

SEASONAL CHANGES IN ABUNDANCE OF THE PEA APHID  
AND ITS ASSOCIATED PARASITES  
IN THE SOUTHERN INTERIOR OF BRITISH COLUMBIA

by

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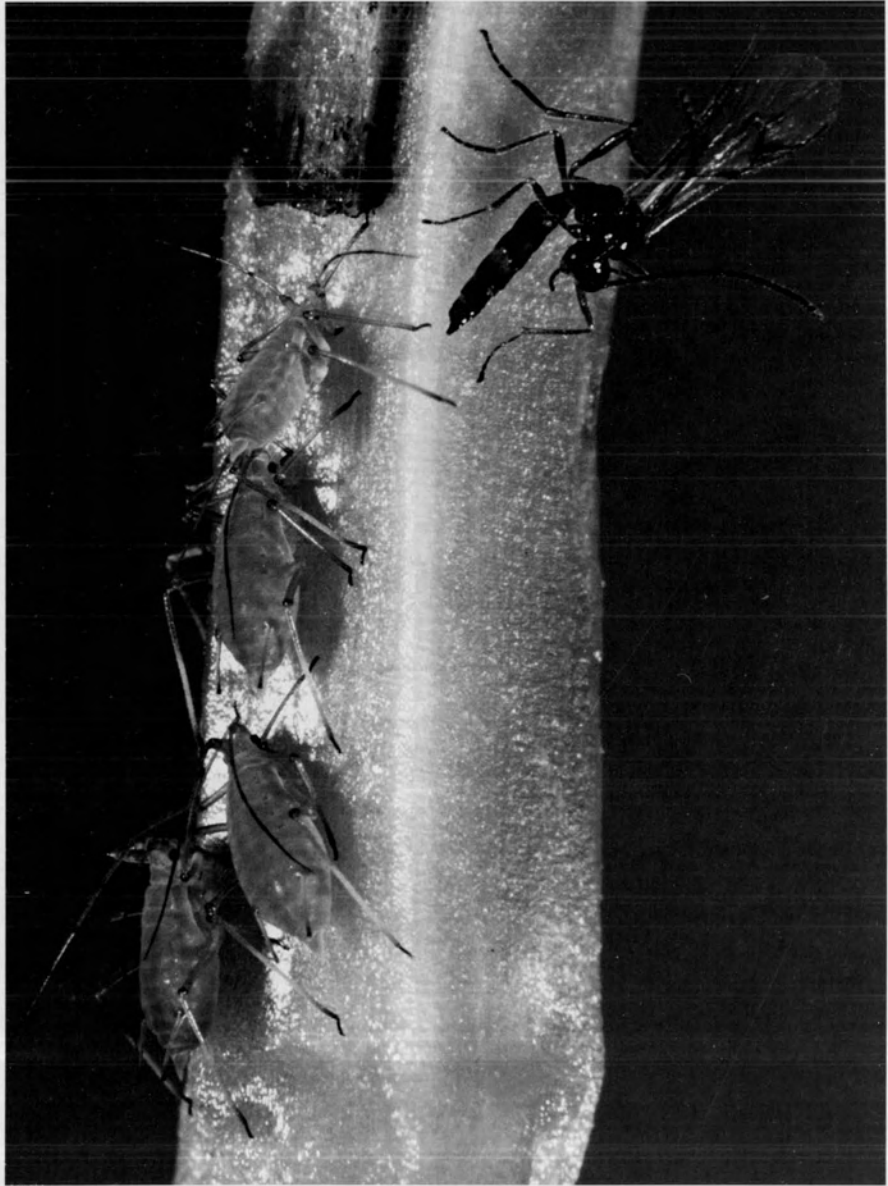
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## ABSTRACT

The study estimates the relative abundance and distribution of four hymenopterous parasites of the pea aphid, *Acyrtosiphon pisum*, in southern British Columbia. The four parasites are: *Aphidius ervi ervi* and *A. smithi*, which were introduced into North America from Europe and India, respectively, and the native *A. e. pulcher* and *Fraon pequodorum*. The effectiveness of the parasites, in particular that of the exotic *A. smithi*, in controlling the pea aphid is evaluated. Life table characteristics, such as the developmental and reproductive rates, of the pea aphid and its associated parasites were determined under laboratory conditions.

