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Cooperating

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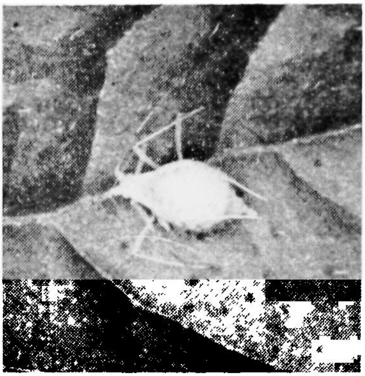

The two most common genera of hymenopterous parasites attacking the potato aphid in northeastern Maine are illustrated by the dead aphids in the pictures above.

A primary parasite of the genus *Aphidius* laid an egg in the abdomen of the potato aphid in the upper left-hand corner. After becoming full grown it killed the aphid and pupated inside, causing the aphid's abdomen to swell.

A primary parasite of the genus *Praon* laid an egg in the abdomen of the aphid immediately above. When full grown, the larva emerged through a slit it made in the ventral side of the aphid's abdomen, then formed its cocoon which it attached to the potato leaf. It pupated beneath the aphid's body, using it as a roof.

The mature adult of *Aphidius* chews a circular emergence hole through the abdomen of the dead aphid, pushes the "cap" up or to one side, then emerges, as it has from the aphid's body, left center.

At lower left are a healthy adult and two small nymphs of the potato aphid, the largest of the four species of potato-infesting aphids in northeastern Maine.

Magnification: 10x — 12x.

Contents

Acknowledgments

The authors are much indebted to the summer assistants who over the years made most of the population counts of aphids and collections of the dead, parasitized aphids on the potato plants, reared the parasites in the laboratory, and preserved each with the aphid mummy from which it emerged. Those who participated in the study for three or more years included E. R. Higgins, L. K. Hunter, R. Q. Jardine, G. A. Towle, and R. D. Wilder. Identifications of parasites belonging to the family Cynipidae were made by the late L. H. Weld, while B. D. Burks identified those belonging to the families Eulophidae, Encyrtidae, Eupelmidae, and Pteromalidae. Corinne C. Gordon gave invaluable assistance in cataloguing the parasite records, summarizing much of the field data, and preparing the figures. To all of these coworkers we express our sincere appreciation.

PARASITES OF POTATO-INFESTING APHIDS IN NORTHEASTERN MAINE

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INTRODUCTION

Four species of aphids infest potatoes in Maine—the buckthorn aphid (*Aphis nasturtii* Kaltenbach), the green peach aphid (*Myzus persicae* (Sulzer)), the potato aphid (*Macrosiphum euphorbiae* (Thomas)), and the foxglove aphid (*Acyrthosiphon solani* (Kaltenbach)). When their populations are large enough, aphids can seriously reduce the yield of Irish potatoes (*Solanum tuberosum* L.) by their feeding damage to the foliage of the plants. Aphids may also transmit certain virus diseases from diseased to healthy potato plants. These diseases often reduce both yield and quality of the tubers produced—not only those produced by the newly infected plants but also those produced by plants growing from tubers that may be unknowingly saved from diseased plants to be used as seed another year. The aphids and the virus diseases they transmit are thus of importance in the production of potatoes for food as well as for seed. The virus-vector aspects of the aphid problem are of particular concern to producers of seed potatoes and also to growers of table stock potatoes whose yields are dependent to a large degree upon the quality of the seed potatoes planted.

Since 1941 a continuing study of potato-infesting aphids in northeastern Maine has been conducted jointly by the U.S. Department of Agriculture and the Maine Agricultural Experiment Station. Phases of investigation have included biology of the aphids and their control on potatoes by means of insecticides, cultural practices, and adverse natural factors. Major emphasis in the studies relating to natural factors has been directed to agents of biological control including arthropod predators, entomogenous fungi, and insect parasites.

The arthropod predators in northeastern Maine include insects and spiders. Among the insect predators are chrysopids, syrphids, and, most important, coccinellids. The coccinellids consume appreciable

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numbers of aphids throughout their larval and adult stages. Many aphids also are killed by both immature and adult spiders. Results of the studies with predators of these aphids will be presented elsewhere.

The results of studies of the entomogenous fungi attacking potato-infesting aphids in northeastern Maine have been reported by Shands et al. (34,[5] 35, 36, 40). The species of fungi found infesting these four species of aphids are *Entomophthora thaxteriana* Petch, *Entomophthora aphidis* (Hoffman), *Entomophthora sphaerosperma* (Fresenius), *Entomophthora planchoniana* Cornu, and *Entomophthora coronata* (Constantin). Two specimens of the dead, diseased buckthorn aphids collected from potatoes at Presque Isle in 1963 were diagnosed by James V. Bell, Department of Biological Control, California Agricultural Experiment Station, as being infected with *Entomophthora lageniformis* (Thaxter). Diagnoses made in 1955 by C. G. Thompson, formerly in charge, Pioneering Insect Pathology Laboratory, Entomology Research Division, showed that one species of introduced fungus, *Acrostalagmus aphidum* Oudemans, infected aphids on potatoes in plots near Presque Isle to which a spray suspension of the spores had been applied three weeks before. This fungus was still present in 1958 but apparently was not abundant.

The relation of insect parasites to the aphid problem in northeastern Maine received much attention between 1941 and 1951, but it was more intensively studied between 1952 and 1963 after the development of more adequate procedures for this kind of research. Our earlier studies emphasized collecting the dead, parasitized aphids and rearing the parasite in each to adulthood for later identification. Much information was obtained on the abundance of the parasitized aphids on their primary hosts and on potatoes, as well as on other secondary hosts. During the later period equal attention was given to the recognition and assessment of the importance of each insect parasite. Results of the early studies have been reported (39); those of the later period are given and discussed in this bulletin. We also include here some suggestions for increasing the importance of insect parasites in the natural control of aphids on field-growing potatoes.

PROCEDURE

The more important field phases of the investigation included surveys to determine the abundance of parasitized aphids, collecting parasitized specimens, and releasing adults of imported species of parasites in experimental plantings of potatoes. Laboratory phases included

[5] Figures in parentheses refer to literature cited beginning on page 75.

rearing and identification of parasites resulting from the field studies. Most of the surveys were made in field plantings of potatoes, but some were made in natural stands of the primary hosts of the aphids and in those of some of the secondary hosts other than potatoes. Surveys were based on sampling procedures that differed somewhat from host plant to host plant but were essentially similar from year to year on any given host plant. The number of sampling units depended to some extent upon the time available for the work, the need for geographical diversity of samples, and experience as to what could be considered a reasonable number of observations.

During all counts of aphids on all sample units, records were made to show, by species, the number of living and dead aphids on each and whether the cause of mortality was an entomogenous fungus, a predator, or a parasite. The method of sampling the primary hosts was to examine 100 or more randomly located plants or sets of leaves at each of a number of locations. Sampling of potatoes, as outlined by Shands and Simpson (32), consisted of examining, *in situ*, all of the foliage of each sample plant until the plants reached a height of about 8 inches, and thereafter of examining only three compound leaves or parts of these leaves per plant. These three leaves were located at random on each plant within the top, middle, and bottom thirds of foliage height or stalk length. Most counts were made on Aroostook Farm, near Presque Isle, Maine; but many were made elsewhere in northeastern Maine both in commercial plantings of potatoes and on primary hosts. Each year some of the potatoes on Aroostook Farm were in small fields, but most were in replicated small plots separated in blocks and columns by strips of oats (41).

Many of the plots and most of those fields of potatoes not situated on Aroostook Farm were treated with insecticides at some time during the summer. A field or series of plots was considered as being "treated" if a systemic insecticide was applied to the soil at planting time, or if regular or specifically scheduled applications of insecticides were made throughout most or all of the season. An "untreated" field or plot was one on which no insecticide was applied or, if an application of a nonsystemic insecticide was made, it was only as the plants were emerging. Where one or more applications of insecticide were made starting in August, the plants prior to that time were considered as being untreated and afterward as being treated.

The potato plants in all fields or plots on Aroostook Farm received weekly applications of a fungicide at recommended rates for the control of late blight, *Phytophthora infestans* (Montagne) DeBary. The fungicide was yellow cuprous oxide during the early 1950's, but in later years zineb or maneb was used. The insecticides, when applied to the growing plants, were incorporated and applied with the fungicide mixtures, nearly all of which were sprays. Most sprays were applied with a tractor-mounted machine equipped with a spray boom. The boom was especially designed to provide superior spray coverage of upper and under surfaces of leaves (42). Dusts were applied with a 6-row power duster equipped with a 10- to 12-foot trailing apron. The rate and frequency of application of insecticides in treated plots varied depending on objectives of each experiment, but such materials were seldom used more often than once in any given week.

Naturally occurring parasites: The procedures for collecting the parasitized aphids and for rearing and preserving the parasites were uniform throughout the study. Each parasitized aphid was put into a separate glass vial (40 X 10 mm.) by gently dislodging the aphid from the leaf with the vial or by placing in the vial a small leaf disc bearing the attached, parasitized aphid. The vial was then closed with a cork stopper, appropriately labeled, and kept in an unheated room. Each vial was usually examined weekly or more frequently throughout each field season or until the adult parasite had emerged from the aphid.

After emergence, and usually allowing time for the insect to harden and darken, the vial containing the parasite and the aphid from which it emerged was filled with a 33% alcohol-water solution and closed again. At that time, the current date was added to the label attached to the vial, together with an indication of whether the parasite was living or dead when preserved. After about November 1 vials containing unemerged parasites were allowed to remain over the winter in this unheated laboratory room in an unheated barn, and similar periodic examinations were resumed in May or early June of the following year. Vials containing unemerged parasites were examined during two successive summers and for at least a part of a third year before any dead, parasitized aphid was discarded. We estimate that parasites emerged from 60 to 90% of the affected aphids depending upon the year, the time of season when collected, the host plant, the species of parasite, and the collector. The overall, average emergence of parasites was thought to be about 75%.

With the aid of a binocular microscope, we subsequently identified each aphid from which a parasite emerged. The aphid, together with its parasite, was again returned to the vial and when necessary, the field identification of the aphid shown on the label was corrected. The vials containing identified aphids and their associated parasites were then forwarded to taxonomists of the Entomology Research Division at the U.S. National Museum.

Introduced parasites: Living parasites shipped via air mail to us from the Moorestown, New Jersey, laboratory of the Insect Identification and Parasite Introduction Branch, Entomology Research Division, were released immediately in designated environments in northeastern Maine. While most of the releases were made during summer in replicated small-plot plantings or in small fields of untreated potatoes on Aroostook Farm, a few were made in stands of the primary hosts at several places in May, 1957, before the time of the aphids' spring migrations. The releases were made by placing the shipping containers in an upright position beneath and at the base of plants and merely removing the lids so the parasites could crawl upward and escape to the aphid-infested host plants. In order to aid survival during the first winter after release, many of the potato stalks in one field were cut in September 1957, and again in 1958, and taken to the edge of nearby woods so that fall or spring plowing in the field would not cover and destroy any parasitized aphids from which parasites had not emerged and which were still attached to the plants.

Limited collections of parasitized aphids from places where releases had been made were handled in the same way as were those of the naturally occuring parasites.

THE PARASITES

The tabulation below lists the primary parasites and hyperparasites thus far reared from potato-infesting species of aphids taken from primary or secondary hosts, including potatoes, in northeastern Maine during the period 1942 through 1962.

Parasites reared from potato-infesting aphids in northeastern Maine, 1942-1962

PRIMARY PARASITES

BRACONIDAE
- Aphidiinae
  - *Ephedrus incompletus* (Provancher)
  - *Praon* spp.
  - *Praon aguti* Smith
  - *Praon americanum* (Ashmead)
  - *Praon occidentale* Baker
  - *Praon pequodorum* Viereck
  - *Monoctonus* sp.
  - *Aphidius* spp.
  - *Aphidius avenaphis* (Fitch)
  - *Aphidius matricariae* Haliday
  - *Aphidius nigripes* Ashmead
  - *Aphidius obscuripes* Ashmead
- Aphidiinae (Cont.)
  - *Aphidius ohioensis* Smith
  - *Aphidius pulcher Baker*
  - *Lysiphlebus testaceipes* (Cresson)
  - *Trioxys* sp.
  - *Diaeretiella* sp.
  - *Diaeretiella rapae* (M'Intosh)

EULOPHIDAE
- Eulophinae
  - *Dahlbominus fuscipennis* (Zetterstedt)
- Aphelinae
  - *Aphelinus semiflavus* Howard

HYPERPARASITES

ENCYRTIDAE
Encyrtinae
Aphidencyrtus aphidivorus (Mayr)
EUPELMIDAE
Eupelmella vesicularis (Retzius)
PTEROMALIDAE
Sphegigasterinae
Asaphes sp.
Asaphes lucens (Provancher)
Asaphes rufipes Brues
Pachyneuron sp.
Pachyneuron altiscutum Howard
Pachyneuron siphonophorae (Ashmead)
Sphegigasterinae (Cont.)
Pachyneuron virginicum Girault
Coruna clavata Walker
Euneura sp.
CYNIPIDAE
Charipinae
Charips sp.
Charips brassicae (Ashmead)
Aloxysta sp.
CERAPHRONIDAE
Lygocerus sp.
Lygocerus attentus Muesebeck
Lygocerus incompletus Muesebeck
Lygocerus niger (Howard)

The extent of the list of reared parasites fluctuated from time to time during the 21 years collections were made. It increased as new species were discovered or described among the individual forms reared from season to season. It decreased as advances in the taxonomic understanding of the limits of variation in the group resulted in the regrouping of forms and the establishment of new synonymies.

In the present state of our knowledge, there are at least 40 species all of which are Hymenoptera, including 15 identified species of primary parasites and 12 of hyperparasites. The primary parasites belong to two families, the Braconidae with seven genera and approximately 20 species and the Eulophidae with two genera and two species. The hyperparasites belong to five families.

ROLE OF PARASITES IN CONTROL OF APHIDS ON UNTREATED POTATO PLANTS

Yearly Variation in Parasitism of the Aphids

Parasitized aphids comprised a very small part of the aphid populations counted on field-growing potatoes. From 1952 through 1963 there were differences of considerable magnitude between years and among species on untreated potatoes (table 1). The percentage of potato aphids was affected much more by parasites than was any of the other three species of aphids. Simple averages of the yearly percentages found parasitized provide some expression of average yearly abundance of parasites. The averages for the 12-year period are 2.39% for the potato aphid, 0.26 for the foxglove aphid, 0.14 for the green peach aphid, and 0.06% for the buckthorn aphid. Above average abundance of parasitization occurred in three out of the 12 years in the instance of the foxglove aphid, in four of the 12 years for the green peach and buckthorn aphids, and in five of the 12 years for the potato aphid. This observation indicates that the variation among years in relative abundance of parasitized aphids was less for the potato aphid than for the other three species of aphids. The highest average percentage of parasitization of each species for any season during the 12-year period was 6.35 for the potato aphid in 1952, 1.52 for the foxglove aphid in 1959, 0.63 for the green peach aphid in 1962, and 0.17 for the buckthorn aphid in 1959.

The year-to-year differences in total-season numbers of aphids counted and shown in table 1 are of interest but have no particular significance since there was variation among years in the number of fields or plots in the study, and in the number of count dates and in sample units examined. For any one year, however, the data show the correct relationship of abundance of each species of aphid to that of the other three species for the entire season. Considering the data in this light, it is apparent that parasitism in aphids on untreated potatoes during the 12-year period was neither consistent from year to year nor particularly common except in the instance of the potato aphid. Our data and observations also show this pattern for the period 1941 through 1951. The next most abundantly parasitized species—the foxglove aphid—ordinarily is not very abundant on potatoes in northeastern Maine. Therefore, major emphasis throughout the remainder

Table 1.—The all-season prevalence of parasitized aphids on foliage of field-growing potatoes not treated with insecticides, 1952-63, inclusive.

The data include only the parasitized aphids recently killed by parasites from which parasites had not emerged at the times of observation. Such aphid specimens were thus infested by parasites in the pupal or late larval stages of development.

Year	Potato aphid		Green peach aphid		Buckthorn aphid		Foxglove aphid	
	In hundreds	Percent par.	In hundreds	Percent par.	In hundreds	Percent par.	In hundreds	Percent par.
1952	148	6.35	25	0	2085	0.02	73	0.04
1953	302	1.34	268	0	5512	.01	189	.03
1954	668	.82	511	0	2400	0	229	.01
1955	209	2.49	230	0	4862	0	43	.21
1956	416	.47	523	.03	2959	.02	465	.06
1957	541	1.18	634	.05	7531	.03	792	.10
1958	269	4.25	289	.16	645	.16	102	.22
1959	169	3.41	101	.26	152	.17	16	1.52
1960	183	1.40	41	.10	99	.05	2	.43
1961	141	2.79	505	.10	2066	.08	3	0
1962	131	2.33	57	.63	42	.14	9	.55
1963	139	1.73	91	.40	811	.06	1	0

of this bulletin is devoted to a consideration of parasitism of the potato aphid.

Parasitism as a Factor in Natural Control of the Potato Aphid

In this bulletin the general approach for assessing the importance of insect parasitism as a factor in natural control of the potato aphids is the same as that in the report of studies in northeastern Maine relating to entomogenous fungi (35). It is based on studies of aphid population dynamics in relation to growth characteristics of aphid populations on field-growing potatoes (33). Essentially, the average overall population trend of any one or of all four species of aphids on untreated potatoes is represented by a sigmoid curve, the time and size of the peak of which is variable because of natural factors. The size of population at the peak is seldom, if ever, limited by factors dependent on density. Because of the parthenogenetic nature of the aphids, their rapidity of development, and length of their reproductive stage on potatoes in the field, the rate of population increase is exponential during much of the summer. Most of the growth phase of the population curve becomes essentially a straight line when the common logs n+1 of the aphid numbers are plotted against time. Once apparent, any appreciable decrease in the slope of this line indicates a decrease in the rate of aphid population increase.

The overall effect of a factor or factors responsible for a decrease in rate of population growth can be approximated by determining the difference in areas beneath the curves showing the actual aphid population trend and those showing the expected trend had the population growth rate not been reduced. Furthermore, the point of separation of the lines indicating actual and estimated population trends will serve to indicate the approximate date when operation of the factor or factors retarding the rate of population increase began. This is especially so if these effects became evident soon afterward.

We have prepared freehand curves representing the actual seasonal population trends of the potato aphid on untreated field-growing potatoes for each of the years 1952 through 1963. Closely associated with each curve we have shown for the same sample units the seasonal trend of abundance of dead, parasitized specimens of the potato aphid from which the parasites had not yet emerged. We have also indicated the point or points of departure of the actual population trends from the ones expected had there been no adverse interference from natural factors. These graphs will be referred to later.

Effect of parasites on population trends

Every year in northeastern Maine natural factors influence to varying degrees the seasonal trend of the potato aphid population. The size of the peak in late summer is affected by the time and size of the aphids' spring migrations, the direct and some indirect effects of weather, and in most years to a large extent by the various biological agents of aphid control. The magnitude of the influence of these biological agents upon numbers of aphids at the peak of their abundance is determined by the time of beginning and the duration of their action during the growth phase of the aphid population.

Figures 1, 2, and 3 show for the years 1952 through 1963 yearly population trends of the potato aphid in relation to prevalence of dead, parasitized potato aphids, from which parasites had not yet emerged. Data were taken on the same sample plants or count leaves of field-growing potatoes that were not treated with an insecticide. The average numbers of potato aphids per 100 three-leaf samples, for all counts each week, are plotted on a semilogarithmic basis at midweek points. The percentages of aphids dead from parasites, but from which parasites had not yet emerged, are also plotted at midweek points. Each point is based on an average figure representing field counts involving 400 to 1,700 plants (1,200 to 5,100 compound leaves) in four to 14 locations. The average weekly count of aphids (dead and alive) involved about 1,100 sample plants (3,300 compound leaves) located in eight fields or replicated plot locations.

