1974

Biology of the asparagus beetle, Crioceris asparagi and Crioceris duodecim punctata, in western Massachusetts.

John Lowell Capinera
University of Massachusetts Amherst

BIOLOGY OF THE ASPARAGUS BEETLES, CRIOCERIS ASPARAGI AND CRIOCERIS DUODECIMPUNCTATA, IN WESTERN MASSACHUSETTS

A Thesis Presented
by
John L. Capinera

Submitted to the Graduate School of the
University of Massachusetts in partial
fulfillment of the requirements for the degree of

MASTER OF SCIENCE
January 1974
Major Subject: Entomology

BIOLOGY OF THE ASPARAGUS BEETLES,
CRIOCERIS ASPARAGI AND *CRIOCERIS DUODECIMPUNCTATA*,
IN WESTERN MASSACHUSETTS

A thesis
by
John L. Capinera

Approved as to style and content by:

John H. Lilly (Chairman of Committee)

Cecil L. Thomson (Member)

Gary L. Jensen (Member)

Adrian G. Gentile (Member)

T. Michael Peters, Head
Department of Entomology

ACKNOWLEDGEMENTS

The author wishes to extend his appreciation to Thesis Committee members Dr. G.L. Jensen, who suggested this study; Professor C.L. Thomson, who provided the asparagus plot; and Dr. A.G. Gentile, who offered many valuable editorial criticisms.

Committee Chairman Dr. J.H. Lilly deserves an extra measure of gratitude for his unfailing advice and counsel as well as his phenomenal patience and understanding.

To Ms. M.L. Capinera, wife, editor and secretary extraordinaire, whose contribution is immeasurable, I express my thanks and deepest devotion.

TABLE OF CONTENTS

INTRODUCTION

The biology of the asparagus beetles, *Crioceris asparagi* (L.) and *Crioceris duodecimpunctata* (L.), has received but cursory attention. Both insects feed only on the asparagus plant, *Asparagus officinalis* L., and occasionally prove very destructive. Any control program should be based on sound knowledge of the biologies of the two beetles.

Most of our information about the common asparagus beetle, *C. asparagi*, was provided by F.H. Chittenden (1897), who reported most of the known natural history and predatory enemies of this beetle. It was not until 1909 that *Tetrastichus asparagi* Crawford, a eulophid parasitoid of *C. asparagi*, was first reported by H.T. Fernald. Watts (1938) later reported a tachinid parasitoid of the beetle from South Carolina.

Less is known about the 12-spotted beetle, *C. duodecimpunctata*. The biology of this insect was studied by D.E. Fink (1913). The reports of natural enemies of this beetle are questionable.

Since their accidental importation from Europe, the asparagus beetles, *C. asparagi* and *C. duodecimpunctata*, have proved to be the most important pests of asparagus, wherever they are found. Asparagus is a valuable vegetable crop grown throughout the United States and southern Canada. The periodic population fluctuations of these beetles, resulting in damage above the economic threshold, have sometimes forced growers to resort to chemical control.

Today there is a rising concern for our environment and a new emphasis on food free of insecticide residues. An investigation of the biology and natural control mechanisms of the asparagus beetles could therefore be a valuable endeavor, perhaps resulting in knowledge that could be used in alternative control programs.

This study reviews and extends our knowledge of the life histories of the two species of asparagus beetles, and reports on the bionomics of these insects in western Massachusetts. The naturally occurring predator/parasite complex is closely examined.

LITERATURE REVIEW

A. Crioceris asparagi (L.), the Common Asparagus Beetle.

Asparagus was introduced to North America by the early settlers and is reported to have been successfully cultivated for two hundred years without being significantly troubled by pests (Chittenden, 1897). The common asparagus beetle, Crioceris asparagi (L.), was first noticed at Astoria, Long Island, in 1859. The actual importation of this insect probably occurred earlier, about 1856 or 1857. By 1860 the beetle proved moderately destructive at Astoria, and by 1862 had spread throughout the asparagus plantations of Queens County, Long Island (Lintner, 1882). Fitch (1862) noted the depredations of the beetle on Long Island and suggested that all asparagus, both cultivated and wild, in the vicinity of New York, be cut down. This would prevent the spread of this pest and "assuredly rid our country of this impending calamity." In 1863 "a small shining black parasitic fly, probably belonging either to the Chalcis or Proctotrupes family" appeared and significantly checked the damage caused by the asparagus beetle. Although the beetle continued to cause some damage to asparagus plants, great loss to the growers had ceased (Riley & Walsh, 1869).

Coupled with the appearance of this beneficial parasitoid was the development of a cultural control technique which also contributed to a decrease in the damage caused by C. asparagi. The growers were careful to destroy any seedlings developing from the seeds of the previous year, thus forcing the beetles to lay their eggs on the mature spears. These mature spears were cut and sent to market every few days, leaving no eggs to hatch and produce a second brood of beetles. Unfortunately it was found impossible to destroy all the volunteer plants growing throughout the area, which provided a reservoir for reinfestation of the growers' beds by the beetles (Riley & Walsh, 1869).

Another widely employed control measure entailed permitting a portion of the stems to grow and serve as a lure for the beetles. The beetles could then be killed with insecticides, or the plants cut and destroyed once a week to eliminate eggs and larvae. Recommended control measures included (1) hand picking, (2) brushing the larvae from the plants to the bare ground in hot weather, and (3) the introduction of chickens and ducks to the asparagus beds where they fed with relish on the pests (Chittenden, 1917).

Insecticides commonly used during this period for the control of C. asparagi included pyrethrum, air-slaked lime, quassia and soap, Paris green, and arsenate of lead (Chittenden, 1917), and also hellebore (Britton, 1902).

C. asparagi spread at a rate of about 20 miles per year after its introduction. The beetle was first observed in New Jersey in 1868 (Lintner, 1893). This insect, spread by a combination of flight and accidental transportation, had been reported in 19 states by 1917, most of them in the East but also including Colorado, California, and southeastern Canada. C. asparagi now appears to be generally distributed throughout the United States and Canada, wherever asparagus is found (Jones & Robbins, 1928).

The common asparagus beetle overwinters as an adult under piles of rubbish, stones, and loose bark of trees (Chittenden, 1917), and also in hollow asparagus stems (Latta, 1928). In Europe the beetle is reported to pass the winter as a pupa (Omerod, 1897; Dingler, 1934). C. asparagi appears in great numbers in April or May at about the time the asparagus is ready for the first cutting. There are at least two generations of C. asparagi in New England, with a possibility of three or four generations in the beetles' southern range (Chittenden, 1917). Jones and Robbins (1928) reported many overlapping generations in southern California.

Both adults and larvae inflict damage by gnawing the tender young shoots. The deposition of eggs makes the shoots less desirable, as does the emission by the larvae of a "black, molasses-like fluid" (Chittenden, 1897). Extensive feeding may result in considerable stunting and crookedness in growth, discoloration, and/or defoliation of the plants later in the season. Such injury may lead to serious losses through death of the plants or undernourishment of the roots, and a subsequent small crop. During the establishment of a new bed, where no cutting is done, the plants are particularly susceptible to damage (Huckett, 1937).

Development of C. asparagi takes about 30 days, depending on weather conditions. Eggs are deposited singly, but often in rows of two to seven. The eggs are white when first deposited but soon turn dark brown. The eggs, about 1.5 mm in length, hatch in three to eight days. The brown or grey larvae begin to feed immediately, attaining a length of 10 to 15 mm in 10 to 14 days. The mature larvae then drop to the ground and burrow into the soil. There they construct cells and pupate. Ten to 20 days after entering the soil the newly emerged adults appear and immediately begin to feed (Chittenden, 1917).

Extremes in temperature have been reported to be fatal to the common asparagus beetle. Severely cold winter temperatures may kill large numbers of overwintering adults (Chittenden, 1917; Latta, 1928). Latta (1928) also indicated that an average annual minimum temperature of -10°F may be the northward limitation for C. asparagi. Abnormally hot, dry weather may also have detrimental effects on larvae and eggs of this insect (Chittenden, 1917; Watts, 1939).

B. Crioceris duodecimpunctata (L.), the 12-Spotted Asparagus Beetle.

Crioceris duodecimpunctata (L.) was first noted in North America in 1881 at Baltimore, Maryland, feeding on volunteer asparagus plants. The insect presumably had been introduced accidentally from Europe several years earlier. By 1892 this beetle was reported from New Jersey, and by 1893 it was found in New York. As C. duodecimpunctata spread northward, its appearance was always accompanied by serious damage. The beetle reached southern Canada by 1898 and began to spread west (Fink, 1913), reaching British Columbia in 1926 (Beirne, 1971). In the United States, this beetle has progressed as far west as Utah and Idaho (Metcalf _et al_, 1962).

Adult 12-spot beetles damage asparagus spears and mature plants in much the same manner as the common asparagus beetle, _C. asparagi_. The larvae, however, do not feed directly on the foliage as do the larvae of _C. asparagi_, but rather on the berries of the "female" plants. The developing larvae dwell internally, consuming both the flesh of the berry and the developing seeds, thus causing significant damage to crops of growers interested in seed production. The adult 12-spot beetles also feed on the berries (Fink, 1913).

Early control recommendations stressed destruction of the adult beetles before the eggs were produced, since the feeding habits of the larvae left them generally impervious to the insecticides of that era. Collection and destruction of the berries was also recommended, should the insect become particularly numerous (Chittenden, 1897). The cultural control practices effective for _C. asparagi_ would, of course, be equally efficient for control of _C. duodecimpunctata_, but these practices soon gave way to improved insecticides (Hutt, 1899; Britton, 1902; Wilson & James, 1942; Westcott, 1964; Hunter, 1971).

There are indications that lower dosages of insecticides may be necessary to control _C. asparagi_ than would be needed to control _C. duodecimpunctata_ as effectively. _C. asparagi_ was found to be 16 to 32 times as susceptible to DDT as was _C. duodecimpunctata_

(Ger dorff & McGovran, 1945).

The 12-spotted beetle overwinters as an adult, although in Europe the second generation may also pass the winter in the pupal state (Chittenden, 1897; Dingler, 1934). The adult emerges from its winter quarters about a week after the appearance of the common asparagus beetle. The beetles begin to copulate immediately but eggs are not produced until three or four weeks later when the blossoms and berries begin to appear on the plants. The female deposits her eggs singly on plants with dense foliage. The egg is attached by its side, not on its end, as is the case with the egg of the common asparagus beetle. The elongate oval eggs are yellow-orange in color, turning green with age. They blend very well with the light green foliage and are extremely difficult to detect. The eggs hatch five to 15 days after being deposited (Fink, 1913).

In form and general appearance the larva of C. duodecimpunctata closely resembles that of C. asparagi. The body color, however, is pale yellow or pale orange, as opposed to the grey-brown hue of the C. asparagi larva.

Two to four berries are consumed during larval development. The larvae pass through three instars in five to eight days, and then drop to the ground where they burrow beneath the soil and prepare a pupal cell. Two to three weeks after entering the soil, the adult beetle emerges and begins feeding on foliage and berries. Two generations of C. duodecimpunctata develop annually in New

England (Fink, 1913).

C. Parasitic Enemies

The eulophid parasitoid Tetrastichus asparagi Crawford is known to be an important parasite of the common asparagus beetle; some authors have believed that T. asparagi is also a parasite of the 12-spotted asparagus beetle, Crioceris duodecimpunctata. This parasite will be stressed later in this summary. Three dipterous parasitoids of the family Tachinidae have also been reported to be parasitic on the common asparagus beetle, Crioceris asparagi.

Meigenia mutabilis (Fall.) is a European tachinid that is parasitic on C. asparagi as well as several other chrysomelid beetles (Lecaillon, 1917; Couturier, 1938; Ruffo, 1938). M. mutabilis was imported to the United States in 1939 to aid control of the common asparagus beetle. Adult parasites were released at several points in southern New Jersey and initially gave a high percentage of parasitism. However, the parasite failed to persist through the winter (Strong, 1940, 1941; Stone et al, 1965). Clausen (1956) suggested that an alternate host may be necessary for permanent establishment.

Paralispe infernalis (Tns.) is found throughout the south and southwest United States. This tachinid was reported by Watts (1938) to be parasitic on the common asparagus beetle. It was reared successfully from beetle larvae collected from July through September. Collections showed that less than ten percent of the larvae generally were parasitized. This was the only parasite Watts found in South Carolina.

The tachinid *Myiobia pumila* Macq. is known to be a parasite of *C. asparagi* in central Europe (Chittenden, 1897; Baer, 1920).

The gregarious eulophid parasitoid *Tetrastichus asparagi* Crawford mentioned above is found both in Europe and North America. When this parasite was first found in Massachusetts (Fernald, 1909) it was thought to be native to North America (Crawford, 1909). However, it is native to Europe and was described there by Nees ab Esenbeck in 1834 (Graham, 1961). Graham (1961) suggested that although the name *Tetrastichus coeruleus* Nees had precedence, it ought to be rejected in favor of *T. asparagi* because of the extensive use of the latter in the economic literature.

T. asparagi is a predator of the eggs of *C. asparagi* as well as an egg-larval parasitoid. In fact it may be more valuable as a predator than as a parasite in the regulation of asparagus beetle numbers (Johnston, 1915). Johnston examined 2,097 eggs on 28 stalks of asparagus in a check row that had been left to attract the beetles from the main crop. He found that 71.2% of the eggs had been destroyed by *T. asparagi*.

In the laboratory, Johnston determined that emerging adult parasites generally fed before beginning to oviposit. The feeding behavior is as follows. The host beetle egg was carefully examined by the adult parasite, utilizing its antennae. If the egg was found acceptable, the parasite climbed upon it, inserted its ovipositor, and worked it up and down with a pumping motion. After a few seconds to three to four minutes the parasite withdrew its ovipositor and backed down from the egg. Placing its mouthparts to the puncture, the parasite sucked up the egg contents until the egg collapsed.

The process of oviposition is similar, but instead of pumping the abdomen, an ovipositing parasite holds the ovipositor motionless within the egg for a few minutes. Eggs that had been parasitized were distinguishable by the small amount of egg contents that oozed from the puncture site. The parasite egg may be laid singly, but in a number of cases the eggs were laid side by side in pairs.

The parasite does not complete its development and emerge from the host egg, as would a true egg parasite. Development is not completed until the host beetle larva enters the soil and prepares the pupal cell. The beetle larva does not pupate, as the developing parasite larvae consume the beetle and pupate within the beetle pupal cell. The adult parasites break out of the cell and make their way to the surface of the soil.

The average length of life of the adult parasites in confinement was 7.5 days, the maximum 25 days. <u>Tetrastichus</u> parasitized 1.9 beetle eggs per day, but consumed 3.9 host eggs per day while confined to vials.

Three generations of the parasite were observed by Johnston in a single season, but he indicated that the third generation, in the autumn, may be partial. He suggested that the third generation may be the exception rather than the rule. The parasite was observed to overwinter as a full-grown larva in the pupal cell of the host. Of the field collected and laboratory reared adults no males were found, indicating that T. asparagi reproduces parthenogenetically.

This valuable wasp was sent from Ohio to Washington in 1937 to aid in reducing damage by the common asparagus beetle. This program met with at least partial success (Johansen, 1957). T. asparagi was also introduced to California but failed to become established there (Clausen, 1956).

Several authors have indicated that T. asparagi is a parasite of the 12-spotted asparagus beetle as well as of the common variety (Thompson, 1943; Peck, 1963; Beirne, 1971). However, a close examination of the literature cited by these authors shows that no real evidence of parasitism of C. duodecimpunctata by T. asparagi actually exists. The confusion seems to stem from (1) a faulty review of Britton's 1921 Connecticut Agricultural Experiment Station Report published in the Review of Applied Entomology, and (2) use of common names instead of Latin names.

Britton (1922) did not report T. asparagi as a parasite of C. duodecimpunctata, but the review of the article plainly stated that the parasitoid was found to parasitize the "beetles". Therefore, it is easy to understand why Thompson (1943) recorded this parasitic relationship, since his Catalogue is based on literature cited in the Review of Applied Entomology, rather than on the original literature.

The interpretation of the references cited by Peck (1963) and Beirne (1971), in reviewing the relationship between T. asparagi and C. duodecimpunctata, may have been influenced by the inaccuracy of Thompson's Catalogue. Burks (1943), in a review of the genus Tetrastichus in North America, indicated that the host of Tetrastichus asparagi was Crioceris asparagi, but that the host record was "questionable".

D. Predatory Enemies

Chittenden (1897) reported that the common asparagus beetle, Crioceris asparagi, has some very efficient natural enemies that assist in preventing damage by this species. He indicated that the spotted ladybird, Coleomegilla maculata Timberlake, consumes larvae of the common asparagus beetle with great efficiency. The spined soldier bug Stiretrus anchorago Fab. also feed on beetle larvae. Also, the wasp Polistes pallipes Lep. and the damselfly Ischnura posita (Hagen) are reported to pounce upon the larvae and carry them away.

