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**LA THÈSE A ÉTÉ
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POPULATION DYNAMICS OF THE ASPARAGUS BEETLE,
CRIOCERIS ASPARAGI (L.) (COLEOPTERA: CHRYSOMELIDAE).

BY

ROBERT GORDON TAYLOR, B.Sc., M.Sc.

A thesis submitted to the Faculty of
Graduate Studies in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

Carleton University
Ottawa, Ontario,
September, 1978

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Plate 1. Life cycle of the asparagus beetle.

FLAMEY-10

The undersigned recommend to the Faculty of
Graduate Studies acceptance of the thesis "Population
Dynamics of the Asparagus Beetle, Crioceris asparagi
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ABSTRACT

To provide a meaningful rationale for pest management, a detailed study on the life system of the asparagus beetle, Crioceris asparagi (L.) was conducted by the writer from 1973-1976.

C. asparagi is the most important insect pest of asparagus in Ontario. The adults overwinter in the hollow stems of old asparagus plants and emerge in the spring to feed and oviposit on the new spears, lessening the market value of the crop. The larvae and adults of the later generations, feed on the ferns, reducing plant vigour resulting in lower yields the next year. Pupation occurs in the soil. There are three generations a year in Eastern Ontario.

Population shrinkage occurs in all of the immature stages. Although a few eggs are infertile and some are attacked by coccinellids, most mortality is due to feeding by Tetrastichus asparagi Cwfd. a small gregarious eulophid which also oviposits in the eggs. Larvae are preyed upon by coccinellids and pentatomids. There is some loss of pupal cells due to physiological reasons; however, the principal mortality agent of this stage is T. asparagi which completes its feeding and destroys the host prior to pupation.

When the immature stages of the beetle were reared at 10 constant temperatures differential rates of survival and development were observed. Duration of all stages decreased with increase in temperature up to 32°C. Eggs tolerated a wider range of temperature than other stages (8-34°C) but hatching and survival were optimal only between 22° and 26°C. Larvae and pupae survived between 10° and 34°C with high mortality only at these limits. At 34°C emerging adults were often deformed. Curves of developmental rates plotted against temperature conformed to the function $1/y = K/(1 + e^{a-bx})$.

Methods were developed for estimating numbers of the different stages in a field of asparagus. The most appropriate sample unit for the egg and larval stages was the individual spear or shoot; for adults it was the whole plant, and for pupal cases, a square foot quadrat of soil from beneath the plant canopy.

Analysis of the variation between samples showed that inter plant variation was the major source of sampling variance. A sampling plan was drawn up for estimating populations during five age intervals. The number of plants required was inversely proportional to population density; this relationship was graphed for four probabilities ($p = .70, .75, .80$ and $.90$) and three levels of precision (10, 15 and 20% standard error).

Based on 261 stage samples life tables were compiled for seven successive generations during the three year period, 1973-1975. Analysis of the data using components and graphical key factor methods showed that mortality in two age intervals was of critical importance to population trend. Regression analysis of the separate mortalities expressed as K-values confirmed that the causal agent Tetrastichus asparagi Cwfd. was the key factor determining generation survival.

Several recommendations are made for pest management of C. asparagi.

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INTRODUCTION

An estimated half billion people in the world suffer from malnutrition. By the turn of the century the global population will grow from 4 billion to an estimated 7 billion, causing severe food shortages (FAO, 1974; NAS, 1971). Total world food losses today are estimated to range up to 48% with pre-harvest losses at 35% (Cramer, 1967) and post-harvest losses at an additional 13% (Pimental et al, 1975).

Since World War II, short sighted, extensive use of pesticides has caused a documented deterioration of our environment, while insect problems continue.

The failure of pesticides to control insects is chiefly attributable to factors such as resurgence, and resistance. The application of pesticides or other depressive factors is nearly always followed by a resurgence of the population to its former density, (Huffaker, 1969). This is as expected since most species have a characteristic population density and distribution. In the case of pesticide application, however, resurgence is frequently large since the pesticide usually removes some of the natural enemies.

of the target species. Predators are more severely affected by pesticide, since they are higher up the food chain and are therefore subject to bioaccumulation of pesticides. The resultant resurgence necessitates repeated application of insecticide to maintain control and this leads to resistance in the pest.

A further complication of pesticides is the elevation of non-pest species to an economic level. For example, in the early years of apple growing in Canada, most of the important pests of today were relatively scarce because they were more in balance with their natural enemies (MacPhee and Sanford, 1956; Sanford and Lord, 1962).

In addition to counter-productive effects there are other disadvantages of chemicals as well. Concern about residues in food and their carcinogenic and teratogenic effects has been widely publicized. Also the persistence of some of these chemicals or their metabolites is of great environmental significance. Furthermore, one must consider the exposure of producers, handlers and applicators of pesticides. Finally, the rising costs of pesticide development and depletion of fossil fuels in formulation and application of pesticides is of mounting importance.

Huffaker coined the phrase "pesticide syndrome" to describe the injudicious use of chemicals. Spray schedules are often based on the time of year or stage of the crop rather than on the pest population. There is often no research to show that the treatment is really necessary, or that it can be justified economically. Worse still, many pesticides are used to maintain what are referred to as "cosmetic standards", (Pimentel, 1977). The minor surface blemishes on fruits and vegetables do not significantly affect the nutritional content, storage life or flavour of the produce. The emphasis given the "cosmetic appearance" of fruits and vegetables is generally alleged to reflect consumer preference, (van den Bosh et al, 1975). The consumer seldom has been educated about the advantage of blemished produce, nor has he had the opportunity to take advantage of the potential price differential.

The inherent problems of a purely chemical control plus strong public opinion have given new impetus to the field of economic entomology. The most promising solution to many of the present problems is offered by a pest management strategy. The basic philosophy behind this approach is that pest control is adequate if populations are held at tolerable levels, rather than aiming to completely eradicate them.

The regulation of insect populations uses , realistic models based on orderly and systematic appraisal of carefully recorded field data integrated with controlled laboratory experiments. Ecologically sound principles are put into practice and pesticides are kept in reserve. When the situation is such that chemicals must be used they are applied at optimum time and rate to control the pest with minimum impact to natural control agents.

The purpose of the present study was to determine the factors and/or processes that regulate natural populations of the asparagus beetle so as to provide a meaningful rationale for pest management.

SECTION I. GENERAL BIOLOGY

OF C. asparagi

Host Plant

Asparagus officinalis L. is a member of the family Liliaceae and is dioecious, the female plants being more robust. In Ontario, it is cropped chiefly in the counties of Essex, Norfolk and Simcoe. About 2800 acres are grown annually in the province yielding an average of about 1600 pounds per acre with a value to farmers of two million dollars.

The culture of asparagus is a long-term investment. The life expectancy of a new planting is 15 to 20 years and peak production is not attained until the fifth or sixth year. Traditional crown transplanting and direct field seeding are two distinct planting systems used in commercial asparagus production. Harvesting typically begins when the plants are three years old, but the harvest period is kept short for the first few seasons to allow the root system to develop and thus provide strong crowns for the duration of the planting. Harvest begins in the latter part of May and continues in a mature planting until the end of June.

The adult beetles of the overwintered generation feed and lay their eggs on the spring shoots, lessening the fresh market value of the spears and rendering them unfit for processing. The larvae and adults of subsequent generations feed on the ferns, reducing plant vigour resulting in lower yields in the next year. Plant stems scarified by the insect feeding are susceptible to breakage from wind and rain.

Taxonomic Position and General Description of Stages

The chrysomelids, commonly known as the leaf beetles, are a large family within the Coleoptera. Entirely phytophagous, they are distinguished by the apparently 4-segmented tarsi with the third segment bilobed. But the tarsi are actually 5-segmented; the fourth segment is small and concealed in the notch of the third. They share this tarsal formula with the Cerambycidae, the long-horned beetles, but usually have much shorter antennae and are smaller and more oval in shape. Adult leaf beetles feed principally on flowers and foliage; the larvae are phytophagous but vary in appearance and habits. Some of the larvae are free feeders, some are leaf miners, some feed on roots, and some bore in stems. Many members of this family are serious pests as can be seen from the following partial list (Borror & DeLong, 1970).

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<u>Subfamily</u>	<u>Common Name(s)</u>
Cassidinae	tortoise beetles
Hispinae	leaf mining leaf beetles
Alticinae	flea beetles
Criocerinae	asparagus beetles, cereal leaf beetle, threelined potato beetle
Chrysomelinae	potato beetle
Galerucinae	cucumber beetles.

The asparagus beetle is a member of the subfamily Criocerinae. Members of this subfamily characteristically have the head narrowed behind the eyes to form a slender neck, and the punctures of the elytra are arranged in rows (Borror and Delong, 1970). The adult is ca. seven millimetres long and is slender. The background colour is metallic blue-black; the thorax is red and the elytra have creamy yellow markings bordered in red (Plate 1).

C. asparagi (L.) occurs throughout Canada and the United States wherever asparagus is grown (Jones and Robbins, 1928). It is a European species that was

introduced into the United States during the last century. It was first found in Canada in Southern Ontario in 1898, in Quebec in 1912 and in British Columbia in 1926 (Beirne, 1971).

The adults overwinter throughout their range in sheltered places, such as hollow stems of old asparagus plants and under plant debris. They emerge in the spring to feed on new asparagus tips and to oviposit. The eggs are slightly over one millimetre long, dark brown and are laid singly or in rows of 2 to 9 on the shoots in the spring, and on the stems and leaves of the ferns later in the season.

The larvae are dark grey, fleshy grubs with a black head. They feed on the apical portions of the ferns through the larval period. When mature, they drop to the ground, burrow beneath the soil surface, and form a tough pupal case composed of particles of soil cemented together by larval secretions.

In eastern Ontario, the species is trivoltine with peaks of egg-laying at the beginning of June, early July, and early August (Taylor and Harcourt, 1975). Adults produced by the third generation feed for a short period before entering diapause. They do not lay eggs until the following spring.

Natural Enemies of C. asparagi

The eulophid Tetrastichus asparagi Cwfd. is the principal natural enemy in eastern Ontario. As early as 1863, Riley and Walsh (1869) noted that a "small shiny black parasitic fly" appeared and significantly checked the asparagus beetle population on Long Island, New York. In 1909, Crawford of the U.S. National Museum described the species and named it T. asparagi. Crawford believed it to be native to North America, but it had already been described in Europe by Nees as Esenbeck in 1834, who named it Tetrastichus coeruleus Nees (Graham, 1961). Graham (1961) suggested that although the latter name had precedence, T. asparagi should be retained due to its extensive use in the literature.

F.A. Johnston (1915) was the first worker to discover that T. asparagi was both a predator and parasitoid. The parthenogenic females feed on the eggs of the asparagus beetle. At the same time they oviposit in the eggs. Parasitoid development is slow during the host egg and larval stages. However, once the larva has constructed its pupal case, the parasite develops quickly, devouring the host and pupating within the pupal case. Multiple ovipositions typically

occur, and as many as 13 parasitoid adults have been known to emerge from a single host, (Johnston 1915; Capinera and Lilly, 1976). There are three generations per year in the Ottawa area and the larvae overwinter within the pupal cases of the host.

Other insects were frequently observed to prey on the egg and larval stages. These included large numbers of larvae and adult Coccinellidae (lady beetles), predominantly of the genus Hypodamia. At no time were significant numbers of aphids found on the asparagus. This is noteworthy since Capinera and Lilly (1975) have speculated that aphids attract large populations of coccinelids which in turn prey heavily on the asparagus beetle.

Other common predators of the larvae were nymph and adult stink bugs. These bugs characteristically impale their prey and hold them up while sucking out the body fluids.

Although pupae were collected throughout the course of this study specimens of the tachinid Paralispe infernalis were not reared. This fly was the only parasite of the asparagus beetle that Watts (1938) reported from South Carolina.