Substantial parts of the curves representing growth phases of population trends in figures 1, 2, and 3 approximate a straight line. Little significance need be attached to the apparent inconformity of the trend during the early part of the season each year. The seeming drop in population occurring immediately preceding the beginning of the straight-line relationship is due chiefly to sampling a smaller fraction of the potato foliage during the period when plants undergo very rapid proliferation. In addition, there is an added complexity associated with increasing aphid populations from the incoming spring migrants during a part of the time. This is followed by cessation of the spring migration and decreasing aphid numbers resulting from the action of predators, parasites, and other natural factors when the number of aphids per plant is extremely small.

At some time during the growth phase of the seasonal population trend of the potato aphid each year, there has been a deceleration in rate of population growth. This is evident in figures 1, 2, and 3 where we have added to the solidline curve each year a broken-line curve to

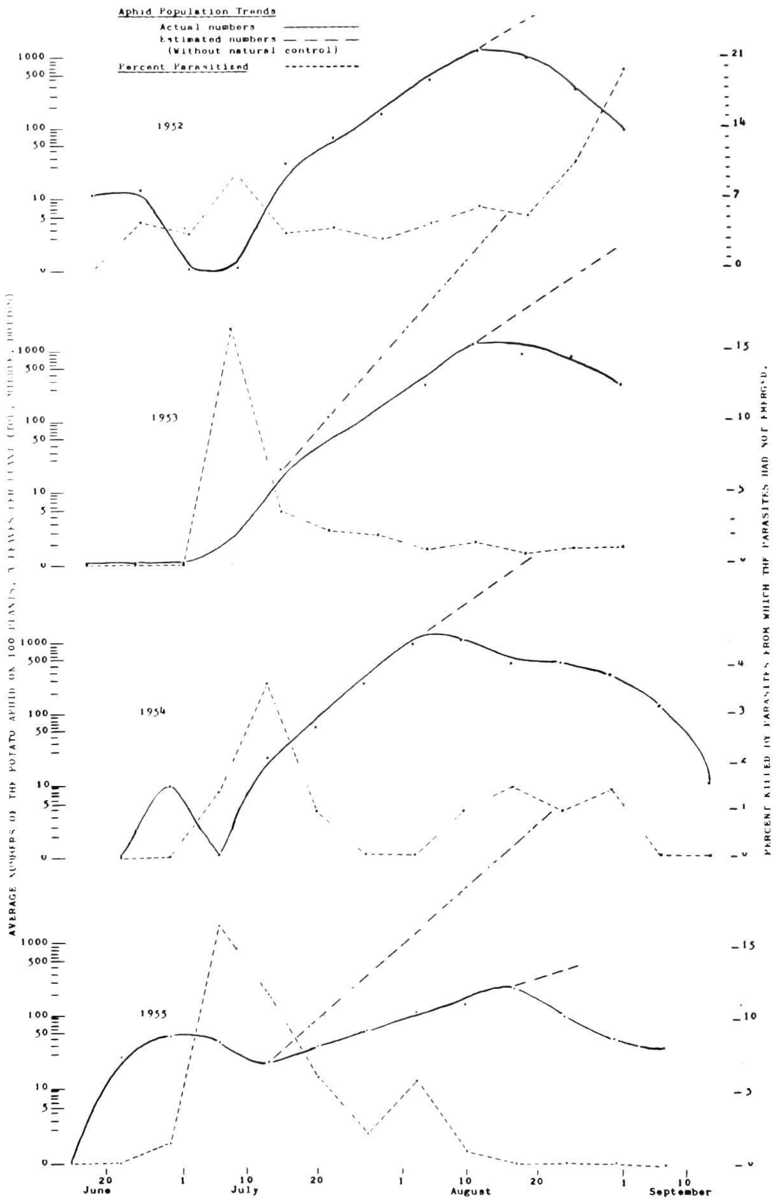

Figure 1.—Relation of parasitism to abundance of the potato aphid on untreated potatoes, in the field, 1952 to 1955, inclusive.

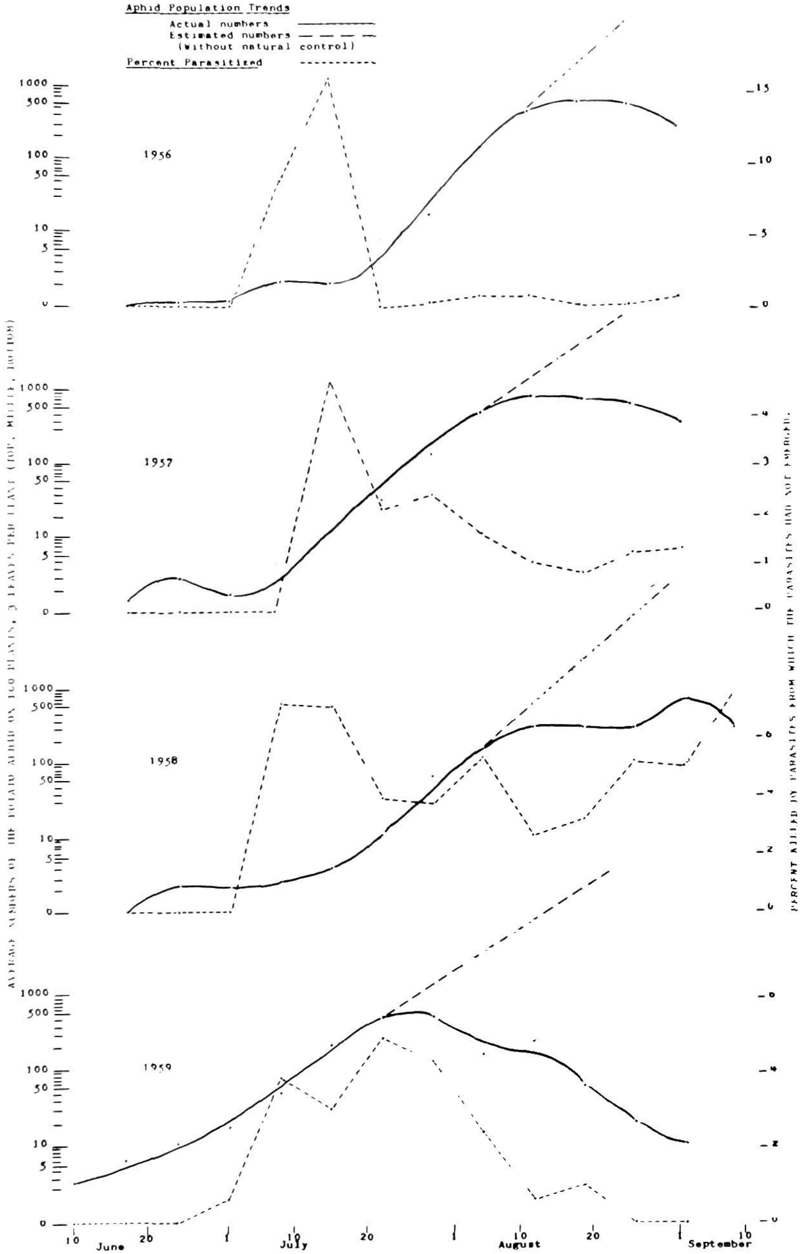

Figure 2.—Relation of parasitism to abundance of the potato aphid on untreated potatoes, in the field, 1956 to 1959, inclusive.

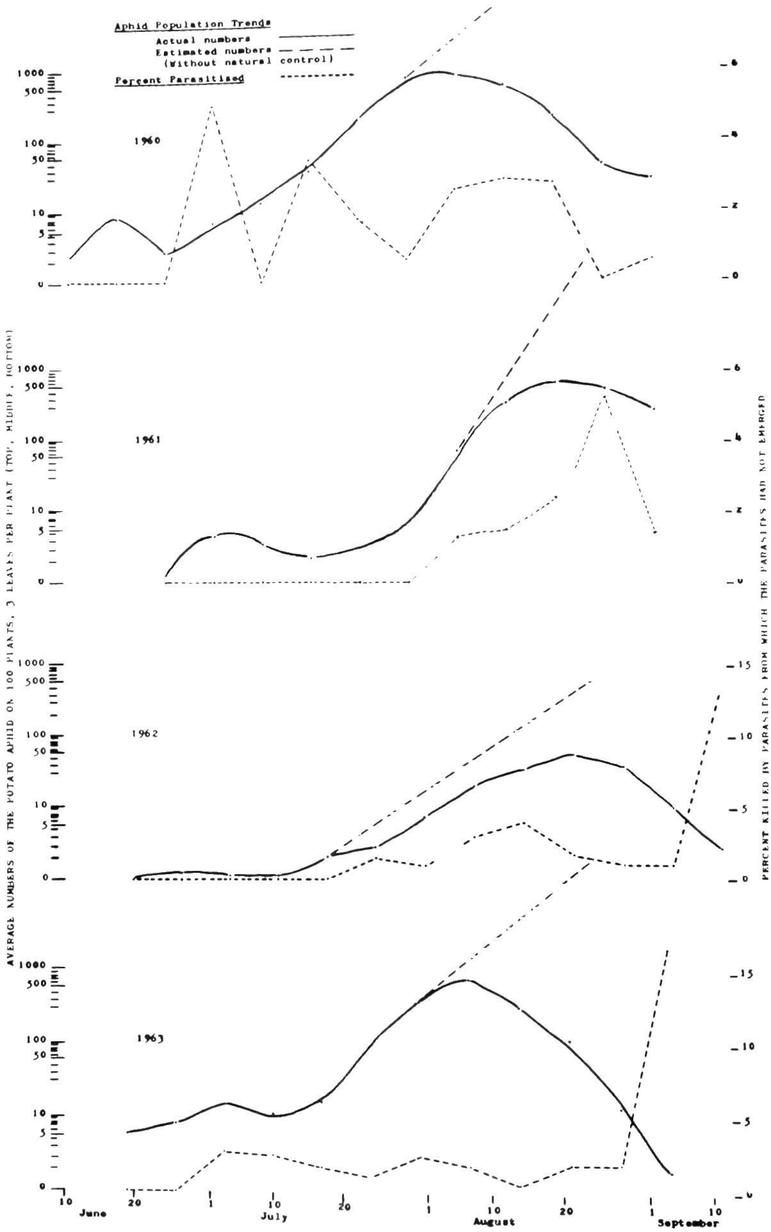

Figure 3.—Relation of parasitism to abundance of the potato aphid on untreated potatoes, in the field, 1960 to 1963, inclusive.

show the approximate beginning time and extent of departure of the actual population trends from the estimated straight-line relationship. The full extent of departure may be estimated by extending this broken-line curve for each year until the beginning of the fall migration since, without interference, the population should increase at least until then. We have made no special effort to do this because the chief purpose of the broken line is to indicate when the suppressive effect of adverse factors first became evident. The start of the fall migration of the potato aphid during the 12-year study ranged from August 21 in 1952 and in 1962 to as late as September 2 in 1953; the average date has been August 25. The broken lines in figures 1, 2, and 3 extend to the correct dates except the uppermost ones in 1953 and 1955, and those for 1960, when it was August 21, and for 1963 when the numbers of fall migrants were so small the beginning of the migration was not determined with accuracy. Our evidence indicates it started about September 1. The lower broken lines for 1953 and 1955 in figure 1 extend to the correct dates.

In both 1953 and 1955 there appeared to be deceleration in the rate of population growth of the potato aphid early in the season, followed by a second deceleration later in the season (figure 1). There was very little basis for establishing the slopes of the broken lines to indicate the rate of growth of a population not affected by adverse natural factors, especially so for 1955, because decelerations in the rates of aphid increase occurred before the slopes were evident. Nevertheless, the slope for 1953 was approximated on the basis of the data available while that for 1955 was made the same as the one for 1954.

Method of assessing importance of parasites.—The extent to which populations of the potato aphid have been reduced by natural factors during this 12-year period has varied from year to year, but the reduction has been very substantial in most years (figures 1, 2, 3). The extent of this reduction is influenced chiefly by the beginning time and degree of deceleration in rate of aphid increase (or the slope of the broken line) when compared with the solid line representing the actual population trend. The average calendar date for the first detection of a reduction in rate of population growth due to the action of natural control agents has fallen near the halfway point on the curve representing the growth phase of the seasonal population trend of the potato aphid. However, inspection of the yearly curves shows a range from as early as the 10% point to as late as the 80% point on the curve representing the growth phase of the population trend of this aphid. The reduction in actual aphid numbers from the decelerating effect of adverse natural factors is large since it occurs during the second half of the population growth phase. Potential reductions in size of aphid populations increase as the effects from natural agencies begin earlier in the season.

The method we use to assess the importance of the various natural factors inimical to aphid increase, including parasites, predators, entomogenous fungi, and weather, is to correlate the actual or relative abundance of each with the observed beginning of the deceleration in rate of population growth of the aphid for which they are responsible. This is appropriate if the adverse effects become immediately evident, as from the action of predators, hurricanes, or severe rainstorms which kill the aphids. The effects of parasites also will become apparent rather quickly since, as Spencer (45) has pointed out, parasitization results in cessation of reproduction about the third day after it has been initiated. Even though the infested aphid may live for several days more, it ceases to reproduce. This two-fold effect of parasitism—quick cessation of reproduction, followed eventually by death of the aphid—should have both immediate and far-reaching effects on the population dynamics of the potato aphid and of other species of aphids on potatoes and on their other host plants.

The decelerative effects upon rate of aphid population growth from attacks by entomogenous fungi differ in some respects from those caused by insect parasites. The initial appearance of these effects after the start of an attack by fungi may be more retarded than for parasites, but the drag upon aphid increase may be more extensive and far reaching. We do not know the length of time between infection by the fungus and the death of the infected aphid, but indications from work by others elsewhere suggest it may vary from several days to a considerably longer period depending upon the temperature and humidity of the microenvironment of both the fungi and the aphids. While there may be some delay in mortality of the aphid, the observations (35) showed that the depressive effect of entomophthoraceous fungi coincided very closely with the first appearance of dead, diseased potato aphids on the potato plants—which was when an average of about 0.4% of the population had died—and that in most years there was very little increase in numbers of the aphids after the first dead, diseased specimens were found.

The deceleration in rate of population growth of the potato aphid found in that study (35)—also shown in figures 1, 2, and 3—was so sudden and pronounced as to suggest that one effect of fungus infection in an aphid population is to reduce the biotic potential of the aphids.

Ullyett and Schonken (48) reported that entomogenous fungi, beyond causing premature death of some host insects, in others produce sterility in the adults. MacLeod (17) wrote that in Siberia one worker concluded that physiological sterilization of the females by infections of entomophthoraceous fungi was the predominant factor in reducing the heavy infestations of grasshoppers. Madelin (18) also mentioned that in Russia several workers reported a species of hyphomycete, belonging to the genus *Isaria*, as causing sterility in females of the beet webworm (*Loxostege sticticalis* (Linnaeus)) by infecting the ovaries.

Assessment of importance of parasites.—Our assessment of the importance of parasitism as a factor in natural control of the potato aphid is based upon the considerations that we have discussed. It has been reached after considering the probable magnitude of the immediate and delayed or continuing adverse effects upon population trends of the aphid arising from periods of extremely unfavorable weather as well as from the three biological agents of aphid control—arthropod predators, entomogenous fungi (35), and insect parasites. The data available from this 12-year study indicate that only during the two hurricanes in 1954 (37) was the direct, adverse effect of weather of enough importance to markedly affect the aphid population trend. Further, these storms and their immediate effects did not occur until after August 30. This was well after the seasonal peak of aphid population. Extremely unfavorable weather thus appears to have had no real significance in this consideration.

In a preliminary assessment of the importance of predators from 1952 through 1962 (35), it was concluded that they appeared to have exerted a substantial degree of aphid control in 1957 and in 1959 (figure 2). They also were of considerable importance in 1963. In 1959 the braking action of predators upon rate of aphid increase became evident one week after that of entomophthoraceous fungi. In 1963 this effect became evident two weeks after the initial influence of fungus disease was detected for the potato aphid, and one week after for the buckthorn aphid. In 1957, the beginning of the effect of predators appeared to coincide with and thus could not be separated from that of entomogenous fungi. In none of these instances was it possible to assess the separate importance of these two biological agents of aphid control.

Entomogenous fungi exerted a detectable adverse effect upon rate of population growth of the potato aphid during each of the years 1952 through 1962. The time of initial detection of the braking action closely coincided with that of the first appearance of dead, diseased specimens of this aphid on the potato plants (35). The unpublished results and conclusion from a continuation of that study in 1963 were similar to those observed before 1952 except that, for the first time since the start of the study of entomogenous fungi, they appeared to exert a substantial adverse effect upon rate of increase of the buckthorn aphid as well as the potato aphid.

After attempting to correlate seasonal abundance of parasitized potato aphids with population trends of that species (figures 1, 2, 3) and allowing for what is considered to be the nature and extent of the adverse effects from entomogenous fungi and arthropod predators, we conclude that parasitism observed in this study resulted in no appreciable, adverse effect upon rate of population increase of the potato aphid, at least by our methods of measurement and assessment. There was no separate, clear-cut effect from parasitism during any of the years for which observations are available. Although each year insect parasites doubtless exerted effects adverse to aphid increase, such effects were probably masked by the effects of the activity of entomogenous fungi in all years and of the arthropod predators in some. The percent of parasitization found in most years likely was too small to reduce appreciably the rate of increase of the potato aphid during the growth phase of the seasonal population trend. There is some possibility, however, that parasitization could have caused a detectable change in population trends of the potato aphid in 1958 (figure 2), 1960, 1961, and 1962 (figure 3) had other biological agents been of no importance during those years. If so, only in 1958 would its action have occurred soon enough to affect population size of the potato aphid at the peak.

Figure 4, showing the 10-year averages for seasonal abundance of the potato aphid and of parasitism in that species, also indicates that insect parasites likely had little influence upon population trends of that aphid on untreated potatoes. The highest percentages of parasitism occurred during the first half of the population-growth phase of the seasonal trend without producing any detectable deceleration in rate of aphid increase. If the increase in parasitism after mid-August became large enough to cause appreciable reduction in aphid abundance, the

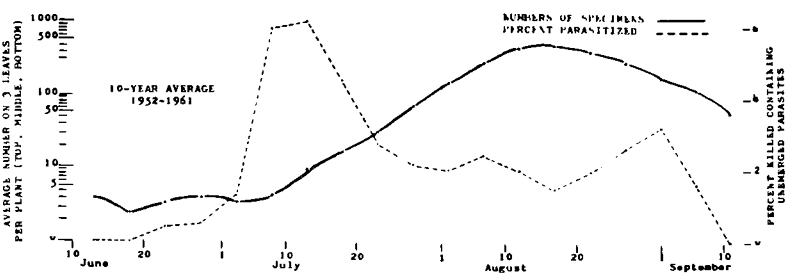

Figure 4.—Relation of parasitism to abundance of the potato aphid on untreated potatoes, in the field, 10-year average, 1952 to 1961, inclusive.

effect was exerted on a declining population and cannot be separated from similar effects caused by other biological agents.