The convergent ladybird, Hippodamia convergens Guer., was once reported to have migrated in large numbers to asparagus fields to feed extensively on the eggs of the asparagus beetle, C. asparagi. This prevented the development of the normally large first generation (Watts, 1939). Coccinella septumpunctata L. was reported to feed on the larvae of C. asparagi in Europe (Balduf, 1935), as was the sphecid Cerceris quinquefasciata Rossi (Chevalier, 1924).

The pentatomid Perillus biculatus F. feeds readily on C. asparagi larvae (Landis, 1937). Watts (1938) indicated that the reduvids *Sinea* sp. and *Pselliopus* sp. preyed extensively on the larvae of the common asparagus beetle. Sanderson (1899) suggested collecting the "wheel bug", *Arilus cristatus* (L.), from apple trees and introducing them to asparagus beds where they would feed voraciously on the larvae and adults of the common asparagus beetle.

Apparently no authoritative reports of insects predaceous on *C. duodecimpunctata*, the 12-spotted asparagus beetle, appear in the literature. The imprecise use of "asparagus beetles" by Britton (1922) seems to have led Thompson (1964) to cite the predatory enemies of *C. asparagi* as predaceous on *C. duodecimpunctata*.

Felt (1901) reported that English sparrows apparently consumed a large number of *C. asparagi* and *C. duodecimpunctata* adults and larvae. However, Jones (1932) found *C. duodecimpunctata* to have a low relative acceptability to several insect-eating birds.

MATERIALS AND METHODS

A. Bionomics of Asparagus Beetles and Associated Insects

Field studies for 1972 and 1973 were carried out at three locations in western Massachusetts: (1) an experimental plot at the University Farm, Deerfield (Franklin County), (2) an asparagus field under normal commercial cultivation and harvesting at Hadley (Hampshire County), and (3) an abandoned field with volunteer asparagus, also in Hadley Township. The experimental plot had been established in 1968. The plants at the other sites appeared to be at least as old.

Asparagus plants were randomly selected for observation at all three sites. Twenty plants were selected at the experimental plot, and 10 each at the asparagus farm and abandoned field. The experimental and volunteer plants were labeled with numbered paper tags; the harvested plants were labeled with numbered stakes.

During 1972 all numbered asparagus plants were visited weekly from May 14 to September 24 (with one exception). During 1973, all plants were visited weekly from May 13 to August 31. All tagged asparagus plants were closely examined, and the abundance and stage of development of each pertinent species of insect was determined by direct observation and then recorded. Observations were always made between 10:00 a.m. and 2:00 p.m., on warm or sunny days when possible.

The population of insects frequenting the ground beneath the asparagus plants was sampled with 10 oz. plastic drinking cups. Three cups were distributed randomly beneath each group of 10 monitored asparagus plants and buried at the depth necessary for the lip of the cup to be level with the surface of the soil. These traps were set out five to seven days each month, and examined daily for trapped insects.

B. Parasitism of Asparagus Beetles

The egg, larval, and adult stages of the asparagus beetles, C. asparagi and C. duodecimpunctata, were collected randomly from the University Farm and from volunteer asparagus plants. Larvae of C. asparagi were collected at least once per week until August, when they could no longer be found in sufficient quantity. The other stages of both beetles were collected when they were abundant. No collections were made from plants under observation, nor from adjacent plants. No more than two larvae of C. asparagi were collected from a single asparagus plant, and the total number collected was kept low enough to minimize the effect their removal might have on the population dynamics of the plot.

The larvae of C. asparagi were collected by shaking the branch bearing the insects over a container. If the larvae dropped readily into the container they were taken back to the laboratory for rearing. If the larvae did not drop readily from the branch, they were not removed, as this indicated immature larvae. Only mature larvae were collected, so as to minimize interference with possible larval parasitoids.

The larvae of C. duodecimpunctata were collected by removing berries from the asparagus plants and by collecting berries from the ground. Berries were placed in individual vials with a small amount of moist soil, and plugged with cotton. If a berry was found to support a beetle larva, additional berries were added to the vial to supply enough food for successful development.

The larvae of C. asparagi were treated in like manner, except that the larvae were supplied with fresh asparagus foliage instead of berries. Larvae collected in the described manner were found to pupate almost immediately upon exposure to the soil, and generally did not require additional foliage.

Beetle eggs were kept in a single vial on asparagus branches until they hatched; larvae were then separated into individual containers and reared to the adult stage. Field-collected adult beetles were also isolated and supplied with asparagus; they were generally kept in vials two to three weeks or until death.

About 120 C. asparagi eggs were field collected and reared; emerging larvae suffered 50% mortality. Asparagus berries containing 180 C. duodecimpunctata larvae were also collected from the field, and demonstrated a similar mortality. Of the 386 mature C. asparagi larvae collected, less than 10% failed to produce either adult parasites or beetles.

The possibility that Tetrastichus asparagi might produce and detect a trail odor was examined during 1973. A technique modified from Price (1972) was used to test for trail odor.

Plastic petri dishes 9.0 X 1.5 cm. were used for the test area. A paper strip 1.3 cm. wide was glued end to end to form a ring 4.5 cm. in diameter. The paper ring was placed in the center of the petri dish. An adult parasitoid was allowed to explore the interior sides of the paper ring and the top and bottom of the central portion of the plastic petri dish, but could not gain access to the petri dish exterior of the ring.

After four to six hours of exposure to the portion of the petri dish delineated by the paper ring, the paper ring was removed and the parasite was allowed access to the interior of the entire petri dish. In some cases another parasite was introduced and the original specimen removed. The exploratory movements of the parasite were recorded for 15 minutes. If a trail odor similar to that reported for many other parasitoids was present, T. asparagi could be expected to avoid the pre-searched area.

Eight newly emerged adults and eight older adults that had fed on C. asparagi eggs were tested using the technique described above. Four parasites of each group were tested to determine whether they could detect their own trail odor or the trail odor of other T. asparagi. Tests were conducted at room temperature (25°C). Light was provided by a single 60-watt incandescent bulb directly over the center of the petri dish at a distance of 30 cm. from the dish.

To determine whether adult T. asparagi were attracted to the odor of C. asparagi egg contents, 10 fresh beetle eggs or 10 three-day-old eggs were crushed in a drop of distilled water. The solution, from which the egg shells were removed, was painted onto the central area of the top and bottom of a petri dish. The area painted with the egg solution was 4.5 cm. in diameter. The remainder of the petri dish was painted with distilled water. The petri dish was allowed to dry and an adult T. asparagi was allowed to explore the interior of the dish. The movements of the parasite were recorded. Four newly emerged parasites and four older, recently fed parasites, were examined in this manner, employing eggs of each age category.

To determine whether adult T. asparagi could differentiate between newly laid C. asparagi eggs and older host eggs, an equal number of eggs from each age category were placed in a plastic petri dish containing five parasites. Some of these parasites were newly emerged and some had previously fed. Five, 10, or 15 eggs of each age category were placed in the petri dish with the parasites. One-day-old eggs were considered to be newly laid; three-day-old eggs were considered to be old eggs. The eggs were exposed to the parasites in this manner for three days before the results were tabulated. At this time several of the "old" eggs had hatched.

The development of the parasitoid T. asparagi in relation to its host C. asparagi was compared through dissection. Parasitized and unparasitized host eggs were field collected. Some eggs were dissected, while others were allowed to develop. Several beetle larvae or pupae were dissected each day between the time of parasitism of the host egg and emergence of the adult parasite or beetle.

C. Predation of Asparagus Beetles

Qualitative evaluation of predation was based on sampling for predaceous insects. Field-collected predators were confined with asparagus beetles and observed in the laboratory. Quantitative evaluation was limited to predation of the egg stage of C. asparagi. Egg predation by Tetrastichus asparagi was determined by counting the number of eggs with the contents removed which resulted in a characteristically collapsed appearance. Eggs fed upon by T. asparagi generally fell from the branch within a few days and were not encountered on the next observation. Eggs preyed upon by coccinellids were either torn completely from the branches or had the distal two-thirds consumed.

D. Pathogens of Asparagus Beetles

Moribund or abnormally colored larvae of C. duodecimpunctata and C. asparagi were collected from the field and brought back to the laboratory for examination. Some larvae were dissected in a drop of distilled water and examined microscopically for abnormalities. Other larvae were fixed in Kahle's solution, imbedded in paraffin, sectioned, stained with Delafield's haematoxylin, and examined microscopically for pathogens.

RESULTS AND DISCUSSION

A. Bionomics of Asparagus Beetles and Associated Insects

Field Studies indicate that the common asparagus beetle, *Crioceris asparagi*, has two full generations per year in western Massachusetts. A third generation may occur under favorable climatic conditions. The abundance of each stage of the common asparagus beetle observed each week during the two summers of the study is shown in Tables 1 and 2, and in Figures 1 and 2. The 12-spotted asparagus beetle, *Crioceris duodecimpunctata*, seems to have two generations per year. The numbers of *C. duodecimpunctata* adults observed weekly are shown in Tables 3 and 4, and in Figures 3 and 4. The very small second generation observed in 1972, and the absence of a second generation in 1973, may have been due to flights of emerging adults to areas where asparagus berries were more abundant, or perhaps to the activities of unknown predators or disease agents.

The development of large aphid populations during the summer months, consisting primarily of *Aphis craccivora* Koch (1972) and *Brachycolus asparagi* Mordvilke (1973), is shown in Tables 3 and 4. The relationship of these aphid populations to coccinellid populations reflected in Tables 3 and 4, and in Figures 5 and 6, will be discussed in the section on predation.

The abundance of the eulophid parasitoid *Tetrastichus asparagi* is shown in Tables 5 and 6. Of the second generation *T. asparagi* obtained in July 1973, 36.7% did not complete their development normally but diapaused as larvae while in the pupal cell of the host beetle. This is the normal overwintering stage of the parasitoid (Johnston, 1915). Generally, all the parasitoids from the same host larva either developed normally or exhibited arrested development. The diapause of some of the second generation parasitoids until the following spring could explain the small size of the third generation and the large size of the subsequent first generation. The relationship of this predator/parasite to its host will be discussed in the sections dealing with parasitism and predation.

The numbers of insects observed in the asparagus field under commercial cultivation in Hadley were so slight and irregular that they were not included in the tabulated results. Therefore, the population trends indicated by the tables and figures cited above reflect population dynamics found on uncultivated asparagus. Actually, during the two years of the study asparagus beetles were rarely observed on cultivated asparagus plants. That asparagus beetles prefer undisturbed asparagus to cultivated plants has been known for many years; this preference has been used to lure the beetles to "trap" rows of asparagus. The asparagus beetles are likely to become pestiferous only (1) during periods of great abundance, when they migrate from volunteer plants to adjacent cultivated asparagus, or (2) when they become very abundant in newly established, uncultivated asparagus beds.

B. Parasitism of Asparagus Beetles

Tetrastichus asparagi was found to be the only significant parasitoid in western Massachusetts. This wasp was found to parasitize only the common asparagus beetle, Crioceris asparagi. No parasitoids of the 12-spotted asparagus beetle, Crioceris duodecimpunctata, were discovered. The percentages of parasitism of C. asparagi by T. asparagi, determined weekly, are shown in Tables 5 and 6, and in Figures 7 and 8. Percent parasitism generally increased with an increase in the number of parasites, whose abundance was closely synchronized with the abundance of the host (Fig. 16 and 17). Thus, T. asparagi is shown to be a density-dependent mortality factor which may serve to dampen oscillations in the abundance of the common asparagus beetle and thereby help prevent increases in beetle numbers which might result in significant crop damage. Average percent parasitism throughout the summer of 1972 was found to be 48.3% and in 1973 it was 47.8%.

An average of 4.75 parasites were reared from each parasitized beetle. The range in the number of parasitoids emerging from one host was two to 12. Curiously, a single parasite was never reared from a common asparagus beetle host, although Johnston (1915) stated that a single parasite egg may be deposited by this gregarious parasitoid. Parasitized host beetle eggs collected from the field and dissected during 1973 always contained at least two parasitoid eggs. When the distribution of parasitoid eggs among host eggs was analyzed, it varied widely from a Poisson series (Table 7 and

Fig. 13), which indicates that the distribution is not random (Askew, 1971). The wasps, then, seem selective in their oviposition behavior. Clausen (1954) suggested that T. asparagi probably oviposits only in eggs containing advanced embryos.

Nasonia vitripennis (Walker), a gregarious parasitoid of muscoid pupae, lacks the power to detect parasite eggs. After inserting the ovipositor, the female can detect the stage of development of the prospective host and the presence of parasite larvae. This parasite avoids ovipositing within the advanced stages of development of the host, and within hosts containing parasite larvae. The ovipositor is apparently capable of detecting changes in the composition of the host hemolymph (King & Rafai, 1970).

In the case of T. asparagi, parasitoid eggs were recovered only from the host eggs containing advanced embryos. The adult parasite cannot detect parasite larvae, as does N. vitripennis, since the parasite hatches during the first larval instar of the host (Fig. 18). T. asparagi may be able to detect the presence of parasite eggs, or the odor of other parasites that have visited the host, as has been shown for Trichogramma evanescens (Salt, 1937). T. asparagi may choose to oviposit within host eggs containing advanced embryos instead of feeding on them because the contents may simply be too difficult to extract through the tiny feeding hole.

When Tetrastichus adults were confined to petri dishes with beetle eggs, 17 out of 30 newly deposited eggs were consumed within three days. Of an equal number of three-day-old eggs, none had been consumed after three days of exposure; several had been parasitized.

When the results of the trail odor tests were examined, no clear evidence of avoidance of pre-searched areas was indicated. The searching behavior of T. asparagi is generally rather erratic, or as Fernald (1909) so eloquently stated, "their actions on the plant were carefully studied and gave the impression of stupidity on the part of the insects." The occasional avoidance of pre-searched areas by the parasites during the trail odor tests may be interpreted to be part of the normal searching behavior of these insects. It is also quite possible that the normal behavioral patterns of the parasites are not exhibited when these insects are confined to petri dishes. A more sensitive test may be needed before any valid conclusions can be drawn as to the ability of Tetrastichus to produce or detect a trail odor. But on the basis of the tests conducted, no trail odor could be detected.

It may not be as critical for T. asparagi to detect the presence of parasite eggs within the host eggs as it is for many other parasitoids that are not gregarious in habit. Up to 12 T. asparagi may develop in a single host. Many of the parasitoids exhibiting discriminatory abilities are superparasitic in habit, and discrimination provides a mechanism to avoid wastage of eggs. King and Rafai (1970), however, showed that the gregarious parasitoid Nasonia vitripennis possesses the ability to discriminate between hosts.

The effects of parasitism by T. asparagi on C. asparagi are not noticeable until the host attains the prepupal stage and the parasite larvae begin to develop rapidly. The presence of larval parasitoids cannot be visually ascertained during the larval stage of the host; the host must be dissected to detect parasitism. Under laboratory conditions the parasitized larvae feed as readily, develop at the same rate, and attain the same size as the unparasitized larvae. Dissection revealed that the principal effect of parasitism appeared to be the poor development of the fat body in the parasitized host larvae. Once the prepupal stage is reached and the host larva has constructed a pupal cell in the soil, the parasite larvae can be detected in the distended host remains.

T. asparagi may gain some adaptive advantage by its gregarious habits. The ability to detect parasitism of the host egg, and parasitize such an egg additionally, may have some survival value. This is suggested by Figure 15, which shows that parasites emerging from heavily parasitized hosts emerge earlier than parasites emerging from less heavily parasitized hosts. The parasites emerging from hosts supporting about 4.75 T. asparagi (the mean number of T. asparagi reared from parasitized C. asparagi during 1972) emerge 16 to 20 days after pupation (Table 8 and Fig. 14).

The difference between host and parasitoid emergence allows time for the host to mate and begin production of eggs. Thus, those parasites emerging from lightly parasitized hosts emerge after many of the available host eggs have been consumed or parasitized, while the parasites emerging from heavily parasitized hosts emerge before food and oviposition sites are generally available. Such discrimination, the selection of a parasitized host egg to be parasitized again, may help explain why such a high proportion of eggs are not parasitized (Table 7 and Fig. 13).

There is no doubt that the host egg is parasitized by more than one adult parasite, or at least on separate occasions. Dissection showed that parasite larvae within the same host could be considerably different in size; also, adult parasites frequently do not emerge synchronously from the same host pupal cell.

A single specimen of the tachinid _Paralispe infernalis_ was reared from an asparagus beetle larva in 1972. This fly was the only parasite of the common asparagus beetle that Watts (1938) reported from South Carolina. This tachinid apparently is not abundant enough in western Massachusetts to exert significant control. Actually, it is quite surprising that more tachinids were not reared from common asparagus beetles, since tachinids were frequently and consistently observed on asparagus plants.