Sexing the adults

In order to select females for experiments, it was necessary to develop a method of sexing the adults. The sex of a beetle can be determined by dissection since the male aedeagus is reasonably conspicuous; however, the work is tedious and of course necessitates killing specimens. Fortunately, Mysner and Schultz (1967), while working on a closely related member of the Criocerinae, the cereal leaf beetle (Oulema melanopus), discovered that the intercoxal process of the first abdominal sternite is somewhat rounded and convex in the female, whereas in the male it is more pointed and flattened. This characteristic held for the asparagus beetle (Fig. 1) and based on dissection proved to be 90 per cent accurate.

Number of Larval Instars

There are a number of gaps in the literature pertaining to the life history and stage descriptions, of the asparagus beetle. One of these pertains to the number of larval instars. Although the insect and its depredations are well documented in the early literature, there is no specific reference to the number of larval instars. This problem was approached in two ways. The first was to rear a number of specimens from egg to pupa in the laboratory and to count the number of cast skins per individual, which invariably was four. However, this method is not entirely reliable in that instar number of a species may vary with temperature. For example, Guppy (1969) showed that the armyworm Pseudaletia unipunctata (Haw.) required an extra moult at 13°C. Therefore, the following procedure was followed. During the summers of 1974 and 1975 a sample of 100 larvae was collected from the study field, care being taken to select a good spectrum of all sizes available. The head capsule width of each larva was measured by means of a microscope equipped with an eyepiece grid calibrated to scale. The measurements, tabulated and plotted in the form of a histogram (Fig.2), indicate that four instars exist.

Fig. 1 Ventral view of adult male and female
asparagus beetles, C. asparagi. Note
difference in shape of intercoxal processes.

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Fig. 2 Histogram of head capsule measurements
for 100 C. asparagi larvae (0.05 mm intervals).

SECTION II. EFFECTS OF TEMPERATURE ON DEVELOPMENTAL RATE OF THE IMMATURE STAGES

INTRODUCTION

In pest management studies, the timing of population sampling in relation to seasonal development of the target species must be precise. This is particularly important when assessing rates of mortality due to parasites or disease since it is essential to separate real from apparent effects, and a poorly timed sample can lead to biased mortality estimates (Miller, 1955). If pilot sampling is not possible, proper timing can best be determined by relating development to temperature; thus development may be predicted using thermal requirements for each stage in terms of degree-days above an established threshold.

Accurate estimation of the rates of development is also basic to the proper integration of population data. The method of integration used in this thesis is that of Southwood and Jepson (1962) and is detailed in Section IV.

The influence of temperature on the development of many insect species has been studied critically and the problem is discussed by Wigglesworth, (1953), Andrewartha and Birch, (1954) and Howe, (1967). However, critical

studies are lacking for the asparagus beetle.

Some authors have approximated the generation time required for C. asparagi as well as that for duration of each of the life stages (eg. Riley, 1869; Chittenden, 1917; Capinera and Lilly, 1975). However, these data were qualitative and based solely on field observations.

The relationship between temperature and developmental rate in insects may be expressed by a number of mathematical formulae such as Van't Hoff-Arrhenius equations, Belehradek's formula, Janisch catenary curve (Davidson, 1944) and Pradhan's equation (1946). Howe (1967) states that there seems to be little basis for choice between the various mathematical relationships proposed except what one is prepared to accept.

In the present study a curve of the form:

$$100/y = K/(1 + e^{a-bx})$$

where y = time for complete development at temperature x and K , a and b are constants, is used to represent the developmental curves at constant temperatures. The formula is a form of the logistic curve developed by Verhulst in 1839 (Pearl and Reed, 1920) and has been used extensively by population biologists to build models of population growth (Lotka, 1925; Andrewartha and Birch, 1954; Watt, 1968). Davidson (1942) used the above form of the curve to describe the relation between embryonic development of insects and temperature.

Methods

A stock culture of C. asparagi was established from field collected adults during the summers of 1974 and 1975. These were placed in a cage (90 x 65 x 105 cm) together with four, two-year old asparagus plants in 8-inch peat pots. The sides of the cage were made of fine

plastic screening but the top was of clear plexiglass in order to allow better light penetration. The light source was two, 40 watt fluorescent tubes placed two inches above the top of the cage. One tube was standard white light and the other was a Gro-lux (Sylvania) to help maintain plant vigour. The solid floor of the cage was covered with one inch of fine sandy loam soil collected from the field plots and sieved to remove debris. The cage was kept in a controlled environment room at $25.0 \pm 0.5^{\circ}\text{C}$ and 55% R.H. with a 16 hour photoperiod. Under these conditions diapause did not occur.

In this manner it was possible to maintain conditions simulating nondiapause conditions in nature. The adults oviposited readily on the "ferns". The larvae completed their development, dropped to the cage floor, and pupated in the soil. The newly emerged adults returned to the plants to complete the life cycle. The potted plants were watered daily and replaced, as required, in rotation so as to minimize the disruption of the life cycle of the insect. From time to time it was necessary to remove some insects

since under these near optimal conditions the population increased to the point where it would have destroyed the limited food source.

Eggs for the incubation studies were collected by placing a fresh potted plant in the cage in the early morning and examining it for eggs at two hour intervals.

The immature stages of the beetle were reared at 10 temperatures: 8, 10, 12, 14, 18, 22, 26, 30, 32, and 34 degrees centigrade. These temperatures were carefully chosen, based on preliminary rearing studies, to cover the entire tolerance range of the insect. Also, the temperatures were carefully chosen to allow selection of values at three equally spaced temperatures on the abscissa since this is crucial to the analysis. Furthermore, the rearing temperatures were selected at closer intervals near the extremes since it is more difficult to fit the ends of the sigmoid curves than the middle, which is approximately linear.

The rearing containers were disposable plastic petri dishes (6 x 2 cm). These were kept in larger plastic vented boxes (17 x 8 x 4 cm) and both were lined at the bottom with layers of moist blotting paper to prevent desiccation. The R.H. in the rearing container

was about 80%. A total of 100 freshly laid eggs was incubated at each temperature. Also, 30 newly hatched larvae (less than 2 hours old) from the stock culture were simultaneously placed on fresh cuttings of asparagus foliage. Larvae that did not feed within the first 24 hours were replaced. Thus 30 individuals were tested at each temperature during the first instar. Those that died after 24 hours were discarded; hence the number of individuals tested decreased slightly from instar to instar. Numbers tested during instars II to IV ranged as follows:

Instar II	Instar III	Instar IV
22-30	16-30	14-30

The pupal stage was considered to begin with the final larval moult which occurred after the larva had crawled to the bottom of the rearing container. Hence, the feeding period of the 4th instar and the prepupal stage were combined. To avoid cumulative effects (Guppy, 1969), 30 newly formed pupae from the stock culture were reared at each temperature. This also enabled a full complement of pupae to be tested at each temperature. Each individual was observed daily, and the time of hatching, moulting and adult emergence were recorded. At the higher temperatures,

and when a change of stage was imminent, observations were made at 6 to 8 hour intervals. Fresh food was provided as required.

Treatment of the Data

The methods used are those of Davidson (1944). The observed data are presented graphically (Figs. 3-4). The closed circles represent the points obtained when time (y) is plotted against temperature (x), so that the distribution of these points indicate the course of the temperature time curve. The open circles represent the points obtained when the reciprocals of time (1/y) are plotted against temperature (x): each of the reciprocals is multiplied by 100, so that values on the ordinate (100/y) represent the average percentage development made per stage day at the given temperature. The observed data are fitted to a curve having the formula:

$$100/y = K/(1 + ea^{-bx})$$

where: K is the parameter representing the distance between the upper and lower asymptote of the curve, a is the parameter which indicates the relative position of the curve on the abscissa, b is the parameter representing the degree of acceleration of development of the eggs in relation to temperature and therefore determines the slope and course of the curve, and e is the base of the Napierian system of logarithms.

If the observed points are distributed over the complete course of the projected logistic curve, the value of K can be visually assessed. In the case of the types of data considered here, it cannot be assessed in this way, because the observed points do not extend far enough along the upper portion of the curve. In fact, due to detrimental effects of higher temperatures, the values decrease drastically at high temperatures.

Therefore K can be calculated from the following formula:

$$K = \frac{2P_1P_2P_3 - P_2^2(P_1 + P_3)}{P_1P_3 - P_2^2}$$

(Davidson, 1944)

where P_1 , P_2 and P_3 are values for $100/y$ on the curve at three equally spaced temperatures on the abscissa. The letter P is used to represent values on the ordinate.

Substituting in the equation:

$$P = K/(1 + e^{a-bx})$$

$$\log e^{(K-P)/P} = a - bx$$

which is the equation of a straight line. Therefore a and b can be determined by a regression and substituted along with K into the equation to determine the temperature-time and temperature-velocity curves. Once the equation of the curve has been determined, the expected value for each of the experimental temperatures can be calculated and compared to the observed value. An analysis of variance after Williams (1959) was used.

Results and Discussion

Survival

Hatching of eggs occurred from 8° to 34°C. However, at these extremes only 44% and 55% survived, respectively (Table 1), and the resultant larvae failed to feed. Percentage hatch increased from 8° to 14°C and was near maximal between 18° and 32°C. As a rule, larvae completed development from 10° to 34°C, although there was some mortality at these limits. Pupae survived at all temperatures above 8°C but there was high mortality at 10° and 34°C and the survivors were often small and deformed.

Table 2 shows that the egg stage can tolerate a wider range of temperatures than the larval or pupal stages. The limits of tolerance for the four larval instars are about equal. The range for pupae is least of all.

Development

Based on number surviving, the duration of each stage at each temperature was calculated.

Duration of the egg and larval stages decreased rapidly with rise in temperature up to 30°C, and slowly thereafter (Table 2). For pupae, the duration decreased rapidly, plateaued between 30° and 32°C, and then declined.

Figures 3-4 show that the time-temperature curves for all stages are of the conventional type (Howe, 1967). For the egg, pupal, and larval stage as a whole, the point of inflection occurred near 26°C. Broadly speaking, this means that two thirds of the temperature range of the insect is below 26°C. Above this temperature, rates of development levelled off or decreased, as did survival.

Thermal Requirements

The foregoing data indicate that a development survival threshold of 10°C would be appropriate for predicting seasonal development of the beetle. A base of 8°C may be more suitable for eggs laid in the spring when temperatures are low; however, larvae from eggs that hatched at 8°C did not undergo complete development at any temperature. The minimum temperature for hatching and subsequent complete development at a given higher temperature has been defined as the "hatching survival threshold" (Hodson and Alrawy, 1958). The hatching-survival threshold for the asparagus beetle for most mid-range subsequent rearing temperatures was approximately 10°C. Choice of a base temperature that is too low predicts events too soon, and vice versa.

The maximal rates of stage development and survival suggest the following optimum temperatures: egg and larval instars I-II, 32°C; larval instars III-IV and pupa, 30°C. For all stages, rates of development decreased with the onset of high mortality; the older larvae suffered greater mortality at high temperature than did the younger stages, possibly because of accumulated harmful effects. A similar phenomenon has been observed in Hypera postica (Gyll.) (Guppy and Mukerji, 1974).

Because of the non-linear relationship between temperature and rate of development, it is evident that the thermal requirement varies with temperature.

Accordingly, to construct a predictive model, a mean value for each stage must be derived based on the different temperatures that occur under field conditions. This was accomplished by averaging thermal requirements calculated at 2-degree intervals from the time temperature curve equations within a range of temperatures from the base (10°C) to the mean daily maximum expected to occur during the main seasonal developmental period in eastern Ontario, viz., 10-26°C.

The thermal requirements in degree days for the six life stages were as follows: egg, 58; instar I, 21; instar II, 26; instar III, 32; instar IV, 88; and pupa, 92.