Failure to find an appreciable or even a detectable effect from the action of parasites by the criteria employed is not particularly surprising, especially since such pronounced effects can occur from the influence of entomogenous fungi and arthropod predators. To provide effective biological control of aphids on potatoes, the biological agents must exert continuing pressure during at least a substantial part of the growth phase of the seasonal population trend, or a catastrophic pressure of short duration is required. The natural infestations of parasites in northeastern Maine have met neither of these requirements. Parasites only intermittently exert pressure against aphid population increase, since the pressure occurs only in the short-lived larval stage of each generation of the parasite. Furthermore, in addition to affecting only the aphids in which parasite eggs are deposited, the numbers of adult parasites apparently are too small to parasitize a large percentage of the potato aphid population.

We do not mean to imply that insect parasites are of no appreciable value in controlling infestations of the potato aphid on potatoes in northeastern Maine or that there is no likelihood their role in biological control of potato-infesting aphids can be improved. The combined depressive effect of parasites, predators, and entomogenous fungi every year is very appreciable. While we have not yet devised a criterion for detecting and measuring the depressive effects from parasitism upon the rate of aphid increase, there is a distinct possibility this can be done. Later in this bulletin we propose and discuss ways of increasing the role of insect parasites in biological control of potato-infesting aphids.

EFFECT OF INSECTICIDES UPON PARASITIZATION OF THE POTATO APHID

Parasitism in Replicated Small Plots

Our studies were extended to include a determination of the effect of insecticide treatments upon abundance of parasitized aphids throughout each season on the treated plants. We accomplished our purpose, as described earlier in this bulletin. Most aphid populations were substantially reduced by the insecticide treatments; thus, there were fewer potential hosts for the parasites to infest. Although under these conditions the potato aphid was not ordinarily the most abundant species, parasitized specimens of this species were far more abundant than were those of the other three potato-infesting aphids. We therefore limit to the potato aphid this consideration of the effects of insecticide treatments upon parasitization.

Complicating factors prevent uniform comparison of the effects of the different insecticides during the 12-year study. Because of the general scarcity of free-flying adult parasites following insecticide application, the number of parasitized aphids was so small and their distribution so uneven that conclusions as to the effects of an insecticide treatment upon parasitization in any one year are not possible. Furthermore, because of the continuing advances in control with insecticides, the materials, methods, and schedules of application underwent change yearly. Except for DDT, which was included each year, it has been necessary to limit comparisons to rather broad categories of insecticides. The three major groupings include DDT, all other nonsystemic insecticides, and systemic insecticides. Comparisons involving fewer years allow separating endosulfan from the nonsystemic group and of further dividing systemic insecticides according to method or time of application—planting furrow, foliar spray, or seedpiece-dip. All comparisons are limited to total-season, relative abundance of parasitized aphids.

Insecticides and rates of application

In most instances DDT was applied weekly throughout the season, largely as a foliar spray. Most spray mixtures were prepared from emulsifiable concentrates of the insecticide but some were from wettable powders. Per-acre application rates were 0.63 or 2.0 pounds of DDT when derived from emulsion concentrates or wettable powders, respectively. For the few tests in which dusts were used, the application rate ranged from 0.7 to 1.5 pounds of DDT per acre.

Endosulfan from an emulsifiable concentrate was applied as a spray mixture at ½ or ¼ pound of active ingredient per acre. The number of applications ranged from 1 to 3 each year, depending upon objectives of each experiment.

The spray mixtures of nonsystemic insecticides contained many materials used singly, such as barthrin, carbaryl, carbophenothion, Chlorthion® (now unavailable) [*O*-(3-chloro-4-nitrophenyl) *O, O*-dimethyl phosphorothioate], DDVP, diazinon, endrin, endothion, ethion, Guthion® (*O,O*-dimethyl *S*-[4-oxo-1,2,3-benzotriazin-3 (4*H*-ylmethyl] phosphorodithioate), parathion, toxaphene, Zectran® (4-dimethylamino-3, 5-xylyl methylcarbamate), various numbered compounds, and other nonsystemic materials. Rates of application varied but in most instances did not exceed ½ pound of active ingredient per acre. The frequency of application depended on the objective of each experiment, but it was never more often than weekly and frequently far less often.

The systemic insecticides applied as foliar sprays included demeton (Systox), Meta-Systox-R® [*S*-2-(ethylsulfinyl) ethyl *O*, *O*-dimethyl phosphorothioate], and menazon. The per-acre rates of application varied from 0.06 to 0.20 pound. The frequency of application varied; in general it was less than for nonsystemic materials.

The systemic insecticides applied in the planting furrow included demeton, Di-Syston® (*O*, *O*-diethyl *S*-[2-(ethylthio) ethyl] phosphorodithioate), phorate, menazon, and dimefox (Hanane). The rates of application ranged from ½ to 2½ pounds of active ingredient per acre.

The Bidrin® (3-hydroxy-*N*, *N*-dimethyl-*cis*-crotonamide dimethyl phosphate) seedpiece dips were water mixtures containing 0.92, 1.82, or 3.62 percent of the active ingredient.

Comparisons of results

During the 12-year study we observed much variation among years and insecticide categories in prevalence of parasitized specimens of the potato aphid on treated potatoes and on untreated potatoes (table 2). In most but by no means all instances the percentage of parasitism in strictly comparable, adjacent or nearby, plots of untreated potatoes was larger than in plots treated with insecticides. Except in the instance of endosulfan, the weighted average percentage of parasitism was greater in strictly comparable plots of untreated potatoes than in the ones treated with insecticides. Endosulfan as a treatment was included in only five of the 12 years, and there were relatively small numbers of aphids in the plots treated with this insecticide.

Weighted average percentages may not reflect the effect of insecticide treatments upon parasitism as accurately as simple averages of the yearly percentages, because there was considerable variation among years in the number of insecticide treatments and plot replications. On the other hand, the simple averages which give equal weight to each year's tests, irrespective of the abundance of aphids and of parasitism or of the number of sample units examined, could be somewhat inaccurate also. We believe simple averages of yearly weighted averages are better than the fully weighted ones for measuring the overall, average effect of insecticide treatments upon parasitism of the aphids over the entire period of the study.

Such averages are shown in table 3 in comparison with like percentages for nearby, strictly comparable plots of untreated potatoes. The deleterious effects of insecticides upon parasitism by this criterion in comparison with weighted average percentages, were slightly larger

Table 2.—The prevalence of parasitized specimens of the potato aphid on potatoes in small plots in which insecticides were or were not applied, 1952 to 1963, inclusive.

Year		Number plant sample units examined	*M. euphorbiae* on sample units: In hundreds	*M. euphorbiae* on sample units: Percent parasitized	Number plant sample units examined	*M. euphorbiae* on sample units: In hundreds	*M. euphorbiae* on sample units: Percent parasitized
		Foliar applications of DDT only			*All foliar applications of non-systemic insecticides other than DDT*		
1952	Treated	7,475	412	6.67	16,700	145	7.78
	Nontreated	6,762	210	10.44	6,762	210	10.44
1953	Treated	10,045	673	1.51	13,045	534	2.23
	Nontreated	6,840	209	1.47	6,110	228	1.77
1954	Treated	40,000	303	1.04	26,850	808	1.28
	Nontreated	4,550	229	1.02	6,350	446	.98
1955	Treated	3,750	78	1.45	28,975	194	2.39
	Nontreated	4,775	37	3.38	6,575	52	3.06
1956	Treated	11,150	261	.42	17,975	356	1.00
	Nontreated	4,425	153	.44	5,650	172	.58
1957	Treated	14,700	1037	.89	13,800	416	1.43
	Nontreated	4,970	294	.83	5,295	373	.75
1958	Treated	4,200	115	2.37	14,490	221	3.31
	Nontreated	1,740	34	3.29	6,970	104	4.21
1959	Treated	7,550	284	1.94	13,350	208	4.13
	Nontreated	1,775	39	2.90	3,900	68	4.20
1960	Treated	1,800	98	.91	12,300	215	2.03
	Nontreated	2,100	70	1.52	4,050	113	1.34
1961	Treated	3,150	39	1.21	9,750	128	1.30
	Nontreated	1,950	52	1.30	3,600	106	2.37
1962	Treated	1,500	30	.20	20,350	176	1.72
	Nontreated	1,523	28	3.43	3,618	59	2.17
1963	Treated	1,950	33	.86	14,400	91	2.12
	Nontreated	3,522	70	1.60	3,600	60	1.46
1952 to 1963	Treated	——	—	1.85[1]	——	—	2.13[1]
	Nontreated	——	—	2.66[1]	——	—	2.47[1]
		Foliar applications of endosulfan only			*Foliar applications of systemic insecticides*		
1952	Treated	——	—	—	15,450	42	11.56
	Nontreated	——	—	—	4,462	151	12.12
1953	Treated	——	—	—	4,995	299	3.41
	Nontreated	——	—	—	4,735	203	1.82
1954	Treated	——	—	—	2,250	92	2.41
	Nontreated	——	—	—	1,375	58	.88
1955	Treated	——	—	—	1,050	9	2.30
	Nontreated	——	—	—	1,800	14	2.23
1956	Treated	750	22	1.83	——	—	——
	Nontreated	1,650	37	.96	——	—	——
1957	Treated	1,250	2	.55	——	—	——
	Nontreated	1,725	190	.71	——	—	——
1958	Treated	2,850	18	4.14	——	—	——
	Nontreated	3,300	39	5.33	——	—	——
1959		No comparison			No comparison		
1960		No comparison			No comparison		
1961	Treated	900	8	1.66	900	6	.52
	Nontreated	1,650	54	3.39	1,650	54	3.39
1962	Treated	1,600	10	1.51	11,300	61	2.38
	Nontreated	1,776	24	2.17	3,426	51	2.52
1963		No comparison			No comparison		
1952 to 1963	Treated	——	—	2.39[1]	——	—	3.73[1]
	Nontreated	——	—	1.79[1]	——	—	4.88[1]

		Soil-applied systemic insecticides (in planting furrow)			*Freshly cut seed-pieces dipped in slurry of systemic insecticide immediately before planting*		
1952	Treated	3,150	13	8.30	——	—	——
	Nontreated	4,462	151	12.12	——	—	——
1953	Treated	2,670	94	1.23	——	—	——
	Nontreated	3,085	124	1.90	——	—	——
1954		No comparison			No comparison		
1955		No comparison			No comparison		
1956	Treated	3,875	1	2.74	——	—	——
	Nontreated	9,275	182	.50	——	—	——
1957	Treated	6,500	7	2.59	——	—	——
	Nontreated	14,595	455	1.06	——	—	——
1958	Treated	5,850	2	2.42	——	—	——
	Nontreated	15,850	237	4.03	——	—	——
1959	Treated	7,475	21	1.34	——	—	——
	Nontreated	11,525	169	3.41	——	—	——
1960	Treated	9,000	45	2.09	——	—	——
	Nontreated	7,950	183	1.40	——	—	——
1961	Treated	10,950	41	2.74	——	—	——
	Nontreated	8,550	238	3.58	——	—	——
1962	Treated	6,900	92	.90	——	—	——
	Nontreated	9,331	131	2.33	——	—	——
1963	Treated	7,140	13	.68	4,650	46	1.12
	Nontreated	7,056	107	1.80	1,650	33	1.81
1952 to	Treated	——	—	1.75[1]	——	—	——
1963	Nontreated	——	—	2.92[1]	——	—	——

[1] Weighted averages.

for DDT, about the same for foliar sprays containing insecticides other than DDT, and substantially less for foliar sprays or furrow applications of systemic insecticides. A complete reversal of about the same magnitude for foliar sprays of endosulfan may have been due to comparisons involving too few aphids, plot replications, and years for both

Table 3.—Average yearly percentage of the all-season populations of the potato aphid killed by parasites on potato plants receiving different insecticidal treatments, 1952 through 1963.

Insecticidal treatment	Inclusive period	Percent parasitized: On treated plants	Percent parasitized: On strictly comparable untreated plants
DDT *(mostly as foliar sprays)*	1952-1963	1.63	2.63
All nonsystemic materials other than DDT[1] *(foliar sprays)*	1952-1963	2.54	2.79
Endosulfan only *(foliar sprays)*	1956-1962	1.94	2.51
Systemic insecticides			
Applied as foliar sprays	[2]	3.76	3.83
Applied in planting furrow		2.50	3.21
Seedpiece dip at planting	1963	1.12	1.81

[1] Includes endosulfan.

[2] 1952, 1953, 1954, 1955, 1961, 1962.

[3] 1952-1963 excluding 1954 and 1955.

the treated and untreated plants. Except for the one year's results from the seedpiece-dip treatment, the other results from this method of comparison differ only in magnitude from those obtained by comparing weighted averages.

The results in table 4 are expressed as simple averages of the yearly weighted average percentages of all-season parasitism after regrouping the data into fewer categories of insecticides and consolidating all plots of untreated potatoes. Any decrease in accuracy caused by not limiting comparisons of treated with strictly comparable untreated potatoes probably is more than offset by an increase in value of the average for untreated potatoes because of the larger number and better distribution of samples. Inaccuracy due to heterogeneity in distribution of the parasites in all of the untreated plots as compared with that in only the nearby, strictly comparable plots, likely was not large since each year all treated and untreated plots were located in a 500 by 700 foot field which in most years was well removed from woods.

Analysis of variance of the regrouped data on which the averages in table 4 are based shows that DDT was the only insecticide treatment that significantly reduced the all-season prevalence of parasitized specimens of the potato aphid. Parasitism was cut nearly in half in these plots. Although less than on untreated potatoes, parasitism was not significantly less in plots treated with other nonsystemic insecticides or with systemic insecticides.

Table 4.—The influence of insecticides grouped into three categories upon parasitization of the potato aphid on field-growing potato plants for the 12-year period 1952 through 1963.

Insecticide treatment	Average percent of population killed by parasites
Nontreated	3.03 a
Foliar sprays of nonsystemic insecticides other than DDT	2.56 a
Systemic insecticides (some foliar sprays but mostly furrow-applied at planting)	2.48 a
DDT (mostly as foliar sprays)	1.62 b

Percentages flanked by the same letter are not significantly different at the 5% level but those separated by the horizontal line differ at the 5%- or 1% levels of significance by the Duncan Range Test.

No differences in parasitism of any significance were found between untreated and treated potato foliage when the yearly, weighted averages for five years in the same treatment categories were compared. An exception was created by regrouping the "all-other" nonsystemic materials to provide a separate category for endosulfan sprays (table 5). The years included in this comparison were 1956, 1957, 1958, 1961, and 1962. Neither was there a significant difference in parasitism between the untreated and any of the insecticide treatment categories when a sixth category was formed by dividing systemic insecticides into foliar and preplant soil applications (table 6). That comparison was limited to 1961 and 1962. From the results of these analyses, we can conclude that variability in parasitism between and within treatment categories was so great that data for more than five years would have been required before the differences could have been significant at the 5% level.

Table 5.—The influence of insecticides (grouped into four categories) upon parasitization of the potato aphids infesting field-growing potato plants during a period of five years (1956, 1957, 1958, 1961, 1962).

Insecticide treatment	Average percent of population killed by parasites[1]
Nontreated	2.30
Nonsystemic insecticides (foliar sprays)	
DDT	1.01
Endosulfan	1.94
All others	1.72
Systemic insecticides	
Preplant soil applications	2.28

[1] Differences between percentages are not significant by the F-test for P=0.05.

Table 6.—The influence of insecticides (grouped into five categories) upon parasitization of the potato aphid on field-growing potato plants in 1961 and 1962.

Insecticide treatment	Average percent of population killed by parasities[1]
Nontreated	2.96
Nonsystemic insecticides	
DDT	0.71
Endosulfan	1.59
All others	1.51
Systemic insecticides	
Foliar sprays	1.45
Preplant soil applications	1.32

[1] Differences between percentages are not significant by the F-test for P=0.05.

Parasitism in Commercial Plantings

Comparisons during six years were made to observe differences in parasitism between commercial fields of potatoes and the plots from which the data in table 2 were obtained. The three commercial fields included in the study were well separated from each other and all were within eight miles of the small experimental plots. All three of these fields were treated each year with the insecticides commonly recommended for control of aphids and other foliage feeding insects. They all received each season at least one application of DDT and from one to three applications of some other nonsystemic insecticide.

Among the commercial fields the yearly differences in parasitism of the potato aphid were less than those shown for the insecticide-treated plots in tables 2 and 6. In fact, in most of the years and on the average, parasitism was numerically slightly higher in the commercially treated fields of potatoes than in the untreated experimental plots. Thus, the level of parasitism in the potato aphid on potatoes in this study was not influenced appreciably by the area of the planting nor by the changes in abundance of the aphids on potato plants caused by the application of insecticides.

ABUNDANCE OF PARASITES REARED FROM FIELD-COLLECTED APHIDS

During the 11-year period 1952 through 1962 in northeastern Maine, many parasitized aphids were collected from primary and secondary hosts of the potato-infesting species of aphids. At all sampling stations the collections were limited to parasitized aphids found on the randomly located sample units when making population counts of the aphids on their host plants. From 1952 through 1959 parasitized aphids were collected from the primary hosts in spring and fall and from potatoes and other secondary hosts during summer. The primary hosts included several species of wild roses (*Rosa* spp.), Canada plum (*Prunus nigra* Ait.), alder-leaved buckthorn (*Rhamnus alnifolia* L'Her.), and several species of hawkweed (*Hieracium* spp.), which are the more important primary hosts of the potato, green peach, buckthorn, and foxglove aphids, respectively. Counts and collections were much less intensive on alder-leaved buckthorn than on the other primary hosts. The great majority of parasitized aphids reported in this bulletin came from potatoes in our replicated, small-plot plantings on Aroostook Farm, but many were from commercial fields of potatoes in widely separated places in northeastern Maine. We used the same procedure indicated earlier to rear parasites from all parasitized aphids collected.

The Potato Aphid

Abundance of the potato aphid during the 12-year period from 1952 through 1963 was intermediate between that of the buckthorn and foxglove aphids and just about the same as that of the green peach aphid (table 1). Despite this, the potato aphid was more heavily parasitized than all of the other species combined.

Primary parasites

Primary parasites reared from the potato aphid belong to two families, Braconidae and Eulophidae (table 7). All of the braconids so far identified are in four genera of the subfamily Aphidiinae, including *Ephedrus, Praon, Aphidius,* and *Diaeretiella.* The eulophids are represented by one genus in each of the subfamilies Eulophinae and Aphelinae, namely *Dahlbominus* and *Aphelinus*, respectively.

The most common species of primary parasite during the 11-year period of this study was *Aphidius nigripes;* 92% of all reared specimens were of that species. A total of 5.7% of the primary parasites belonged to two or more species of *Praon* as yet undescribed. Also represented in each year's collections except 1962 was *Praon pequodorum*, which comprised 1.5% of the reared, primary parasites. Aside from a few specimens of *Praon aguti* and of *Aphidius* spp., as yet undescribed, there were only trace numbers of the other five species belonging to the Aphidiinae.

The family Eulophidae was barely represented among the primary parasites of the potato aphid. A single specimen of *Aphelinus semiflavus* was reared from a parasitized potato aphid collected in 1959. The three specimens of *Dahlbominus fuscipennis* reared from potato aphids collected in 1958 are of interest since this hymenopteron is ordinarily a parasite of sawflies rather than of aphids. Because of the procedure we used in collecting the parasitized aphids, and in the rearing and handling of the parasites described earlier, there seems little, if any, question but that *D. fuscipennis* parasitized these three specimens of the potato aphid.

Hyperparasites

Hyperparasites comprised 22% of all parasites emerging from the collections of parasitized potato aphids (table 7). Three of the five families represented in the collections accounted for over 99% of the hyperparasites, as follows: Pteromalidae, 59.5%; Ceraphronidae, 30.5%; and Cynipidae, 9.6%. Only trace numbers belonged to the families Encyrtidae or Eupelmidae.