C. Predation of Asparagus Beetles

The biology of the common asparagus beetle, _Crioceris asparagi_, is such that the eggs and larvae are generally vulnerable to the many predators frequenting asparagus. The eggs and larvae of the 12-spotted asparagus beetle, _Crioceris duodecimpunctata_, lead a much more protected existence, as has been mentioned previously. The eggs are extremely difficult to detect among the asparagus branchlets. In one instance a female 12-spot was observed to manipulate asparagus branchlets with her mandibles in such a manner as to glue the vegetation to the sides of a newly deposited egg, providing additional camouflage.

Tetrastichus asparagi was confined with eggs of the 12-spotted asparagus beetle in the laboratory but the predator/parasite did not feed upon, nor parasitize, these eggs. It should be noted that the egg-laying populations of the 12-spot and the peak abundance of the eulophid parasitoid do not generally coincide in nature. The eggs of the 12-spotted asparagus beetle suffer little exposure to the predatory habits of this parasite. The larvae of these beetles spend much of their time feeding within the asparagus berries and are vulnerable to predators only when in transit between berries or when seeking a location to pupate.

Percentages of predation of C. asparagi eggs by T. asparagi are shown in Tables 5 and 6. These data reflect predation by coccinellids also, but coccinellid predation was significant only in the late summer. The abundance of coccinellids is indicated in Tables 3 and 4. Figures 9 and 10 illustrate the decrease in numbers of C. asparagi eggs observed as the numbers of coccinellids increased. The abundance of ladybird beetles is believed to be a response to the numbers of aphids (Tables 3 and 4) found on asparagus during June and July of 1972, and July and August of 1973. Once the adult coccinellids were attracted to the aphid colonies and began to lay eggs, the ladybird progeny were more or less condemned to feed on whatever food was available. As the number of aphids diminished in July of 1972 and in August of 1973, the ladybird larvae probably fed heavily on the eggs and larvae of the asparagus beetles. Adult and larval coccinellids, when confined to petri dishes in the laboratory, fed with relish on small *C. asparagi* larvae, and fed on the eggs of this beetle when no other food was available. The coccinellid species involved in predation of the common asparagus beetle were primarily *Coccinella transversoguttata* Falderman, *C. novemnotata* Herbst, *Hippodamia convergens* Guerin, and *Coleomegilla maculata* Mulsant.

Coccinellid predation was noted principally at the Deerfield observation site. The aphid that exhibited the dramatic population increase during 1972, the cowpea aphid, *Aphis craccivora* Koch, is not normally associated with asparagus and was not observed in great numbers at the Hadley site. The asparagus aphid, *Brachycolus asparagi* Mordvilke, was present only in small numbers at both sites during 1972, but in 1973 the populations reached high levels and attracted large numbers of predators.

Percent predation of *C. asparagi* eggs averaged 52.6% during 1972 (Table 5) and 52.1% during 1973 (Table 6). Predation generally increased as the numbers of parasites and host eggs increased (Figs. 11 and 12), and thus can be regarded as a density-dependent mortality factor. Percent egg predation at periods when parasite numbers were low was considerably higher than percent parasitism during this same period. This may be due to an inherent error in the method of determining egg predation; that is, the remains of some of the consumed eggs may not have fallen from the asparagus plants within one week and may have been tabulated more than once. This did not seem to be generally the case, however. DeBach (1943) reported that predation of the black scale, Saissetia oleae (Bern.) by the parasite Metaphycus helvolus (Comp.) also was relatively more effective at lower parasite levels. Finally, mutual interference between searching insect parasites may be involved at higher population levels (Hassel, 1971).

Newly emerged T. asparagi generally feed before parasitizing any beetle eggs (Johnston, 1915). Many parasitoids are known to discriminate against parasitized hosts (Price, 1972; Vinson & Guillot, 1972). T. asparagi may have some mechanism that allows it to detect parasitized eggs and to avoid feeding on them, thus insuring survival of the species. If this is the case, at periods of high percentage of parasitism the parasites may not feed as frequently as might be desirable for optimal egg production. This could explain why the percent predation is higher at periods of low parasite population density. The parasites at this time have a proportionally greater number of host eggs to choose from and may feed more readily. An additional factor of this discriminatory mechanism could be the production of fewer eggs by each parasite at higher parasite densities due to reduced protein intake. This could help insure that some beetle eggs survive to provide for the next generation.

Discrimination could also involve production and recognition of a trail odor by the adult parasitoid, which could result in avoidance of pre-searched areas and dispersal from high density areas. The parasites might also be able to detect the small amount of host egg contents that escape the egg when it is punctured by the ovipositor of the parasite. When a solution of egg contents and distilled water was painted onto one area of a petri dish, however, *Tetrastichus* did not seem to discriminate against this area. Ganesalingam (1972) reported that the ichneumonid *Devorgilla canescens* (Grav.) could detect a parasitized host by piercing the host cuticle with the ovipositor. Tarsal or antennary contact was not necessary for discrimination to occur. Salt (1937) found that the chalcid parasitoid *Trichogramma evanescens* could discriminate between healthy and parasitized hosts by detecting external odor or by inserting the ovipositor. Insertion of the ovipositor may be necessary before *T. asparagi* can distinguish parasitized from unparasitized eggs, or freshly laid eggs from eggs containing advanced embryos -- if indeed *Tetrastichus* can make the former distinction.

Predaceous ground beetles frequented the soil beneath the asparagus plants, especially when additional cover was provided by weeds. The most common carabids collected included *Pterostichus lucublandus* Say, *P. melanarius* Illiger, *Harpalus pennsylvanicus* DeGeer, *H. erraticus* Say, and *Agonum melanarium* Dej. These predators were all found to consume *C. asparagi* and *C. duodecimpunctata* larvae when exposed to them in the laboratory. With the exception of *A. melanarium*, these carabids might be expected to consume mature asparagus beetle larvae as they dropped to the ground to pupate. A. melanarium is too small to attack mature asparagus beetle larvae and can be considered an effective predator only on small asparagus beetle larvae, which are rarely found on the ground.

It was observed in the laboratory that frequently a common asparagus beetle larva would sever an asparagus branchlet supporting another C. asparagi larva, resulting in the separation of the larva from the main plant. The larva would cling to the severed branchlet until the foliage was consumed or began to dry up. It then began to wander rather aimlessly, with scant hope of regaining the plant. This destructive mechanism was obviously more prevalent under densely populated conditions.

No attempt was made to determine whether larval carabids, dwelling in the soil, preyed on the pupae of asparagus beetles.

During June and July of 1972, 147 asparagus berries were removed from asparagus plants; 15.6% of these berries were found to support larvae of C. duodecimpunctata, the 12-spotted asparagus beetle. All of these larvae were still quite small. During this same period, 148 berries were collected from the soil beneath the asparagus plants; 91.2% of these berries supported C. duodecimpunctata larvae, and the contents of an additional 6.7% of the berries had been consumed by 12-spot larvae which were no longer present. Clearly, the feeding activities of the maturing larvae caused the berries to drop from the plant.

Each larva of the 12-spotted beetle requires about three berries to complete its development. Larvae were frequently observed wandering about asparagus plants searching for additional food. Often they were found on "male" plants, which do not produce berries. Surely the wanderings of these larvae left them vulnerable to predation.

Fink (1913) reported that he never found an asparagus berry supporting more than one larva simultaneously. Under the conditions in western Massachusetts, by mid-July of 1972 nearly all asparagus berries within the observation plots supported a C. duodecimpunctata larva. In several instances berries were found supporting two larvae, which may be interpreted to indicate severe competition for food and shelter. This phenomenon was not apparent in 1973 when the first generation of C. duodecimpunctata was much smaller (Table 4 and Fig. 4).

The pentatomid Podisus maculiventris Say was frequently observed feeding on C. asparagi larvae during late July and August. The nabid predator Nabis rufusculus Reuter was more commonly observed as a predator of the larvae earlier in the summer. Occasional predators observed include Sinea diadema Fab. (Reduviidae) and Chrysopa oculata Say (Chrysopidae).

D. Pathogens of Asparagus Beetles

Moribund Crioceris asparagi larvae frequently were encountered in the field, particularly during the late summer. Examination of these larvae usually revealed some evidence of predation. If a nabid or reduviid was disturbed while feeding on a beetle larva, the predator would sometimes drop the prey, leaving the beetle to die slowly. Frequently a blackened C. asparagi larva was discovered adhering to an asparagus plant. Well developed Tetrastichus asparagi larvae could usually be dissected from such host remains. On several occasions moribund larvae were found that did not appear to have suffered the effects of either predation or parasitism. The causes of death of these individuals could not be determined, but no indication of disease could be ascertained.

SUMMARY AND CONCLUSIONS

The findings of this study are as follows:

1) The common asparagus beetle, Crioceris asparagi, has two full generations in western Massachusetts. This agrees with Chittenden's (1917) contention that there are "at least two" generations annually in New England.

2) The second generation of C. asparagi produces eggs that could develop into a third generation if the season were long enough; they provide food for the third generation of Tetrastichus asparagi, the subject of a major portion of this investigation.

3) The number of second generation C. asparagi reaching maturity is much smaller than the number of first generation beetles attaining adulthood. This may be due to the activity of predators and parasites or, perhaps, asynchronous development of the beetle populations. Age specific mortality of C. asparagi is presented in the form of life tables (Tables 9-12).

4) Aphid populations on asparagus attracted large numbers of coccinellids which fed heavily on the eggs and young larvae of C. asparagi.

5) The larvae of C. asparagi are fed upon by several other insect predators associated with asparagus in western Massachusetts, principally Podisus maculiventris (Pentatomidae) and Nabis rufusculus (Nabidae).

6) A small second generation of Crioceris duodecimpunctata,

the 12-spotted asparagus beetle, was observed in 1972, but no evidence of a second generation of this insect was observed in the field during 1973.

7) Laboratory rearing of field-collected 12-spot beetle larvae indicated that a second generation of C. duodecimpunctata should have emerged in the field during 1973, but the field data did not indicate such emergence. Migration or subterranean predators may explain the absence of beetles from the observation sites, but we found no evidence to support these contentions. Fink (1913) reported two generations per year in New York.

8) C. duodecimpunctata seemed to escape significant predation and parasitism under the conditions of this study.

9) Availability of asparagus berries may be an important factor in C. duodecimpunctata population development.

10) The absence of important natural enemies of the 12-spotted asparagus beetle, Crioceris duodecimpunctata, indicates that (a) abundance of berries is the critical factor in C. duodecimpunctata population dynamics, and/or (b) an undiscovered predator/parasite/disease factor is important in determining abundance, and thereby determines economic importance as well.

11) Microbial pathogens and the tachinid, Paralispe infernalis, were not significant mortality factors in asparagus beetle biology in western Massachusetts under the conditions of this investigation.

12) Any program to control asparagus beetles, or other insects that become economically important on asparagus, should take into

consideration the bionomics of the insects, as partially illustrated by this manuscript. More importantly perhaps, any control program should be planned to minimize interference with the valuable predator/parasite, Tetrastichus asparagi.

13) Tetrastichus asparagi is a density-dependent mortality factor. It accounted for about 65% of the common asparagus beetle mortality found in this investigation.

14) Egg predation by T. asparagi accounted for about 50% of the C. asparagi mortality observed during this study, and about half of the larvae were found to be parasitized by T. asparagi.

15) T. asparagi deposits about five eggs in each parasitized host egg. Two to 12 parasites have been reared from single beetle hosts and 13 parasite larvae have been dissected from a single host larva.

16) The eggs of T. asparagi are not distributed randomly, as determined by comparison to a Poisson distribution.

17) The reason that so many host eggs remain unparasitized, while the parasitized eggs receive about five parasitoid eggs, may be related to an adaptive advantage associated with this degree of parasitism. That is, those parasitoids developing under the conditions described above may emerge at a particularly opportune time, at least from the standpoint of survival of the parasite.

18) Under laboratory conditions the adult parasite prefers to feed on recently-deposited common asparagus beetle eggs, but to parasitize eggs containing advanced embryos.

19) Under the conditions of the tests *T. asparagi* did not seem to avoid or seek either a trail odor or the contents of the host egg.

20) Reports that *Tetrastichus asparagi* parasitizes *C. duodecimpunctata* appear to be unfounded, and seem to be based on misinterpretation of the literature.

21) The common asparagus beetle predator/parasite *Tetrastichus asparagi* has three generations per year. The third generation does not appear to be the "exception instead of the rule", as Johnston (1915) hypothesized.

22) Some second generation *Tetrastichus* diapaused as full-grown larvae within the pupal cell of the host until the subsequent spring. Other parasite larvae did not diapause, but went on to produce the third generation. Nearly 37% of the 1973 second generation parasites diapaused.

23) With the exception of the egg stage, the developmental stages of *T. asparagi* are slightly longer than the corresponding developmental stages of the host *C. asparagi*.

24) Stated simply, the abundance, and hence the economic status, of the common asparagus beetle, *Crioceris asparagi*, apparently is determined largely by the activity of the eulophid predator/parasite *Tetrastichus asparagi*.

LITERATURE CITED

Askew, R.R. 1971. Parasitic Insects. American Elsevier, New York. 316 p.

Baer, W. 1920. Tachinids as parasites of injurious insects. Their life history, economic importance, and systematic characters. Z. Angew. Entomol. 6: 185-246. Original not seen; abstract in Rev. Appl. Entomol. (A) 9: 61-3.

Balduf, W.V. 1935. Bionomics of Entomophagous Coleoptera. J.S. Swift Co., St. Louis, Mo. 220 p.

Beirne, B.P. 1971. Pest Insects of Annual Crop Plants in Canada. Entomol. Soc. Can. Mem. 78. 124 p.

Britton, W.E. 1902. Report of the Connecticut Agricultural Experiment Station. Rep. State Entomol. 2: 172-4.

1922. The asparagus beetles. Conn. Agr. Exp. Sta. Bull. 234: 171-5.

Burks, B.D. 1943. The North American parasitic wasps of the genus <u>Tetrastichus</u> - a contribution to biological control of insect pests. U.S. Nat. Mus., Proc. 93: 505-606.

Chevalier, L. 1924. Un manger de crioceres, le <u>Cerceris quinfasciata</u>, Rossi. Bull. Soc. Sci. Seine & Oise. 5: 77-80. Original not seen; abstract in Rev. Appl. Entomol. (A) 13: 399.

Chittenden, F.H. 1897. The asparagus beetles. USDA Yearb., 1896. 341-52.

1917. The asparagus beetles and their control. USDA Farmers' Bull. 837. 13 p.

Claus~n, C.P. 1954. The egg-larval host relationship among the parasitic Hymenoptera. Boll. del Lab. di Zool. Gen. Agr., Portici. 33: 119-33.

1956. Biological control of insect pests in the United States. USDA Tech. Bull. 1139. 151 p.

Couturier, A. 1938. Remarques sur la tendance au parasitisme de Meigenia mutabilis Fall. sur le doryphore (Leptinotarsa decemlineata Say). Rev. Path. Veg. 25: 195-210. Original not seen; abstract in Rev. Appl. Entomol. (A) 27: 194-5.

Crawford, J.C. 1909. Two new species of the genus Tetrastichus. Entomol. Soc. Wash., Proc. 2: 150.

DeBach, P. 1943. The importance of host-feeding by adult parasites in the reduction of host populations. J. Econ. Entomol. 36: 647-58.

Dingler, M. 1934. On our asparagus beetles (Crioceris duodecimpunctata L. and C. asparagi L.). Z. Angew. Entomol. 21: 415-42. Original not seen; abstract in Rev. Appl. Entomol. (A) 23: 138-9.

Felt, E.P. 1901. Sixteenth report of the state entomologist. N.Y. State Mus. Bull. 36: 952-1063.

Fernald, H.T. 1909. A parasite of the asparagus beetle. Mass. Agr. Exp. Sta. Cir. 23. 1 p.

Fink, D.E. 1913. The asparagus miner and the twelve-spotted beetle. N.Y. (Cornell) Agr. Exp. Sta. Bull. 331: 410-35.

Fitch, A. 1862. The asparagus beetle. Country Gentleman 20: 81-2.

Ganesalingam, V.K. 1972. Anatomy and histology of the sense organs of the ovipositor of the ichneumonid wasp Devorgilla canescens. J. Insect Physiol. 18: 1857-67.

Gersdorff, W.A., and E.R. McGovran. 1945. Insecticide toxicity studies. Experimental results on the comparative toxicity of benzene hexachloride, DDT, and pyrethrum. Soap and Sanit. Chem. 21: 117, 121.

Grahm, M.W.R. de V. 1961. The genus Aprostocetus Westwood, sensu lato (Hymenoptera, Eulophidae); Notes of the synonomy of European species. Ent. Monthly Mag. 97: 34-64.