The reliability of the method of thermal requirements for predicting seasonal development was assessed during 1976. Population peaks for different stages, except pupae, were determined during the course of three generations in a half-acre field of Viking asparagus near Richmond, Ontario. Weather data were obtained from the Central Experimental Farm, Ottawa, which lies ca. 10 miles to the northeast. Using the dates on which peak numbers

were observed in the field, degree-days above 10°C accumulating during development of each stage were calculated. These data were compared with the thermal requirement derived for each stage, and tested by chi-square. Table 3 shows that the observed degree-days accumulated between stages did not differ significantly from those predicted. It may be concluded that proper timing for samples of eggs, larvae, or adults of C. asparagi can be determined by using pertinent daily temperatures to plot the seasonal progress of field populations.

Table 1. Percentage survival for the immature stages of C. asparagi at 10 constant temperatures*

Stage	Temperatures (°C)				
	8	10	12	14	18
Egg	44	74	84	85	92
Instar I	0	73	100	100	100
Instar II	0	73	97	93	93
Instar III	0	88	93	100	96
Instar IV	0	86	93	93	100
Total Larva	0	40	83	90	90
Pupa	0	10	83	90	90
	22	26	30	32	34
Egg	100	100	98	95	55
Instar I	100	100	100	100	90
Instar II	100	97	97	100	89
Instar III	100	100	100	93	83
Instar IV	100	100	100	89	75
Total larva	100	97	97	83	50
Pupa	93	93	87	73	37**

*All egg percentages were based on 100 individuals. Instar I percentages were based on 30 individuals; those for the remaining instars were based on surviving individuals. Pupa percentages were based on 30 individuals.

**Some adults deformed.

Table 2 Duration in days of the immature stages of C. asparagi at 10 constant temperatures*

Stages	Temperatures (°C)			
	8	10	12	14
Egg	35.5 $\pm$ 0.4	27.50 $\pm$ 0.2	14.5 $\pm$ 0.2	10.4 $\pm$ 0.2
Instar I	-	8.5 $\pm$ 0.1	5.8 $\pm$ 0.1	4.3 $\pm$ 0.1
Instar II	-	11.3 $\pm$ 0.1	8.5 $\pm$ 0.1	7.0 $\pm$ 0.1
Instar III	-	12.1 $\pm$ 0.3	8.5 $\pm$ 0.1	6.0 $\pm$ 0.1
Instar IV**	-	23.1 $\pm$ 0.4	20.5 $\pm$ 0.2	18.0 $\pm$ 0.1
Total larval stage**	-	54.6 $\pm$ 0.5	41.4 $\pm$ 0.2	35.4 $\pm$ 0.2
Pupa	-	38.0 $\pm$ 3.1	28.5 $\pm$ 0.4	22.3 $\pm$ 0.5

Stages	18	22	26	30
Egg	7.5 $\pm$ 0.1	4.8 $\pm$ 0.1	3.3 $\pm$ 0.1	3.00 $\pm$ 0.1
Instar I	3.0 $\pm$ 0.1	2.0 $\pm$ 0.1	1.6 $\pm$ 0.1	1.2 $\pm$ 0.1
Instar II	3.3 $\pm$ 0.1	2.3 $\pm$ 0.1	1.8 $\pm$ 0.1	1.3 $\pm$ 0.1
Instar III	4.6 $\pm$ 0.1	3.0 $\pm$ 0.1	2.2 $\pm$ 0.1	1.8 $\pm$ 0.1
Instar IV**	12.0 $\pm$ 0.2	8.3 $\pm$ 0.1	6.0 $\pm$ 0.1	5.0 $\pm$ 0.7
Total larval stage**	22.8 $\pm$ 0.2	15.6 $\pm$ 0.1	11.6 $\pm$ 0.1	9.2 $\pm$ 0.1
Pupa	13.0 $\pm$ 0.2	8.0 $\pm$ 0.1	5.8 $\pm$ 0.1	4.0 $\pm$ 0.1

Stages	32	34
Egg	2.9 $\pm$ 0.1	2.9 $\pm$ 0.1
Instar I	1.2 $\pm$ 0.1	1.1 $\pm$ 0.1
Instar II	1.1 $\pm$ 0.1	1.1 $\pm$ 0.1
Instar III	1.6 $\pm$ 0.1	1.5 $\pm$ 0.1
Instar IV**	4.2 $\pm$ 0.1	4.1 $\pm$ 0.1
Total larval stage**	7.9 $\pm$ 0.1	7.9 $\pm$ 0.2
Pupa	4.0 $\pm$ 0.1	4.1 $\pm$ 0.3

*Based on numbers surviving.

**Included prepupal period.

The significance of the decimal may be variable because observations were not in every case made to one tenth of a day.

Table 3. Comparison between observed and expected degree-days required for development of the asparagus beetle at Ottawa (1976) for three generations

Generations				
Stage	Date of peak numbers	Degree-days (°C) from one peak to the next		Chi-square
		Observed	Expected	
<u>Generation I</u>				
Egg	June 2	48.2	58	1.6559
Instar I	June 10	20.7	21	.0043
II	June 12	20.1	26	1.3388
III	June 15	35.4	32	.3613
IV	June 18	154.0	180	3.7556
Adult	July 2			7.1159*
<u>Generation II</u>				
Egg	July 4	51.8	58	.6628
Instar I	July 8	28.9	21	2.9719
II	July 11	35.3	26	3.3265
III	July 15	27.6	32	.6050
IV	July 18	169.8	180	.5780
Adult	Aug. 6			8.1442**
<u>Generation III</u>				
Egg	Aug. 7	44.9	58	2.9588
Instar I	Aug. 12	21.7	21	.0233
II	Aug. 14	23.3	26	.2804
III	Aug. 17	25.9	32	1.1628
IV	Aug. 20	154.6	180	3.5842
Adult	Sept 8			8.0095**

*.20 > P > .10 ** .10 > P > .05

Fig. 3 Relationship between temperature and
development for the egg stage of C. asparagi.
Deviation from the fitted curve is not significant
at the 5% level.

Fig. 4 Relationship between temperature and development for larval and pupal stages of C. asparagi. Deviations from the fitted curves are not significant at the 5% level.

SECTION III. DESIGN OF A SAMPLING PLAN FOR FIELD POPULATION STUDIES

Introduction

Early workers in population biology frequently measured the degree of mortality caused by different biotic factors. This resulted in the publication of lists of "percent mortality" for a factor such as parasitism, since this is often easy to estimate; unfortunately, these early attempts contributed little to overall understanding of population dynamics.

However effective a factor may be against a given stage of a pest species, its value is limited if it does not make for a significant contribution to population trend. Variation is the most important attribute of mortality, and as pointed out by (Morris, 1957), low but variable mortalities may have more influence on the population dynamics of a species than high but relatively constant mortalities. These variations in individual mortalities should be interpreted according to their effect on population trend, rather than on generation mortality alone. It is necessary, therefore, to measure population changes within and between generations and to study all of the factors responsible for these changes. This is only

possible through an approach utilizing sampling techniques that provide for the collection of data of the required quantity and quality.

In the study of insect populations, a primary objective is to measure the interaction between the life stages of the subject species and pertinent mortality factors. Such data are essential to a proper understanding of population dynamics and the role played by mortality factors acting singly, or in concert, in the population regulation of the species (Morris, 1957). These data will provide the key to a precise understanding of agroecosystems and can facilitate the intelligent and practical manipulation of mortality factors and/or husbandry practices for the purpose of pest control in crop habitats. Basic to this holistic approach is that all stages of the pest population (and its natural enemies) be measured in terms of a common population unit and that such data be collected during the course of several generations.

Sample Unit

In agricultural insect sampling, the universe, viz., specified area in which the population of a given species occurs, is predetermined by the size and limits of the crop. However, the basic sample unit must be selected carefully. This may be part of a plant

(Harcourt, 1961), the whole plant (Hudon and LeRoux, 1961) or a quantity of soil (Cameron and Morrison, 1974). Morris (1955) has stated that where the object is to assess absolute populations, selection of the most appropriate sample unit should be based on the following criteria:

1. "In order for the sample to be representative of the universe, the sample unit should be of such a nature that all units in the universe have an equal chance of selection". This is a fundamental principle in sampling.
2. "The sample unit must have stability. This is, the number of units available to the insect population must not be affected by changes in the growth habits of the plant caused either by intrinsic factors or by repeated insect damage." LeRoux and Reimer (1959) chose the leaf cluster, a unit of foliage that in mature apple trees, does not vary significantly during the growing season or from year to year.
3. "The proportion of the insect population using the sample unit as a habitat must remain constant."

Harcourt (1962) found that the imported cabbageworm Pieris rapae (L.), oviposited on the leeward side of the plant during windy periods of the day and as a result significant quadrant-to-quadrant differences, occurred in numbers of the immature stages on the crown

of the plant. Accordingly, he used the half plant as a sample unit; this was obtained by splitting the crown according to direction of the prevailing wind.

4. "The sample unit should be reasonably small so that enough units can be examined on a given plot and date to provide an adequate estimate of variance. The other advantage of a small unit is flexibility, so that, after a certain amount of pilot sampling, the investigator will be able to choose the combination of units per plant and plants per plot that will assure the most economic allocation of sampling resources".

5. "In absolute population work, where estimates of population per acre are required, the sample unit must lend itself to quantitative assessment of the total number of units per plant and per acre". This is not a problem with most agricultural pests since crops are often planted in rows at regular intervals. Working with a nonrow crop, alfalfa, Guppy and Harcourt (1977) found it practical to report stand densities of the crop on a square foot basis. Then, on the basis of these stand counts, estimates were adjusted to numbers per ft² (0.09m²) for the purposes of life table construction. It is only when the samples are themselves counted and the whole converted into numbers per unit area that it is possible to make a valid comparison between populations differing in time

and space, which is the essence of life table or budget construction. The labour of obtaining additional data on the plant unit density is comparatively slight.

6. "An important practical consideration is the facility with which the sample unit can be delineated in the field and collected without serious loss or disturbance of the insect population". Here the mobility of the insect is a factor which must be taken into account. Mukerji (1973) used a hydraulically operated platform mounted on a truck to avoid disturbing the tarnished plant bug in a field of birdsfoot trefoil. Non-destructive sampling, where possible, is desirable.

Sample Units for C. asparagi

(i) Eggs and feeding stages.

Based on a knowledge of the life cycle of the insect, preliminary sampling, and Morris' criteria, the primary sample unit chosen was the whole plant. However Waters and Henson (1959) suggest that at the outset of a study, one should take sample units of at least two different sizes; one of these should be towards the smallest possible limit, because in general, a higher level of reproducibility may be obtained for the same cost by taking more smaller units, than by taking fewer large ones (Southwood, 1966). Small sample units

may also increase precision by distinguishing between favourable and unfavourable microhabitats. To this end, the individual asparagus shoot was chosen as the secondary sample unit. During 1974 and 1975, counts were taken for each shoot in each sample plant; this approach allowed the two sample units to be taken simultaneously.

The selection of a sample unit for the asparagus beetle presents a number of problems and illustrates Southwood's (1966) point that plant habitats are, in many ways, the most difficult to sample. The number of asparagus shoots is not consistent from plant to plant and in fact, varies within the plant during the growing season. Therefore, in order to relate the sample unit to the universe, it is necessary to randomly select a shoot from each plant; and to estimate the mean number of shoots per plant on each sample day. Also the disadvantage of sampling small units is the number of zeros that may result at low densities; this truncation may make analysis difficult and has led some authors to conclude that larger sized sample units should be taken (Pradhan and Menon, 1945; Spiller, 1948, 1952). The decision must be related to the density of the animal,

although moderate truncation may be overcome by suitable transformation; in other cases it may be necessary to increase the size of the unit (Anderson, 1965). Southwood (1966) points out that because population density, and hence, variance is continually fluctuating, too much stress should not be placed on a precise determination of optimum size of the sample unit. When studying phytophagous insects, the nature of the host plant often dictates possible unit sizes, eg. shoot, branch or leaf.

(ii) Pupal Cases

It is not always possible to restrict sampling to a single habitat since many insects spend parts of their life cycle in totally different habitats. The stages of such species must be recorded using different sample units and the data converted to a common denominator for expression in the life table. Working with the winter moth in an oak forest, Embree (1965) found it convenient to trap the mature larvae as they dropped from the tree; these numbers were then converted to absolute values (numbers per tree) and related to larval counts in the foliage.