Over 71% of the pteromalids were *Asaphes lucens* while 6% were *A. rufipes* and 16% were *Coruna clavata*; other species of *Pachyneuron* and of *Euneura* comprised 5%. There were trace numbers of what appeared to be undescribed species of *Pachyneuron* or of *Asaphes.*

Table 7.—Total number of each species of parasite reared from dead, parasitized specimens of the potato aphid collected in northeastern Maine, 1952-1962, inclusive.

Species of parasite	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1952-62
Primary parasites												
BRACONIDAE												
Aphidiinae												
Ephedrus incompletus	1	0	0	0	0	0	0	0	0	0	0	1
Praon spp.	58	17	4	55	44	81	128	105	31	5	47	575
Praon aguti	3	2	5	0	0	1	5	1	4	1	0	22
Praon occidentale	0	0	0	0	1	0	0	0	0	0	0	1
Praon pequodorum	38	6	2	24	2	3	12	51	11	3	0	152
Aphidius spp.	4	4	8	1	1	3	7	4	5	0	4	41
Aphidius matricariae	0	0	0	0	0	0	0	1	0	0	0	1
Aphidius nigripes	1684	1539	583	377	364	830	715	1713	779	209	514	9307
Aphidius obscuripes	2	5	0	0	1	1	0	0	1	0	0	10
Diaeretiella rapae	0	0	0	0	1	0	1	1	1	0	0	4
Other Aphidiinae	2	0	0	0	0	0	0	1	0	0	0	3
EULOPHIDAE												
Eulophinae												
Dahlbominus fuscipennis	0	0	0	0	0	0	3	0	0	0	0	3
Aphelinae												
Aphelinus semiflavus	0	0	0	0	0	0	0	1	0	0	0	1
Hyperparasites												
ENCYRTIDAE												
Encyrtinae												
Aphidencyrtus aphidivorus	0	0	0	0	0	0	0	0	9	0	0	9
EUPELMIDAE												
Eupelmella vesicularis	0	1	0	0	0	0	0	1	0	0	0	2

Table 7, continued—Total number of each species of parasite reared from dead, parasitized specimens of the potato aphid collected in northeastern Maine, 1952-1962, inclusive.

Species of parasite	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1952-62
PTEROMALIDAE												
Sphegigasterinae												
Asaphes sp.	1	0	2	1	0	0	0	0	0	0	0	4
Asaphes lucens	132	49	73	49	4	124	399	224	38	94	28	1214
Asaphes rufipes	5	18	3	15	3	26	17	13	1	5	0	106
Pachyneuron sp.	0	1	2	0	0	0	0	2	3	0	1	9
Pachyneuron siphonophorae	20	7	1	3	0	0	1	0	6	0	0	38
Pachyneuron virginicum	16	10	0	1	0	1	0	18	9	0	0	55
Coruna clavata	72	35	22	27	8	34	23	38	7	4	7	277
Euneura sp.	0	0	0	0	1	0	0	0	0	0	0	1
CYNIPIDAE												
Charipinae												
Charips sp.	1	5	1	6	1	7	5	16	29	0	4	75
Charips brassicae	25	58	10	9	1	12	32	36	1	4	0	188
Alloxysta sp.	1	0	0	0	2	4	0	1	0	1	2	11
CERAPHRONIDAE												
Lygocerus spp. (after 1957 only *Lygocerus* sp.)	61	130	124	77	55	50	2	2	2	0	1	504
Lygocerus incompletus	—	—	—	—	—	—	17	27	23	48	21	136
Lygocerus niger	—	—	—	—	—	—	53	59	12	19	12	155
Lygocerus attentus	—	—	—	—	—	—	8	45	12	2	11	78
Percent of parasitized aphids from which hyperparasites were reared	16	17	28	29	15	22	39	20	15	45	13	22*

*Weighted average.

While ceraphronids were common most years, the distribution by species can be indicated only for collections since 1958 when two additional species were described (22). From 1958 through 1962, 41% of the *Lygocerus* were *L. niger*, 36% were *L. incompletus,* and 21% were *L. attentus.* Among those identified as *Lygocerus* sp., there were probably a few specimens of an undescribed species.

Over 96% of the cynipids were *Charips* spp., mostly *Charips brassicae;* but possibly a few specimens were of an undescribed species. *Alloxysta* sp. was represented in six of the 11 years, but only in small numbers. Only in 1961 and 1962 were specimens reared from parasitized potato aphids taken from potatoes; in the other years the parasitized specimens came from swamp rose, *Rosa palustris* Marshall, the most important primary host of the potato aphid. Possibly *Alloxysta* sp. is parasitic principally in another species of aphid living on this primary host along with the potato aphid.

There was considerable variation among years in the prevalence of hyperparasites of the potato aphid. Of all parasites emerging, from 13 to 45% were hyperparasites depending upon the year. The 11-year weighted average was 22%.

The Green Peach Aphid

The green peach aphid on untreated potatoes during the period 1952 through 1963 was only slightly less abundant than the potato aphid but was parasitized to a far lesser extent (table 1). The percentage of green peach aphids parasitized was considerably more than that of buckthorn aphids but slightly less than that of foxglove aphids.

Primary parasites

Primary parasites reared from the green peach aphid were almost entirely braconids (table 8). *Aphidius nigripes* was probably the most abundant species. Although numerically *Praon* spp. predominated, this group was comprised possibly of two or three species, as yet undescribed. Other species of *Aphidius* included single specimens of *A. avenaphis* and *A. ohioensis,* a few specimens of *A. matricariae,* and small numbers of possibly two or more species not yet described.

Three specimens of the eulophid *Dahlbominus fuscipennis* were reared from green peach aphids collected from potatoes in 1958 (table 8). These parasitized specimens were collected the same year but from a potato field about one-half mile away from the one in which potato aphids were found to be infested with the same parasite (table 7). As we indicated in that instance, this is an unusual record.

Hyperparasites

The most abundant hyperparasite reared from the green peach aphid was *Asaphes lucens*, followed by *Coruna clavata, Lygocerus incompletus* and *Asaphes rufipes*. Also included were small numbers of *L. niger, Pachyneuron siphonophorae, Charips brassicae, Charips* sp., and *Pachyneuron* sp. Hyperparasitism on the average appears to have been considerably more common in the green peach aphid than in the potato aphid; the 11-year averages for these two species were 38.7% and 22.0%, respectively. The numbers of parasites reared from the green peach aphid, however, were smaller and the difference among years in percent of hyperparasitization was much larger than for the potato aphid. The range in yearly percentages was 0 to 53 and 13 to 45 for these two species of aphids, respectively (tables 7, 8).

The Foxglove Aphid

Although the foxglove aphid ordinarily was the least abundant species on untreated potatoes in the field, it ranked intermediate in the extent to which it was attacked by insect parasites.

Primary parasites

The largest numbers of braconid parasites reared from the foxglove aphid belong to two or more undescribed species of *Praon* and two or more undescribed species of *Aphidius*. Small numbers of other braconids found parasitising the aphid included *Aphidius nigripes, Praon pequodorum, Monoctonus* sp., and *Aphidius avenaphis* (table 9). A few specimens of the eulophid *Aphelinus semiflavus* were reared from parasitized specimens collected in 1958 and 1959. This parasite, which apparently attacks aphids most abundantly when infesting short-growing thick stands of plants, was fairly common in some of the grain-infesting species of aphids in 1963; but unfortunately there were then only trace numbers of the foxglove aphid on potatoes or on its primary hosts, *Hieracium* spp.

Hyperparasites

Hyperparasites from the foxglove aphid, in decreasing order of numbers of reared specimens, were *Asaphes lucens*, one or more species of *Lygocerus*, and *Coruna clavata*; and there were trace numbers of *Asaphes* sp., *Pachyneuron* sp., and *Charips* sp. While total-season hyperparasitism ranged from 0 to 43%, depending upon the year, the average was about 25% (table 9).

Table 8.—Total number of each species of parasite reared from dead, parasitized specimens of the green peach aphid collected in northeastern Maine, 1952-1962, inclusive.

Species of parasite	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1952-62
Primary parasites												
BRACONIDAE												
Aphidiinae												
Praon spp.	4	3	0	1	3	10	93	25	1	24	28	192
Praon aguti	0	0	0	0	0	0	7	0	0	0	0	7
Aphidius spp.	1	0	0	4	0	1	10	4	1	0	1	22
Aphidius avenaphis	0	0	0	0	0	0	0	0	0	0	1	1
Aphidius matricariae	0	0	0	1	0	0	6	2	0	1	0	10
Aphidius nigripes	0	2	0	1	10	4	31	26	13	30	23	140
Aphidius ohioensis	0	0	0	0	0	0	1	0	0	0	0	1
Diaeretiella rapae	0	2	1	0	0	1	0	1	0	1	3	9
EULOPHIDAE												
Eulophinae												
Dahlbominus fuscipennis	0	0	0	0	0	0	3	0	0	0	0	3
Hyperparasites												
ENCYRTIDAE												
Encyrtinae												
Aphidencyrtus aphidivorus	0	0	0	0	0	0	0	1	0	0	0	1
PTEROMALIDAE												
Sphegigasterinae												
Asaphes lucens	1	0	0	0	0	1	139	5	0	13	3	162
Asaphes rufipes	0	0	0	0	0	0	10	0	0	1	0	11
Pachyneuron sp.	0	0	0	0	0	0	0	0	1	0	0	1
Pachyneuron siphonophorae	0	0	0	0	0	0	3	0	0	0	0	3
Coruna clavata	1	1	0	1	0	3	12	4	1	2	0	25
CYNIPIDAE												
Charipinae												
Charips sp.	0	0	0	0	0	0	4	0	0	0	0	4
Charips brassicae	0	0	0	0	0	0	1	1	0	0	0	2
CERAPHRONIDAE												
Lygocerus spp. (after 1957 only *Lygocerus* sp.)	0	1	0	1	3	3	0	0	0	1	0	9
Lygocerus incompletus	—	—	—	—	—	—	0	7	0	9	2	18
Lygocerus niger	—	—	—	—	—	—	3	0	0	4	0	7
Percent of parasitized aphids from which hyperparasites were reared	28	22	0	22	19	30	53	24	12	35	8	39*

*Weighted average.

Table 9.—Total number of each species of parasite reared from dead, parasitized specimens of the foxglove aphid collected in northeastern Maine, 1952-1962, inclusive.

Species of parasite	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1952-62
Primary parasites												
BRACONIDAE												
Aphidiinae												
Praon spp.	3	5	0	0	7	21	17	6	1	0	26	86
Praon pequodorum	1	1	0	2	0	0	1	0	0	0	0	5
Monoctonus sp.	0	0	0	0	0	2	1	0	0	0	0	3
Aphidius spp.	0	0	0	33	1	13	3	0	0	0	2	52
Aphidius avenaphis	0	0	0	0	0	0	0	0	0	0	1	1
Aphidius nigripes	0	1	0	1	6	3	5	0	0	0	1	17
EULOPHIDAE												
Aphelinae												
Aphelinus semiflavus	0	0	0	0	0	0	2	1	0	0	0	3
Hyperparasites												
PTEROMALIDAE												
Sphegigasterinae												
Asaphes sp.	0	0	0	1	0	0	0	0	0	0	0	1
Asaphes lucens	0	0	0	0	0	5	18	0	0	0	2	25
Pachyneuron virginicum	1	0	0	0	0	0	0	0	0	0	0	1
Coruna clavata	1	0	0	3	0	2	3	0	0	0	0	9
CYNIPIDAE												
Charipinae												
Charips sp.	0	1	0	0	0	0	0	0	0	0	0	1
CERAPHRONIDAE												
Lygocerus sp. (possibly *Lygocerus* spp. prior to 1958)	0	0	0	13	3	1	1	0	0	0	0	18
Percent of parasitized aphids from which hyperparasites were reared	33	13	0	32	18	17	43	0	0	0	6	25*

*Weighted average.

The Buckthorn Aphid

The buckthorn aphid usually has been by far the predominant species on untreated, field-growing potatoes in northeastern Maine, yet it has been least parasitized (table 1). Possibly because of its small size, some species of parasites may not reach maturity in this aphid, particularly in the small nymphs. However, we cannot say whether lack of parasitism in the buckthorn aphid is due to host selection by the parasites because of this or related factors.

Primary parasites

The most common species of primary parasite reared from the buckthorn aphid has been *Aphidius nigripes.* The largest number in a single group belonged to possibly two or three undescribed species of *Praon* (table 10). In addition to small numbers of *Aphidius obscuripes* and of possibly two undescribed species of *Aphidius,* the other aphidiines included *Diaeretiella rapae, Ephedrus incompletus,* and an undescribed species of *Diaeretiella.* Our records indicate that *Diaeretiella* spp. have been more commonly reared from the turnip aphid, *Hyadaphis pseudobrassicae* (Davis) than from the potato-infesting species.

Hyperparasites

As with the other potato-infesting aphids, *Asaphes lucens* was the most abundant species of hyperparasite reared from the buckthorn aphid (table 10). *Lygocerus incompletus* and *Coruna clavata* were next most common. Also represented by small numbers were two or more additional, as yet undescribed, species of *Lygocerus, Asaphes rufipes, Charips brassicae,* and an undescribed species of *Charips.* Ranging from 0 to 35% by years, hyperparasitism over the 11-year period averaged 22%, as it did in the potato aphid.

Miscellaneous Species of Aphids

Parasites were reared also from aphids of other species found on the sample units examined while making counts of potato-infesting species of aphids on the primary hosts and on secondary hosts other than potatoes. The identities of these are shown in table 11. These data are of interest chiefly because they reveal the kinds of parasites that affected several species of aphids competing with the potato-infesting species on the same plants. In some instances the host plants of record may be incorrect, especially in the instance of the nonhost oats which closely bordered the plots of potatoes. Undoubtedly some parasitized aphid specimens moved from the nonhost or the host plant

Table 10.—Total number of each species of parasite reared from dead, parasitized specimens of the buckthorn aphid collected in northeastern Maine, 1952-1962, inclusive.

Species of parasite	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1952-62
Primary parasites												
BRACONIDAE												
Aphidiinae	1	0	0	0	0	0	0	0	0	0	0	1
Ephedrus incompletus	0	0	0	0	0	0	1	0	0	0	0	1
Praon spp.	17	8	0	1	8	78	36	41	4	45	8	246
Aphidius spp.	5	1	1	3	1	3	3	1	1	5	2	26
Aphidius nigripes	4	1	1	0	17	13	10	3	9	29	2	89
Aphidius obscuripes	14	2	0	0	1	3	0	0	0	0	0	20
Diaeretiella sp.	1	0	0	0	0	0	0	0	0	0	0	1
Diaeretiella rapae	0	2	1	0	0	1	0	1	0	0	1	6
Hyperparasites												
PTEROMALIDAE												
Sphegigasterinae												
Asaphes lucens	3	0	0	1	0	3	21	2	0	23	1	54
Asaphes rufipes	0	0	0	0	0	2	1	1	0	1	1	6
Coruna clavata	0	2	0	0	0	3	0	4	0	3	1	13
CYNIPIDAE												
Charipinae												
Charips sp.	0	0	0	0	0	1	1	0	0	0	0	2
Charips brassicae	4	0	0	1	0	1	0	0	0	0	0	6
CERAPHRONIDAE												
Lygocerus sp. (possibly *Lygocerus* spp. prior to 1957)	1	1	0	0	2	3	0	1	0	1	0	9
Lygocerus incompletus	—	—	—	-	—	—	2	2	0	14	0	18
Lygocerus niger	—	—	—	—	—	—	1	0	0	0	0	1
Percent of parasitized aphids from which hyperparasites were reared	16	18	0	33	7	12	34	18	0	35	19	22*

* Weighted average

Table 11.—The numbers of parasites reared from miscellaneous species of aphids, 1952-1962, inclusive.

Species of host plant	*Prunus nigra* Aiton			*Rosa* spp.		*Avena sativa* Linnaeus[1]				Secondary weed host	
Species of parasite	*Anuraphis cardui* (Linnaeus)	*Phorodon humuli* (Schrank)	*Rhopalosiphum* sp.	*Capitophorus* sp.	*Myzaphis bucktoni* Jacob	*Acyrthosiphon pisum* (Harris)[1]	*Macrosiphum avenae* (Fabricius)	*Macrosiphum* sp.[1]	*Rhopalosiphum fitchii* (Sanderson)	*Hyalopterus atriplicis* (Linnaeus)	*Myzus certus* (Walker)
Primary parasites											
BRACONIDAE											
Aphidiinae											
Praon spp.	4	11	0	5	4	1	29	3	6	0	0
Praon pequodorum	0	0	0	0	0	4	0	0	0	0	0
Aphidius spp.	0	0	0	0	0	0	7	0	6	0	0
Aphidius matricariae	0	0	0	12	0	0	0	0	0	0	0
Aphidius nigripes	0	0	0	1	0	0	14	3	5	0	0
Aphidius obscuripes	0	0	0	0	0	0	89	8	1	0	0
Aphidius ohioensis	0	0	0	0	0	0	0	0	1	0	0
Aphidius pulcher	0	0	0	0	0	1	0	0	0	0	0
Aphidius ribis	0	0	0	2	0	0	0	0	0	0	0
Lysaphidus adelocarinus	0	0	0	1	0	0	0	0	0	0	0
Lysaphidus rosaphidis	0	0	0	2	0	0	0	0	0	0	0
Trioxys sp.	0	0	0	0	0	0	0	0	1	0	0
Trioxys gahani	0	0	0	1	0	0	0	0	0	0	0
Diaeretiella rapae	0	0	0	0	0	0	0	0	3	1	1
EULOPHIDAE											
Aphelinae											
Aphelinus semiflavus	0	0	0	1	0	0	0	0	0	0	0
Hyperparasites											
PTEROMALIDAE											
Sphegigasterinae											
Asaphes lucens	1	5	1	5	1	0	6	0	1	0	0
Pachyneuron siphonophorae	0	1	0	0	0	0	9	3	0	0	0
Pachyneuron virginicum	0	0	0	0	0	0	1	0	0	0	0
Coruna clavata	0	1	0	0	0	0	3	0	0	0	0
CYNIPIDAE											
Charipinae											
Charips sp.	0	1	0	0	0	0	5	0	1	0	0
Charips brassicae	0	1	0	0	0	0	19	6	0	0	0
CERAPHRONIDAE											
Lygocerus sp.	0	0	0	0	0	0	3	1	0	0	0
Lygocerus attentus	0	0	0	0	1	0	1	0	0	0	0

[1] The oats grew in strips bordering plots of potatoes and at times had intermixed plants of young clover and weeds.

and became attached to the other before dying. The parasitized specimens of the pea aphid shown as coming from oats most likely came from young clover plants which during some years grew with the oats.

Altogether, approximately 17 species of primary parasites and 10 species of hyperparasites were reared from this miscellaneous group of aphids during the 11-year period (table 11). Largest numbers came from the English grain aphid *Macrosiphum avenae* (Fabricius) and the apple grain aphid, *Rhopalosiphum fitchii* (Sanderson) in part because of their larger populations, also because of the more frequent counts on and collections from the oats than from the other plants. Five species of primary parasites not found infesting the potato-infesting species of aphids were reared from this miscellaneous group of aphids (tabulation on page 9 and table 11). These were *Aphidius ribis* Haliday, *Lysaphidus adelocarinus* Smith, *Lysaphidus rosaphidis* Smith, and *Trioxys gahani* Smith, from *Capitophorus* sp. on *Rosa* spp., and *Trioxys* sp. from *Rhopalosiphum fitchii* on oats. *Asaphes virginicum* was the only species of hyperparasite, reared from the miscellaneous group, we can be certain did not occur also in the potato-infesting species. We do not know whether the specimens of *Lygocerus* sp. from the English grain aphid and *Macrosiphum* sp. shown in table 11 were of the undescribed species mentioned earlier or whether they may have been that and/or *L. incompletus*, since the determinations were made before *L. incompletus* was described (22). These specimens were reared in 1953, 1956, and 1957, and the determinations were made in the years following. Several species of primary parasites and of hyperparasites were reared from potato-infesting aphids that did not occur in the miscellaneous group of aphids, likely because of more collections of affected specimens of the potato-infesting group (tabulation on page 9 and table 11).