Hassell, M.P. 1971. Mutual interference between searching insect parasites. J. Anim. Ecol. 40: 473-86.

Huckett, H.C. 1937. The asparagus beetle. N.Y. (Geneva) Agr. Exp. Sta. Cir. 171. 4 p.

Hunter, B.T. 1971. Gardening without Poisons. Houghton-Mifflin Co., Boston. 318 p.

Hutt, W.N. Asparagus beetles. Entomol. Soc. Ont. Annu. Rep. 10: 71-3.

Johansen, C.A. 1957. History of biological control of insects in Washington. Northwest Sci. 31: 57-79.

Johnston, F.A. 1915. Asparagus-beetle egg parasite. J. Agr. Res. 4: 303-13.

Jones, H.A. and W.W. Robbins. 1928. The asparagus industry in California. Cal. Agr. Exp. Sta. Bull. 446: 3-105.

Jones, F.M. 1932. Insect coloration and the relative acceptability of insects to birds. Entomol. Soc. Lond., Trans. 80: 345-86.

King, P.E. and J. Rafai. 1970. Host discrimination in a gregarious parasitoid Nasonia vitripennis (Walker) (Hymenoptera: Pteromalidae). J. Exp. Biol. 53: 245-54.

Landis, B.J. 1937. Insect host and nymphal development of <u>Podisus maculiventris</u> Say and <u>Perillus biculatus</u> F. (Hemiptera, Pentatomidae). Ohio J. Sci. 37: 252-9.

Latta, R. 1928. The effect of the extreme temperature of Dec. 7, 8, and 9, 1927 on hibernating <u>Crioceris asparagi</u> L. and <u>Hippodamia convergens</u> Guer. at Ames, Iowa. Psyche 35: 229-31.

Lecaillon. 1917. Observations on <u>Meigenia floralis</u>, a Dipterous parasite of the Lucerne "Negril" (<u>Colaspidema atrum</u>) in France. Monthly Bull. Agr. Intell. & Plant. Dis. 8: 1299-1300. Original not seen; abstract in Rev. Appl. Entomol. (A) 6: 171.

Lintner, J.A. 1882. First annual report of the state entomologist. N.Y. Sen. Doc. 93: 239-46.

1893. Eighth annual report of the state entomologist. N.Y. State Mus. Rep. 45: 250-3.

Metcalf, C.L., W.P. Flint, and R.L. Metcalf. 1962. Destructive and Useful Insects. 4th ed. McGtaw-Hill, N.Y. 1087 p.

Ormerod, E.A. 1897. Report of Observations of Injurious Insects and Common Farm Pests. Simpkin, Marshall, Hamilton, Kent and Co., London. 160 p.

Peck, O. 1963. A Catalogue of the Nearctic Chalcidoidea (Insecta: Hymenoptera). Can. Entomol. Supp. 30. 1092 p.

Price, P.W. 1972. Behavior of the parasitoid <u>Pleolophus basizonus</u> (Hymenoptera: Ichneumonidae) in response to changes in host and parasitoid density. Can. Entomol. 104: 129-40.

Riley, C.V. and B.D. Walsh. 1869. The asparagus beetle. Amer. Entomol. 1: 114-5.

Ruffo, S. 1938. Studi sui Crisomelidi (Insecta: Coleoptera). Boll. Inst. Entomol. Bologna 10: 178-222. Original not seen; abstract in Rev. Appl. Entomol. (A) 27: 471-2.

Salt, G. 1937. The sense used by Trichogramma to distinguish between parasitized and unparasitized hosts. Roy. Soc. Lond., Proc. (B) 122: 57-75.

Sanderson, E.D. 1899. A destroyer of asparagus beetles. Amer. Gardening 20: 349.

Stone, A., C.W. Sabrosky, W.W. Wirth, R.H. Foote, and J.R. Coulson. 1965. A Catalogue of the Diptera of America North of Mexico. USDA Agr. Handb. 276. 1696 p.

Strong, L.A. 1940. Report of the Chief of the Bureau of Entomology and Plant Quarantine, 1938-39. USDA, Washington, D.C. 117 p.

1941. Report of the Chief of the Bureau of Entomology and Plant Quarantine, 1939-40. USDA, Washington, D.C. 128 p.

Thompson, W.R. 1943. A Catalogue of the Parasites and Predators of Insect Pests. Parasite Host Catalogue. 1: 36-7.

Thompson, W.R. and F.J. Simmonds. 1964. A Catalogue of the Parasites and Predators of Insect Pests. Predator Host Catalogue. 3: 13.

Vinson, S.B. and F.S. Guillot. 1972. Host marking: source of a substance that results in host discrimination in insect parasitoids. Entomophaga 17: 241-5.

Watts, J.G. 1938. Insect control studies. S.C. Agr. Exp. Sta. Rep. 51: 190-2.

1939. Insect control investigations. S.C. Agr. Exp. Sta. Rep. 52: 193-4.

Westcott, C. 1964. The Gardener's Bug Book. Doubleday, Garden City, N.Y. 625 p.

Wilson, H.F. and R.L. Janes. 1942. Lower concentrations of rotenone. Soap 18: 93-5, 117.

APPENDIX: TABLES AND FIGURES

Table 1. - Numbers of eggs, larvae, and adults of the common asparagus beetle, *Crioceris asparagi*, per 10 plants (average of three replicates) in western Massachusetts, 1972.

Week of observation	*C. asparagi* eggs	*C. asparagi* larvae	*C. asparagi* adults
MAY 14	0	0	0
21	12.7	0	7.7
28	90.0	1.0	5.5
JUNE 4	66.0	11.0	6.3
11	65.7	4.7	5.3
18	59.7	32.0	3.3
25	62.7	15.7	3.3
JULY 2	39.0	35.3	7.3
9	67.7	50.3	14.0
16	99.9	12.3	11.3
23	53.7	29.3	1.3
30	51.5	16.0	1.0
AUG. 6	7.5	7.5	0
13	15.5	1.5	2.5
20	0	5.0	4.5
27	0	2.0	3.0
SEPT. 3	0	3.0	0.5
10	-	-	-
17	0	4.0	0
24	0	1.0	0

Table 2. - Numbers of eggs, larvae, and adults of the common asparagus beetle, *Crioceris asparagi*, per 10 plants (average of three replicates) in western Massachusetts, 1973.

Week of observation	*C. asparagi* eggs	*C. asparagi* larvae	*C. asparagi* adults
MAY 13	0	0	0
20	18.5	0	8.0
27	27.3	0	7.7
JUNE 3	204.7	2.0	18.0
10	139.6	75.7	6.0
17	148.0	63.7	7.7
24	89.0	52.0	11.7
JULY 1	98.3	43.0	7.7
8	108.0	49.7	16.7
15	48.0	33.3	1.7
22	9.0	12.7	1.3
29	14.6	3.7	1.7
AUG. 5	8.0	2.7	2.3
12	1.0	2.3	2.0
19	3.3	1.0	0.7
26	1.0	0.3	0

Table 3. - Numbers of adult 12-spotted asparagus beetles, *Crioceris duodecimpunctata*; coccinellids; and aphids, per 10 plants (average of three replicates) in western Massachusetts, 1972.

Week of observation	*C. duodecimpunctata*	Aphididae[a]	Coccinellidae[b]
MAY 14	0	0	0
21	18.0	0	0
28	94.0	7.0	0
JUNE 4	64.0	0	0
11	36.3	37.0	0.7
18	27.3	37.5	0.3
25	20.0	92.0	0
JULY 2	12.6	126.5	1.0
9	11.7	131.0	1.0
16	19.6	7.5	1.7
23	4.6	2.0	2.0
30	0	10.0	5.0
AUG. 6	0.5	3.0	4.0
13	1.0	5.0	13.0
20	0.5	21.0	6.0
27	2.0	0	8.0
SEPT. 3	1.5	10.0	6.0
10	-	-	-
17	0.5	1.0	3.0
24	0	0	1.0

[a]Primarily *Aphis craccivora* Koch.
[b]Primarily *Coccinella novemnotata* Herbst, *C. transversoguttata* Falderman, *Hippodamia convergens* Guerin, and *Coleomegilla maculata* Mulsant.

Table 4. - Numbers of adult 12-spotted asparagus beetles, *Crioceris duodecimpunctata*; coccinellids; and aphid-infested asparagus plants, per 10 plants (average of three replicates) in western Massachusetts, 1973.

Week of observation	*C. duodecimpunctata*	Aphid-infested plants[a]	Coccinellidae[b]
MAY 13	0	0	0
20	6.5	0	0
27	15.7	0	0.3
JUNE 3	24.3	0.7	2.0
10	7.6	1.0	0
17	5.7	0.7	0
24	3.0	0.7	1.0
JULY 1	2.7	0.7	0.3
8	1.0	1.0	0.3
15	1.3	1.0	0.7
22	0.3	4.0	6.0
29	0.3	4.7	12.3
AUG. 5	0	7.0	8.7
12	0.3	3.3	2.0
19	0	1.3	1.3
26	0.7	2.0	2.7

[a]Infested primarily by *Brachycolus asparagi* Mordvilke.
[b]Primarily *Coccinella novemnotata* Herbst, *C. transversoguttata* Falderman, and *Coleomegilla maculata* Mulsant.

Table 5. - Numbers of *Tetrastichus asparagi* per 10 plants (average of three replicates) in western Massachusetts; percent parasitism of *Crioceris asparagi*; and percent predation of *C. asparagi* eggs by *T. asparagi* and several coccinellid species, 1972.

Week of observation	*T. asparagi*	Parasitism (%)	Predation (%)
MAY 14	0	-	0
21	0	-	0
28	12.5	76.9	52.2
JUNE 4	1.0	60.0	40.1
11	0.3	36.3	16.2
18	0	0	39.9
25	0.6	33.3	23.3
JULY 2	3.0	71.0	54.6
9	6.3	-	69.9
16	2.6	38.0	43.3
23	2.0	62.5	72.0
30	1.5	57.1	61.6
AUG. 6	2.0	-	58.5
13	0	-	100.0
20	3.5	-	0
27	0	-	0
SEPT. 3	0	-	0
10	-	-	-
17	2.0	-	-
24	1.0	-	-

Table 6. - Numbers of Tetrastichus asparagi per 10 plants (average of three replicates) in western Massachusetts; percent parasitism of Crioceris asparagi; and percent predation of C. asparagi eggs by T. asparagi and several coccinellid species, 1973.

Week of observation	T. asparagi	Parasitism (%)	Predation (%)
MAY 13	0	-	-
20	6.0	-	45.9
27	8.0	-	45.1
JUNE 3	18.7	62.5	41.2
10	0	30.3	64.9
17	0.7	18.1	56.0
24	1.7	3.5	43.0
JULY 1	4.3	75.0	48.4
8	3.0	85.7	55.5
15	1.3	79.1	64.5
22	0.3	28.5	37.0
29	3.0	-	56.8
AUG. 5	1.0	-	66.6
12	0	-	-
19	0	-	-
26	0	-	-

Table 7. - Frequency of the wasp parasite *Tetrastichus asparagi* in its host, the common asparagus beetle, *Crioceris asparagi*, 1972.

No. parasites per host	Observed	Expected from Poisson Distribution
11	1	0.001
10	0	0.007
9	2	0.037
8	4	0.160
7	4	0.612
6	9	2.050
5	13	5.885
4	12	14.073
3	7	26.922
2	11	38.628
1	0	36.948
0	80	17.671

Table 8. - Emergence times of the parasite *Tetrastichus asparagi* and its beetle host *Crioceris asparagi*, 1972.

Length of pupation of *Crioceris asparagi* (Days)	No. insects emerging: *Tetrastichus asparagi*[a]	No. insects emerging: *Crioceris asparagi*
10	0	0
11	0	1
12	0	15
13	0	19
14	0	15
15	7.5	8
16	5.0	7
17	3.7	6
18	5.0	2
19	5.5	3
20	5.0	0
21	4.0	0
22	5.0	0
23	0	0
24	0	0

[a]Mean number wasps emerging.

Table 9. - Life table for first generation of *Crioceris asparagi*, 1972.

Age interval	No. per 10 plants	Causative factors	Mortality: Per 10 plants	Apparent (%)	Real (%)
EGGS	294.1	predation[a]	108.8	37.0	37.0
		other[b]	118.9	40.4	40.4
LARVAE	66.4	parasitism by			
		T. asparagi	27.4	41.3	9.3
		other[c]	16.1	24.2	5.5
PUPAE	22.9	pupal mortality[d]	8.9	38.8	3.1
ADULTS	14.0				
GENERATION TOTALS			280.1	95.3	95.3

[a]almost entirely by *Tetrastichus asparagi*
[b]some of this mortality probably occurred in early larval period
[c]much of this was probably due to predation
[d]determined in the laboratory

Table 10. - Life table for second generation of *Crioceris asparagi*, 1972.

Age interval	No. per 10 plants	Mortality: Causative factors	Mortality: Per 10 plants	Mortality: Apparent (%)	Mortality: Real (%)
EGGS	382.0	predation[a]	206.6	54.1	54.1
		other[b]	23.2	6.0	6.0
LARVAE	152.2	parasitism by *T. asparagi*	79.9	52.5	21.0
		other[c]	56.9	37.5	14.9
PUPAE	15.4	pupal mortality[d]	10.9	70.8	2.9
ADULTS	4.5				
GENERATION TOTALS			377.5	98.9	98.9
TREND INDEX[e], 1.3					

[a] primarily by *Tetrastichus asparagi*, but coccinellid predation was significant in the later part of the generation

[b] some of this mortality probably occurred in early larval period

[c] mostly predation, especially by coccinellids

[d] determined in the laboratory

[e] trend index = $\frac{\text{eggs laid in new generation}}{\text{eggs laid in old generation}}$

Table 11. - Life table for first generation of *Crioceris asparagi*, 1973.

Age interval	No. per 10 plants	Causative factors	Mortality Per 10 plants	Apparent (%)	Real (%)
EGGS	390.1	predation[a]	192.2	49.3	49.3
		other[b]	56.5	14.5	14.5
LARVAE	141.4	parasitism by			
		T. asparagi	52.1	36.9	13.4
		other[c]	53.6	37.5	13.7
PUPAE	35.7	pupal mortality[d]	19.0	53.2	4.9
ADULTS	16.7				
GENERATION TOTALS			373.4	95.8	95.8
TREND INDEX[e], 1.0					

[a] almost entirely by *Tetrastichus asparagi*
[b] some of this mortality probably occurred in early larval period
[c] much of this was probably due to predation
[d] based on 1972 laboratory data
[e] trend index = $\frac{\text{eggs laid in new generation}}{\text{eggs laid in old generation}}$

Table 12. - Life table for second generation of *Crioceris asparagi*, 1973.