The sample unit chosen for pupal cases, was a square foot quadrat of soil one inch deep. This was taken from beneath the plant canopy.

Timing of Samples.

The life history of the insect determines the timing of sampling (Morris, 1955). Samples should be taken during peak numbers of each age interval under study. Ideally the age intervals chosen should be easily detectable, relatively immobile and not prone to loss due to disturbance. In a study of the diamondback moth (Plutella maculipennis (Curt.)); Harcourt (1961) sampled the egg, late larval and pupal stages but not the first instar, which is concealed within leaf mines. However, with the imported cabbageworm, Pieris rapae (L.), all of the larval stages were conspicuous on the plant and could be examined in situ without unduly disturbing the foliage (Harcourt, 1962).

The time available for obtaining population fixes for multivoltine species is very short as the population peaks and declines very rapidly. As pointed out by Pottinger and LeRoux, (1971) storing samples at

temperatures below the developmental threshold is an effective way of arresting development or mortality until time is available for their examination.

Samples for the purpose of assessing rates of mortality from parasites should be taken during the "emergence period" (Miller, 1955). Thus, errors due to differential mortality between parasitized and unparasitized hosts are limited to the actual time of emergence. Fortunately in the case of pupal parasites this difficulty is not severe, owing to the residual nature of the stage. In some cases the same is also true for egg parasites (Morris, 1955; LeRoux and Reimer, 1959; Hudon and LeRoux, 1961).

The actual dates of sampling are dictated by the prevailing rates of development, which may be determined by the use of indices such as developmental curves (Harcourt, 1962). Guppy and Mukerji (1974) used thermal requirements (cumulative degree-days) to successfully predict peaks of the alfalfa weevil (Hypera postica). Alternatively, the progress of infestations may be followed in an outdoor study cage (Harcourt, 1961).

METHODS

Study Plots

The population study was conducted on the grounds of a 5-acre field station operated by Agriculture Canada near Richmond, Ontario in Nepean Township, 15 miles southwest of Ottawa. A half-acre field (ca. 0.2 hectare) was planted in early May 1971 with 3,200 three-year old asparagus roots. Fertilizer was applied before planting as follows: 700 lbs. 15-15-15 nitrogen, phosphorous and potash, plus 160 lbs. muriate of potash.

According to commercial practice, the rows were spaced 5 feet apart with plants at 18-inch centres in the row. The field was bordered by annual plantings of vegetables and corn as well as several acres of pasture. The soil was light sandy loam. Clean cultivation was practiced, but at no time were insecticides used on or near the experimental plots.

The plots were sampled intensively during 7 successive generations of the beetle (1973, 1974 and 1975), and several population fixes were made for each age interval in each generation.

Sampling Intervals

Proper timing is extremely important when sampling a multivoltine species, due to overlap of generations and short generation interval. Accordingly, the stage of development was determined by considering the mean temperature during the time interval since the previous sample in relation to development rate curves. It was thus possible to determine the predominant stage of development. In this study, all stages present in addition to the target stage were counted on each sample day since the additional data were valuable in proving the approach was viable.

Estimates of population density were obtained for each of five age intervals, namely eggs, larvae (Periods 1 and 2), pupal cases and adults. Because the life cycle of C. asparagi is short there was a rapid day-to-day change in populations. Consequently, it was necessary to complete assessments of population of certain age intervals within a few hours of the same day. The calendar dates of peaks, even in corresponding generations, varied from year to year.

Eggs Sampling for this stage embraced the oviposition period. Females mate and begin to oviposit within a day of emergence from the soil or, in the case of

overwintering adults, from the litter. The eggs are small (1 mm), but can be counted readily in the field. Egg populations were estimated by direct sampling; in addition, substantial numbers were collected and reared in the laboratory to determine viability. Counts also were made to determine percentage predation.

Larvae. - The larvae begin feeding in the area where they emerge but continue to disperse over the plant in search of food as they mature.

To isolate possible mortality factors, the larval stage was divided into two periods.

Period 1 "Small larvae": This interval included the first and second instars. Populations of larvae in Period 1 were estimated by direct sampling, and mortality caused by predators was based on population reduction between samples.

Period 2 "Large larvae": This interval included the third and fourth instars. Populations of larvae in Period 2 were estimated by direct sampling, and mortality caused by predators was based on population reduction between samples.

Pupal Cases.- Populations were estimated during late June, early August and early September, after the fourth instar peak. Examination of empty and full cases in the laboratory revealed the rate of attack of T. asparagi.

Adults. - Populations were estimated by direct sampling of the spears and foliage. Overwintering populations were estimated by sampling the litter in spring before the adults had emerged from hibernation. Percent mortality due to frost was recorded at this time.

Sampling Procedures

a) Above Ground Stages

As previously noted the units chosen for sampling the egg and ~~feeding~~ stages of C. asparagi were the individual plants and shoots. At Richmond, each plant produced an average of five to six shoots; these developed into a tall "fern" as the season progressed. Although the "ferns" tended to become entwined, there was no appreciable difficulty in delineating individual shoots.

The field was laid out in a 4 x 4 grid to give 4 equal blocks that were divided into 16 plots of equal size. The plots were 60 feet long and 5 rows wide. Thus there were 200 plants per plot. On each sample day, six plants were chosen at random from each plot, for a total of 96 plants. Populations were estimated

twice a week from the latter part of May to mid September, an average of 32 sample days each year. On each occasion each shoot of the 96 sample plants was examined from base to tip for eggs, larvae and feeding adults of C. asparagi and the results recorded separately. The data for July 12, 1974 are typical (Figs. 5-8). To avoid possible border effects, a buffer row was left on both sides of the field. In addition, the plants at the end of each row were not sampled.

Total stage counts for each sample date are shown (Tables 4-6).

b) Other Stages

(i) pupal cases

Initially it was hoped that pupal mortality could be estimated by trapping the adult beetles as they emerged from the soil. Labour saving emergence traps have been used successfully for a number of different insects (Nicholls, 1963; Southwood, 1966). Accordingly, pilot studies were carried out using a series of one-meter metal cones complete with trapping jar. These were inverted beneath the canopy of the plants; unfortunately, numbers recovered by this

technique were negligible. This method relies on a strong positive phototactic response, that these insects apparently failed to exhibit. ■

As pointed out by Southwood (1966), mechanical methods that can be used to separate animals from the soil include sieving, flotation, sedimentation, centrifugation and differential wetting. The disadvantage of mechanical methods is that they are far more labour intensive than methods that take advantage of behavioural habits; however, one reward is that they extract all stages, mobile and sedentary, thus providing a more complete set of data, particularly on the causes of mortality. In this study both dry and wet sieving were used depending on the moisture content of the soil to extract the pupal cases. Dry sieving consisted of simply sieving the soil sample through a screen (mesh 1/8 inch) that prevented the passage of the pupal cases, which were then hand sorted from the remaining debris. Variations of this method have been used by a number of authors (Jacot, 1935; Stage, Gjullin and Yates, 1952; Wallace, 1956). Wet sieving consisted of washing the soil sample through a sieve using a garden hose. Wet sieving is often used in studies of the bottom fauna of aquatic habitats to

remove the mud (Berg, 1938; Jonasson 1955; Hairston et al, 1958). In this work, soil washing was found to be preferable when samples were too wet to be dry sieved easily.

The sample unit selected for pupal cases was a quadrat of soil, one foot square and one inch deep. Choice of this depth assured that no pupal cases would be missed since they occur "just beneath the soil surface", (Jones and Robbins, 1928). Test samples were taken at depths greater than one inch but no pupal cases were found. Numbers of cases were estimated on a total of 22 occasions. On each date of sampling, two plants were selected at random from each of the 16 plots, and four quadrats of soil, oriented according to the cardinal points of the compass, were chosen from beneath the canopy of each plant. The quadrat was delineated with a metal square and the soil was trowelled into a labelled bag. Each sample required a total of 10 man hours to collect and 16 hours to process. As a result there was not time enough to extract soil samples immediately and they were stored at 4°C. Short term cold storage (1-2 weeks) did not affect mortality. The data are shown (Tables 7-9).

(ii) overwintering adults.

In order to assess the mortality of overwintering adults, a litter sample was taken each spring.

It was necessary to choose a sample size large enough to obtain reasonable representation, yet small enough not to interfere with the level of population. Thus two samples, each comprising 60 feet of row (ie. 2.5% of the field in total) were taken each April before the adults emerged from hibernation. When sampling, all of the ground litter was collected from the portions of row selected. This was placed in shallow trays in the laboratory and examined for overwintering adults. The adults were almost always found in the hollow stalks of the previous year's growth. Most dead adults were discoloured and brittle. Other adults that did not move after one day at room temperature were also scored as dead. Percentage mortality was recorded for each year.

Treatment of Data

Analysis of Variance

i) Above ground stages

The statistical methods used in this study were similar to those of Harcourt et al. (1974) and especially designed for the treatment of nested population data. All of the counts were assessed by analysis of variance. Because the disposition of counts conformed to an aggregated distribution (Taylor and Harcourt, 1974) a transformation of the form $\log(x + 1)$ was applied to the data prior to analysis. The method of analysis is illustrated (Table 10), using one of the 202 sets of data. Based on this model, the total variation of the transformed responses as measured by the corrected total sum of squares was divided into components associated with differences among blocks (σ_b^2), among plots within blocks (σ_p^2), and between plants within plots (σ_s^2).

ii) Pupal cases

For this age interval the total variation of the transformed responses was divided into components associated with differences among blocks, among plots within blocks, between plants within plots and among quadrats within plants. The method of analysis is illustrated in Table 10, using one of the 22 sets of data.

Sources of Variation

The reliability of a population estimate depends upon two concepts conveniently termed accuracy and precision (LeRoux and Reimer, 1959). Accuracy in this special sense denotes the absence of bias, which stems from systematic errors. Precision is a measure of the reproducibility of an estimate; it is concerned with random errors. An estimate can rank high in accuracy and low in precision, and vice versa.

For eggs, larvae and adults, variation between blocks was statistically significant ($p=.05$) in only 2 of the 202 samples and the variation between plots was statistically significant in only 9 samples. The analysis of variance thus indicates that block and plot differences need not be taken into account in designing a sampling plan. At the same time it is evident that inter-plant variance was the major source of sampling variation. Hence, this is the chief factor to be considered in design of the sampling procedures for the above-ground stages of C. asparagi.

For pupal cases, the analysis of variance revealed the variation between blocks and plots was not significant in any of the 22 samples. That for plants predominated; significant variation occurred in 7 samples.

Optimum Allocation of Sampling Resources

Number of Plants per Plot

i) Above ground stages

An approximation procedure (Sukhatme and Sukhatme, 1970) was used to determine the sampling requirements for specified probabilities and levels of precision. The number of plants per plot was derived as:

$$n_p = (t_{\alpha}^2 / 16d^2 s_p^2)$$

where d is the level of precision (10, 15 or 20% of mean), t_{α} is the $1 - \alpha/2$ percentage point of Student's t distribution and s_p^2 is the plant variance.

Numbers of plants required were calculated for probabilities of 70, 75, 80 and 90% - these are probabilities of obtaining an estimate of the mean that is within 10, 15 or 20% of its true value. Tables 11-18 give the calculated values for $p = .70$ as an example of the calculations.

Graphic illustrations of the data for all probabilities (Figs. 9-12) show that numbers of plants required are inversely proportional to population density; this is not surprising since the distributional pattern of all stages is of an aggregated type (Taylor and Harcourt, 1974).

ii) Pupal cases

Numbers of quadrats required were calculated for a probability of 70% and levels of precision of 10, 15 and 20% of mean. These data are illustrated in Fig. 13.