SEASONAL HISTORY AND ABUNDANCE OF THE PARASITES

To gain some concept of the seasonal histories of the parasites we have charted the seasonal distribution of each of the more abundant species or groupings of species of parasites reared from potato-infesting species of aphids during the 20-year period 1942-1961 irrespective of the aphid host or of the plant host of the aphid (figures 5, 6, 7). The percentages of the total number of identified specimens, irrespective of time of emergence, are shown at the midpoints of 5-day intervals of collection of the parasitized aphids. Since the parasites in the dead, parasitized aphids at the time of collection most likely were in the pupal or late-larval stages, the seasonal distribution of the free-flying

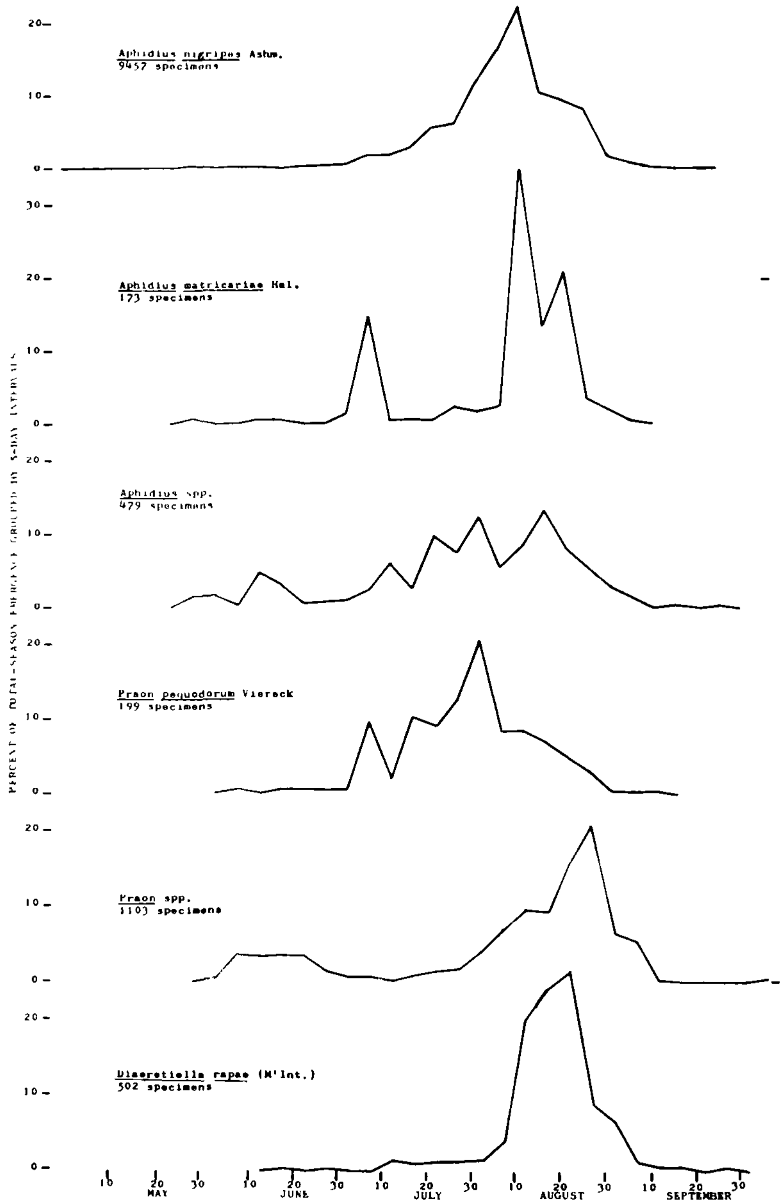

Figure 5.—Seasonal distribution of primary parasites of potato-infesting aphids reaching maturity based on the time the aphid mummies were collected from the overwintering and summer hosts, principally potatoes, 1942 to 1961, inclusive.

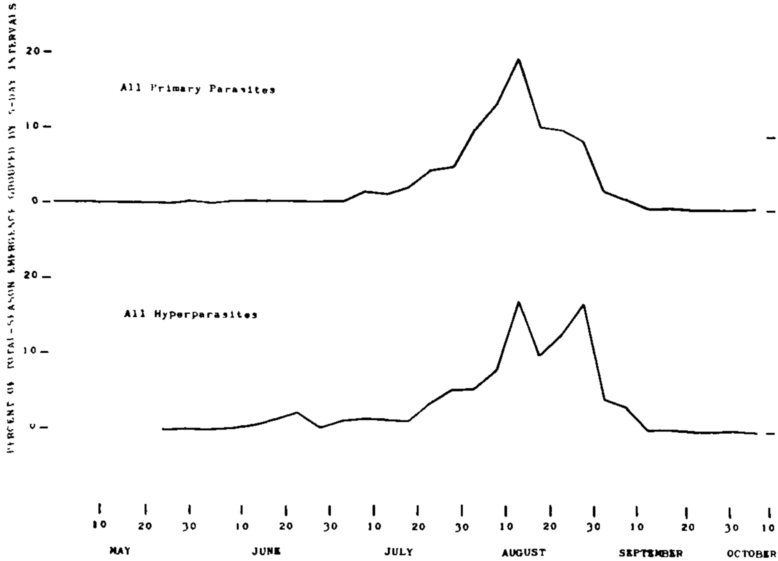

Figure 6.—Seasonal distribution of all primary and hyperparasites of potato-infesting aphids reaching maturity based on the time the aphid mummies were collected from the overwintering and summer hosts, principally potatoes, 1942 to 1961, inclusive.

adults should be similar to but slightly later than that shown in the figures.

Little, if any, extrapolation of the seasonal histories of the parasites can be made from figures 5, 6, or 7 because of the relatively small number of individuals for which records are available, and because no studies of the bionomics of these species of parasites were made. Furthermore, there were differences among years and seasons in various physical factors affecting the seasonal history and abundance of both the parasites and the aphids.

Primary Parasites

The parasitized aphids from which primary parasites emerged were largely potato aphids (figure 5). From mid-June until early in September the parasitized aphids came mostly from field-growing potato plants but some were taken on other secondary hosts. Before and after those times the aphids came mostly from primary hosts. There was some overlapping in the seasons of collecting from primary and secondary hosts during spring and fall, both before and after the spring and the fall migrations of the aphids.

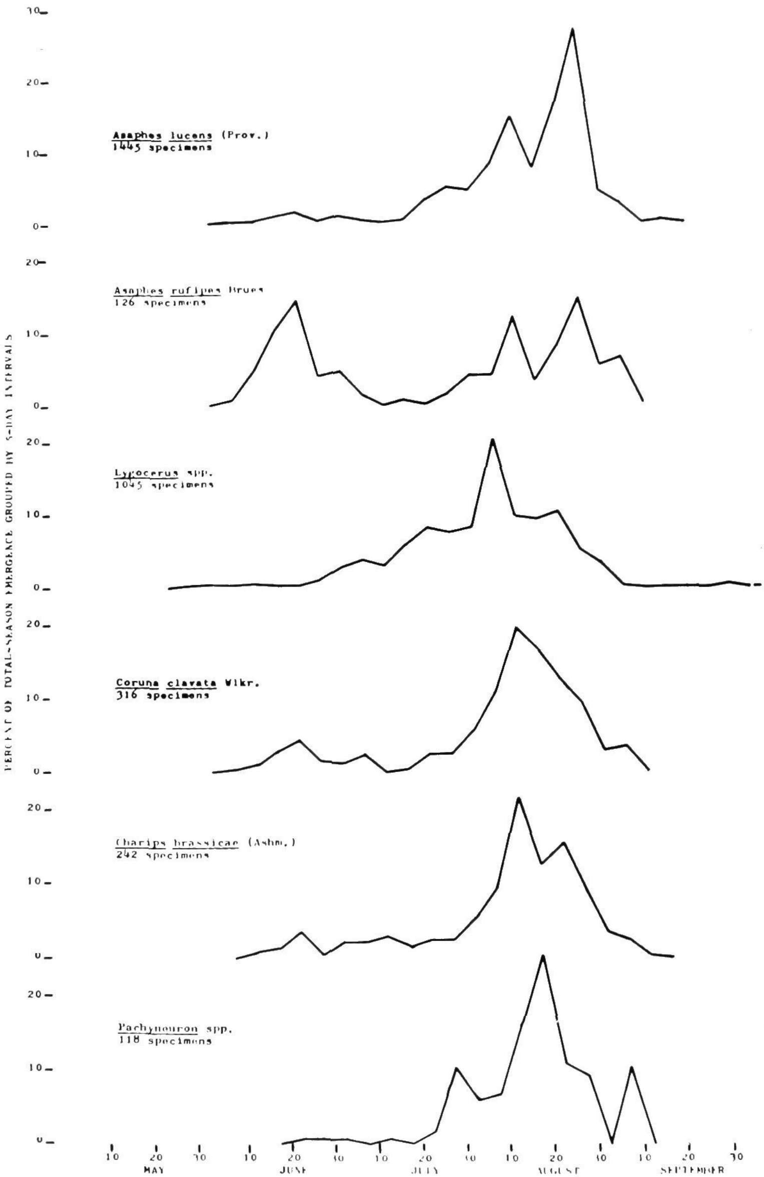

Figure 7.—Seasonal distribution of hyperparasites of potato-infesting aphids reaching maturity based on the time the aphid mummies were collected from the overwintering and summer hosts, principally potatoes. 1942 to 1961, inclusive.

Aphidius nigripes was the species that started earliest to parasitize the aphids. Its activities were evident early in May, which was before maturation of the stem mother aphids. Parasitization by *Aphidius matricariae* and the undescribed species of *Aphidius* began somewhat later since the first affected aphids were not collected until after May 20. Seasonal activity of *Praon* spp. started slightly later, but a little before that of *Praon pequodorum*, while that of *Diaeretiella rapae* was latest in starting.

All these primary parasites infested aphids on their primary hosts in spring, but not all of them were collected again in fall (figure 5). The only ones taken from primary hosts in fall included *Praon* spp., *D. rapae, Aphidius* spp., and *A. nigripes*. Other species of parasites may have been active also, since dissections of living aphids taken late in fall from primary hosts revealed the presence of living, internal parasites (38).

We cannot suggest with accuracy the number of generations per year for the species of parasites included in figure 5. In most instances there probably are at least four, one in the aphids on the primary host plants in spring and again in fall, and at least two in the aphids on potatoes and on other secondary host plants in summer.

The grouping of all primary parasites offered no resolution to the question of the number of generations each year; in fact, complete obscurement resulted (figure 6). Very likely this was caused by variations in seasonal histories of the several species and in overlapping of generations both within and among species. However, relative abundance of the primary parasites rather closely followed that of the potato aphid. The primary parasites were active in some years as early as about May 1; an occasional parasite was active until early in October. Overall abundance began gradually to increase in mid-July. The increase was, in general, greatest from August 1 to 10. There was then a rapid decrease for about one week, followed by a more gradual decrease for about one week. Dead, parasitized aphids were scarce after September 10.

Hyperparasites

Manifestations of hyperparasitization appeared later in spring than did those of parasitization by primary parasites. The activity of the hyperparasites continued as late in fall as did that of the primary parasites (figure 7). *Lygocerus* spp. started activity earliest, followed by *Asaphes* spp., *Coruna clavata, Charips* spp., and *Pachyneuron* spp. *Lygocerus spp. and A. lucens* appeared to continue their activities latest in fall. These were the only two species reared from parasitized aphids taken in fall from the primary hosts. Although the number of generations of the hyperparasites cannot be stated with any degree of accuracy, there probably are four: one in the aphids living on the primary host plants in spring, two or more in those found on potatoes and other secondary host plants in summer, and one on the aphids living on their primary hosts in fall.

No clarification of seasonal history of the hyperparasites resulted from grouping all reared specimens (figure 6). The pattern of relative seasonal abundance of the hyperparasites closely followed that of the primary parasites except activity was about three weeks later in starting. The period of greatest abundance was spread over a slightly longer interval, and there were two peaks of equal size, one about August 12 and the other about August 27. The two peaks may have been due in part to differences in relative abundance of the species of aphids or of the hyperparasites. The potato aphid (the most abundantly parasitized species) ordinarily reaches its seasonal peak about the time of the first of the two peaks shown for hyperparasites. After that peak there is a generally steady or even a sharp drop in numbers of this aphid. The other three species of aphids ordinarily continue to increase in abundance until sometime during the latter part of August, however. Even though these three aphids are parasitized less frequently than the potato aphid, the activity of hyperparasites within this larger overall population represented by these three species of aphids is probably sufficient to account for the second peak shown in figure 6.

SOME GENERAL CONSIDERATIONS OF PARASITISM

Our studies permitted us to examine several factors that influence year-to-year importance of parasites as biological agents for aphid control on potatoes. Among these factors were the numbers of species, as well as the abundance of each; how well adapted each species is for surviving from one year to another, or even over a period of several years of low abundance of the aphid hosts; and the relative abundance and probable effects of the hyperparasites upon abundance of the primary parasites and their aphid hosts.

Stability in Numbers of Parasites

Insect parasites can play an important role in control of aphids on potatoes if one or more species are present every year in large enough numbers to parasitize a large percentage of the aphids at any given time but particularly in the early part of the season. Fewer individuals of a larger number of species of parasites also can provide a like effect

Table 12.—Distribution of parasites reared from potato-infesting species of aphids during two periods, 1942 through 1950 and 1952 through 1962.

	Potato		Green peach		Foxglove		Buckthorn	
	1942 -50	1952 -62	1942 -50	1952 -62	1942 -50	1952 -62	1942 -50	1952 -62
Primary Parasites								
BRACONIDAE								
Aphidiinae								
Ephedrus incompletus	—	X	—	—	—	—	—	X
Praon spp.	X	X	X	X	X	X	—	X
Praon aguti	X	X	X	X	X	—	—	—
Praon americanum	—	—	X	—	—	—	—	—
Praon occidentale	—	X	—	—	—	—	—	—
Praon pequodorum	X	X	X	—	—	X	—	—
Monoctonus sp.	—	—	—	—	—	X	—	—
Aphidius spp.	X	X	X	X	X	X	X	X
Aphidius avenaphis	X	—	X	X	—	X	—	—
Aphidius matricariae	X	X	X	X	X	—	X	—
Aphidius nigripes	X	X	X	X	—	X	X	X
Aphidius obscuripes	—	X	—	—	—	—	—	X
Aphidius ohioensis	X	—	—	X	—	—	—	—
Aphidius pulcher	X	—	X	—	—	—	—	—
Lysiphlebus testaceipes	—	—	—	—	—	—	X	—
Trioxys sp.	—	—	—	—	—	—	X	—
Diaeretiella sp.	—	—	—	—	—	—	—	X
Diaeretiella rapae	X	X	X	X	—	—	X	X
EULOPHIDAE								
Eulophinae								
Dahlbominus fuscipennis	—	X	—	X	—	—	—	—
Aphelinae								
Aphelinus semiflavus	—	X	—	—	—	X	—	—
Hyperparasites								
ENCYRTIDAE								
Encyrtinae								
Aphidencyrtus aphidivorus	—	X	—	X	—	—	—	—
EUPELMIDAE								
Eupelmella vesicularis	—	X	—	—	—	—	—	—
PTEROMALIDAE								
Sphegigasterinae								
Asaphes sp.	—	X	—	—	—	X	—	—
Asaphes lucens	X	X	X	X	X	X	—	X
Asaphes rufipes	X	X	—	X	—	—	—	X
Pachyneuron sp.	X	X	—	X	—	—	—	—
Pachyneuron altiscutum	X	—	—	—	—	—	—	—
Pachyneuron siphonophorae	X	X	—	X	—	—	—	—
Pachyneuron virginicum	—	X	—	—	—	X	—	—
Coruna clavata	X	X	—	X	—	X	—	X
Euneura sp.	—	X	—	—	—	—	—	—
CYNIPIDAE								
Charipinae								
Charips sp.	X	X	X	X	—	X	—	X
Charips brassicae	X	X	X	X	—	—	—	X
Alloxysta sp.	—	X	—	—	—	—	—	—
CERAPHRONIDAE								
Lygocerus sp.	—	X	—	X	—	X	—	X
Lygocerus attentus	—	X	—	—	—	—	—	—
Lygocerus incompletus	—	X	—	X	—	—	—	X
Lygocerus niger	X	X	X	X	—	—	X	X

if the overall numbers are large enough. For parasites to exert dependable aphid control of any degree, however, there must be substantial stability from year to year in the overall abundance and effectiveness of parasites at the most critical times for controlling the aphids.

Tables 7, 8, 9, and 10 show there were large differences among years during the 11-year period 1952 through 1962 both as to the number of species and the number of individuals of the reared parasites for each of the four species of potato-infesting aphids. There were only a few species of primary parasites having an appreciable degree of abundance. These included *Aphidius nigripes,* two undescribed species of *Praon* and two of *Aphidius,* and *P pequodorum.* The most common hyperparasites reared from all species of parasitized aphids included *Asaphes lucens, Coruna clavata,* and *Lygocerus* spp. *Charips brassicae* was commonly reared only from the potato aphid. Relatively speaking only one species of primary parasite—*A. nigripes*—was abundantly reared from all species of aphids, while several species of hyperparasites were found to be common.

The number of species of parasites taken during the 9-year period 1942 through 1950 (39) differed substantially from that found during the 11-year period 1952 through 1962 (table 12). During the earlier period, when aphid populations on potatoes were generally much larger, and when the green peach aphid was much more abundant than in the later period, we found a total of about 15 species of primary parasites and nine species of hyperparasites. During the later period there were about 18 species of primary parasites and 17 species of hyperparasites. Of a total of about 22 species of primary parasites reared during both periods, four were found only during the early period while seven occurred only during the later period. Among the hyperparasites, only one species was found during the early period that did not occur also during the later period but nine that were not found during the earlier period occurred during the later one.

Differences between periods for each species of aphid are shown in table 12. During the 20-year period a total of approximately 17 species of primary parasites and 18 species of hyperparasites were reared from the potato aphid. Corresponding numbers reared from the green peach aphid were 14 and 11, while from the buckthorn and foxglove aphids the numbers of species were 12 and eight, 11 and six, respectively. Altogether about 40 species of parasites were reared from the four species of aphids, of which 22 were primary parasites and 18 were hyperparasites.

The following tabulation, from data in tables 7, 8 9, and 10 and from Shands et al. (39), strongly indicates that intensity of hyperparasitism varied between year groupings or periods as well as among species of aphids. Except for the foxglove aphid—which was represented in this study by only a few parasitized specimens—hyperparasitization was substantially lower during the period 1942-1950 than from 1952 through 1962. Reasons for this are not clear.

Species of aphids	Parasites reared		Proportion that were hyperparasites	
	1942-1950	1952-1962	1942-1950	1952-1962
	Number		Percent	
Potato	547	12,983	15	22
Green peach	416	628	8	39
Buckthorn	49	499	4	22
Foxglove	8	222	25	25

Ability of the Parasites to Survive

Starting in 1953, records were kept of the emergence dates of the parasites as well as collection dates of the dead, parasitized aphids. From these records it soon became apparent that a small percentage of the parasites may survive a winter within the aphid mummy and emerge the following year or later. Some emergence of parasites occurred during the second and third years after collection; but there has, as yet, been none during the fourth year. We therefore discarded, after the third year of observation, all parasitized aphids from which parasites had not emerged. Emergence records for all parasites reared from aphids collected during the eight-year period 1953-1960, inclusive, are shown by years on a percentage basis in table 13.