In the field, pea aphid populations increased rapidly during early alfalfa growth, but aphid densities generally levelled off and sometimes declined before each crop was cut. Weather conditions subsequent to hay harvesting influenced aphid recovery. Mild weather after the first crop allowed rapid aphid population recovery, while hot and dry weather after the second crop decimated aphid and parasite populations. The numbers of parasitized and unparasitized aphids surviving from the previous crop and the numbers of immigrant alatae were important factors in determining the peak density of aphid populations in alfalfa fields.

Aphidiid parasites appeared to be the most important natural enemies of the pea aphid in the Kamloops area. *Aphidius smithi* was the numerically dominant parasite under hot, dry climatic conditions in the Interior of British Columbia, while *A. e. ervi* was numerically dominant under the relatively wet and mild climatic conditions of the lower Fraser Valley. All parasite species showed a density dependent response to changes in aphid abundance. On occasion, the density dependent response was masked by the early spring emergence of parasites from diapause, by the immigration of

large numbers of adult parasites from neighbouring fields, or by harvesting practices.

Low spring temperatures affected the developmental rates of the different parasites in a different way. *Aphidius smithi* and *A. e. pulcher* develop at lower temperatures than *Praon pequodorum* and therefore appeared earlier in spring. Discrete generations, and their coincidence with the availability of suitable hosts, caused changes in the abundance of parasite species during the first spring crop. However, with increasing temperatures in summer and parasite responses to aphid population growth there was an overlapping of parasite generations. This resulted in a steady mean contribution of 70 to 80% by *A. smithi*, 13 to 20% by *A. e. pulcher*, and 5 to 10% by *P. pequodorum* to aphid parasitism rates during the second and third crops.

Hyperparasites did not have a major effect on the growth periods of the parasite populations, as during these periods hyperparasitism of parasitized aphids rarely exceeded 15 to 40%. After aphid and parasite populations had peaked hyperparasitism sometimes increased rapidly to 70 to 85%. This was probably due to a reduction in the numbers of parasitized hosts rather than to an increase in hyperparasite abundance.

The high rate of parasitism of the aphid fundatrix generation during spring, 1972, was important in reducing aphid population growth and numbers during the rest of the season. Parasites, especially *A. smithi*, effectively contributed to the biological control of the pea aphid in Kamloops during 1971 and 1972.

A simulation model constructed from field and laboratory data predicted aphid and parasite population growth and age structures up to the peak population levels. However, the model was unable to predict the decline in aphid numbers to levels actually experienced in the field. The model was

useful in placing particular research results in perspective and in suggesting areas for further research. ' .

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CHAPTER I  
GENERAL INTRODUCTION

A. The Problem

The pea aphid, *Acyrtosiphon pisum* (Harris) (Homoptera: Aphididae), was accidentally introduced into North America prior to the 20th century and has since become widely distributed (Campbell, 1926; Cooke, 1883; Davis, 1915). It has become a pest on crops such as canning peas (*Pisum sativum* L.) and alfalfa (*Medicago sativa* L.) grown for seed and hay. Beirne (1972) reviewed the pest status of the pea aphid in Canada. Although the pea aphid is known to be a vector of some 20 plant viruses (Kennedy *et al.*, 1962), it may also damage crops directly when abundant. Infestations usually occur in localized areas, causing a loss of up to 20% of proteins, carotene, and dry matter in alfalfa yield (Kindler *et al.*, 1971). Severe pea aphid outbreaks can cause the alfalfa leaves to wilt and turn yellow as well as reduce flowering and cause heavy blossom drop (Harper, 1972).

Attempts to control the pea aphid by biological means have included: (1) the use of resistant alfalfa varieties (Cartier *et al.*, 1965; Kehr *et al.*, 1968; Pimentel and Wheeler, 1973); (2) the modification of harvesting practices to increase the probability of survival of mortality agents of the pea aphid (van den Bosch *et al.*, 1967); and (3) the importation of several parasite species belonging to the family Aphidiidae (Hymenoptera) into North America to supplement the impact of indigenous parasites (Mackauer, 1971).