Age interval	No. per 10 plants	Causative factors	Mortality Per 10 plants	Mortality Apparent (%)	Mortality Real (%)
EGGS	500.3	predation[a]	253.5	50.7	50.7
		other[b]	52.4	10.5	10.5
LARVAE	194.4	parasitism by *T. asparagi*	105.3	54.3	21.0
		other[c]	73.8	38.1	14.8
PUPAE	15.3	pupal mortality[d]	13.0	84.9	2.6
ADULTS	2.3				
GENERATION TOTALS			498.0	99.6	99.6
TREND INDEX[e], 1.2					

[a]primarily by *Tetrastichus asparagi*, but coccinellid predation was significant in the later part of the generation
[b]some of this mortality probably occurred in early larval period
[c]mostly predation, especially by coccinellids
[d]based on 1972 laboratory data
[e]trend index = $\frac{\text{eggs laid in new generation}}{\text{eggs laid in old generation}}$

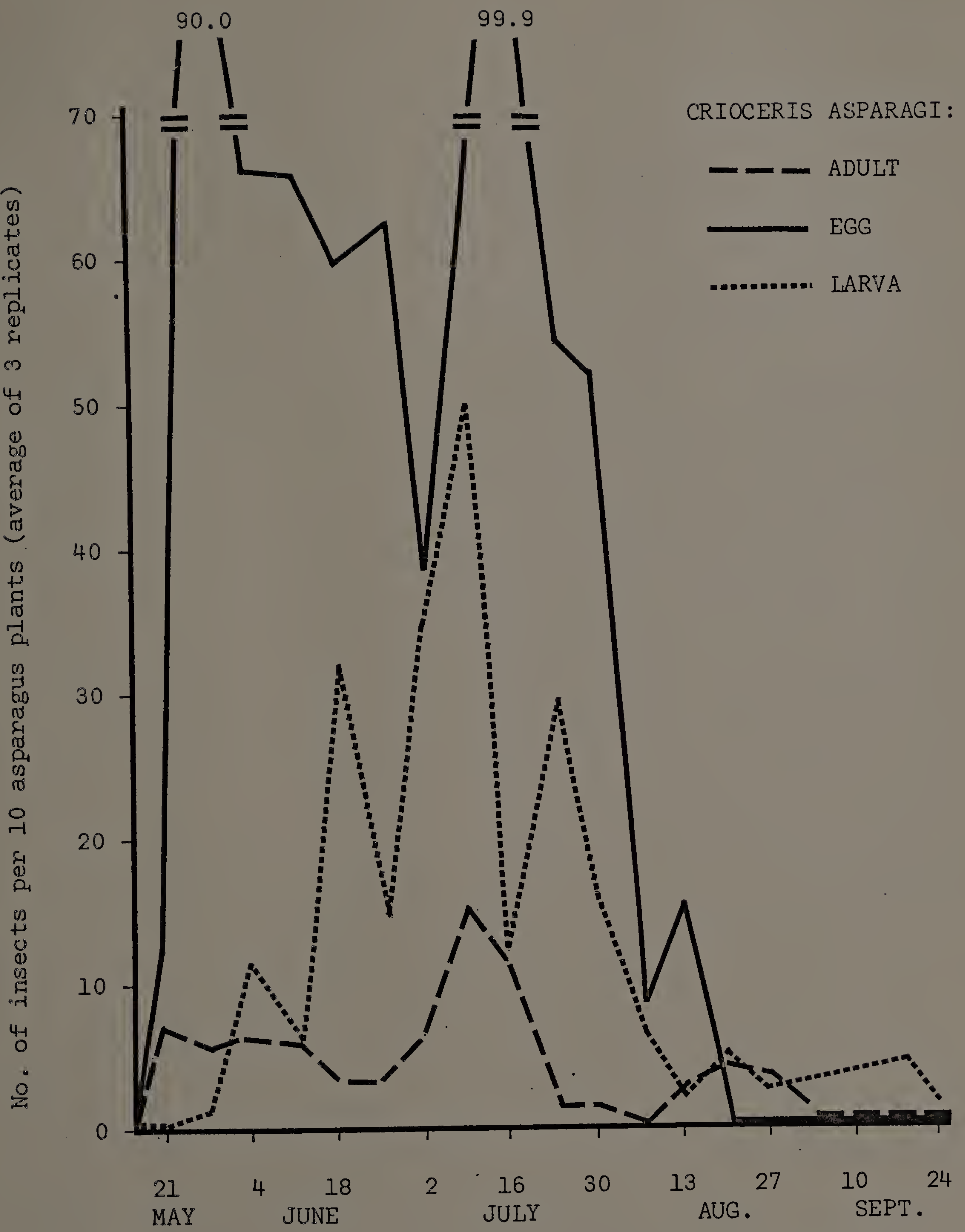


Fig. 1. - Numbers of eggs, larvae, and adults of the common asparagus beetle, Crioceris asparagi, in western Massachusetts, 1972.

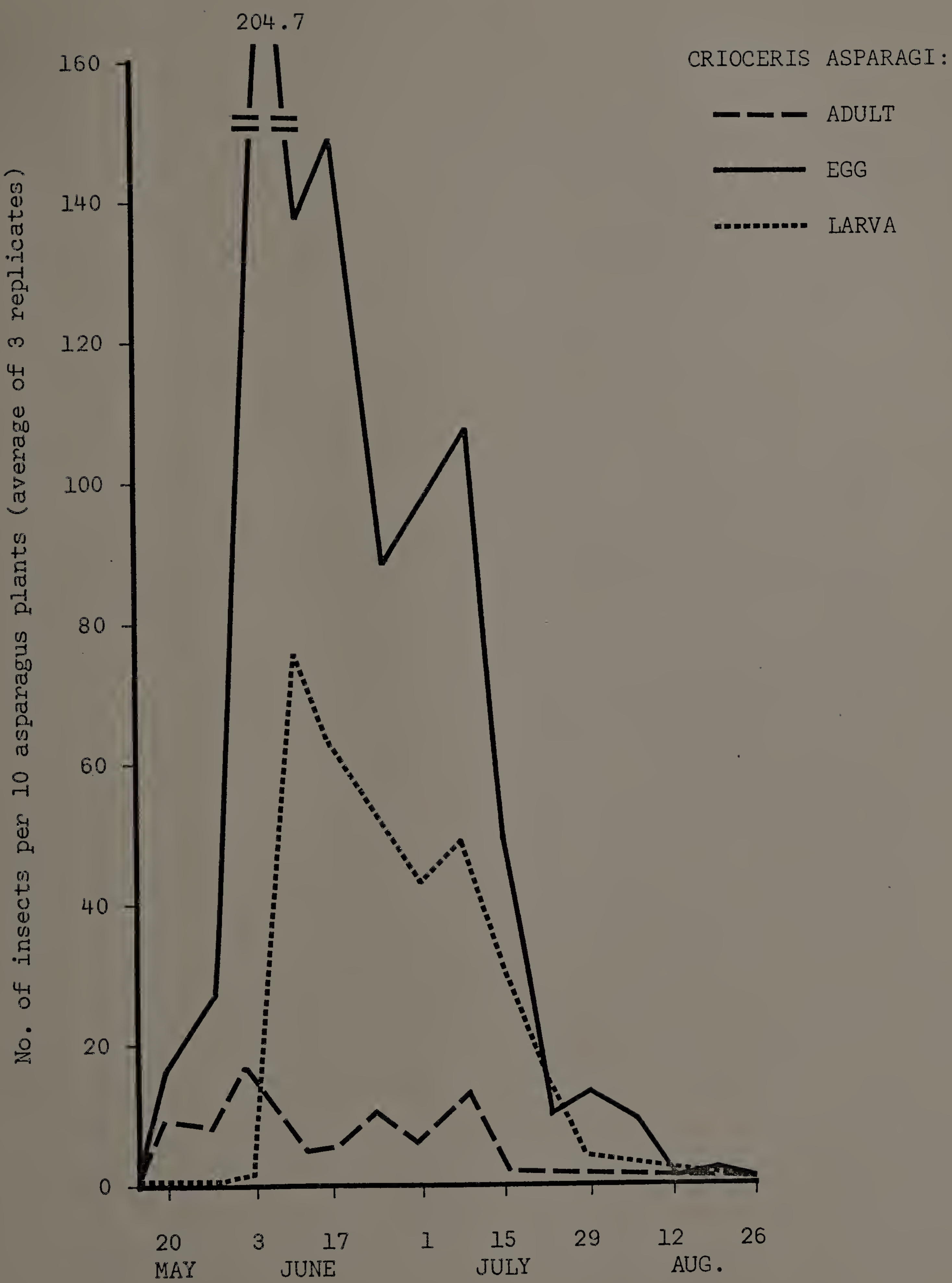


Fig. 2. - Numbers of eggs, larvae, and adults of the common asparagus beetle, *Crioceris asparagi*, in western Massachusetts, 1973.

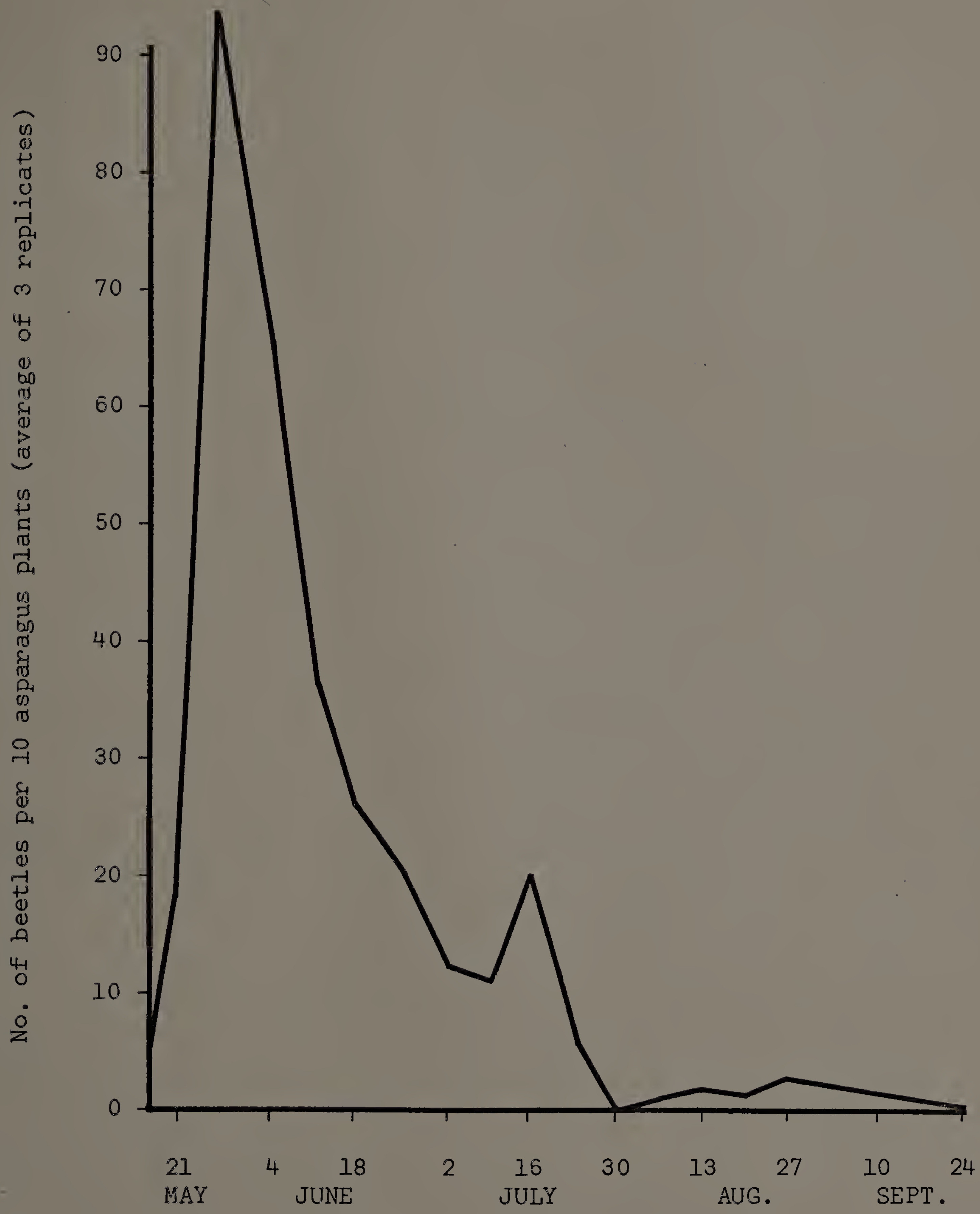


Fig. 3. - Numbers of adult 12-spot asparagus beetles, *Crioceris duodecimpunctata*, in western Massachusetts, 1972.

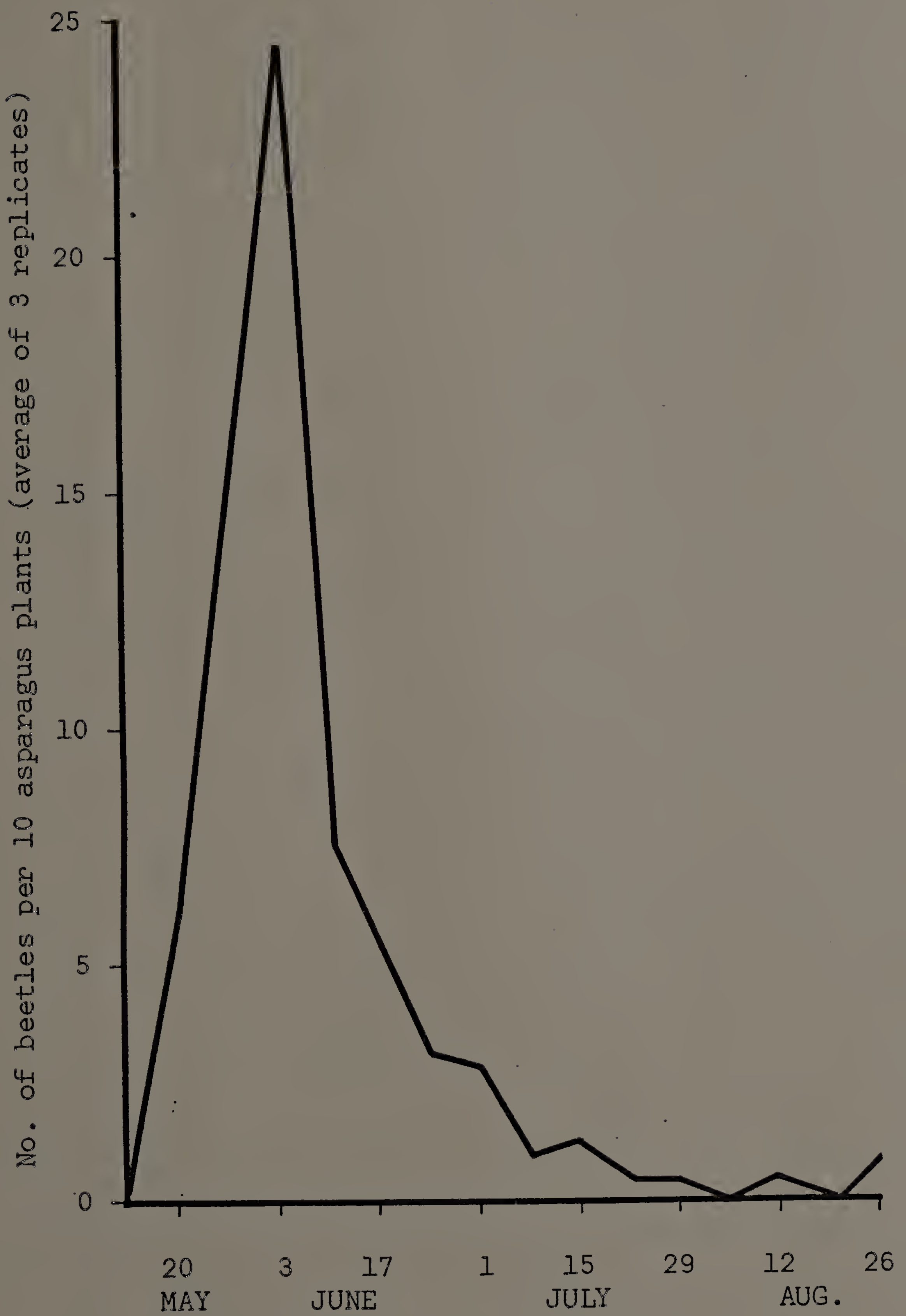


Fig. 4. - Numbers of adult 12-spot asparagus beetles, *Crioceris duodecimpunctata*, in western Massachusetts, 1973.

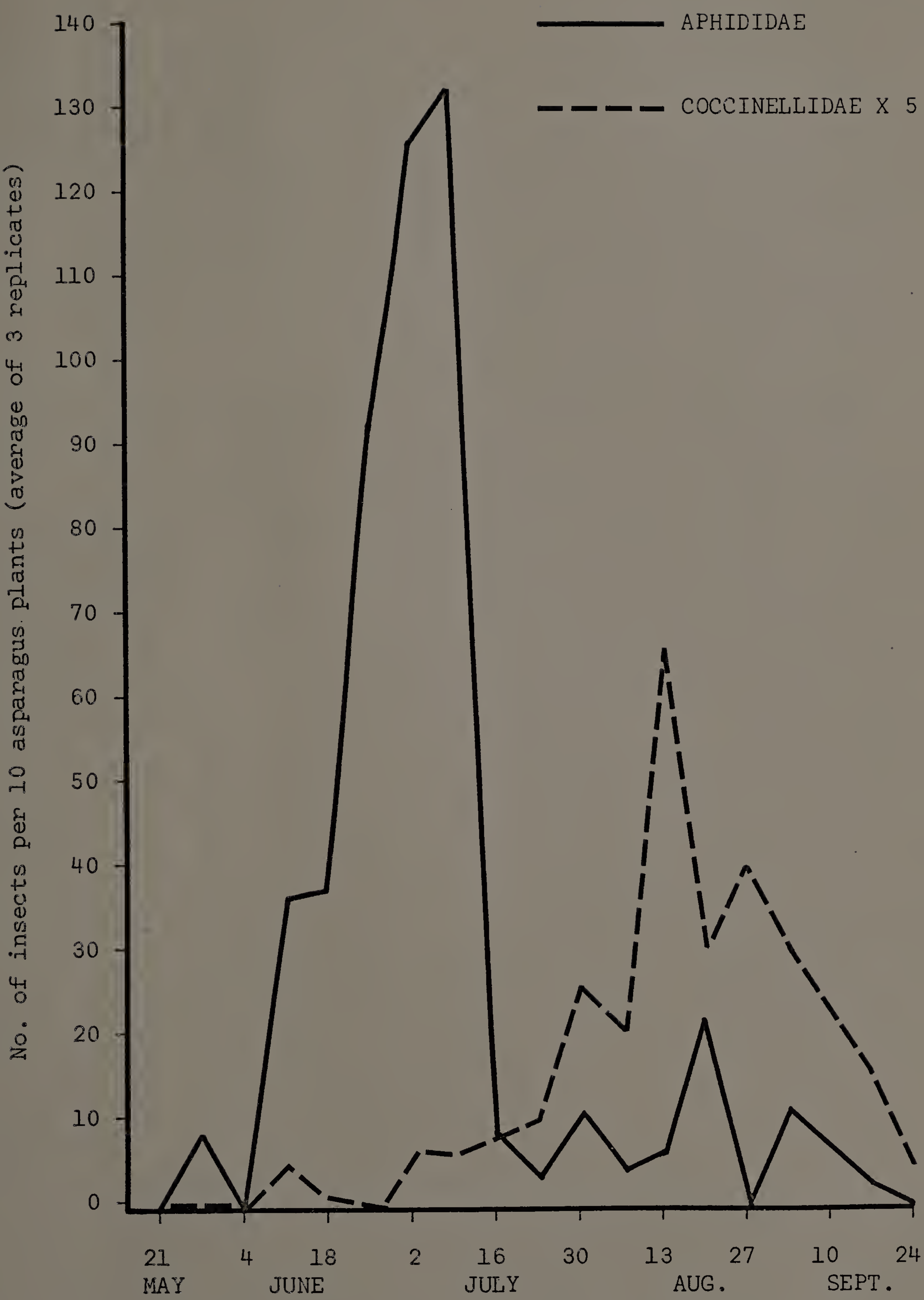


Fig. 5. - Numbers of coccinellid predators and aphid prey in western Massachusetts, 1972.