While most emergence of both primary and hyperparasites occurred during the year of collection, small numbers emerged in the second and third years (table 13). It is both interesting and probably significant that the species of primary parasites most common over the 20-year period were those having some carry-over of emergence to the third year, including *Aphidius nigripes* and the undescribed species of *Praon* and of *Aphidius*. Six species of the hyperparasites had some carryover of emergence to the third year after collection. This characteristic is likely of importance for the survival of both primary parasites and hyperparasites, more especially the latter since their survival and abundance depend upon the survival and abundance of the primary parasites as well as of the aphids.

Effect of Hyperparasitism upon Primary Parasitism and Aphid Infestations

Our attempt to detect any relationships between abundance of hyperparasites and the sizes and trends of the aphid populations is based

Table 13.—Three-year emergence records of parasites from potato-infesting species of aphids collected 1953 through 1960.

Species of parasite	Total number of specimens	Percent emerging		
		1st year	2nd year	3rd year[1]
Primary Parasites				
Ephedrus incompletus	1	100	—	—
Praon spp.	888	97	2	T
Praon aguti	25	96	4	—
Praon occidentale	1	100	—	—
Praon pequodorum	120	97	3	—
Monoctonus sp.	3	100	—	—
Aphidius spp.	135	89	8	3
Aphidius avenaphis	6	100	—	—
Aphidius matricariae	22	100	—	—
Aphidius nigripes	7,071	98	2	T
Aphidius obscuripes	105	98	2	—
Aphidius ohioensis	2	100	—	—
Aphidius pulcher	1	100	—	—
Aphidius ribis	2	100	—	—
Lysaphidus adelocarinus	1	100	—	—
Trioxys gahani	1	100	—	—
Diaeretiella rapae	19	100	—	—
Dahlbominus fuscipennis	6	100	—	—
Aphelinus semiflavus	5	100	—	—
Hyperparasites				
Aphidencyrtus aphidivorus	10	90	10	—
Eupelmella vesicularis	2	100	—	—
Asaphes sp.	4	50	50	—
Asaphes lucens	1,057	94	6	—
Asaphes rufipes	99	92	8	—
Pachyneuron sp.	10	70	20	10
Pachyneuron siphonophorae	34	97	3	—
Pachyneuron virginicum	40	93	8	—
Coruna clavata	238	82	18	1
Euneura sp.	1	—	100	—
Charips sp.	86	92	8	—
Charips brassicae	187	75	22	2
Alloxysta sp.	7	100	—	—
Lygocerus sp.	474	93	7	T
Lygocerus attentus	67	93	6	1
Lygocerus incompletus	79	95	1	4
Lygocerus niger	128	96	4	—

[1] T = less than 0.5%

on comparisons of total-season hyperparasitization in one year with early-season populations and parasitism of the potato aphid in the year following. By imposing this limitation, the important confounding effects of entomogenous fungi upon population trends of this aphid are excluded, since experience (35) indicates that activity of the fungi in most years does not start before late in July. The possible, confounding influence of hyperparasitism cannot be avoided, however. Theoretically, excessive hyperparasitism in one year might cause a reduction in parasitism in the year following, which in turn could be reflected as an increase in rate of aphid population growth.

We have selected two periods for observing possible effects of hyperparasitism upon aphid populations, July 1 to 11 and July 11 to 23. An expression for the first period should indicate the effect of hyperparasitism upon the size of the aphid population at the end of the aphids' spring migrations; it should be rather comparable from year to year. The aphid population of the second period, when compared with the first, should indicate its rate of increase as influenced by physical and biotic factors excluding entomogenous fungi.

The prevalence of hyperparasitism in one year appears to have had no appreciable or consistent effect upon prevalence of parasitism in that year or the one following, either during the early part of the field season or for the entire field season (table 14). Neither was prevalence of hyperparasitism in one year consistently associated with that in the year before or after. Two of the three years of highest early-season parasitism—1955 and 1956—followed one and two years of high hyperparasitism, respectively. By contrast early-season parasitism was high in 1953 and low in 1957 following years of low hyperparasitization. No parasitism was observed before July 23 in 1961 or 1962 following years of low and high hyperparasitization, respectively.

The relative abundance of hyperparasites in one year appears to have had no appreciable or consistent influence upon the early-season size of populations of the potato aphid the year following (table 14).

Table 14.—The relation of hyperparasitism to parasitism and populations of the potato aphid on field-growing potato plants not treated with insecticides, 1952 to 1963[1]

Year	Percent of hyperparasitization[2]	Percent of potato aphids parasitized			Av. no. potato aphids on 3 leaves per plant[3]	
		July 1-11	July 12-23	All season	July 1-11	July 12-23
1952	15.7	10.0	3.6	6.35	0.08	0.34
1953	16.6	16.7	3.8	1.34	.04	.22
1954	28.3	1.4	3.7	.82	.08	.24
1955	29.1	16.5	5.9	2.49	.48	.41
1956	15.3	0	15.8	.47	T[4]	.01
1957	21.9	0	4.7	1.18	.03	.05
1958	39.0	7.1	7.0	4.25	.02	.03
1959	20.4	3.8	3.0	3.41	.50	2.16
1960	15.4	5.1	3.5	1.40	.07	.37
1961	44.8	0	0	2.79	.04	.01
1962	13.3	0	0	2.33	.01	.10
1963	—	2.8	1.8	1.73	.15	.16

[1] The number of sample units examined for these two dates of observation ranged from 400 and 600 in 1952 to 2,050 for both dates in 1955. The average number for each date exceeded 1,100.
[2] Overall, total-season hyperparasitization as identified from all reared parasites (table 8).
[3] The unit of sample was 3 leaves per plant (top, middle, bottom).
[4] T = less than 0.005.

Aphid populations in early July were larger in 1955 and 1959 following years of high hyperparasitization, than at the same time the preceding year. However, in 1962, in a similar sequence, the aphid population was slightly smaller than it was in 1961. Likewise, following two years of relatively high hyperparasitism the aphid population was very small in early July, 1956.

The percent of parasitism in the potato aphid in July of one year was not consistently or appreciably associated with the all-season prevalence of parasitism in the preceding year; neither was all-season prevalence of parasitism related to that of the preceding year or the year following (table 14). In general, there was a tendency for the percent of parasitized aphids to decrease as the season advanced. In July this decrease likely resulted from the rapidly increasing size of aphid populations in conjunction with longevity of the adult parasites and the break between generations resulting from mortality of the brood of adult parasites first reaching the potato fields.

Early-season abundance of the potato aphid was not consistently associated with the all-season level of parasitism of the aphid in the preceding year (table 14).

The rate of aphid increase in July appeared not to have been influenced consistently by percent of hyperparasitism the preceding year (table 14). The rate was high or relatively so in two years—1962 and 1959—following years of high hyperparasitism, and low in 1955 following a year of high hyperparasitism. Likewise following years of low hyperparasitism the rate of aphid increase up to July 23 was high in 1953 and in 1960 and low in 1958 and in 1961.

The rate of aphid increase in July was not consistently associated with the percent of parasitism at the time (table 14). In two years when no parasitism was detected before July 23—1961 and 1962—the rate of aphid increase was high one year, while a drop in numbers occurred in the other. When early-season parasitism was relatively high, the early-season rates of aphid increase were high in 1952 and in 1953, while a slight drop in aphid abundance during the period occurred in 1955.

Lack of consistent relationships among hyperparasitism, parasitism, and abundance or rate of increase of the potato aphid during the 12-year period (table 14) likely was due in part to conditions difficult to avoid or compensate for. Ordinarily, parasitism in the aphid and populations of the aphid are so small during the first part of July that large samples are required to provide adequate estimates of abundance. While each figure in table 14 was based on the examination of 600 to 2,050 sample units (1,800 to 6,150 leaves), with an average of over

1,100 units or 3,300 leaves, even these large numbers may have been inadequate at very low levels of abundance of parasitism or of the aphid. Variation among years in abundance of predators likely accounted for some of the lack of consistency found in relationships of the parasites and the aphids when the early-season populations of insects used as food by the predators were so small on the young potato plants.

RELEASES AND RECOVERY OF PARASITES

Releases of parasites were made in fields of potatoes and in patches of primary hosts of three of the potato-infesting species of aphids during 1957, 1958, and 1962 (table 15). Altogether, we released in northeastern Maine a total of about 25,000 adult parasites belonging to four

Table 15.—Liberations of adult insect parasites of aphids in northeastern Maine, 1942-1963, inclusive.

Number liberated	Host plant	Location	Date
	Aphelinus semiflavus from France[1]		
100	*Rhamnus alnifolia*	1 mi. S. Bridgewater	May 13, 1957
192	*Rosa palustris*	3.5 mi S. Bridgewater	do
1609	do	4.0 mi. S. Presque Isle	May 30, 1957
	Aphidius matricariae from France[1]		
1739	*Rhamnus alnifolia*	1 mi. S. Bridgewater	May 13, 1957
1399	*Rosa palustris*	3.5 mi. S. Bridgewater	do
920	*Rhamnus alnifolia*	1 mi. S. Bridgewater	May 16, 1957
900	*Rosa palustris*	3.5 mi. S. Bridgewater	do
1115	do	4.0 mi. S. Presque Isle	May 20, 1957
1936	*Prunus nigra*	2.9 mi. E. Smyrna Mills	May 23, 1957
2900	*Rhamnus alnifolia*	4.5 mi. S. Mapleton	May 27, 1957
2267	do	do	May 29, 1957
1166	*Rosa palustris*	7.8 mi. W. Houlton	May 31, 1957
1068	*Solanum tuberosum*	1 mi. S. Presque Isle	June 18, 1957
1776	do	do	June 20, 1957
2287	do	do	June 23, 1957
814	do	do	June 27, 1957
1128	do	do	Aug. 6, 1958
367	do	do	Aug. 8, 1958
286	do	do	Aug. 11, 1958
464	do	do	Aug. 14, 1958
479	do	do	Aug. 16, 1958
608	do	do	Aug. 19, 1958
152	do	do	Aug. 20, 1958
	Aphidius sp. (near *A. medicaginis*) from India[1]		
75	*Solanum tuberosum*	1 mi. S. Presque Isle	Aug. 16, 1958
64	do	do	Aug. 19, 1958
169	do	do	Aug. 20, 1958
	Aphidius sp. from France[2]		
25	*Solanum tuberosum*	1 mi. S. Presque Isle	Aug. 28, 1962

[1] Reared at and shipped from Moorestown, New Jersey, by D. W. Jones.

[2] Collected in France by R. I. Sailer, reared at and shipped from Moorestown, New Jersey, by L. B. Parker.

species. The 25 specimens of *Aphidius* sp. liberated in 1962 emerged at the Moorestown (New Jersey) Station of the Entomology Research Division from dead, parasitized aphids collected from potatoes several days earlier in France. All of the other specimens were reared at Moorestown. France was the initial source of the breeding stocks of *Aphidius matricariae* and *Aphelinus semiflavus,* while India was the source of the *Aphidius* sp. (near *A. medicaginis* Marshall) released in 1958.

Except for intensive searches daily during much of August, 1959, in one field of potatoes on Aroostook Farm where many parasites were released in 1957 and 1958, our efforts to recover parasites at points of liberation were limited to rearings from collections of dead, parasitized aphids. These specimens we found on sample units of randomly located plants at each place when making periodic counts of the aphids. Our recovery efforts on all plantings of potatoes were quite intensive, since we made weekly counts of aphids in all untreated plots or fields in or near release sites on Aroostook Farm. The counts on swamp rose were at weekly intervals in spring and fall of 1957, 1958, and 1959; those on Canada plum were in early June of each year, including 1957. We made very limited efforts to recover parasites at stations where parasites were released in stands of alder-leaved buckthorn, the primary host of the buckthorn aphid.

There were no recoveries of *Aphidius* sp. (near *A. medicaginis*). Identifications have not yet been made of parasites reared from dead, parasitized aphids collected in 1963 in the potato field where the *Aphidius* sp. from France were released in 1962. Chances appear very limited for its establishment because of the single, small, late-season release in a potato field having a very small aphid population.

There appears to be little likelihood of establishment of *Aphidius matricariae* or of *Aphelinus semiflavus* from releases made during this study. *A. matricariae* has been reared in small numbers for a number of years from potato-infesting aphids in northeastern Maine. There was no substantial increase in its distribution, abundance, or frequency of representation in rearings from parasitized aphids collected since the releases of 1957 and 1958. In the 20-year period, only six specimens of *A. semiflavus* were reared from all of the dead, parasitized aphids collected. One of these was found in 1942, three in 1958, and two in 1959. All came from Aroostook Farm, approximately two miles north of the nearest station where a release was made in 1957. Three were from the foxglove aphid on the primary host, *Hieracium* sp.; only one of the six came from the potato aphid on potatoes.

SYNOPSIS OF THE BIOLOGIES OF SOME INSECT PARASITES OF APHIDS

Primary Parasites

Insect parasites are important in biological control of aphids infesting potatoes in northeastern Maine. Their role would be more impressive if parasite abundance could be increased throughout the period of aphid breeding each year, especially from the time of the spring migrations to potatoes until the end of the field season. At the end of the spring migrations the aphid populations on the potatoes are very small.

Efforts can be made to increase the usefulness of insect parasites as biological agents of aphid control. The abundance and effectiveness of the species of parasites already present may be increased by supplemental releases at appropriate times. Non-native species that appear to be more efficient than the locally occurring ones could be introduced to complement the latter. A prerequisite for either course is knowledge of the biologies of both the parasites and the hyperparasites that attack them. We have included, from available published sources and from our observations, information relating to some aspects of the biologies of the more abundant, locally occurring primary and secondary parasites of the potato-infesting aphids, as well as a few of the species of primary parasites that have been imported and released elsewhere in the United States.

The primary insect parasites of aphids we have found in Maine belong to two families, Braconidae and Eulophidae. All of the braconids reared to maturity thus far belong to the subfamily Aphidiinae. All of the Aphidiinae are solitary, internal parasites of aphids (2, 43). All species of both families reared from aphids in Maine have been solitary, internal, primary parasites. Some species of Eulophidae are external primary parasites of other insects. In our observations, even though more than one egg may have been deposited, only one primary or one hyperparasite adult ever emerged from a parasitized aphid.

Braconidae

(Aphidiinae)

Spencer (45) and Smith (43) gave generalized accounts of the biology of parasites belonging to the subfamily Aphidiinae. Usually the females lay their eggs in half-grown aphids. The female parasite is ready for mating soon after maturation and oviposition may occur with or without mating. Ordinarily only one egg is laid in an aphid, but under some conditions many may be deposited. Timberlake (47) found that superparasitism occurred in two-thirds of the specimens of the rose aphid (*Macrosiphum rosae* (Linnaeus)) in the greenhouse. Dunn (3) observed as many as 10 eggs to hatch within a single aphid. Wheeler (53) found that when aphids were scarce the Aphidiinae females would return to oviposit in the same individual. Our observations in Maine agreed with those of Spencer (45), who said that even though superparasitism by two species of primary parasites may occur, only one parasite specimen is able to complete development.

Not all species of the Aphidiinae appear to have the same number of larval stages. Spencer (45) indicated there are four. Wheeler (53) found five for *Aphidius matricariae*. Schlinger and Hall (26, 28) recorded only three for *Praon palitans* Muesebeck and three for *Trioxys utilis* Muesebeck.

In addition to killing the aphid host eventually, the developing parasite exerts an immediate, striking effect upon reproductive tissues of the aphid being infested. According to Spencer (45), development of all embryos in the aphid, irrespective of stage, is arrested at the time the parasite larva hatches. The embryos finally degenerate into vacuolated masses. The host aphid is killed about the time the parasite larva completes its development and is ready to pupate. Immediately after death of the aphid, the parasite larva makes a ventral slit in the abdomen of the aphid through which it moves either to pupate beneath its host, or to anchor the host to the foliage of the host plant. The matured adult chews a circular emergence hole through the cocoon and/or the abdomen of the aphid host.

Not all species of aphids respond to parasitization as related by Spencer (45). In Czechoslovakia Stary (46) found that when adults of the aphid *Megoura viciae* Bckt. are parasitized by *Aphidius megoura* Stary, the host aphid produces progeny in the usual manner. When the aphid is parasitized in the third or fourth instar, it matures and produces progeny for several days. Parasitism in these stages does not delay maturity of the aphid but does reduce duration of the reproductive period and the number of nymphs deposited.

The time required for a generation of parasites to develop may vary from 10 days to several weeks depending upon factors such as temperature and humidity. In warmer climates, both aphids and parasites continue to reproduce throughout the winter months, but in more northerly areas the parasites can pass the winter as mature larvae or as pupae in the mummified aphid. Spencer (45) found that one species, *Diaretiella rapae*, could withstand long periods of winter temperatures ranging from 10° F. to 50° F. but not an entire winter because of starvation. This parasite doubtless survives the severe winter in northeastern Maine in an immature stage in the dead aphid hosts.

In southerly areas, where the summers are long and relatively high temperatures prevail for extended periods, many species of the Aphidiinae undergo a facultative diapause, during which they, of course, cease to exert pressure against aphid increase (51, 25, 24, 27). There is no evidence of summertime diapause in the aphidiine parasites in northeastern Maine.

Praon spp.

Parasites of the genus *Praon* rank second in abundance only to those of the genus *Aphidius* in attacking potato-infesting aphids in Maine. A dead aphid parasitized by a *Praon* can be recognized readily. After the parasite larva becomes full-grown, it emerges through a slit which it has made in the ventral side of the host aphid's abdomen. The larva then forms its cocoon which it attaches to the leaf or other surface and, using the dead aphid's body as a roof, pupates beneath it.

Praon pequodorum was probably the most common species of this genus we reared from potato-infesting species of aphids in Maine. We have reared it from the green peach, foxglove, and potato aphids. All specimens reared from the buckthorn aphid were identified as *Praon* sp. Difficulty in identifying as to species may have been due in part to deformities and reduced size of undernourished adult specimens emerging from the small buckthorn aphid. Other *Praon* spp. reared from the other three potato-infesting species included *P. aguti*, *P. americanus*, and *P. occidentale*. Among the most common of the unidentified species of *Praon* from our rearings were two or more undescribed species.

Parasites of the genus *Praon* occur throughout southern Canada and over a large part of the United States (43, 23, 15, 27), although according to studies of Schlinger and Hall (27), except possibly for *P. unicus* Smith, they apparently were not common in southern California before the introduction of *P. palitans* in 1956 (49). Schlinger and Hall (27) suggested that diapause exhibited by *P. pequodorum* in winter or spring may explain why in Kern County, California, this species had not been an effective parasite of the pea aphid, *Acyrthosiphon pisum* (Harris). We have no evidence of summertime diapause in *P. pequodorum* in Maine.

Little is known of the biology of *Praon* spp. under field conditions in Maine. However, some aspects of the biology have been studied elsewhere by Timberlake (47), Wheeler (53), Spencer (45), Schlinger (24), and others. Sekhar (30) found that in *P. aguti* the maximum number of offspring reached 230; also, while mated females produced more females than males, the number of female progeny decreased more rapidly than the male progeny as the oviposition period advanced. Schlinger and Hall (25, 26) found a complete life cycle of *Praon palitans* required about 12 days in southern California, and that the insect may have as many as 15 generations a year in the field. They found that *P. palitans* had a facultative diapause of about 140 days in winter at Riverside. The adults lived from 12 hours to 56 days depending upon temperature and relative humidity.