Hagen and van den Bosch (1968) considered the introduced Indian parasite *Aphidius smithi* Sharma and Subba Rao as a major controlling agent of the pea aphid in most alfalfa-growing areas of California (Hagen and

Schlinger, 1960; van den Bosch *et al.*, 1966). Hagen and van den Bosch (1968) also listed *A. smithi* as one of the most successful biological control agents of *A. pisum* to date. *A. smithi* and another introduced parasite from Europe, *Aphidius ervi ervi* Haliday, have become established in the eastern United States and in Canada, as well as in the Pacific Northwest (Halfhill *et al.*, 1972; Mackauer, 1971); however, the degree of biological control varies from one geographic area to another and the parasite complex present.

The pea aphid is distributed throughout southern British Columbia. It is considered a pest of canning peas in the Lower Fraser Valley (Arrand, 1959) and of alfalfa in the Peace River district and the Thompson and Okanagan River Valleys in southern British Columbia (Arrand and Neilson, 1958). Alfalfa is the most important forage crop in the interior of British Columbia (Hubbard and Mclean, 1961) and is grown mainly to produce hay and silage for dairy and feeder cattle.

Little is known of the aphid's seasonal population fluctuations in British Columbia. Neither is there information on the natural mortality agents that may be involved in the aphid's control. Indeed, there have been no attempts made in British Columbia to manage pea aphid populations except by pesticide applications. This contrasts with Oregon and Washington, where an extensive campaign was waged to mass release *A. smithi* and *A. e. ervi* during the past decade. This campaign resulted in the successful establishment of both parasite species in the northwestern United States (Halfhill *et al.*, 1972). As a consequence of these releases *A. smithi* and *A. ervi* have spread northwards from the northwestern United States and are now established in British Columbia (Mackauer and Campbell, 1972).

## B. The Objectives

The objectives of this thesis are:

- 1) To determine:
  - a) The composition of the parasite complex which attacks the pea aphid.
  - b) The relative abundance and distribution of each parasite species in southern B.C.
- 2) To evaluate:
  - a) Parasite effectiveness in the control of the pea aphid.
  - b) The impact of the exotic *Aphidius smithi* on the pea aphid and its indigenous parasites.

## C. The Approaches

Three main approaches were used to achieve the above objectives:

1. *Laboratory experiments.* Some basic parameters, only obtainable under controlled laboratory conditions, were considered to be important in the interpretation of the field results. Thus life table characteristics, such as developmental and reproductive rates, of the pea aphid and its associated parasites were determined. These laboratory results and observations are reported in the first part of the thesis; e.g. aphid biology is discussed in Chapter II; parasite biology in Chapter III; and aphid-parasite interactions in Chapter IV.

2. *Field study.* The hymenopterous parasites of the pea aphid were surveyed throughout southern British Columbia alfalfa fields during the summers of 1971 and 1972. The observed distribution and abundance of the aphidiid parasites is reported in Chapter VI. The main study was conducted in an alfalfa field at the Canada Department of Agriculture Research Station,



Kamloops, B.C. Aphid and parasite numbers were monitored to elucidate the population dynamics of the pea aphid and its parasites. The effects of hay harvesting practices, weather, hyperparasitism, and insect predation on aphid and parasite abundance were also observed. The results of this field study are discussed in Chapters V and VI.

3. *Simulation model.* The third approach involved the construction of a descriptive "alfalfa-pea aphid-parasite" computer simulation model using some of the techniques described by Hughes and Gilbert (1968) and Gilbert and Gutierrez (1973). The model was used as a method of analysis, synthesizing both the laboratory and field findings in an attempt to understand the population dynamics of the pea aphid and its associated parasites in an alfalfa ecosystem. The model is discussed in Chapter VII.

A general discussion is made in Chapter VIII.