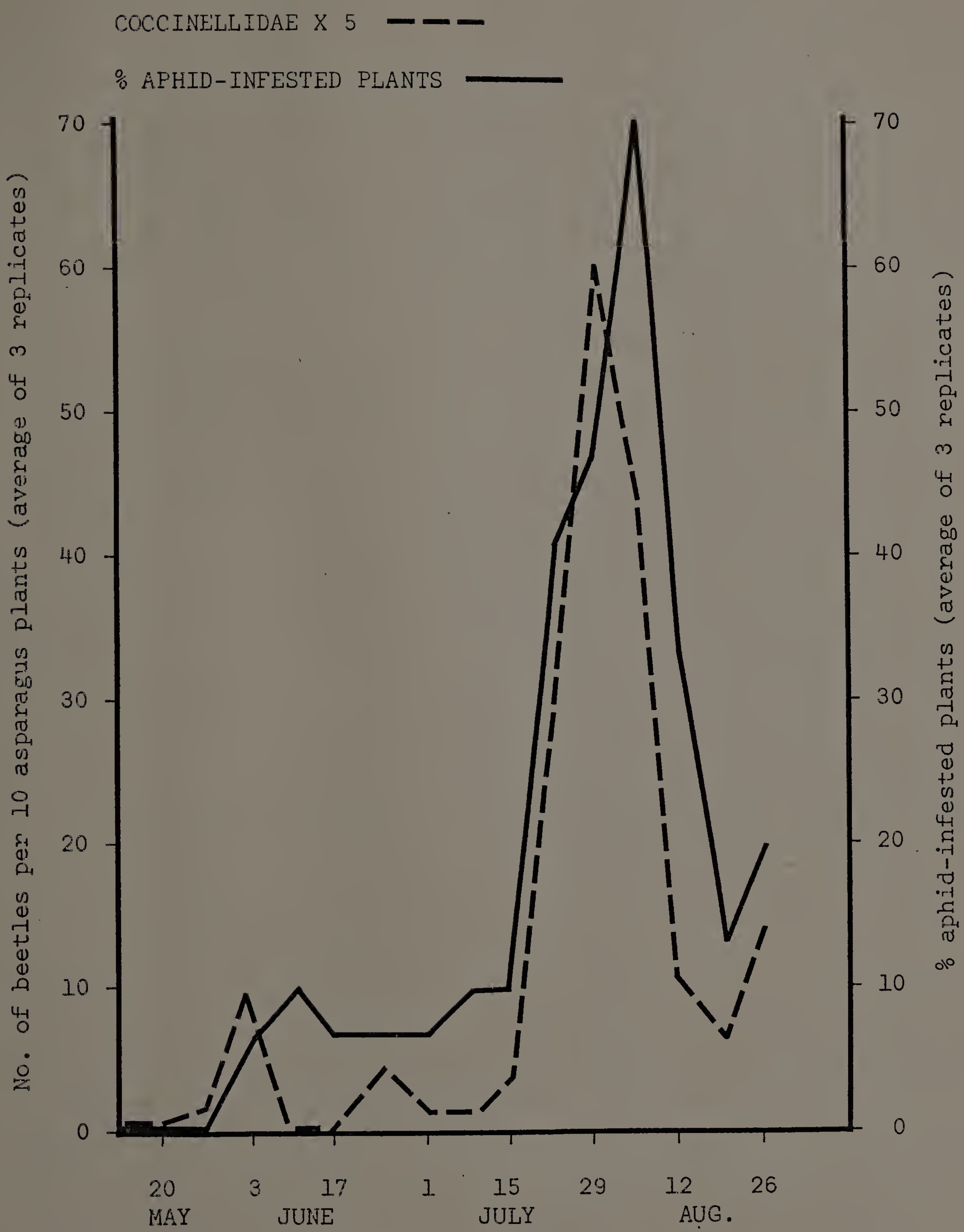


Fig. 6. - Numbers of coccinellid predators and percent aphid-infested asparagus plants in western Massachusetts, 1973.

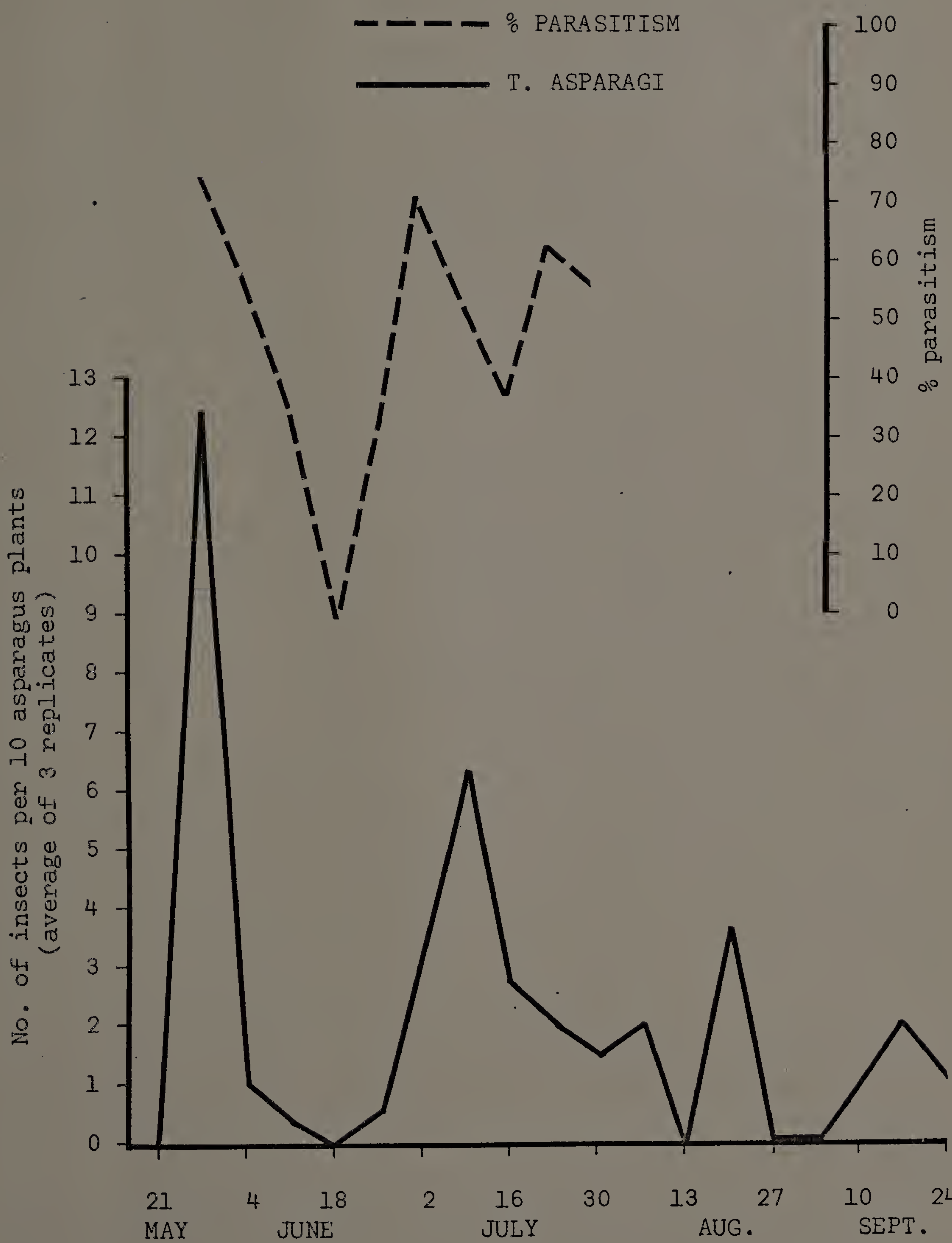
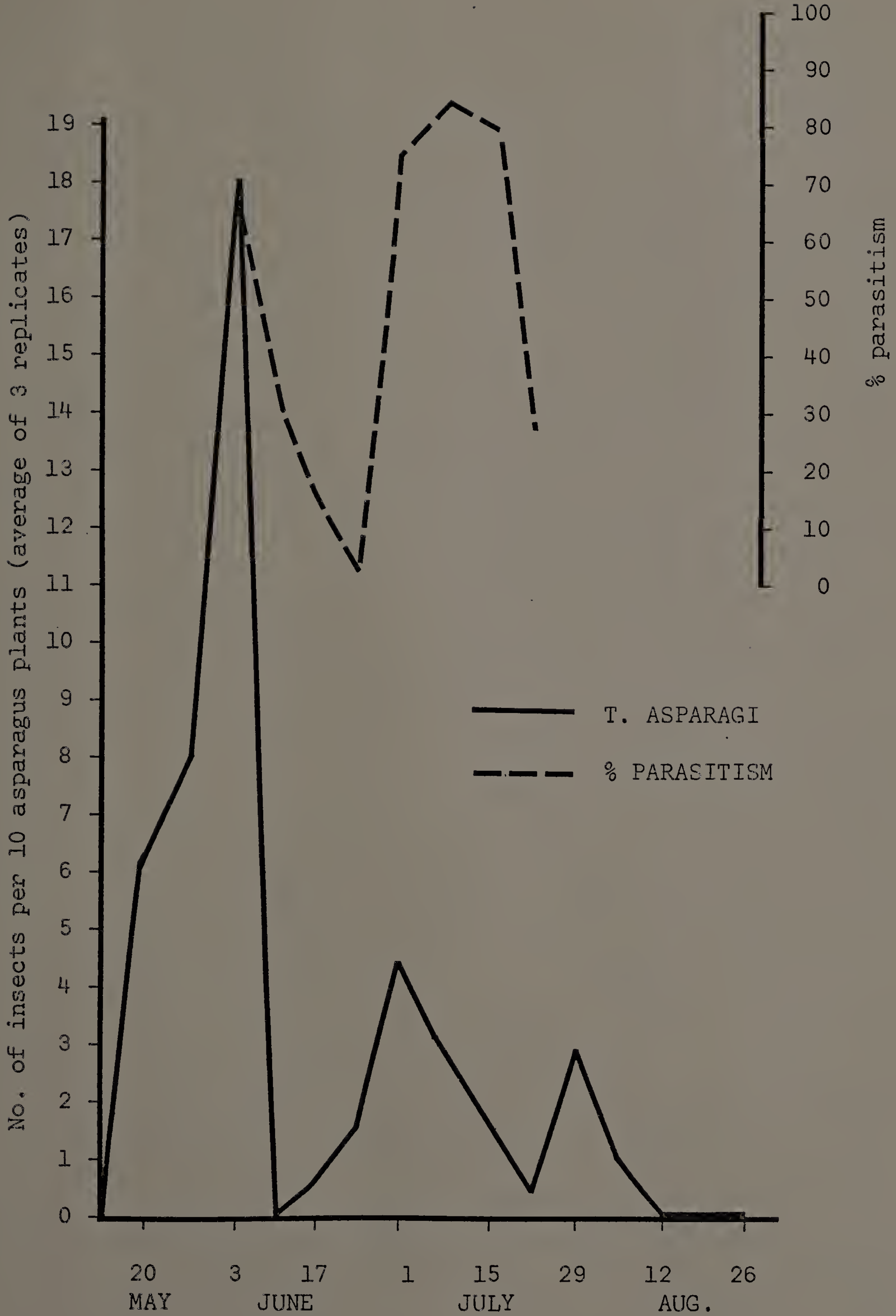


Fig. 7. - Percent parasitism of the common asparagus beetle, Crioceris asparagi, and numbers of its primary parasite, Tetrastichus asparagi, in western Massachusetts, 1972.

Fig. 8. - Percent parasitism of the common asparagus beetle, *Crioceris asparagi*, and numbers of its primary parasite, *Tetrastichus asparagi*, in western Massachusetts, 1973.



No. of insects per 10 asparagus plants (average of 3 replicates)
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19
% parasitism
0 10 20 30 40 50 60 70 80 90 100
T. ASPARAGI
% PARASITISM
20 3 17 1 15 29 12 26
MAY JUNE JULY AUG.

Fig. 9. - Numbers of *Crioceris asparagi* eggs and numbers of egg predators in western Massachusetts, 1972.

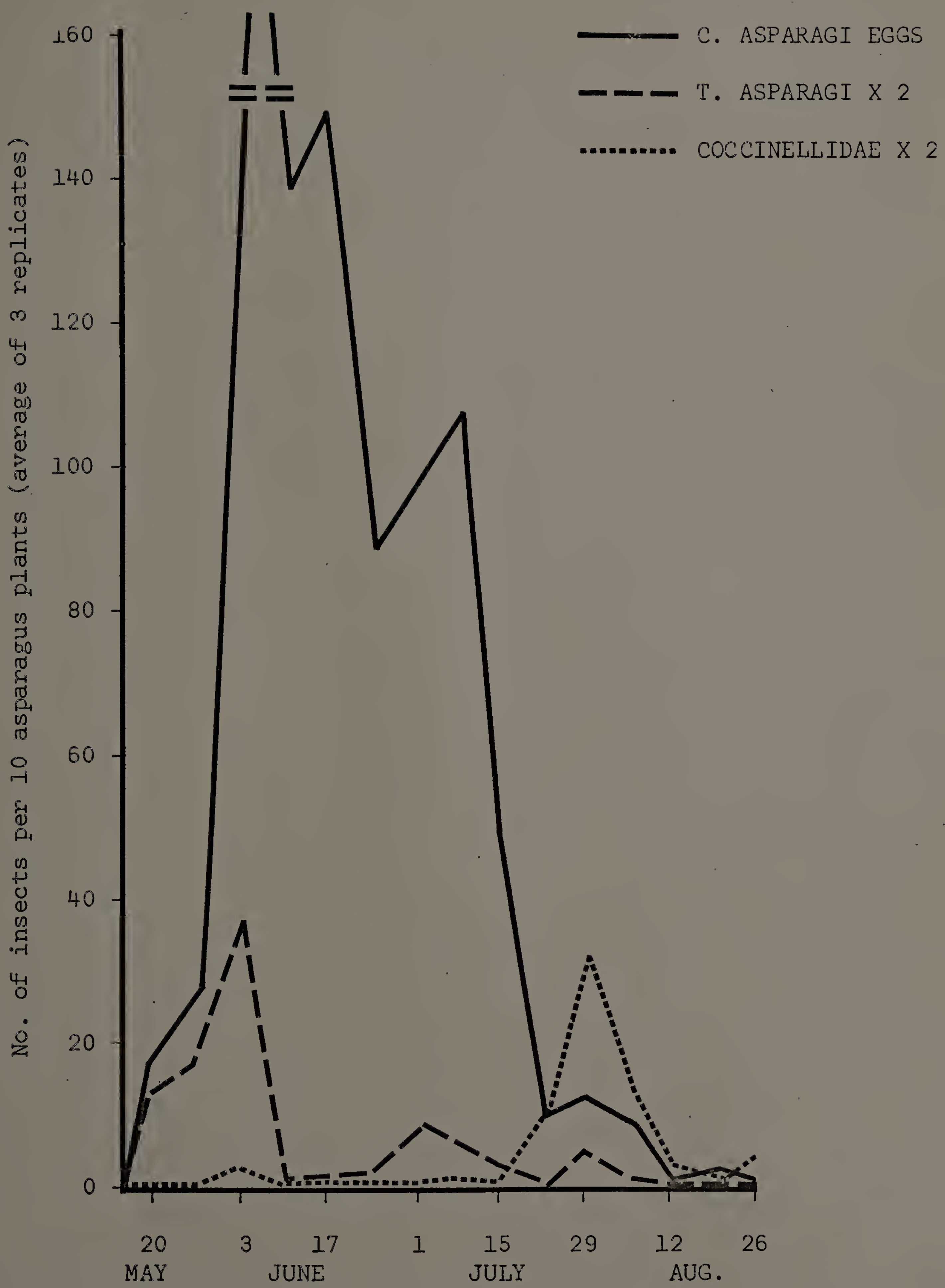


Fig. 10. - Numbers of Crioceris asparagi eggs and numbers of egg predators in western Massachusetts, 1973.