Aphidius nigripes Ashmead

Aphidius nigripes was the most abundant primary parasite of potato-infesting aphids in northeastern Maine. In addition to the potato, green peach, and buckthorn aphids, we have reared *A. nigripes* from the English grain aphid (*Macrosiphum avenae*), the apple grain aphid (*Rhopalosiphum fitchii*), and also from *Cryptomyzus galeopsidis* (Kaltenbach), *Amphorophora sp., Capitophorus* sp., and *Macrosiphum* sp. It occurs from New Brunswick, Canada, and from the northeastern part of the United States southward to North Carolina, westward to Minnesota, and as far south as Kansas; more recently also at Riverside, California, (15, 23, 27).

Little is known of the life history and habits of *A. nigripes.* Schlinger (24) stated that diapause substantially limits its productivity as well as that of several other species of primary parasites at Riverside, California. We have no evidence of summer diapause in this species in Maine. Its pattern of emergence during the year in which it was collected indicated that no interruption occurred in its development. Relatively few specimens of *A. nigripes* emerged from aphid mummies during the year following collection, and only one *A. nigripes* and three *Aphidius* sp. emerged in the second year following collection.

There is some question as to the manner in which *A. nigripes* overwinters. Spencer (45) thought the species did not survive the winter out-of-doors in many places, and that such places were reinfested annually in waves of adult parasites from more southerly regions where both aphids and parasites breed throughout the winter. He reported that *A. nigripes* in 1921 reached Raleigh, N. C., May 7 and disappeared June 1, while it reached Columbus, Ohio in early June and disappeared by July 15. In Maine there appears to be little question that many of the primary parasites of aphids overwinter in the aphid mummy, including some *A. nigripes* as we pointed out in the preceding paragraph.

Determination of the number of generations of *A. nigripes* annually in northeastern Maine would be difficult because of the seasonal histories and development of the wide variety of aphid species which it utilizes as hosts, and the large number of primary and secondary host plants on which these species of aphids occur. While there are possibly two generations and a partial third of *A. nigripes* on potatoes, there is at least one generation before the spring migrations of the aphids and at least a partial generation after the fall migrations.

In northeastern Maine *A. nigripes* appears to be the native parasite offering greatest possibility of increased effectiveness against the potato-infesting species of aphids through artificial culture and field release because of its natural abundance and the relatively large number of aphid species it utilizes as hosts. It is well adapted to the climate and the host aphids available. However, it is more than likely attacked by several species of hyperparasites in Maine. In California it is attacked by more than four including *Asaphes californicus* Girault and *Charips* sp. (24, 26).

Aphidius matricariae Haliday

A. matricariae (= *A. phorodontis* Ashmead and *A. nigriteleus* Smith) has been reported from North America, Europe, North Africa, the middle East, Mongolia, Peru, and Brazil according to Schlinger and Mackauer (29). In North America they indicated it has been found in Ontario and New Brunswick in Canada, and in Maine, Massachusetts, Connecticut, Maryland, Washington, D.C., Virginia, Ohio, Michigan, Indiana, Oregon, Idaho, and California.

A. matricariae has a wide variety of aphid hosts. Schlinger and Mackauer (29) assembled a list containing 41 species of aphid hosts including seven in California and seven in New Brunswick, Canada. In Maine we have reared *A. matricariae* from six species, including *Cryptomyzus galeopsidis*, *Capitophorus* sp., and from all four of the potato-infesting species of aphids.

In northeastern Maine, during the period 1942-1950, *A. matricariae* was reared chiefly from *C. galeopsidis* on hempnettle (*Galeopsis tetrahit* Linnaeus), from *Capitophorus* sp., and from the potato aphid on swamp rose, the most important primary host of the potato aphid in that area. Few specimens of *A. matricariae* have been reared since 1950, very likely because the collection of parasitized aphids from hempnettle was largely discontinued. Among aphids on potatoes *A. matricariae* was exclusively a parasite of the green peach and potato aphids. It occurred only in very small numbers during the period 1942 through 1961 in fields of potatoes or elsewhere.

Evidence indicates there may be two or more strains or geographical subspecies of *A. matricariae*, and that one of these is more effective than the locally occurring one as a parasite of the green peach aphid. Schlinger and Mackauer (29) found that a strain in California increased in abundance and effectiveness against the green peach aphid from 1957 to 1960. They pointed out that although *A. matricariae* has been recognized since 1911 in California, all of the early collections were from the greenhouse, and its presence out-of-doors at Riverside was not detected until 1957. By 1959 this species became so abundant at Riverside that it could be found in practically all large colonies of the green peach aphid. By 1960 it had spread to the Imperial Valley. Therefore, they think the *A. matricariae* observed since 1956 was introduced and became established some time after 1950. Certainly the strain now so common in that state is much more abundant and effective against the green peach aphid than the locally occurring one in Maine. Very likely the strain we have observed since 1942 occurring naturally in Maine is different from the strain introduced into California.

The European strain of *A. matricariae* is an efficient parasite of some species of aphids. Smith (44) said it gave a high degree of control of the green peach aphid in the greenhouse. In a garden plot of potatoes, Dunn (3) found that its attacks were confined to the green peach and foxglove aphids and that 57% of the parasites reared from each of these species of aphids were *A. matricariae*. In the field, however, only the green peach aphid yielded this parasite. Vevai (52) said that the progeny of a single, mated pair of *A. matricariae* eradicated in 11 to 12 weeks a colony of the green peach aphid caged on tulip. The colony had started with 25 viviparous adults. Large numbers of the parasite developed before the colony of aphids was eradicated. *A. matricariae* was the only primary parasite that emerged from parasitized green peach aphids collected by George (5) during August from field-growing cabbage at Harlow, Essex, England. He reared it also from this aphid taken from potatoes in fields adjacent to a field of "sprouts."

Among the accounts of various aspects of the biology of the native strain of *A. matricariae* are those given by Wheeler (53), Spencer (45), McLeod (20), and of that of the imported and/or European strains by Smith (44), Vevai (52), Dunn (3), George (5), Schlinger and Hall (27), Mackauer and Müller (16), Schlinger and Mackauer (29), and others. In Massachusetts, Wheeler (53) found larvae of this parasite in the green peach aphid within four or five days after the eggs of the parasite were deposited. Her observations showed that when the adult females were confined in lots of three or four with a relatively small number of aphids, over a period of four to six days, each female deposited from 1.2 to 3.0 eggs per day. Under more nearly natural conditions, however, the number of eggs laid per female greatly exceeded this.

Wheeler (53) found the time necessary for development of *A. matricariae* to be 19 to 23 days in April and 13 to 18 days in May and June. About 10 days were required for the larval stages and four or five days for the pupal stage. The adults lived two to seven days without food and longer than eight days with food. In northeastern Maine this parasite was not abundant enough to detect the number of generations annually. However, the number does not seem to differ markedly from that of *A. nigripes,* viz., possibly two or three on potatoes, and two on the primary hosts—one before the spring migrations and one after the fall migrations of the aphids.

In view of the increased abundance and effectiveness of *A. matricariae* observed by Schlinger and Mackauer (29), consideration should be given to the introduction of this California strain into the potato-growing area of northeastern Maine. On the basis of the information available, however, it may be effective only against the green peach aphid.

Lysiphlebus testaceipes (Cresson)

Lysiphlebus testaceipes is a widely distributed primary parasite of many species of aphids. More than 30 aphid species have been reported as hosts in the United States, southern Canada, and Mexico (23, 15, 14, 27). In southern California it is a very common parasite of several species of aphids. In fact, the species is so abundant it should be considered a potential aid to any program of natural control of aphids in that area (27).

In Maine the buckthorn aphid is the only one of the potato-infesting species from which *L. testaceipes* was reared (39). In the two years—1947 and 1949—that it was reared during the 20-year period 1942 through 1961, the parasitized buckthorn aphids containing it were collected only from alder-leaved buckthorn, the primary host of this aphid.

Little is known of the biology of *L. testaceipes* in Maine. Wheeler (53) and Sekhar (30) reported their observations on mating, egg deposition, and host discrimination. Spencer (45) thought it did not survive the winter at Raleigh, N. C., and Columbus, Ohio. Instead, he thought that the adult parasites move northward each year in a wave, following a similar wave of aphids from more southerly regions where both aphids and parasites continue breeding during winter. He reported that the adults of *L. testaceipes* reached Raleigh, N. C., on June 10 in 1921 but did not appear at Columbus, Ohio, until September 6. Our records indicate this parasite over-winters as pupae in dead aphids in northeastern Maine, instead of flying into the area each year. At Presque Isle, all of our reared specimens came from dead, parasitized buckthorn aphids collected June 15 to 23. To have killed aphids by that time, the adult parasites must have laid eggs in them by June 1. This date is likely too early for adult parasites to have moved in from southern areas.

Trioxys spp.

More than 10 species of the genus *Trioxys* are known to be primary parasites of aphids in North America (23, 15). They probably have little overall importance as biological agents of aphid control. Few appear to attack more than one species of aphid. Relatively few records of rearings appear to have been reported, but those available show that the species of this genus are widely distributed. In northeastern Maine we have reared a single specimen of *Trioxys gahani* from *Capitophorus* sp. and two specimens of *Trioxys* sp., one from the buckthorn aphid (collected in 1950 on alder-leaved buckthorn) and one from *Rhopalosiphum fitchii* (collected in 1960 on oats).

Along with two other species of primary parasites imported and released in California in 1955-56 for control of the spotted alfalfa aphid (*Therioaphis maculata* (Buckton)) was a European species of *Trioxys* (49), subsequently described as *T. utilis* (21). It became established without delay (8, 50) and appears to be well suited for the warmer parts of California but probably not for colder sections of the state (51).

Little is known about the biology of the species of *Trioxys* native to North America. Brief mention is made here of some aspects of the biology of the introduced *T. utilis* because of its potential importance in aphid control. According to Schlinger and Hall (25, 28), from nine to 11 days are required for development of *T. utilis* from deposition of the egg until maturation of the adult, as follows: egg, two days; larva, three to four days; prepupa, one day; and pupa, four to five days. The sex ratio of mated females is 1:1; unmated females produce males only. The adults live only 12 hours at 100° F. and 37% relative humidity, but up to 27 days at 50° F. and 86% relative humidity. Under laboratory conditions there are probably up to 32 generations per year, but in the field in southern California there are likely only 17. The three reported aphid hosts of *T. utilis* belong to the genus *Therioaphis*. They include *T. maculata, T. trifolii* (Monell), and *T. riehmi* (Börner). Early observations indicate that *T. utilis* plays a secondary role to predators and fungus diseases in controlling the spotted alfalfa aphid at Calexico, California. However, this species was very effective in its attacks upon low population densities of the aphid after the predators and fungus diseases had operated. Possibly its reduced effectiveness may be due in part to diapause which, according to Schlinger and Hall (28), lasts for about 120 days during summer and fall.

Diaeretiella rapae (M'Intosh)

Diaeretiella rapae is one of the most widely occurring primary parasites of aphids in the United States. It occurs from Maine to North Carolina and west to Oregon and California (23, 39). It is also common in England and in mainland Europe (5, 7). Wherever the species occurs it appears to utilize chiefly as hosts the cabbage aphid (*Brevicoryne brassicae* (Linnaeus)) and green peach aphid, although in California Schlinger and Hall (27) indicated it is not well adapted to the latter. In northeastern Maine, in addition to the green peach, buckthorn, and potato aphids, we have reared *D. rapae* from the turnip aphid, from the apple grain aphid, from *Hyalopterus atriplicis,* from *Cryptomyzus galeopsidis,* and *Myzus certus* Walker (tables 7, 8, 9, 10, 11; Shands et al. (39) and unpublished records). *D. rapae* was common as a parasite of the green peach and turnip aphids during the period 1942-50 (39); since 1951 it has been very scarce (tables 7 to 11).

Wheeler (51) described the mature larva of *D. rapae,* and Spencer (45) worked upon the bionomics and some aspects of the ecology of this parasite. In England, George (5) made a two-year field study of the seasonal abundance of *D. rapae* as a parasite of the cabbage aphid on brussels sprouts. The most intensive study of this parasite, however, is that by Hafez (7) in the Netherlands. The following information about its life history and bionomics is based chiefly upon these sources.

Approximately 60% of the adults of *D. rapae* are females. The adult females mate soon after emergence; if they do not mate, all of their progeny are males. The female lives one to two weeks; during that time she lays 25 to 175 eggs, averaging about 83. She deposits only one egg at each insertion of her ovipositor into an aphid. In depositing eggs, the female does not discriminate between parasitized and nonparasitized aphids. Although half-grown aphid nymphs are selected for ovipositing, the female of *D. rapae* will accept larger nymphs and both apterous and alate adults of the cabbage aphid.

A generation of *D. rapae* is completed in 37 to 47 days in spring, 14 to 16 days in the warmer part of summer, and up to 110 days in winter. While in the Netherlands there are five to 11 generations per year, the number in Maine is doubtless smaller. Hibernation does not occur in *D. rapae*. The parasite completes development, and the adults emerge at any time in winter when the parasitized aphid mummies are brought in from outside and exposed to room temperature. In fact, in warmer areas the parasites continue to emerge throughout the winter. *D. rapae* appears to have a summertime diapause in California (27), but we have no indication that it may in Maine.

Eulophidae

(Eulophinae)

The family Eulophidae was represented in our rearings from parasitized aphids in northeastern Maine by one species from each of two genera. One, *Dahlbominus fuscipennis,* was never before recorded from aphids; the other, *Aphelinus semiflavus,* is a well recognized primary parasite of aphids. Although *D. fuscipennis* is ordinarily a parasite of sawflies (23, 14), because of our earlier-described procedure, there is no doubt that in this case it was a primary parasite of both the potato and green peach aphids. We reared it from three specimens of the potato aphid collected from potatoes in one field and from three specimens of the green peach aphid collected from potatoes in a field about one-half mile distant.

(Aphelinae)

Aphelinus semiflavus Howard

Aphelinus semiflavus is a rather distinctive primary parasite of aphids in that the specimens parasitized by it turn black about the time the parasite pupates inside. *A. semiflavus* is a parasite of many species of a wide variety of insects, including some that are parasitic upon pests of economic importance (1). It is one of a relatively few species of eulophids known to be primary parasites of aphids and it occurs in Europe and in the United States. Until recently it was recorded chiefly from aphids in the midwest (9, 45, 23). Although less important than two other species of primary parasites introduced at the same time in 1955 and 1956 for control of the spotted alfalfa aphid, a European strain of *A. semiflavus* appears to have become established in California (49, 8, 50, 51).

Although more than 15 species of aphids are known to serve as hosts for *A. semiflavus,* we have reared it from only four species in northeastern Maine, viz. *Myzus cerasi* (Fabricius) in 1942, *Capitophorus* sp., the potato and foxglove aphids (tables 7 and 11). In general it was very scarce. Schlinger and Hall (25) found four species of aphids serving as hosts of the imported strain of *A. semiflavus* in California.

Substantial contributions to knowledge of the biology of the native strain of *A. semiflavus* were made by Hartley (9) and Spencer (45), and to that of the European strain by Hagen et al. (8), van den Bosch et al. (51), Schlinger and Hall (25), and Finney et al. (4). Some but perhaps not all aspects of the biology of the two strains may be alike although Schlinger and Hall (25) expressed some doubt that the two are conspecific.

According to Hartley (9) and Spencer (45), in Ohio reproduction in the "native" strain is parthenogenetic, with few males ever being produced. In that state the eggs hatch in about three days, the larval stage requires six to eight days, and the pupal stage averages seven to eight days but may vary from five to 15 days. A total of about 20 to 30 days is thus required for a generation to develop. The emerging female has eight to 10 fully developed eggs in the oviducts. The number of generations per year is dependent largely upon temperature. While there could be 12 or more generations in a year, it is likely there are only four or five in northeastern Maine. As in Ohio, *A. semiflavus* probably overwinters in the pupal stage in Maine.

Schlinger and Hall (25) said the imported, Old World strain of *A. semiflavus* may have more than 20 generations per year at Riverside, California. They found the total time from egg to adult to be only 11 to 13 days, as follows: egg stage three days, and the larval, prepupal, and pupal stages a total of nine to 11 days. In parthenogenetic progeny the proportion of sexes varied from 99% males at temperatures of 78° to 85° F. to 95 to 98% females at 65° to 72° F. Although relative humidity had some effect, temperature was the most important factor in controlling sex in uniparental progeny.

Although we released small numbers of the Old World strain of *A. semiflavus* early in 1957, consideration should be given to the possibility of making releases in Maine of the strain now common in California because of the apparent readiness with which it became established there. Large numbers for release can be reared with ease under controlled conditions (4). Schlinger and Hall (25) found that adults of the imported strain lived only 12 hours at 90° F., but 70 days at 50° F. Hartley (9) found that adults of the native strain of this parasite live as long as 39 days. Longevity in the adult likely is due in part to its habit of feeding on juices exuding through holes made in the aphid's abdomen with the parasite's ovipositor. Adult longevity *per se* is a factor also favoring establishment of the parasite, since the longer the female lives the greater are the chances of encountering host aphids in which eggs may be deposited. Hartley (9) indicated that, on the average, a female deposits 500 or more eggs. Eggs of both the native and the imported strains are deposited chiefly in aphids in the first and second instars.

Characteristics that may limit abundance and effectiveness of the introduced strain of *A. semiflavus* as a parasite of aphids in Maine include little, if any flight by the adults, and death of the larva when in competition with aphidiine parasites inside an aphid (45). For oviposition, nonflying females are thus confined to aphids on host plants or aphids not distant from each other. Although it readily became established and occurred in considerable abundance at release sites in California through 1957, the introduced strain appeared to be less abundant than two species of Aphidiinae released with it in 1956 (50, 51).

Hyperparasites

Hyperparasites are highly detrimental in a program of biological control since they attack and kill the primary parasites which otherwise would emerge and lay eggs in many individual insect pests. Hyperparasites thus serve as a brake on population increase of the primary parasites and on their effectiveness against the pest species.

The hyperparasites reared to date from potato-infesting species of aphids in northeastern Maine belong to five families of Hymenoptera. In decreasing order of number of individuals the three families most commonly represented by reared specimens from all four species of potato-infesting aphids were Pteromalidae, Ceraphronidae, and Cynipidae. A few specimens belonging to the Encyrtidae or Eupelmidae were reared from the potato aphid, and a single eupelmid from the green peach aphid.

The degree of hyperparasitism of aphids varies greatly among districts, years, and even among fields. Schlinger (24) found that up to 70% of parasitized specimens of the rose aphid were attacked by various hyperparasites but that parasitization of one primary parasite—*Praon palitans*—was of little importance in California (26).

In a two-year field study of the parasites of the cabbage aphid in England—where *Diaeretiella rapae* was the only primary parasite reared—George (5) found that 55% of the aphid mummies contained hyperparasites in 1953, and 66% in 1954. Hafez (7) found that only hyperparasites emerged from 58% of the 17,000 mummies of this aphid collected in the Netherlands in 1959, while in 1960, 63% of 8,000 mummies yielded hyperparasites. In another two-year study of the cabbage aphid—in Australia, where the only primary parasite found was *D. rapae*—10% were affected by hyperparasites in 1960, and 18.8% in 1961 (13).

In northeastern Maine the yearly variation in hyperparasitization in the potato-infesting species of aphids ranged from 0 to 53% for the period 1952-1961, inclusive (tables 7 and 10); the weighted average percentages for the potato, buckthorn, foxglove, and green peach aphids were 22.5, 21.9, 27.9, and 42.0, respectively, during this period. Because hyperparasites can have such a detrimental effect upon primary parasites, we include brief summaries of the biologies of several of the more abundant species in northeastern Maine and of some closely related ones occurring elsewhere.