Number of Units per Plant

The cost of moving from one plant to the next is a factor that should be taken into consideration in field sampling. In forestry work such as Morris' (1955) the cost of moving the vehicles and ladders from one sample tree to the next was large and therefore it was advantageous to take a larger number of samples from each sample plant. However, in most field crops the cost of moving is usually a fraction of the cost of analyzing the sample, (Guppy and Harcourt, 1977). In these cases it is usually more advantageous to take a smaller number of subsamples from a larger number of sample plants. In the present study the relative cost of moving was small when sampling the immature stages; however, when sampling for the adult stage, the cost of moving was about as great as the cost of examining the plant (Table 19).

Error limits of 10% have been adopted for life table studies on a number of field, forest and orchard insects, (Stark, 1952; Morris, 1955; LeRoux and Reimer, 1959; Paradis and LeRoux, 1962; Harcourt, 1961, 1962, 1964). Unfortunately, one would require a prohibitive number of sample plants, to attain such a high degree of precision for a highly over-dispersed population of an insect such as the asparagus beetle. However, if a smaller sample unit could be found, a higher degree of precision would be attainable.

As noted earlier, the data for individual shoots or quadrats within each plant were recorded. However, prior to comparing the efficiency of sample units of different sizes it is necessary to compute the variance to a common basis - the size of the smallest unit. For the above-ground stages, this was done for each sample by dividing plant variance by the total number of shoots in that particular sample, (Southwood, 1966). Relative efficiency, defined as:

$$\frac{1}{\text{cost per sample (min.)} \times \text{variance per shoot}}$$

(Cameron and Morrison, 1974; Guppy and Marcourt, 1977) was then calculated for each age interval for each sample (one example given, Table 20). The results of the comparisons are summarized (Table 21) and show that for the egg, and both larval age intervals the shoot is the more efficient unit. Similarly, the quadrat was more efficient for pupal cases. However, the situation was less decisive for the adult stage and it is concluded that the whole plant should be retained in this case for the following reasons:

- 1) As discussed earlier, too small a sample unit results in a large number of zeros and makes analysis difficult. Since the adult counts are lower than for any other stage, this problem would be accentuated with the shoot as a unit.
- 2) The adults drop to the ground when disturbed (see also Capinera, 1976) and this makes counting difficult. Since the adult is relatively large and conspicuously coloured it is actually faster to examine the whole plant (Table 19), since delineation of individual shoots takes additional time.

Discussion

Following the choice of an acceptable probability and level of precision, sampling requirement, based on a single unit per plant can be determined from Figs. 9-13.

The cost per plot in man-minutes may be computed as follows:

$$C = n_p(C_p + C_c)$$

where n_p is the number of plants required; C_p is the cost of selecting a plant and C_c is the cost of examining a sample unit for the specified stage.

As pointed out earlier, the sampling requirement is a function of population density - and resources may be a limiting factor. Based on the densities encountered at Richmond from 1973-75, Table 22 presents a sampling plan for life table studies where resources are limited. It is based on one unit per plant. This plan pertains to moderate infestations of all stages of the insect.

It gives the cost, in man-hours, required for a 70% probability of obtaining a 10% level of precision for all of the stages save pupal cases. For the latter, a 20% level of precision is recommended in light of practicality.

Table 4

Above Ground Counts of C. asparagi, Richmond, 1973.

(96 plants)

Sample	Date	Egg	Larval Period 1	Larval Period 2	Adult
1	July 25	102	98	43	22
2	29	16	0	4	47
3	Aug. 4	186	155	34	61
4	9	193	148	40	114
5	15	239	167	89	95
6	18	24	49	93	59
7	20	2	53	157	73
8	25		8	51	36
9	29			44	12
10	Sept. 5			36	73
11	9				88
12	14				82

Table 5

Above Ground Counts of C. asparagi, Richmond, 1974.

(96 plants)

Sample	Date	Egg	Larval Period 1	Larval Period 2	Adult
1	May	25	213		12
2		28	155		20
3		30	188		21
4	June	4	153	62	19
5		7	49	77	17
6		10	21	69	26
7		13		24	33
8		16		26	28
9		20			41
10		24	48	12	13
11		28	115	21	51
12	July	2	470	137	26
13		7	452	146	11
14		9	223	71	14
15		12	96	75	76
16		14	107	62	74
17		16	74	71	33
18		22	68	38	40
19		27	73	31	23
20		29	70		14
21	Aug.	2	251	66	17
22		6	493	147	11
23		9	431	153	41
24		11	183	176	24
25		15	147	189	55
26		18	48	78	96
27		21	51	49	88
28		25		56	84
29		31		29	65
30	Sept.	3			51
31		7			17
32		8			
33		12			
34		15			

Table 6

Above Ground Counts of C. asparagi, Richmond, 1975.

(96 plants)

Sample	Date	Egg	Larval Period 1	Larval Period 2	Adult
1	May 22	54			31
2	25	358			23
3	June 3	40	98		22
4	6	36	43	31	24
5	12	28	48	38	20
6	14	89	24	91	25
7	16	18		35	11
8	21	20		43	11
9	24	55	19	22	36
10	28	96	33	26	58
11	July 1	403	152	48	26
12	5	111	173	24	28
13	9	46	86	16	32
14	13	90	40	84	25
15	16	103	50	82	34
16	21	77	62	61	33
17	26	70	3	29	63
18	29	51	5	35	125
19	Aug. 4	515	289	27	44
20	9	256	232	110	23
21	14	94	115	90	16
22	16	52	109	118	14
23	19	33	62	100	11
24	21		68	97	16
25	27		15	113	96
26	30			54	87
27	Sept. 4			8	92
28	13				109
29	20				62

Table 7

Pupal Counts of C. asparagi, Richmond, 1973

(128 quadrats)

Sample	Generation	Date	Total	Parasitized	Dead
1	3	Sept. 2	20	8	2
2	3	Sept. 4	27	13	2
3	3	Sept. 5	31	15	3
4	3	Sept. 7	17	8	1

Table 8

Pupal Counts of C. asparagi, Richmond, 1974

(128 quadrats)

Sample	Generation	Date	Total	Parasitized	Dead
1	1	June 25	5	3	0
2	1	June 27	7	4	0
3	1	June 30	7	7	0
4	2	Aug. 3	12	8	1
5	2	Aug. 5	16	9	2
6	2	Aug. 7	14	10	1
7	2	Aug. 10	16	9	3
8	3	Sept. 4	21	6	2
9	3	Sept. 9	18	4	0

Table 9

Pupal Counts of C. asparagi, Richmond, 1975

(128 quadrats)

Sample	Generation	Date	Total	Parasitized	Dead
1	1	June 25	11	4	0
2	1	June 27	14	6	2
3	1	June 30	12	4	0
4	1	July 3	13	5	2
5	2	July 30	22	7	0
6	2	Aug. 5	17	3	2
7	3	Sept. 6	20	5	2
8	3	Sept. 8	25	7	0
9	3	Sept. 11	26	5	1

Table 10

Analysis of variance of egg counts of C. asparagi,
Richmond August 4, 1975

Source of Variation	df	Expected Mean Square	Observed Mean Square	F
Blocks	3	$\sigma_s^2 + 6\sigma_p^2 + 24\sigma_b^2$	223.51	1.53 ns.
Plots within blocks	12	$\sigma_s^2 + 6\sigma_p^2$	145.77	1.42 ns.
Plants within plots	80	σ_s^2	102.31	

Analysis of variance of pupal case counts of
C. asparagi, Richmond July 30, 1975

Source of Variation	df	Expected Mean Square	Observed Mean Square	F
Blocks	3	$\sigma_s^2 + 4\sigma_t^2 + 8\sigma_p^2 + 32\sigma_b^2$	0.004	0.25 ns.
Plots within blocks	12	$\sigma_s^2 + 4\sigma_t^2 + 8\sigma_p^2$	0.016	0.53 ns.
Plants within plots	16	$\sigma_s^2 + 4\sigma_t^2$	0.030	2.31 *
Quadrats within plants	96	σ_s^2	0.013	

* significant at $p = 0.05$

Table 11

Number of plants to be sampled for three levels of precision for eggs of C. asparagi, 1974, ($p = .70$).

Mean no. per plant	% S.E.	Numbers required for S.E. of:		
		10%	15%	20%
2.22	29.8	59	26	15
1.61	31.9	67	30	17
1.96	26.3	46	20	12
1.59	34.5	78	35	20
0.51	44.8	132	59	33
0.22	57.8	219	98	55
0.50	47.3	147	65	37
1.20	31.2	64	29	16
4.90	18.8	24	11	6
4.71	21.8	32	14	8
2.32	24.7	40	18	10
1.00	31.2	64	29	16
1.11	29.6	58	26	15
0.77	38.9	99	44	25
0.71	41.5	113	50	29
0.76	43.3	123	55	31
0.73	42.5	118	53	30
2.61	23.5	37	17	10
5.14	23.8	37	17	10
4.49	17.8	21	10	6
1.91	25.3	42	19	11
1.53	30.6	62	28	16
0.50	40.9	110	49	28
0.53	41.3	112	50	28

Table 12

Number of plants to be sampled for three levels of precision for eggs of C. asparagi, 1975, ($p = .70$).

Mean no. per plant	% S.E.	Numbers required for S.E. of:		
		10%	15%	20%
0.56	38.2	96	43	24
3.73	17.3	20	9	5
0.42	46.4	141	63	36
0.38	41.0	110	49	28
0.29	51.7	175	78	44
0.93	30.7	62	28	16
0.19	70.8	328	146	82
0.21	45.0	133	59	34
1.57	44.9	132	59	33
1.00	38.0	95	42	24
4.20	17.7	21	10	6
1.16	34.3	77	35	20
0.48	36.7	88	40	22
0.94	28.9	55	25	14
1.07	29.4	57	26	15
0.80	29.5	57	26	15
0.73	38.1	95	43	24
0.53	40.1	106	47	27
5.36	14.2	14	6	4
2.67	33.0	72	32	18
0.98	51.8	176	78	44
0.54	44.8	132	59	33
0.34	41.3	112	50	28

Table 13

Number of plants to be sampled for three levels of precision for larval period 1 of C. asparagi, 1974, ($p = .70$).

Mean no. per plant	% S.E.	Numbers required for S.E. of:		
		10%	15%	20%
0.65	36.1	85	38	22
0.80	44.9	133	59	33
0.72	35.7	84	37	21
0.25	38.4	97	43	25
0.27	41.4	112	50	28
0.22	44.8	128	57	32
1.43	24.5	40	18	10
1.52	23.8	37	17	10
0.74	31.6	66	30	17
0.78	32.5	70	31	18
0.65	37.2	91	41	23
0.74	34.0	76	34	19
0.40	45.5	136	61	34
0.32	41.2	111	50	28
0.69	33.3	73	33	19
1.53	25.5	43	19	11
1.59	26.3	46	21	12
1.83	21.9	32	14	8
1.97	24.1	38	17	10
0.81	33.5	74	33	19
0.51	41.1	111	50	28
0.58	36.2	86	39	22
0.30	44.9	132	39	33

Table 14

Number of plants to be sampled for three levels of precision for larval period 1 of C. asparagi, 1975, ($p = .70$)

Mean no. per plant	% S.E.	Numbers required for S.E. of:		
		10%	15%	20%
1.02	25.0	41	19	11
0.45	33.9	76	34	19
0.50	23.6	37	17	10
0.25	34.4	78	35	20
0.20	45.8	137	61	35
0.34	38.9	99	44	25
1.58	23.1	35	16	9
1.80	21.1	29	13	8
0.90	24.9	41	18	11
0.42	25.7	44	20	11
0.52	31.1	64	28	16
0.65	21.7	31	14	8
3.01	11.1	9	4	2
2.42	25.9	44	20	11
1.20	36.0	85	38	22
1.14	22.7	34	15	9
0.65	25.6	43	19	11
0.71	28.8	55	25	14
0.16	46.6	143	64	36

Table 15

Number of plants to be sampled for three levels of precision for larval period 2 of C. asparagi, 1974, ($p = .70$).