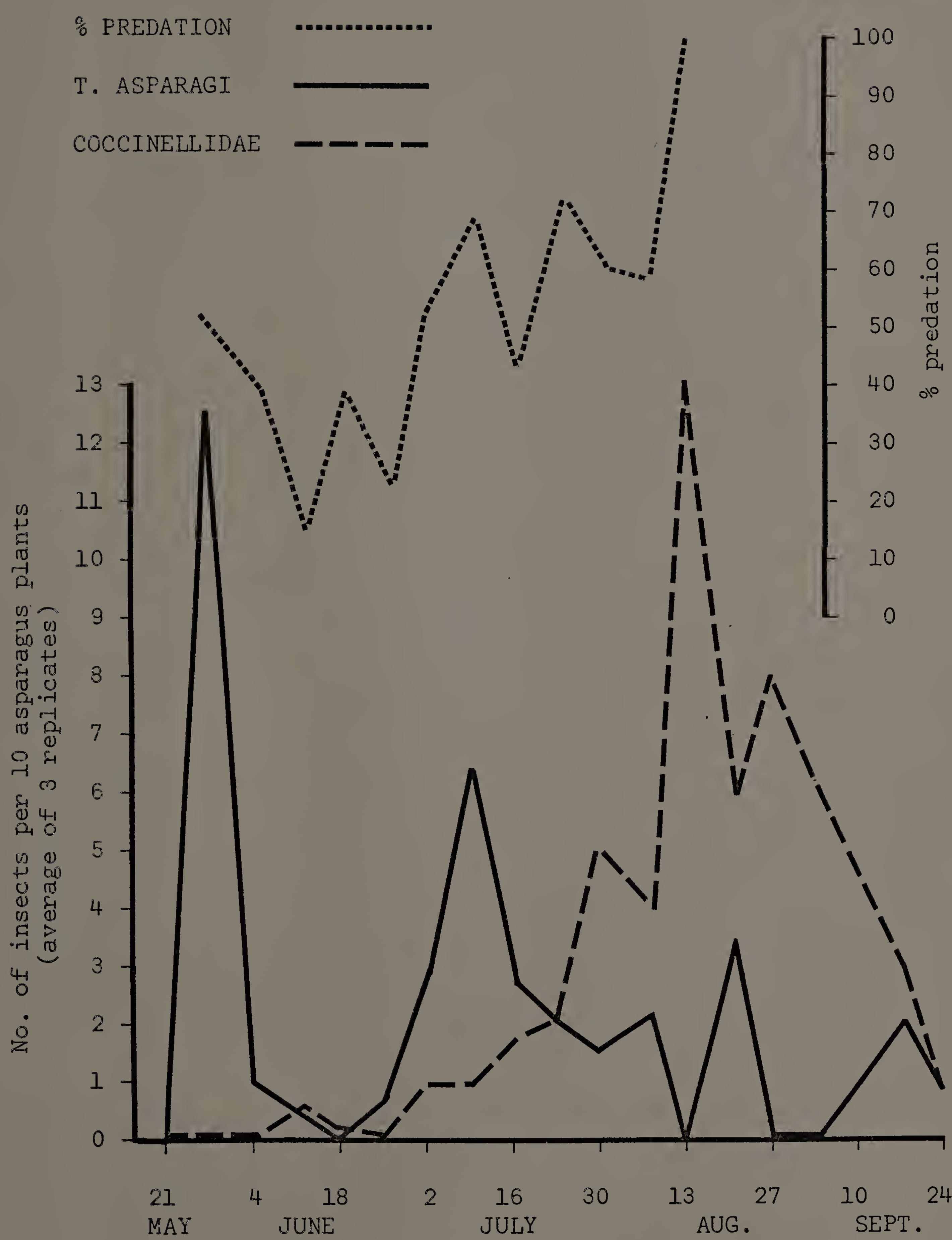
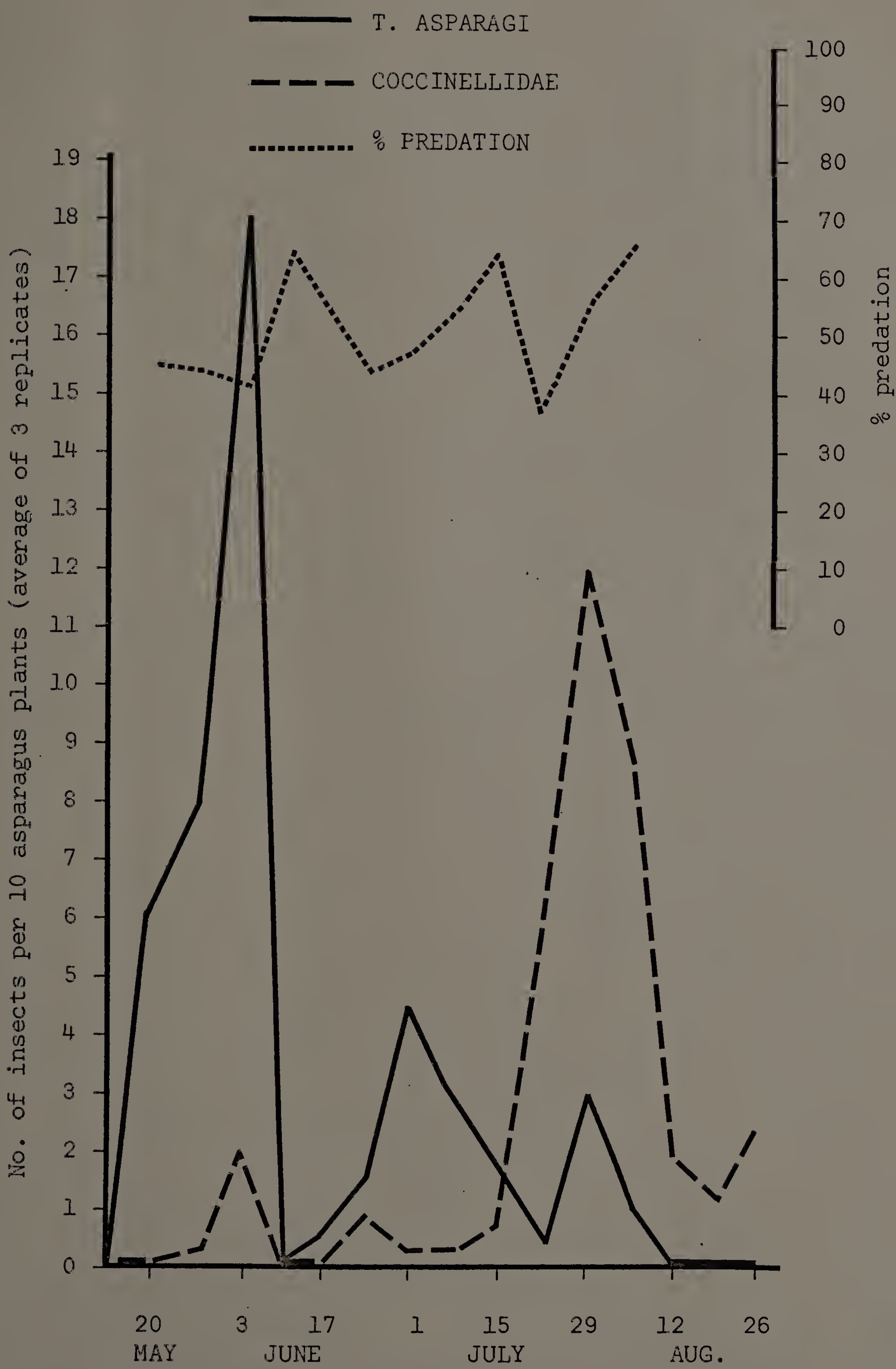


Fig. 11. - Percent predation of common asparagus beetle eggs and numbers of egg predators (adult Tetrastichus asparagi and coccinellid spp.) in western Massachusetts, 1972.

Fig. 12. - Percent predation of common asparagus beetle eggs and numbers of egg predators (adult *Tetrastichus asparagi* and coccinellid spp.) in western Massachusetts, 1973.



T. ASPARAGI
COCCINELLIDAE
% PREDATION
No. of insects per 10 asparagus plants (average of 3 replicates)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
% predation
0
10
20
30
40
50
60
70
80
90
100
20
3
17
1
15
29
12
26
MAY
JUNE
JULY
AUG.

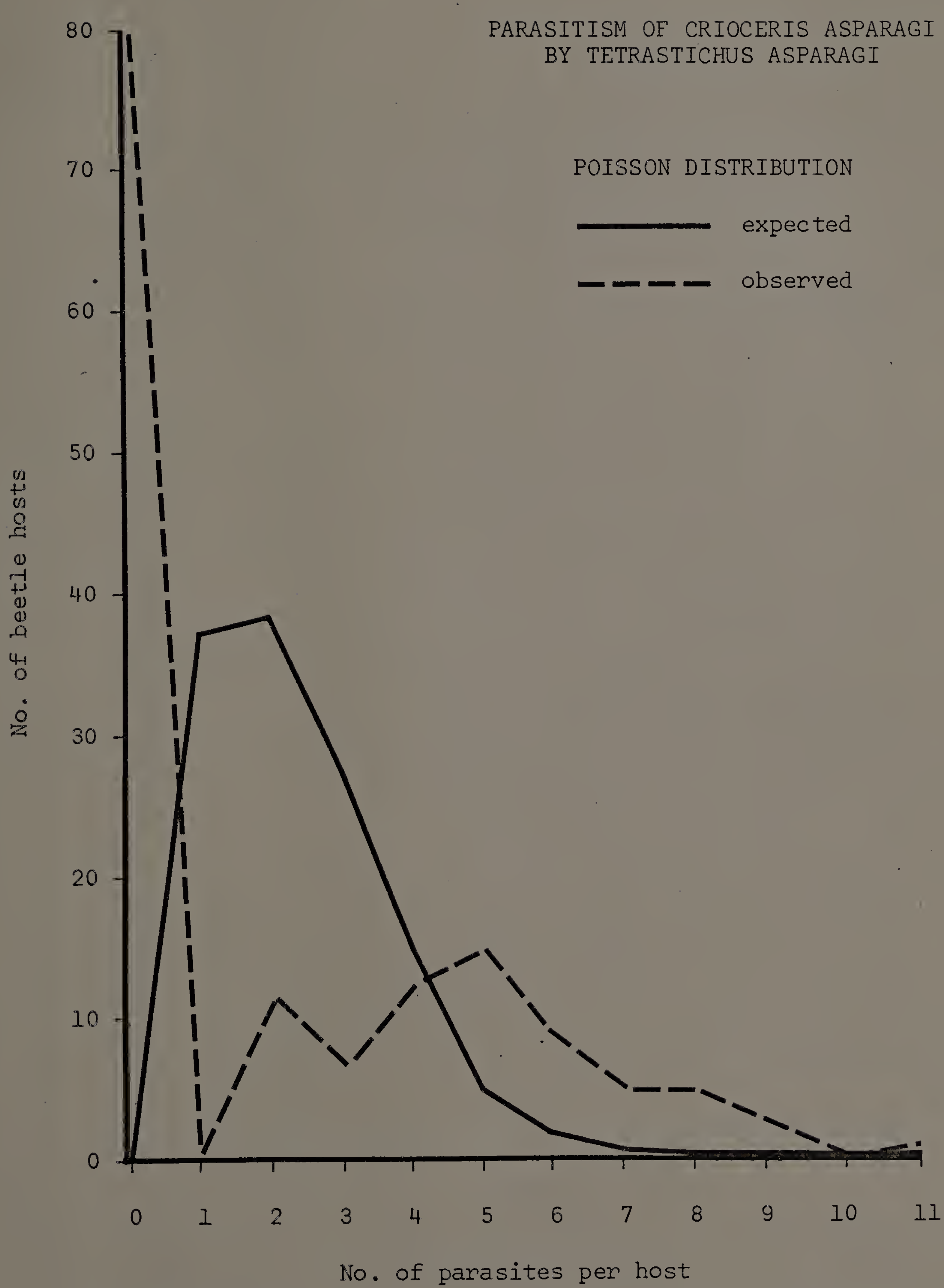


Fig. 13. - Parasitism of the common asparagus beetle, _Crioceris asparagi_, by the eulophid parasite, _Tetrastichus asparagi_, 1972.

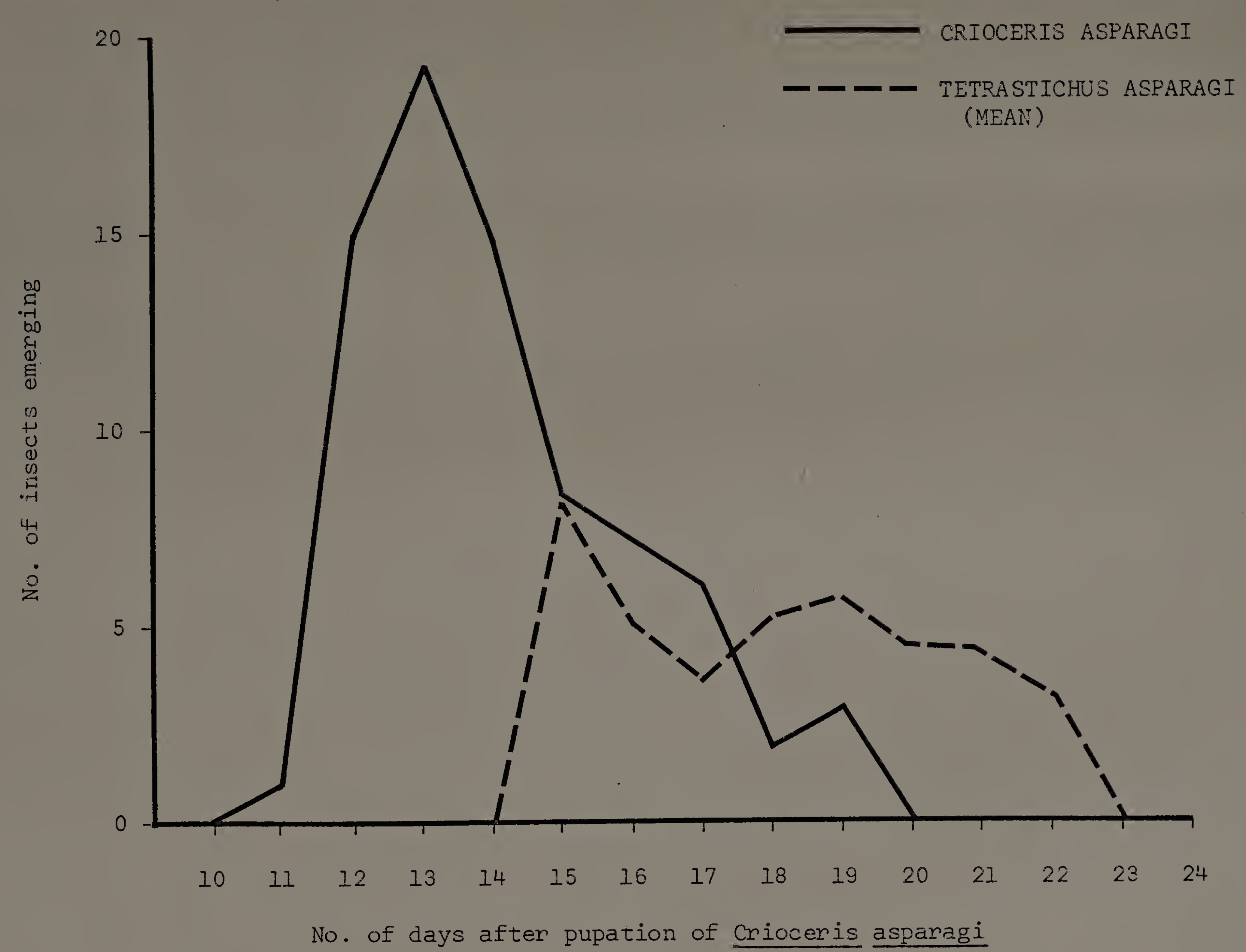


Fig. 14. - Comparison of emergence times of the eulophid wasp _Tetrastichus asparagi_ and its host, the common asparagus beetle, _Crioceris asparagi_.