Hyperparasites of aphids usually exhibit host preference for particular species of primary parasites. Each species, however, ordinarily will accept a larger number of species of primary parasites than a primary parasite does of aphid hosts. The hyperparasites may lay their eggs inside or outside the body of the primary parasite inside the aphid's body. Parthenogenetic reproduction of some species of hyperparasites results in all of the progeny being males or in a predominance of males (45, 6).

Asaphes spp.

Among the Pteromalidae, parasites of the genus *Asaphes* have been the most abundant in rearings from potato-infesting aphids in northeastern Maine. These have included, in decreasing order of abundance, *A. lucens, A. rufipes,* and *Asaphes* sp.

Insects of the genus *Asaphes* are not only secondary parasites; to some extent they may be tertiaries as well (6, 7). They are externally parasitic (10, 45, 6, 3) and attack a large number of species of parasitized aphids, including those parasitized by species of *Aphidius, Lysiphlebus, Praon, Trioxys, Diaeretiella,* and *Aphelinus* (47, 9, 45, 25, 5, 7).

The females of *Asaphes* are very selective as to where they place their eggs. For example Spencer (45) and Sekhar (31) found that from five to six minutes are required for *A. lucens* to place one egg in an aphid. While more than one egg may be deposited in an aphid, only one parasite emerges (7). Never does *A. lucens* deposit an egg in an aphid that is not parasitized (45), and deposition is in an aphid already killed by the primary parasite (31). Deposition comes when the primary parasite is in its last larval stage or in the pupal stage (12, 3, 31). Females of *Asaphes* may deposit fertile eggs with or without mating (6, 31).

Unmated females of *A. lucens* deposit eggs that develop into males only (31) while eggs from mated females may or may not produce a majority of females (6, 31). Females live about two weeks; males are less robust and shorter-lived (45, 31). The females oviposit throughout most of their lifetime but lay only 25 to 54 eggs (45, 31). Depending upon conditions, a generation of *Asaphes* requires from 10 to 27 days (12, 31). Males complete development in less time than females (31).

It appears there are at least two generations of *A. lucens* each year in northeastern Maine.

Pachyneuron spp.

At least some of the pteromalids of the genus *Pachneuron* are external hyperparasites (12). They have been reared from primaries of several species of *Aphidius, Praon, Lysiphlebus, Trioxys, Diaretiella* and *Aphelinus* (12, 45, 5, 25, 24), in numerous species of aphids. A generation of *P. siphonophorae* can be completed in 12 to 15 days, but each female deposits only about 11 eggs (45). Working with a different species of *Pachyneuron,* Haviland (12) found that the female deposits her eggs on full-grown larvae of the primary parasites just before they are ready to pupate within the aphid, and that about three weeks are required for development. She thought there were at least two generations each year of that hyperparasite in the area where she worked.

Coruna clavata Walker

Although *Coruna clavata* had not been recorded in the United States prior to 1944 (39), it has since been the third most abundant hyperparasite reared from the primary parasites in potato-infesting species of aphids in northeastern Maine. MacGillivray and Spicer (15) also reared it from the potato and green peach aphids collected in New Brunswick, Canada, on August 9 and 19, 1950. It has also been reported from Washington (14). For many years, it has been known in Europe as a hyperparasite of certain aphids not attacking potatoes, as well as of the green peach aphid on potatoes (12, 3).

Coruna clavata probably attacks several species of primary parasites, including *Aphidius* spp. and *Praon* spp. (14). We have reared it from parasitized aphids of 10 species, including *Cryptomyzus galeopsidis, Capitophorus* sp., the hop aphid, (*Phorodon humuli* (Schrank)), English grain aphid, apple grain aphid, the pea aphid, and all four of the potato-infesting aphids (tables 7, 8, 9, 10, 11; Shands et al (39); unpublished records).

According to Haviland (12), *Coruna clavata* is hyperparasitic through primaries of the genus *Aphidius*. After mating, the female deposits the egg on the full-grown larva of the primary parasite. The larva feeds externally on the body of the primary parasite inside the aphid. The life history of *C. clavata* requires about three weeks, and there are at least two generations per year.

Lygocerus spp.

The second most important group of hyperparasites of potato-infesting aphids in northeastern Maine includes four species of the genus *Lygocerus*, belonging to the family *Ceraphronidae* (tabulation on page 9). In addition to being externally parasitic upon several species of primary parasites of the genera *Aphidius* and *Diaretiella*, they will parasitize members of the hyperparasitic genus *Charips*, and even their own kind (10, 45, 5, 7).

The eggs of some species of *Lygocerus* are laid on the full-grown larva or the pupa of the primary parasite (45) and the larva lives on the pupa of the primary (10, 3). Completion of the four larval stages requires about six days, while the pupal stage of the hyperparasite requires six to 14 days depending upon species and environmental conditions (10, 45). There are two or more generations each year (10). Oviposition may occur with or without mating. Parthenogenetic reproduction results in male progeny only (45).

The four species of this genus reared from parasitized aphids in northeastern Maine are *L. attentus, L. incompletus, L. niger,* and an as yet undescribed species.

Charips spp.

Except for trace representations of two other families mentioned earlier, cynipids were the least abundant of the hyperparasites of potato-infesting aphids in northeastern Maine. Of the cynipids, two species of *Charips* were most abundant, *C. brassicae* and *Charips* sp.

Charips spp. have been reared from several species of primary aphid parasites belonging to the genera *Aphidius, Praon, Lysiphlebus, Trioxys,* and *Diaretiella* (46, 11, 45, 3, 5, 24, 25, 27). The eggs are deposited through the integument of the aphid and in the body cavity of the primary parasite (11, 45, 7). Development of the primary parasite is arrested so that metamorphosis is not complete and the *Charips* larva feeds and develops internally. When full grown, the larva of *Charips* emerges from the pupa of its host, consumes the remainder of it, then pupates in its own cocoon (11, 45, 3, 7). *Charips* sp. has been reared from diapausing and from nondiapausing larvae or pupae of *Aphidius nigripes* (27). In The Netherlands from 19 days in July to 37 days in May and early June are required for development from egg to adult, and there are four to seven generations per year (7).

Hafez also said that as many as 259 days are required for *Charips ancylora* Cam. to complete a generation during winter. Spencer (45) found that while *C. brassicae* attacked several species of primary parasites, it was especially destructive of *Diaeretiella rapae*.

DISCUSSION AND CONCLUSIONS

The level of parasitism in the potato aphid was relatively high in the early part of the seasons of 1953, 1955, and 1956; but it had no appreciable effect upon population growth of the potato aphid by our criterion (figures 1, 2, 3). Parasitism may have risen enough to affect the population trends adversely in the later part of the seasons of 1952, 1962 and 1963, but not until well after the peak of the aphid's population had passed and populations of this aphid were small. Parasitism may have been high enough at times during 1958 and possibly 1959 to have had some effect. If this is so, the depressing effect from parasites was simultaneous with and could not be separated from that of other biological agents of control. Based on the work of George (5), Hafez (7), and Hughes (13), and in view of our experience, the percent of parasitism at crucial times in these years probably was too small to have reduced potato aphid populations very much.

Despite this there are several possibilities for increasing the effectiveness of insect parasites of potato-infesting aphids, some of which appear worthy of consideration. The most promising ones include (1) introducing species of parasites more effective against each species of aphid than those now present in northeastern Maine; (2) releasing parasites of introduced or native species in potato fields at critical times each year in large enough numbers to control the aphids in early season; or (3) combining the introduction of new species or strains with large, early-season releases of introduced or native species in potato fields at critical times.

Introduction of Parasites

During our 20-year study the potato aphid was the only species affected appreciably by insect parasites. Parasitism in the most abundant species—the buckthorn aphid—was least. Only occasionally were parasites present to any degree in the green peach or foxglove aphids. Thorough exploration may reveal species of parasites occurring elsewhere that are more effective against all these aphids than those occurring locally. *Aphidius matricariae* is one possibility. The California and European strains of this species appear to be much more effective against the green peach aphid than the strain occurring locally. Exploratory efforts may disclose other species or strains that are equally effective or more so against the other three species of aphids.

Introduced species or strains of parasites may be more or less effective than in their former environments because of better or poorer sequences of aphid hosts, hyperparasitization, and other factors. Our data indicate that primary parasites of potato-infesting aphids exhibit far less specificity as to the species of aphids they will attack than suggested by Marshall (19), George (5), and others. For example, *Aphidius nigripes*, the most important primary parasite reared in northeastern Maine, has parasitized all four of the potato-infesting aphids on both their primary and secondary host plants and at least four additional species of aphids in widely varying kinds of environments. The importance of this species may be due in part to the large number of aphid species it attacks. On the other hand the less important, locally occurring strain of *A. matricariae*, although never abundant, was also reared from all the potato-infesting species of aphids (table 12) and from *Capitophorus* sp. on swamp rose (table 11).

The evidence is not clear cut, but indications are that the susceptibility of a species of primary parasite to attacks by hyperparasites could critically influence its abundance and effectiveness against the aphids. Although in northeastern Maine hyperparasites are less abundant than the few common species of primary parasites, in number of species and stability of abundance they rank with, or in some respects even slightly above, the primary parasites. We suspect the more common hyperparasites may be fully as polyphagous as or more so than the most abundant primary parasites (tables 11, 12). Even if an introduced species of primary parasite finds a favorable abundance and sequence of aphid hosts and other environmental factors are favorable, hyperparasites could prevent it from becoming an effective primary parasite. However, the only way to determine this is through observations following introduction.

Any efforts to introduce primary parasites should follow carefully considered plans, including efforts to create environmental conditions designed to enhance chances for establishment. Such plans should include a follow-up study to determine the likelihood of establishment, the desirability of continuing releases, and to take any steps possible to create conditions more favorable for establishment. Chances for establishment might be increased by sequential releases in environments where there are primary host plants of the aphids as well as secondary hosts, and by colonizing the host plants at release sites, or artificially supplementing the natural aphid infestations there.

Releases of Parasites at Critical Times

If the adult parasites are thorough searchers, efficient and long-lasting control of aphids on field-growing potatoes may be achieved by releasing them in the potato field at or near the end of the aphids' spring migrations. Our studies have shown that in northeastern Maine there is a period of about three weeks between the end of the spring migrations and the time virtually all plants harbor at least one aphid (33). During this period the numbers of aphids per plant or per acre are quite small; in fact, the infestation on the small but rapidly growing potato plants during this period can be expressed more meaningfully in terms of percent of plants infested than numbers of aphids per plant. When all plants become infested, interplant movement of the aphids ceases to hold down the apparent level of infestation because the interchange of aphids between plants is equalized. The number of aphids per plant thus begins to increase rapidly. Until that time relatively few adult parasites should suffice to parasitize all of the aphids on the plants, provided they are efficient searchers and will continue searching until all aphids that are large enough are parasitized.

Potatoes kept free or made free of aphids after completion of the aphids' spring migrations will remain so until again infested by summer dispersal forms maturing on potatoes or other secondary hosts. Such plants thus should remain rather free of aphids until early in August. Experience has shown that aphid populations developing on potatoes infested that late in the season seldom, if ever, could attain a level high enough to be of economic importance in fields of potatoes grown for table use. In most if not all instances, under present conditions the aphid populations developing from summer dispersal forms do not become appreciable before the onset of effects of other natural controls, including entomogenous fungi, predators, and the start of the aphids' fall migrations.

The number of adult parasites needed per acre and the technique of making releases to obtain adequate distribution of the parasites in fields of potatoes are considerations that can be readily resolved through experimentation. Also to be determined in a similar manner is the probable need for or frequency of sequential, supplemental releases during a three to four-week period from late June until the latter part of July.

Two additional or supplemental approaches to the control of aphids on potatoes with parasites also are worthy of mention. Mass releases of the adult parasites in patches of the primary host plants of the aphids in spring or fall, when the aphids are breeding there, may offer some possibility for reducing the numbers of the spring migrants or of the overwintering eggs, respectively. This approach appears impractical in northeastern Maine because of the large number and relative inaccessibility of patches of primary host plants which moreover vary greatly in size. Furthermore, there are vast differences between seasons, years, and locations in the levels of aphid infestation supported in these patches or areas of primary hosts.

If for example the species of parasite to be released will attack grain-infesting aphids, supplementary control of the aphids on potatoes during the latter part of the summer may be obtained by planting strips of grain inside or bordering fields of potatoes where mass releases of parasites are made in July. Most of the adult parasites we have observed appear to be able to move to and infest aphids on grain plants some distance away. The first-generation adult parasites emerging from aphids on the grain would soon be searching elsewhere for aphid hosts, since by that time the grain likely would be infested by few, if any, aphids. These adult parasites should be able to infest aphids on the nearby potato plants.

The Combined Approach

We believe the greatest likelihood of success from the use of parasites in controlling aphids on field-growing potatoes lies in the combined-effort approach. This includes establishing new species or strains of parasites that will be more effective than the ones now occurring in northeastern Maine and, at the same time making annual mass releases of parasites in potato fields from late June until about July 20. Mass releases would use one or more introduced or locally occurring species, such as *Aphidius matricariae* or *A. nigripes*. The establishment of more effective parasites than those now found here is desirable, irrespective of whether the degree of aphid control they provide proves to be consistently adequate. If the mass field releases result in adequate control, they could well be sufficiently inexpensive to be adopted as a regular means of aphid control. In that event, as shown in table 4, careful attention must be given to the selection of insecticides to be used in the "parasite" fields for control of insects other than aphids. Mass releases of parasites from other areas also may enhance the chances of establishment of species new to northeastern Maine. Mass releases could also increase the general abundance of native parasites.

SUMMARY

Since 1941 natural agents of aphid control have been a part of joint investigations by the U. S. Department of Agriculture and the

Maine Agricultural Experiment Station on biology and control of potato-infesting aphids in northeastern Maine. During the period 1941 through 1951 exploratory observations revealed the identities of the more important species of entomogenous fungi, arthropod predators, and insect parasites and permitted estimates of the yearly variability in their importance as agents for controlling the aphids on their primary hosts as well as on potatoes and other secondary hosts. Altogether, six species of entomogenous fungi were found to occur there, only four of which were common. The arthropod predators of major importance included spiders and coccinellids, and also syrphids and chrysopids.

After development of more adequate procedures than those formerly available, greater emphasis from 1952 through 1963 was placed upon assessing the importance of natural agents, including parasites, in controlling four species of potato-infesting aphids. Records and collections were made of the parasitized aphids found on all plant-sample units. At the same time quantitative data were obtained on aphid abundance on primary hosts and on field-growing potatoes in many places in the area by sequential sampling at designated intervals each year. The reared parasites were preserved with the aphids from which each emerged. The field identification of each parasitized aphid was verified by examining it in the laboratory under a binocular microscope. The parasites were identified by specialists at the U.S. National Museum at Washington, D.C. Many of the fields and replicated, small-plot plantings of potatoes used in these studies were treated with insecticides and many were not.

Abundance of dead, parasitized aphids on untreated potatoes varied greatly from year to year. The potato aphid was most commonly parasitized and the buckthorn aphid least, while the foxglove and green peach aphids were intermediate. Attempts to detect adverse effects from parasites upon population trends of aphids were confined to possible effects on the potato aphid since it was the most commonly parasitized one on potatoes. Parasitization during the 12-year period 1952 through 1963 ranged from 0.5 to 6.4% of the total numbers of potato aphids on untreated potatoes.

Adverse effects of biological agents upon population trends of the potato aphid appeared to be manifested chiefly as a reduction in rate of population growth. Since the growth phase of the seasonal curve of aphid population trend on untreated potatoes is essentially a straight line when numbers of aphids are plotted on a semilogarithmic basis, a downward departure in the slope of the curve represents deceleration in rate of aphid increase brought about by natural factors. The effect of parasites upon potato aphid populations was assessed by noting divergences from the straight-line relationship and correlating such divergences with the percentages of potato aphids then parasitized, together with evidence as to the importance of other natural factors near these times. After making due allowances for adverse effects caused by other biological agents and weather, we concluded that by this criterion parasitism had no appreciable adverse effect upon rate of population increase of the potato aphid on untreated field-growing potato plants during the period 1952 through 1963.

A study was made throughout the same period to determine whether, or to what extent, insecticides applied in the planting furrow or as foliar sprays affected the all-season prevalence of parasitized potato aphids on field-growing potatoes. Weekly applications of DDT throughout the field season, mostly as a spray at 0.63 pound per acre, reduced parasitism in the potato aphid by nearly 50%. Parasitism in plots treated with other nonsystemic insecticides or with systemic insecticides was less than in untreated plots, but not significantly so. The level of parasitism on the average was not less in commercial fields treated with insecticides for control of aphids than in untreated plots and fields. Level of parasitism did not appear to be influenced by size of the treated area.

During the 20-year period of study, about 40 species of parasites were reared from the potato-infesting species of aphids, of which about 22 were primary parasites and 18 were hyperparasites. The most common species of primary parasite was *Aphidius nigripes*. Other common species also reared from all four species of aphids included two undescribed species of *Praon* and two of *Aphidius*. Several species of hyperparasites were reared from parasitized specimens of each of the four species of aphids; in decreasing order of consistent abundance these were *Asaphes lucens, Coruna clavata,* and an undescribed species of *Charips*. *Lygocerus* spp., as a group, ranked next to *A. lucens* in abundance. Several other species of primary parasites and of hyperparasites were reared from other species of aphids occurring on primary and secondary hosts of the potato-infesting species of aphids. Altogether 17 species of primary parasites and 18 species of hyperparasites were reared from the potato aphid; the corresponding numbers of species reared from the green peach, buckthorn, and foxglove aphids were 14 and 11, 12 and 8, and 11 and 6, respectively. The percentage of hyperparasitization in parasitized specimens of each species of aphid varied greatly from year to year; but during the 11-year period 1952 through 1962, it was 39% in the green peach aphid, 25% in the foxglove aphid, and 22% each in the buckthorn and in the potato aphid.

The seasonal distribution was charted for each of the more common species of parasites reared from potato-infesting species of aphids over the 20-year period. This provided little information on seasonal histories of the parasites. However, in most instances there were probably at least four generations per year of both the primary parasites and the hyperparasites, one each in spring and fall in the aphids on their primary hosts and at least two in populations on potatoes and other secondary hosts.

After examining three factors affecting year-to-year importance of the parasites, it was concluded (1) there has been substantial variability from year to year in the number of species of parasites and in the proportion of hyperparasites to primary parasites, but not in the number of the most common species, (2) the species of parasites consistently most common and abundant from year to year have some carryover of emergence into the second and third years in the dead, parasitized aphids, and (3) hyperparasitism has had no appreciable, consistent effect upon abundance of primary parasites, of aphids, or of the hyperparasites themselves.

There is little likelihood that there has been establishment in northeastern Maine, of the four introduced species of primary parasites liberated in 1957, 1958, and 1962, perhaps because of the small number of releases made and the small numbers of each parasite released. Three of the released species coming from France were *Aphidius matricariae, Aphidius* sp., and *Aphelinus semiflavus,* while one, *Aphidius* sp. (near *A. medicaginis*) came from India.

Brief synopses of the biology of several of the more common species or genera of primary parasites and of hyperparasites occurring in northeastern Maine are given.

Three approaches are discussed for increasing effectiveness of insect parasites against the potato-infesting species of aphids. These include (1) the introduction of new species of parasites or strains of species better adapted and more effective against each species of aphid than the naturally occurring ones, (2) the mass releasing of parasites in potato fields at times critical for the population dynamics of the aphids, and (3) a combination of these. The combined-effort approach is considered most likely to succeed.

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