## CHAPTER II

## BIOLOGY OF THE APHID

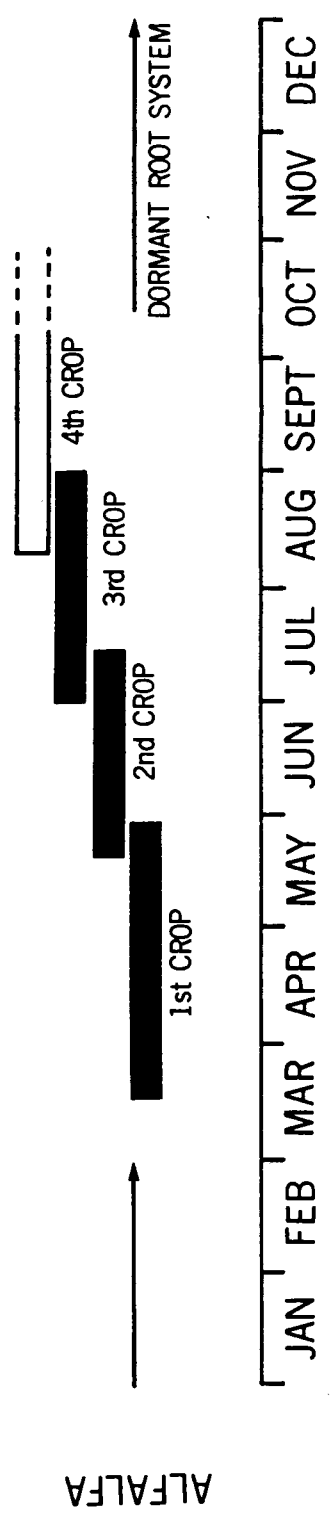
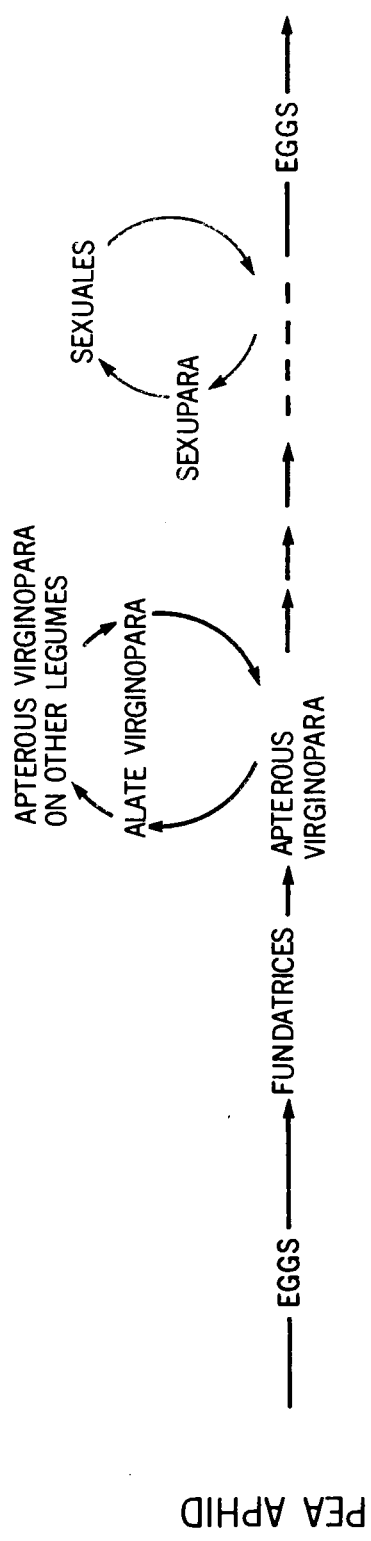
A. General Life History

The pea aphid, *Acyrtosiphon pisum* (Harris), is a common aphid on the herbaceous Papilionaceae (Hille Ris Lambers, 1947). It may become a pest on crop plants such as alfalfa, *Medicago sativa* L., and peas, *Pisum sativum* L. The aphid infests the growing tips of the plant, feeding on the sap from leaves, stems, petioles, and flower buds (Dunn and Wright, 1955; Emery, 1946; Smith, 1926). Numerous studies on aspects of the life history and economic importance of the pea aphid have been conducted (e.g. Campbell, 1926; Cooke, 1963).

In Kamloops the pea aphid overwinters in the egg stage on leaves and stems of alfalfa and clover (Fig. 1). In the lower Fraser Valley where the winters are milder, adult females may overwinter on clover (Buckell, 1940). In Kamloops during late March to mid-April the surviving eggs usually hatch, giving rise to the first or fundatrix generation (Fig. 1). The fundatrix, or stem mother, which is parthenogenic, usually matures during the last week of April and first two weeks of May, giving birth to the first generation of the viviparous parthenogenic females. When these viviparous females mature, they may be winged (alatae) or wingless (apterae) and produce other parthenogenic viviparae. The first few generations of virginopara consist of both apterous and alate viviparous females.