Mean no. per plant	% S.E.	Numbers required for S.E. of:		
		10%	15%	20%
0.27	41.7	114	51	29
0.34	36.7	89	40	22
0.29	39.8	104	46	26
0.43	34.6	79	35	20
0.13	59.8	235	105	59
0.27	26.4	46	21	12
0.11	33.8	75	34	19
0.15	41.1	111	50	28
0.79	32.0	67	30	17
0.77	26.9	48	21	12
0.34	36.6	88	39	22
0.42	29.2	56	25	14
0.24	35.4	82	37	21
0.15	39.2	101	45	26
0.18	36.9	90	40	23
0.11	35.7	84	38	21
0.43	38.3	96	43	24
0.25	44.8	132	59	33
0.57	45.0	133	59	34
1.00	29.2	56	25	14
0.92	29.4	57	26	15
0.88	32.2	68	30	17
0.68	38.3	96	43	24
0.53	26.4	46	21	12
0.18	50.1	164	73	41

Table 16

Number of plants to be sampled for three levels of precision for larval period 2 of C. asparagi, 1975, ($p = .70$).

Mean no. per plant	% S.E.	Numbers required for S.E. of:		
		10%	15%	20%
0.32	35.2	82	37	21
0.40	32.2	69	31	18
0.95	26.4	46	21	12
0.36	31.3	65	29	16
0.45	28.5	54	24	14
0.23	29.1	56	25	14
0.27	35.7	84	37	21
0.50	19.9	26	12	7
0.25	28.8	55	25	14
0.17	25.6	43	20	11
0.88	14.4	14	7	4
0.85	18.2	22	10	6
0.64	17.9	21	10	6
0.30	33.9	75	34	19
0.36	20.5	28	13	7
0.28	24.8	41	18	11
1.15	16.6	19	8	5
0.94	21.3	30	14	8
1.23	19.6	26	12	7
1.04	30.0	59	27	15
1.01	15.3	16	7	4
1.18	19.0	24	11	6
0.56	38.8	99	44	25

Table 17

Number of plants to be sampled for three levels of precision for adults of C. asparagi, 1974, ($p = .70$)

Mean no. per plant	% S.E.	Numbers required for S.E. of:		
		10%	15%	20%
0.13	30.2	60	27	15
0.21	29.7	58	26	15
0.22	29.8	59	26	15
0.20	35.4	82	37	21
0.18	31.4	65	29	17
0.17	33.9	75	34	19
0.13	42.3	117	52	30
0.08	50.0	164	73	41
0.09	50.3	166	74	42
0.14	44.8	132	59	33
0.53	23.6	37	17	10
0.50	17.6	21	9	6
0.27	25.9	44	20	11
0.23	24.3	39	18	10
0.29	26.5	46	21	12
0.22	29.5	57	26	15
0.25	28.4	53	24	14
0.34	28.0	52	23	13
0.16	36.7	88	40	22
0.18	31.4	65	29	17
0.55	17.5	20	9	5
1.16	18.9	24	11	6
0.75	22.0	32	14	8
0.47	23.9	38	17	10
0.55	22.3	33	15	9
0.28	27.8	51	23	13
0.22	37.3	91	41	23
0.09	41.9	115	51	29
0.26	35.4	82	37	21
0.85	21.2	30	14	8
1.02	21.6	31	14	8
0.91	25.2	42	19	11
0.79	27.0	48	22	12
0.66	25.2	42	19	11

Table 18

Number of plants to be sampled for three levels of precision for adults of C. asparagi, 1975, ($p = .70$)

Mean no. per plant	% S.E.	Numbers required for S.E. of:		
		10%	15%	20%
0.32	21.3	30	14	8
0.24	23.8	37	17	10
0.23	28.2	52	24	13
0.25	22.2	33	15	8
0.21	32.4	69	31	18
0.26	25.0	41	19	11
0.11	41.3	112	50	28
0.11	42.0	116	52	29
0.38	27.6	50	23	13
0.60	20.3	27	12	7
0.27	24.9	41	19	11
0.29	24.3	39	18	10
0.33	19.3	25	11	7
0.26	22.7	34	15	9
0.35	20.9	29	13	8
0.34	17.6	21	9	6
0.66	16.2	18	8	5
1.30	9.2	6	3	2
0.46	16.3	18	8	2
0.24	30.2	60	27	15
0.17	28.4	53	24	14
0.15	31.3	64	29	16
0.11	42.0	116	52	29
0.17	27.5	50	22	13
1.00	17.3	20	9	5
0.91	23.7	37	17	10
0.96	21.9	32	14	8
1.13	21.6	31	14	8
0.65	18.5	23	10	6

Table 19

Comparison of mean time to examine a shoot vs. whole plant (minutes)

Age Interval	Shoot	Whole Plant
Egg	0.37	2.10
Small larval	0.32	1.75
Large larval	0.21	1.00
Adult	0.33	0.27

Cost of moving = .0.25 min.

Table 20

Relative efficiency of sample sizes
(eggs, July 9/1974)

	<u>Sample Size</u>	
	<u>Shoot</u>	<u>Whole Plant</u>
Cost per sample (min)	0.37	2.10
Variance per shoot	4.33	7.21
Relative efficiency	1.00	0.11

Table 21

Comparison of relative efficiency of sample units
for C. asparagi

Age Interval	No. of Samples	More Efficient Sample Unit	
		Shoot	Plant
Egg	47	47	0
Small larval	44	44	0
Large larval	48	48	0
Adult	60	27	33
		<u>Quadrat</u>	<u>4 Quadrats</u>
Pupal case	22	22	0

Table 22

Suggested sampling plan for moderate* infestations
of C. asparagi ($p = .70$, 10% S.E.)

<u>Age interval</u>	<u>Sample unit</u>	<u>Number of units</u>	<u>Cost (man-hours)</u>
Eggs	shoot	320	3.3
Larvae			
Period I	shoot	480	4.6
Period II	shoot	448	3.4
Pupal case	quadrat	160	28.2 **
Adults	whole plant	320	2.8

*viz; 5, 3, 1 and 1 eggs, larvae and adults per plant
respectively, and .25 pupal cases per quadrat.

** 20% S.E.

Fig. 5-8 Raw field data for the above
ground stages of one sample day.

SAMPLE NO: 15

BLOCK: A

DATE: July 12/74

S	E	I	II	III	IV	A	S	E	I	II	III	IV	A
2							1						
11							6						1
9							8						
5							4						
7							8						1
5					4 5		5					3 4	
6							10						
4			3		4		3						
5							5						
9							10						
9							7	2	7				
7							5						
7							8						
6				5 4	3		7						

SAMPLE NO: 15

BLOCK: B

DATE: July 12/74

S	E	I	II	III	IV	A	S	E	I	II	III	IV	A
2							1						
6							10						
6							6						
4							5						2
5	8 6 5	5 4 4				5	8			6 7			
5							5						3
6							5						
4							3						
12							9						
7							8						
9					4		9						
4							5						
5							6	5 3					
4		1					6				5		

2 2

OF/DE

SAMPLE NO: 15

BLOCK: C

DATE: July 12/74

	S	E	I	II	III	IV	A	S	E	I	II	III	IV	A
2								1						
6								6						
6								5						2
6	7 3	4	7				1	7						
6							1 1	6			8 5			
7	11		6					8						3
5								7						
4								3	9					
8								5						
6								5						
5								5					3	
7								12						
5								5						
								6						

SAMPLE NO: 15

BLOCK: D

DATE: July 12/74

S	E	I	II	III	IV	A	S	E	I	II	III	IV	A
2							1						
6							9						
5					3		5						
5							8						
8							9						
5	6					2	9						
7							6	5					1
6							5						
5	8						13						
5			5 3 3				8						
9							6	6 6	4				2
6							6						
6							6						

Fig. 9 Relationship between population density
and numbers of plants per plot required for
specified confidence limits in sampling for

C. asparagi eggs.

Fig. 10 Relationship between population density
and numbers of plants per plot required for
specified confidence limits in sampling for
C. asparagi small larvae.

Fig. 11 Relationship between population density
and numbers of plants per plot required for
specified confidence limits in sampling for
 C. asparagi large larvae.

Fig. 12 Relationship between population density
and numbers of plants per plot required for
specified confidence limits in sampling for
C. asparagi adults.

Fig. 13 Relationship between population density
and numbers of quadrats per plot required for
specified confidence limits in sampling for
C. asparagi pupae.

SECTION IV. MAJOR MORTALITY FACTORS
IN THE LIFE SYSTEM OF C. asparagi

INTRODUCTION

Life tables were initially devised for studies of human populations. They are still used by actuaries to form stochastic models of longevity. However, a life table in this form is neither applicable nor desirable in the study of animal populations.

In 1933 Leopold discussed "life equations" and was the first author to apply the concept of a life table to natural populations. E.C. Deevey (1947) wrote a lengthy paper applying the techniques to animal populations in nature. He illustrated three ways in which they could be developed: (1) Cases where the age at death (dx) is directly observed for a large and reasonably random sample of the population; (2) cases where the survival (lx) of a large cohort (born more or less simultaneously) is followed at fairly close intervals throughout its existence; (3) cases where the age structure is obtained from a random sample of the population, and dx is inferred from the shrinkage between successive age classes. The first and third cases can be used only if the population is stable in time. The result is a time specific (or vertical) life

table. The second case results in an age specific (or horizontal) life table which is the type more commonly seen in studying animal species, especially those of economic importance. This type of life table is based on the fate of a real cohort, conveniently the members of a population belonging to a single generation. The population may be stationary or fluctuating. Morris and Miller (1954) were the first workers to prepare life tables for the study of insect populations. In their classic paper on the development of life tables for the spruce budworm, they introduced a modification of Deevey's second method in which survivorship is measured by periodic sampling of the same population but not the same individuals. Survivorship figures are consequently subject to a sampling error and this is the major difference between a laboratory life table and one based on field data.

Morris and Miller also made a number of innovations in the format of the life table. Since birth itself is not an age of universal equivalence, apart from the placental mammals, they measured mortality from the fertilized ovum to obtain a broader view of comparative mortality. The major difference was that they emphasized the causes of mortality and therefore they inserted a new column "dxF" (mortality)

factor responsible for the corresponding dx) immediately to the left of the dx column. Whereas the age intervals (x column) in human life tables are generally equal, this is not practical with insects since population measurement is not always possible owing to mobility. Therefore the age intervals represent the major stages in the life history of the insect with such subdivisions as are feasible.

Conventionally, the l_x column considered was a cohort of 1000 individuals. However, Morris and Miller stressed how the effect of each mortality factor varied with changes in the population density of the insect and thus they recommended that l_x represent actual population figures in terms of some absolute sampling unit. Similarly q_x , which is generally given in human tables as 1000 q_x , is more conveniently given as 100 q_x , ie. percentage mortality. They also incorporated the concept of Balch and Bird (1944), Index of Population Trend, which is simply l_x for the new generation expressed as a percentage of l_x for the old generation, at the same point in the life cycle.

Leopold (1933) introduced the idea of subtracting known factors of mortality from the known annual increment to determine factors of mortality in between,

which did not lend themselves to direct measurement. Morris and Miller incorporated this into their life tables as well as other factors in the dx column to balance the table eg. decreases or increases in population due to unequal sex ratio, loss of fecundity due to reduced body size, migration, mortality of females prior to completion of oviposition, and mating failure. Some of these factors are measured as the difference between expected and actual number of eggs. Morris and Miller based the expected numbers of eggs on the mean number of eggs laid by females of normal size, protected from predators, but under field conditions. They did not use values such as "biotic potential" or "reproductive potential" as defined by Chapman (1931).

The following column headings were proposed by Morris and Miller (1954) and by Morris (1963):

- x - Age interval at which the sample was taken.
- l_x - The number alive at the beginning of the age interval.
- dx - The number dying during the age interval.
- dx_F - The mortality factor responsible for dx .
- $100 q_x$ - Percentage mortality.
- s_x - Survival rate within x .

THE INTEGRATION OF DATA

While field counts serve to provide a reading of the number of insects present at a given point in time, one cannot properly estimate the total population that passes through a stage without integrating the data. To carry out this process, information is needed on rates of development in relation to temperature.