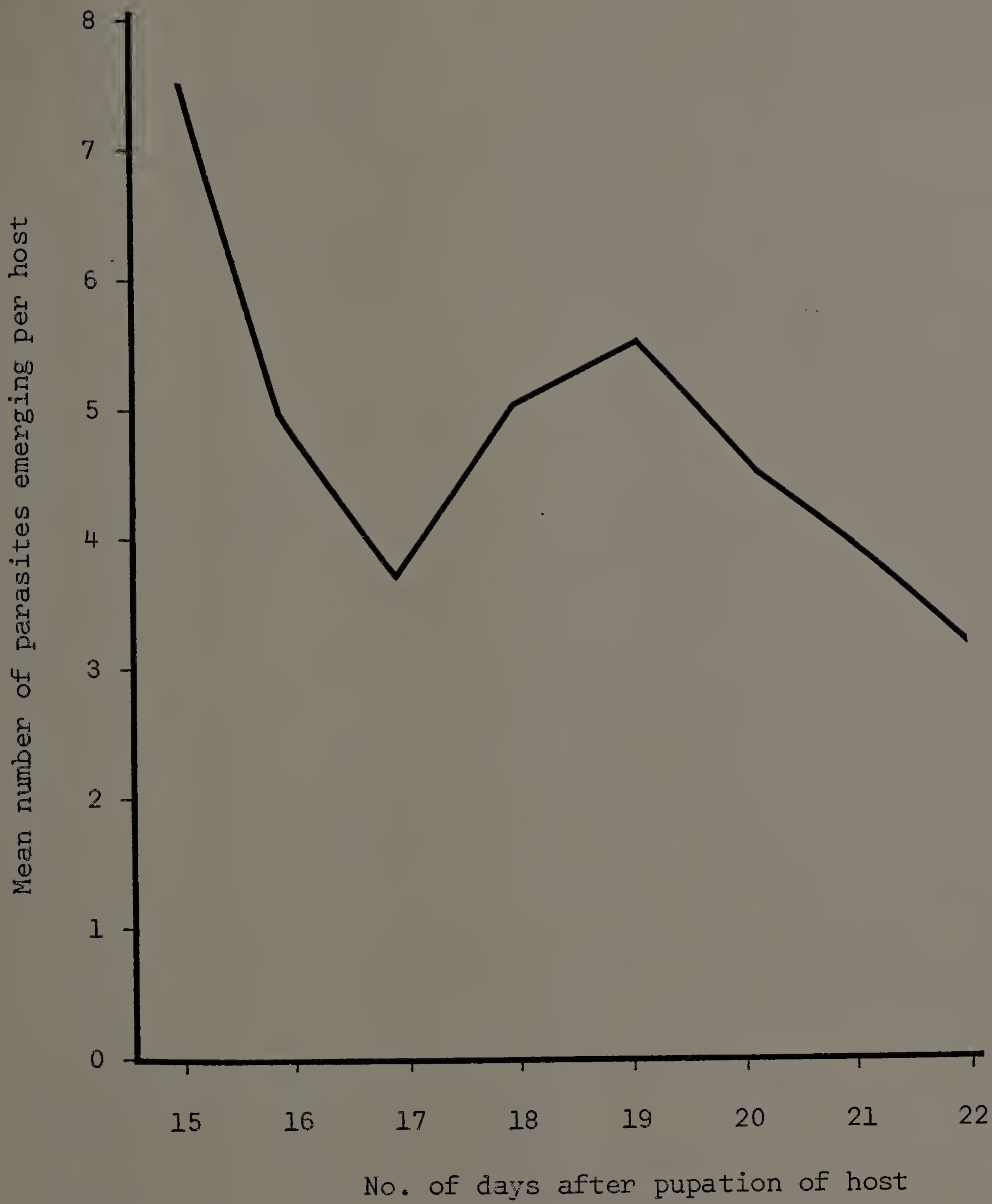
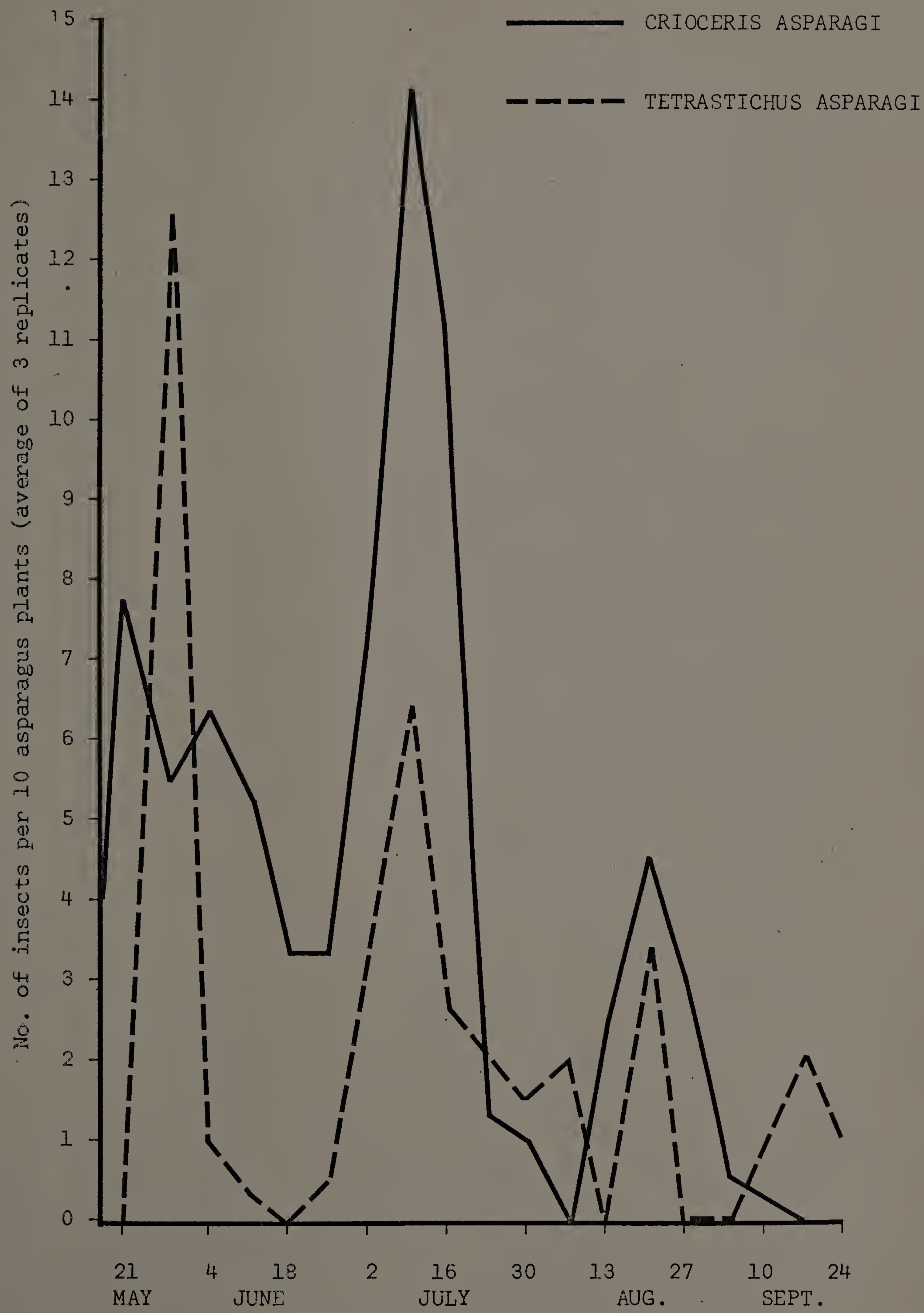


Fig. 15. - Emergence times of the eulophid parasite *Tetrastichus asparagi* at varying parasite densities per host.

Fig. 16. - Numbers of the common asparagus beetle, *Crioceris asparagi*, and the eulophid parasite, *Tetrastichus asparagi*, in western Massachusetts, 1972.


CRIOCERIS ASPARAGI
TETRASTICHUS ASPARAGI
No. of insects per 10 asparagus plants (average of 3 replicates)
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
21
4
18
2
16
30
13
27
10
24
MAY
JUNE
JULY
AUG.
SEPT.

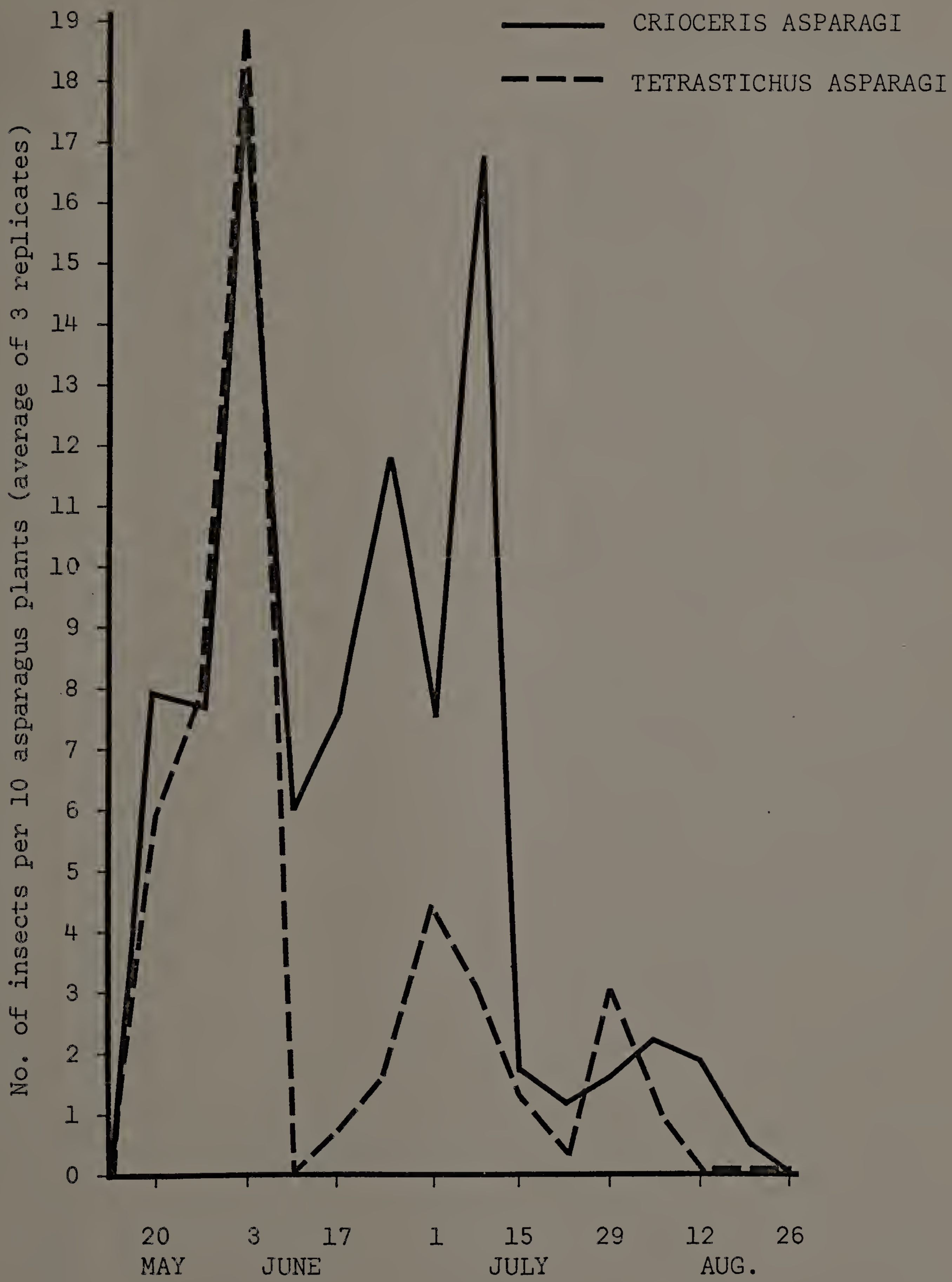


Fig. 17. - Numbers of the common asparagus beetle, Crioceris asparagi, and the eulophid parasite, Tetrastichus asparagi, in western Massachusetts, 1973.

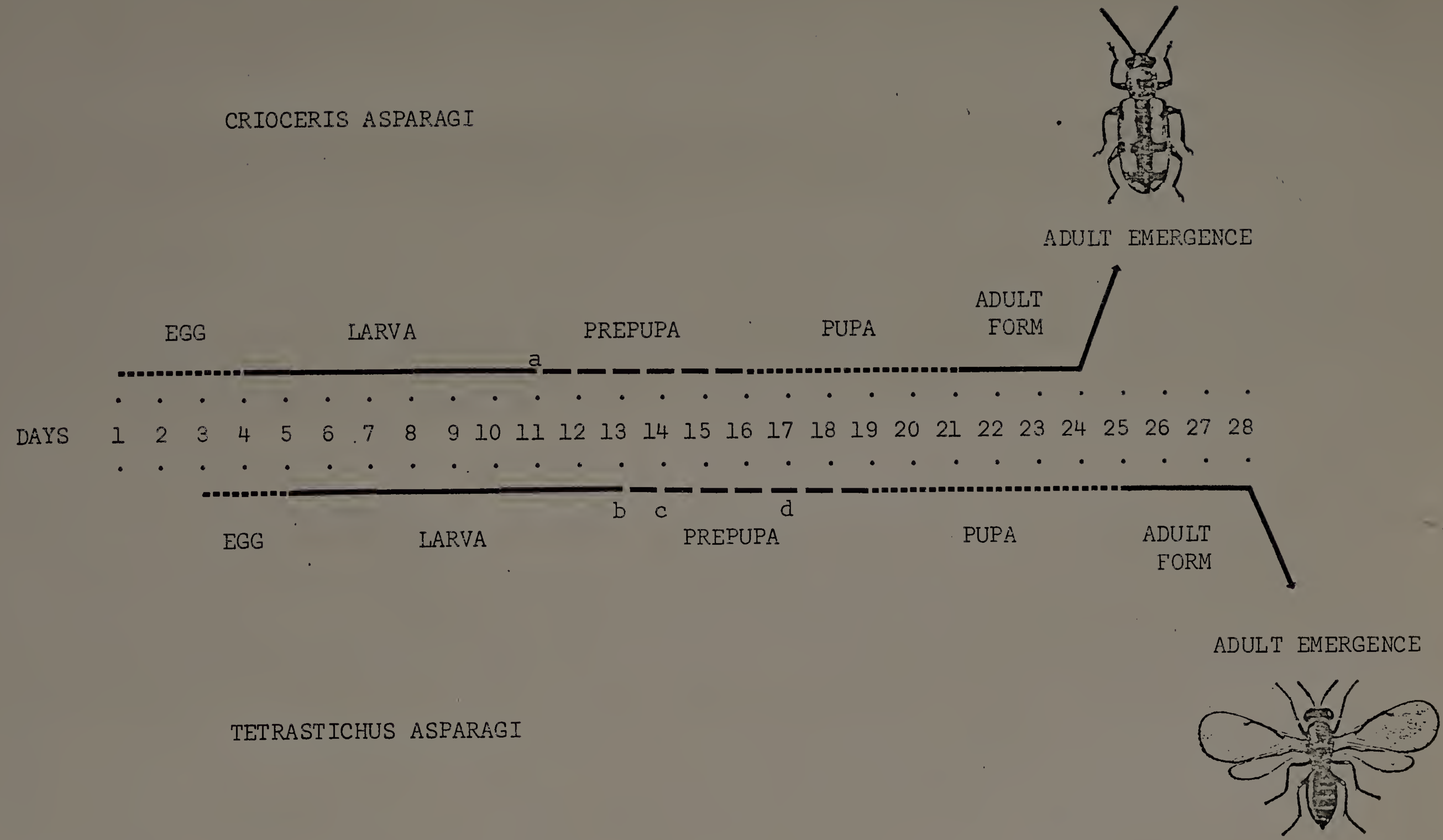
Fig. 18. - Comparative development of *Tetrastichus asparagi* and its host *Crioceris asparagi* at 25° ± 5°C.

[a]*C. asparagi* larva enters soil to form pupal cell.

[b]Cessation of feeding activity by *T. asparagi* within remains of *C. asparagi*.

[c]*T. asparagi* escapes from the host cuticle but remains within the host pupal cell.

[d]Gut contents of *T. asparagi* evacuated prior to pupation.


CRIOCERIS ASPARAGI
ADULT EMERGENCE
ADULT
FORM
EGG
LARVA
PREPUPA
PUPA
a
DAYS 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
b c d
EGG
LARVA
PREPUPA
PUPA
ADULT
FORM
ADULT EMERGENCE
TETRASTICHUS ASPARAGI