The apterous (wingless) viviparous females are the predominant form found on alfalfa during the summer months (Fig. 1). Rapid embryonic and nymphal development produces many overlapping generations during the summer. There are four nymphal instars followed by a short pre-reproductive

Figure 1. Phenology of alfalfa, pea aphid, and primary parasite populations  
at Kamloops, B.C.



period in the adult stage. The four instars differ in a number of morphological features. In this thesis differences in the relative antennal lengths (Fig. 2, Table I) were used to distinguish between the nymphal and adult apterous stages. The fourth instar and adult apterae by the presence of wing buds and wings respectively, are easily distinguished from the apterous morphs. Third instar alates, having small wing buds, are less easily separated from the apterous stages.

Normally apterous virginopara produce both apterous and alate young. However, in some strains alate virginopara produce only apterous young (Sutherland, 1970).

Two main factors have been demonstrated to promote the production of alate virginoparae: (1) physical contact between aphids caused by crowding; and (2) the nutritional quality of the plant sap (Bonnemaïson, 1951, 1971, 1972; Sutherland, 1967, 1969a, b). A number of environmental variables such as photoperiod and temperature may modify the response to crowding and the physiological condition of the plant (Sutherland, 1969b). Sutherland (1970) suggested that the ability of the pea aphid to respond to environmental factors which cause alate production is dependent on an intrinsic factor within the aphid.

Winged virginopara usually migrate from one alfalfa field to another or to other host plants such as clovers and peas. During the flights the alatae deposit a few nymphs wherever they stop, thus insuring a wide distribution (Cooke, 1963). Alate production and alate migration usually occurs throughout the summer in Kamloops. The first mass migration of alates usually occurs shortly before the alfalfa blossom appears in the first crop of the season. The early spring alate migration is usually the

Figure 2. The antennae of the first (1), second (2), third (3), fourth (4) instar and apterous adult (5) of the pea aphid, *Acyrtosiphon pisum* (Harris) (courtesy of Dr. M. Mackauer).