A number of methods of integration have been developed, depending on what aspect of the population one wishes to determine. Southwood and Jepson (1962) have outlined a procedure that will give an approximation of the total population that reaches the median of the age interval. Richards and Waloff (1954) developed a method to determine the number entering a stage. Waloff and Baker (1963) presented a method of estimating the total population change due to migration, and Dempster (1961) has supplied a means of assessing rates of mortality and migration in a population.

The procedure adopted for integrating counts of the egg and larval stages of C. asparagi was that of Southwood and Jepson. When using their method successive field counts are plotted on a graph as shown in the example illustrated in Fig 14.

Podoler and Rogers Method

Podoler and Rogers (1975) have expressed dissatisfaction with the graphical key factor method since it does not provide a quantification of the mortality. They outlined a new method to select the set of values which contributed most to changes in total mortality. Their method is to regress k on K : the submortality with the largest regression coefficient is, by definition, the key factor. They proposed that this new method could be usefully employed to follow the graphical presentation of life table data and could identify the key factor in a less arbitrary way than previous correlation methods.

The method of Podoler and Rogers was applied to the data, (Figs. 17,18). As expected, the submortalities corresponding most closely with the changes in total mortality are k_1 and k_4 , and the relationship between K and $k_1 + 4$ again gives the best fit. Furthermore, since the slope of the regression of $k_1 + 4$ has a value of ca. 1.0, then changes in the individual k -value almost exactly reflect changes in total K . (Podoler and Rogers, 1975).

Since this species is trivoltine in eastern Ontario (Taylor and Harcourt, 1978) it was possible to develop three life tables a year. Accordingly, seven consecutive life tables were developed between August 1973 and September, 1975 (Tables 23-29).

Eggs

lx was based on integration of the sample counts. To determine viability, samples of 100 eggs from each generation were brought to the laboratory and reared at 25°C and 80% R.H. The dx value was obtained from the percentage that were inviable. Mortality caused by predators was classified according to appearance. Eggs attacked by T. asparagi are characteristically collapsed inwards and those preyed upon by coccinellids are torn from the spears or leaves, leaving only the basal parts attached to the substrate. Hatched eggs, on the other hand, have the top of the egg removed where the larva has emerged.

• The dx value for T. asparagi was obtained by careful scrutiny of all eggs observed on two sample days during each generation. The dx value for coccinellid predation was determined by subtraction.

At no time was egg cannibalism observed. In fact, adults kept in a cage with no food did not eat their eggs.

Larvae, Period 1

This interval consists of instars 1 and 2. lx was based on integration of the sample counts. dx for predation was determined by subtracting the lx value for Period 2 from that of Period 1. No mortality was caused by disease and deaths due to rainfall were so few as to be obscured by the sampling error. Larvae parasitized by T. asparagi survived to the next stage.

Larvae, Period 2

This interval consists of instars 3 and 4. lx was based on integration of the sample counts. Again, dx for predation was determined by subtracting the lx value for pupal cases from that of Period 2. Once more, no disease was found, deaths due to rainfall were insignificant, and parasitized larvae survived to the next stage.

Pupal Cases

For purposes of life table construction, counts of the pupal cases were averaged for each generation.

To obtain data on mortality rates, the pupal cases were kept at room temperature for several days prior to laboratory examination. They were then classified as sound or parasitized. Sound cases contained healthy pupae, adult beetles, or already had been vacated by the adult which removes one end of the pupal case. Parasitized cases contained T. asparagi or had been vacated by this parasite leaving a small emergence hole at one end. In each generation a small additional percentage of cases contained shrivelled larvae; reasons for their death were unknown and hence, attributed to physiological causes.

Because the pupal cases were recorded on an area basis it was necessary to convert these counts to a common denominator for purposes of life table construction. Since the area covered by the canopy of a plant averaged 7.5 square feet the following conversion was used:

average count $(7.5 \times 96)/128 = \text{average count} \times 5.625$

The converted data were incorporated directly into the life tables.

Adults

The lx value for adults was estimated indirectly as the product of pupal case density and survival rate for this interval. These data compared favourably to actual counts of the adults; discrepancies reflected migration to and from the plots.

Major Mortality Factors

Parasitoid

Tetrastichus asparagi has an unusual relationship with C. asparagi in that it both eats and oviposits in the eggs. The parasitoid larvae develop slowly within the host larva, finally devouring the mature larva just prior to pupation. This behaviour provides an unusual opportunity to study the impact of a single agent on two distinct stages of its host (egg and pupal case). The fact that the two stages are separated by the larval period makes the study even more unique.

Predators

Coccinellids, mainly of the genus Hippodamia, are important predators of the small larvae, although the eggs and larger larvae are attacked as well. Pentatomids were also frequently observed to prey on the larvae, which they impale on their beaks.

Frost

The numbers of adults found in hibernation were consistent with expectations based on the peak numbers for the third generation in each year, indicating that

the adults do not leave the field for purposes of wintering. Winter mortality was very consistent over over three winters, being 52.1, 52.5 and 48.1 per cent for 1973, 1974 and 1975 respectively.

Even though frost kills a high proportion of the adults each winter, this factor has little or no predictive value since it is very consistent and hence, unrelated to population fluctuation. Since the species is trivoltine in this area, frost only affects every third generation.

Analysis of Life Table Data

The life table data were analysed to identify the stage(s) in the life cycle that made the greatest contribution to population trend. Following Watt (1963) and Morris (1963), within-generation survival (SWG) was expressed as the product of the individual survival rates:

$$SWG = SE \cdot SL_1 \cdot SL_2 \cdot Sp$$

where SE = survival of eggs; SL_1 = survival of larvae in Period 1; SL_2 = survival of larvae in Period 2; and Sp = survival of pupae.

Thus, $.0769 = (.7604) (.3499) (.6351) (.4552)$,
(Table 23).

Components Method

To determine which of the components in the equation was most responsible for variation in intrageneration survival, a series of correlation analyses was carried out relating S_{WG} (Y) to each of the age interval survivals (X) using the formula:

$$r^2 = \frac{[\sum XY - (\sum X \sum Y)/n]^2}{[\sum X^2 - (\sum X)^2/n][\sum Y^2 - (\sum Y)^2/n]}$$

The coefficient of determination (r^2) gives the proportion of total variance contributed by the various age intervals.

The results of the correlation analyses are summarized in Table 30. There was no significant correlation between the survival in the larval age intervals and within-generation survival (S_{WG}). There were, however, significant correlations between S_{WG} and survival of eggs and pupal cases. Hence, T. asparagi may be regarded as the key factor that explains fluctuations in intrageneration survival.

Graphical Key Factor Method

The components method determines the relative importance of the different age intervals by the degree of simple linear correlation between the separate components (S_x) and survival (S_{WG}), the dependent variable. This approach has been criticized on both biological and mathematical grounds by Varley and Gradwell (1970) who point out that correlation analysis is valid only when there is no intercorrelation between the variables. In biological systems such intercorrelations are widespread. Increases in population density will often be accompanied by increases in percentage mortality caused by agents such as predators and disease. Such covariance could invalidate the use of any straightforward statistical analysis (Mott, 1966).

Varley and Gradwell (1960, 1963, 1968) have therefore adopted an alternative method which relies heavily on graphical correlation. Using Haldane's equation for total mortality in a generation, $K = k_1 + k_2 + \dots + k_n$, they calculated a k value for each mortality factor based on the difference

between common logarithms of numbers per unit area before and after its action. When these data are plotted against time, the contribution of each mortality factor to the variation in K can be seen. Alternatively, the correlation coefficients can be calculated (Harcourt, 1971) (Table 38).

Application to C. asparagi is as follows:

k_1 = mortality of eggs.

k_2 = mortality of Period 1 larvae.

k_3 = mortality of Period 2 larvae.

k_4 = mortality of pupal cases.

k_{1+4} = mortality of eggs plus pupal cases.

The budgets prepared for Varley-Gradwell's method are shown in Tables 31-37. Using these k values for the different age intervals, changes in total K for each generation were plotted. Fig. 15 shows that when total K and the two larval periods are plotted, no obvious visual correlation is evident. However, the graphs of the eggs and pupal cases (Fig. 16) show a definite visual trend with K , indicating that these three curves are related. A still better fit is obtained by plotting K against $k_1 + 4$.

Table 38 summarizes the key factor data and gives the results of correlation analyses between K and the various submortalities. It is apparent that the Varley-Gradwell method yields exactly equivalent results to the method of components. Hence, by either criterion, T. asparagi is clearly the key factor.

Podoler and Rogers Method

Podoler and Rogers (1975) have expressed dissatisfaction with the graphical key factor method since it does not provide a quantification of the mortality. They outlined a new method to select the set of values which contributed most to changes in total mortality. Their method is to regress k on K : the submortality with the largest regression coefficient is, by definition, the key factor. They proposed that this new method could be usefully employed to follow the graphical presentation of life table data and could identify the key factor in a less arbitrary way than previous correlation methods.

The method of Podoler and Rogers was applied to the data, (Figs. 17,18). As expected, the submortalities corresponding most closely with the changes in total mortality are k_1 and k_4 , and the relationship between K and $k_1 + k_4$ again gives the best fit. Furthermore, since the slope of the regression of $k_1 + k_4$ has a value of ca. 1.0, then changes in the individual k -value almost exactly reflect changes in total K . (Podoler and Rogers, 1975).

Discussion

The key factor concept was introduced by Morris (1959, 1963) who used the term to describe the factor mainly responsible for variation in abundance from one generation to the next. This study supports the viewpoint of Morris (1957) that variable (as opposed to consistently high) mortalities are most often the factors that determine population trend. They are also the most useful in predictive models.

In this study, it is apparent that overall mortality is controlled by the magnitude of mortality during two age intervals. This is unusual because in most animals, one stage in the life cycle controls generation mortality (Harcourt and LeRoux, 1967; Podoler and Rogers, 1975). To the knowledge of the writer, this is the first life table study to document the impact of a single key factor on two widely separated stages.

Conclusion

Based on the three methods of analysis of the life tables constructed, it can be concluded that the Eulophid parasitoid M. asparagi was the key factor governing intrageneration population trends of the asparagus beetle in Richmond, Ontario for the seven generations from August 1973 to September 1975. This parasitoid produced mortality in two stages of the life cycle that significantly correlated with overall mortality.

General Discussion

Damage caused by the asparagus beetle to fresh market asparagus in early spring, is primarily cosmetic since the presence of eggs and adult scarification is superficial and does not reduce yield or nutritional value. Based on observations made during this study it is concluded that populations of less than two adults per plant do not result in significant damage to the spears. However, the asparagus beetle often reaches populations of up to 12 adults per plant and these higher populations result in severe losses.

At no time during the course of studies at Richmond, Ontario from 1971 to 1976 was a population density greater than 1.6 adults per plant recorded. This is well below the economic threshold level. However, during a preliminary survey carried out by the writer in 1971-1972, counts in commercial fields near Collingwood, Ontario and St. Jean, Quebec often showed means of 2-12 adults per plant. This is significantly above the economic threshold. Furthermore, percent parasitism at Richmond averaged 40.4 percent but based on 249 pupal cases collected near St. Jean, the rate of parasitism was only 12.0 percent. It is entirely possible that the high population levels of the asparagus beetle observed in the commercial fields resulted from suppression of T. asparagi by the widespread use of methoxychlor, malathion and carbaryl which are applied routinely to control the spring adults.

Recommendations

1) Commercial growers of asparagus should be advised about the necessity and timing of insecticide applications so as to minimize the impact on the parasitoid T. asparagi. For this purpose a monitoring system to detect economic infestations could be derived from the sampling data reported herein; timing of sprays would reflect seasonal dynamics of the host and parasitoid.

2) Pesticides registered for use on asparagus should be screened for toxicity to the parasitoid T. asparagi and spray calendar recommendations should be based on those with minimum toxicity.

3) Superficial insect damage should not be considered a factor in grading asparagus and consumers should be educated to accept superficial damage in light of the disadvantages of cosmetic spraying.