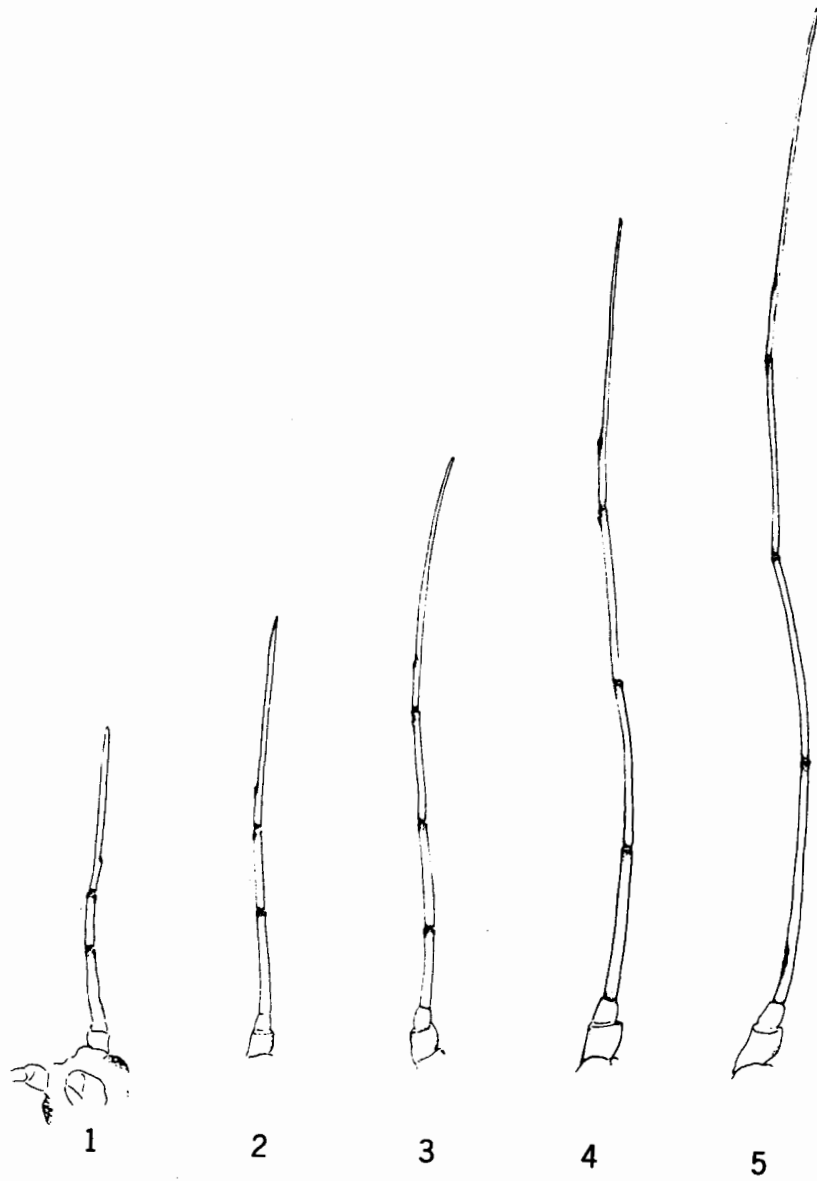


TABLE I. Mean antennal lengths of apterous pea aphids, *Acyrtosiphon pisum*, reared at 20°C (n = 20).

Nymphal Instar	Mean Antennal Length* mm	Range
I	1.085 ± .025	0.950 - 1.250
II	1.701 ± .016	1.500 - 1.875
III	2.432 ± .037	2.100 - 2.600
IV	3.528 ± .027	3.300 - 3.810
Adult	4.663 ± .024	4.501 - 4.800

\* Mean ± 1 SE.



largest for the whole of the season. 'Alate migration is an important mechanism in the recolonization of an alfalfa field, especially after most aphids in the field have been removed or killed by hay harvesting and a subsequent hot, dry period. After several days of flying alatae eventually settle and remain on a plant and lose their capacity for flight due to flight muscle autolysis (Johnson, 1953).

Sexuals start to appear in a population generally in response to changes in the fall temperatures and photoperiod (Lamb and Pointing, 1972). In Kamloops apterous and alate males and apterous oviparous females appear from late September until late October. The sexuals mate and the females lay their eggs on alfalfa leaves and stems. When first laid the eggs are yellow, but eventually they turn black. The eggs that survive the freezing winter temperatures in Kamloops will hatch into fundatrices the following spring.

B. The Influence of Temperature on Life Table Characteristics of the Pea Aphid

1. *Introduction.* The effects of temperature on insects have been reviewed by Andrewartha and Birch (1954), Bursell (1964), Howe (1967), Messenger (1959), and Watt (1968). Many authors have studied the effect of temperature on the development and reproductive capacity of various aphid species. Some of the recent studies on *Acyrtosiphon pisum* (Harris) are by Frazer (1972a, b), Harrison and Barlow (1972), Kenten (1955), Murdie (1969a, b), Siddiqui and Barlow (1973); on *Aphis craccivora* Koch by Gutierrez *et al.* (1972); on *Aphis fabae* Scop. by Banks and Macauley (1964); on *Brevicoryne brassicae* (L.) by Bonnemaïson (1951), Hafez (1961), Hughes (1963); on *Macrosiphum euphorbiae* (Thomas) by Barlow (1962), MacGillivray and

Anderson (1958); on *Masonaphis maxima* (Mason) by Gilbert and Gutierrez (1973); on *Myzus persicae* (Sulzer) by El-Ibrashy *et al.* (1972); and on *Therioaphis maculata* (Buckton) by Messenger (1964).