4) Old asparagus stems should be destroyed each fall since they serve as overwintering sites for the adult beetles. The best method would be to swirl cut the stems late in the fall when it is too cold for the beetles to seek new refuge. This would not affect the parasitoid since it overwinters in the subterranean pupal case of its host. Flaming may be an alternative but would result in loss of organic matter, erosion and loss of cover for beneficial insects.

Table 23

Life table for 3rd generation of C. asparagi on
asparagus, Richmond, Ontario, 1973
(numbers calculated to common base of 96 plants)

X	1X	dxF	dx	100qx	sx
Eggs	793	Infertility	16	2	
		<u>T. asparagi</u>	143	18	
		Coccinellids	<u>31</u>	<u>4</u>	
		TOTAL	190	24	.7604
Larval Period 1	603	Predators	392	65	.3499
Larval Period 2	211	Predators	77	36	.6351
Pupal Cases	134	<u>T. asparagi</u>	62	46	
		Physiological	<u>11</u>	<u>8</u>	
		TOTAL	73	54	.4552
Adults	61				

SWG = .0769

Table 24

Life table for 1st generation of C. asparagi on
asparagus, Richmond, Ontario, 1974
(numbers calculated to common base of 96 plants)

X	lx	dxF	dx	100qx	sx
Eggs	239	Infertility	5	2	
		<u>T. asparagi</u>	105	44	
		Coccinellids	<u>20</u>	<u>8</u>	
		TOTAL	130	54	.4561
Larval Period 1	109	Predators	73	67	.3303
Larval Period 2	36	Predators	0	0	1.0000
Pupal Cases	36	<u>T. asparagi</u>	26	72	
		Physiological	<u>0</u>	<u>0</u>	
		TOTAL	26	72	.2778
Adults	10				

SWG = .0419

Table 25

Life table for 2nd generation of C. asparagi on
asparagus, Richmond, Ontario, 1974
(numbers calculated to common base of 96 plants)

X	lx	dxF	dx	100qx	sx
Eggs	1052	Infertility	53	5	
		<u>T. asparagi</u>	484	46	
		Coccinellids	3	8	
		TOTAL	620	59	.4106
Larval Period 1	432	Predators	338	78	.2176
Larval Period 2	94	Predators	12	13	.8723
Pupal Cases	82	<u>T. asparagi</u>	51	62	
		Physiological	10	12	
		TOTAL	61	74	.2561
Adults	21				

SWG = .0200

Table 26

Life table for 3rd generation of C. asparagi on
 asparagus, Richmond, Ontario, 1974
 (numbers calculated to common base of 96 plants)

X	lX	dxF	dx	100qx	sx
Eggs	849	Infertility	8	1	
		<u>T. asparagi</u>	272	32	
		Coccinellids	<u>29</u>	<u>3</u>	
		TOTAL	309	36	.6360
Larval Period 1	540	Predators	411	76	.2389
Larval Period 2	129	Predators	19	15	.8527
Pupal Cases	110	<u>T. asparagi</u>	28	25.5	
		Physiological	<u>6</u>	<u>5.5</u>	
		TOTAL	34	31	.6909
Adults	76				

SWG = .0895

Table 27

Life table for 1st generation of C. asparagi on
asparagus, Richmond, Ontario, 1975
 (numbers calculated to common base of 96 plants)

X	lx	dxF	dx	100qx	sx
Eggs	385	Infertility	12	3	
		<u>T. asparagi</u>	85	22	
		Coccinellids	<u>17</u>	<u>4</u>	
		TOTAL	114	29	.7039
Larval Period 1	271	Predators	175	65	.3542
Larval Period 2	96	Predators	26	27	.7292
Pupal Cases	70	<u>T. asparagi</u>	27	38.6	
		Physiological	<u>6</u>	<u>8.6</u>	
		TOTAL	33	47	.5286
Adults	37				

SWG = .0961

Table 28

Life table for 2nd generation of C. asparagi on
asparagus, Richmond, Ontario, 1975
(numbers calculated to common base of 96 plants)

X	1X	dxF	dx	100qx	sx
Eggs	800	Infertility	8	1	
		<u>T. asparagi</u>	208	26	
		Coccinellids	<u>29</u>	<u>4</u>	
		TOTAL	245	31	.6938
Larval Period 1	555	Predators	431	78	.2234
Larval Period 2	124	Predators	14	11	.8871
Pupal Cases	110	<u>T. asparagi</u>	28	25.5	
		Physiological	<u>6</u>	<u>5.5</u>	
		TOTAL	34	31	.6909
Adults	76				

SWG = .0950

Table 29

Life table for 3rd generation of C. asparagi on
asparagus, Richmond, Ontario, 1975
(numbers calculated to common base of 96 plants)

X	lx	dxF	dx	100qx	sx
Eggs	931	Infertility	19	2	
		<u>T. asparagi</u>	55	6	
		Coccinellids	<u>8</u>	<u>1</u>	
		TOTAL	82	9	.9119
Larval Period 1	849	Predators	675	78	.2049
Larval Period 2	174	Predators	41	24	.7644
Pupal Cases	133	<u>T. asparagi</u>	32	24	
		Physiological	<u>6</u>	<u>5</u>	
		TOTAL	38	29	.7143
Adults	95				

SWG = .1020

Table 30

Analysis of seven life tables of C. asparagi
using the components method

S_{WG}	S_E	S_{L1}	S_{L2}	S_P
.0769	.7604	.3499	.6351	.4552
.0419	.4561	.3303	1.0000	.2778
.0200	.4106	.2176	.8723	.2561
.0895	.6360	.2389	.8527	.6909
.0961	.7039	.3542	.7292	.5286
.0950	.6938	.2234	.8871	.6909
<u>.1020</u>	<u>.9119</u>	<u>.2049</u>	<u>.7644</u>	<u>.7143</u>
r^2	.7713*	-.0006	.2284	.8418*

*Significant at $p = .05$

Table 31

A budget prepared for Varley and Gradwell's analysis
for 3rd generation of C. asparagi, Richmond, Ont. 1975

	Number per 96 plants	Log number per 96 plants	K-values
Eggs	931	2.96895	
k ₁ (infertility, <u>T. asparagi</u>)			0.04004
Larval Period 1	849	2.92891	
k ₂ (predation)			0.68836
Larval Period 2	174	2.24055	
k ₃ (predation)			0.11670
Pupal Cases	133	2.12385	
k ₄ (<u>T. asparagi</u> , physiological)			0.14613
Adults	95	1.97772	
Total K			0.99123

Table 32

A budget prepared for Varley and Gradwell's analysis
for 2nd generation of C. asparagi, Richmond, Ont. 1975

	Number per 96 plants	Log number per 96 plants	K-values
Eggs	800	2.90309	
k ₁ (infertility, <u>T. asparagi</u>)			0.15880
Larval Period 1	555	2.74429	
k ₂ (predation)			0.65087
Larval Period 2	124	2.09342	
k ₃ (predation)			0.05203
Pupal Cases	110	2.04139	
k ₄ (<u>T. asparagi</u> , physiological)			0.16058
Adults	76	1.88081	
Total K			1.02228

Table 33

A budget prepared for Varley and Gradwell's analysis
for 1st generation of C. asparagi, Richmond, Ont. 1975

	Number per 96 plants	Log number per 96 plants	K-values
Eggs	385	2.58546	
k ₁ (infertility, <u>T. asparagi</u>)			0.15249
Larval Period 1	271	2.43297	
k ₂ (predation)			0.45070
Larval Period 2	96	1.98227	
k ₃ (predation)			0.13717
Pupal Cases	70	1.84510	
k ₄ (<u>T. asparagi</u> , physiological)			0.27690
Adults	37	1.56820	
Total K			1.01726

Table 34

A budget prepared for Varley and Gradwell's analysis
for 3rd generation of C. asparagi, Richmond, Ont. 1974

	Number per 96 plants	Log number per 96 plants	K-values
Eggs	849	2.92891	
k ₁ (infertility, <u>T. asparagi</u>)			0.19652
Larval Period 1	540	2.73239	
k ₂ (predation)			0.62180
Larval Period 2	129	2.11059	
k ₃ (predation)			0.06920
Pupal Cases	110	2.04139	
k ₄ (<u>T. asparagi</u> , physiological)			0.16058
Adults	76	1.88081	
Total K			1.04810

Table 35

A budget prepared for Varley and Gradwell's analysis
for 2nd generation of C. asparagi, Richmond, Ont. 1974.

	Number per 96 plants	Log number per 96 plants	K-values
Eggs	1052	3.02202	
k ₁ (infertility, <u>T. asparagi</u>)			0.38654
Larval Period 1	432	2.63548	
k ₂ (predation)			0.66235
Larval Period 2	94	1.97313	
k ₃ (predation)			0.05932
Pupal Cases	82	1.91381	
k ₄ (<u>T. asparagi</u> , physiological)			0.59159
Adults	21	1.32222	
Total K			1.69980

Table 36

A budget prepared for Varley and Gradwell's analysis
for 1st generation of C. asparagi, Richmond, Ont. 1974

	Number per 96 plants	Log number per 96 plants	K-values
Eggs	239	2.37840	
k ₁ (infertility, <u>T. asparagi</u>)			0.34097
Larval Period 1	109	2.03743	
k ₂ (predation)			0.48113
Larval Period 2	36	1.55630	
k ₃ (predation)			0.00000
Pupal Cases	36	1.55630	
k ₄ (<u>T. asparagi</u> , physiological)			0.55630
Adults	10	1.00000	
Total K			1.3784

Table 37

A budget prepared for Varley and Gradwell's analysis
for 3rd generation of C. asparagi, Richmond, Ont. 1973

	Number per 96 plants	Log number per 96 plants	K-values
Eggs	793	2.89927	
k ₁ (infertility, <u>T. asparagi</u>)			.11895
Larval Period 1	603	2.78032	
k ₂ (predation)			.45604
Larval Period 2	211	2.32428	
k ₃ (predation)			.19718
Pupal Cases	134	2.12710	
k ₄ (<u>T. asparagi</u> , physiological)			.34177
Adults	61	1.78533	
Total K			1.11394

Table 38

Analysis of seven life tables of C. asparagi
using the key factor method

K	=	k ₁	k ₂	k ₃	k ₄	k ₁₊₄
1.11394		.11895	.45604	.19718	.34177	.46072
1.37840		.34097	.48113	.00000	.55630	.89727
1.69980		.38654	.66235	.05932	.59159	.97813
1.04810		.19652	.62180	.06920	.16058	.35710
1.01726		.15249	.45070	.13717	.27690	.46616
1.02228		.15880	.65087	.05203	.16058	.31938
<u>.99123</u>		<u>.04004</u>	<u>.68836</u>	<u>.11670</u>	<u>.14613</u>	<u>.18617</u>
r ²		.80809*	.00843	.18994	.83431*	.86921*

*Significant at p = .05

Fig. 14 The determination of the total number of individuals in the small larval stage from a series of estimates, by graphical summation (Southwood and Jepson, 1962). Data are from generation 2, 1974. The area of one small larva-day equals 5 sq. mm.

Area under curve = 11476.0 sq mm
 . . Total number of stage days = $\frac{11476.0}{5}$

Mean temperature June 24-July 29 = 20.1

Time for development at 20.1°C = 5.31

. . . Actual number of small larvae in
 stage = $\frac{2295.1}{5.31} = 432.2$

Fig. 15 Visual comparison of the relationship
between total mortality (K) and age interval
mortalities for small larvae (k_2) and large
larvae (k_3) values for seven generations of C.
asparagi using the method of Varley and Gradwell.

Fig. 16 Visual comparison of the relationship between total mortality (K) and age interval mortalities for eggs (k_1) pupae (k_4) and eggs plus pupae (k_{1+4}) for seven generations of C. asparagi using the method of Varley and Gradwell

Fig. 17 Plot of the k-values for individual
submortalities against total K.

Fig. 18 Plot of $k_1 + 4$ for sum of
egg and pupal mortalities against total K

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