The influence of temperature on the development and reproduction of the pea aphid has been studied for different reasons; for example, to show: (1) life table characteristics of various pea aphid biotypes (Cartier, 1959; Frazer, 1972b; Kilian and Nielson, 1971; Markkula, 1963); (2) the effect of temperature on alfalfa clone resistance to the pea aphid (Cartier *et al.*, 1965; Isaak *et al.*, 1963); (3) the pea aphid as a virus vector at different temperatures (Sylvester and Richardson, 1966); (4) the effect of temperature and light on morph determination (Kenten, 1955; Lamb and Pointing, 1972); (5) temperature effects on pea aphid size and fecundity variations (Murdie, 1969a, b); and (6) pea aphid population growth after exposure to extreme temperatures (Harrison and Barlow, 1972) and fluctuating laboratory temperatures (Siddiqui and Barlow, 1972). Few authors have actually attempted to apply their laboratory findings on aphid developmental and reproductive rates to field observations using a comparative and/or predictive approach. Notable exceptions are studies on aphid species other than the pea aphid. For example, Hughes and Gilbert (1968) used developmental rates obtained by Hughes (1962) to predict the population trends of *Brevicoryne brassicae* on kale. Gilbert and Gutierrez (1973) have used the life table characteristics of *Masonaphis maxima* (Mason) to predict the aphid's population trends on thimbleberry.

A knowledge of the life table characteristics of the pea aphid was essential for the interpretation of the field observations (Chapter VI) and the construction of an aphid-parasite model (Chapter VIII). Campbell *et al.*

(1973) suggested that there is a considerable variation in the temperature requirements for development between different aphid species as well as within one aphid species from one geographic area to another. Thus a laboratory study was initiated to determine the effect of constant temperatures on the developmental, survival, and reproductive rates of the pea aphid as found in the Kamloops area.

The objectives of this chapter are to determine the developmental, survival, and reproductive rates of apterous and alate forms of the pea aphid, *A. pisum*, at various constant temperatures in the laboratory so that the effects of field fluctuating temperatures on the aphid could be assessed.

2. *Materials and Methods.* Two experiments were conducted between 15 June and 4 August, 1972, at Kamloops. In the first experiment, apterous and alate *A. pisum* individuals were exposed to different constant temperatures ranging from 10 to 28°C (Table II). Pea aphid adults collected in the field were used to supply newly born nymphs of known age (1 to 4 hours). These nymphs were placed individually into small plastic rearing cages having a diameter of 9.5 cm (Mackauer and Bisdee, 1965) (Fig. 3) and containing alfalfa stems. The cages were maintained in Precision Scientific environmental cabinets with a light regime of 18 L/6 D and relative humidity of 50 to 70%.

In the second experiment, apterous pea aphids were exposed to fluctuating temperatures in an alfalfa field. In this experiment the rearing cages were attached to stakes and protected by sheets of galvanized iron (20 x 20 x .1 cm) against sun and rain (Fig. 3). Temperatures within the plastic containers in both the laboratory and field experiments were measured with thermocouple probes and recorded on thermographs (Weksler Instrument Corp., Type 12MR1-2P).

Figure 3. Rearing cages in incubator (top), modified cage attached to stake in field (middle), rearing cages in alfalfa field (bottom).



The aphid host plant used for both experiments was *Medicago sativa* L. var. Vernal. In the laboratory experiment fresh 10 to 15 cm long alfalfa tips were cut from field grown alfalfa and placed individually into a plastic rearing cage with the cut end in tap water. In the field experiment the growing alfalfa tips were placed individually in the modified cages, but the tips were always left attached to the plant; the cages were raised on the stakes as the alfalfa stems grew. Alfalfa tips were replaced weekly in both experiments. Care was taken to insure that all extraneous insects were removed before placing the tips into the cages.

The developmental periods of each aphid instar under constant temperatures were determined by checking each container for aphid ecdysis and/or cast skins every six hours. In the field experiment only the total pre-reproductive period (birth to first larviposition) was measured. After all aphids had begun to reproduce, they were examined daily and all progeny produced were counted and removed with a camel's hair brush. From these data the mean developmental period for each instar, the pre-reproductive periods, and the mean total fecundity of each age group of alatae and apterae were calculated.

Linear regression equations were calculated to show the relationship between temperature and the rates of aphid development expressed as reciprocals of time:  $y = a + bt$ , where  $y$  is the rate of development or  $1/D$ ;  $D$  is the number of days taken for each instar period at a particular temperature  $T$  in degrees centigrade;  $a$  and  $b$  are constants calculated by using the least sum of squares method. The lower threshold temperature for development is  $t = -a/b$  when  $y = 0$ . The physiological time period (in day - degrees C) for each instar or "time to adult" is  $K = 1/b$ . The physiological thermal



constants for each nymphal instar were calculated using the methods described by Hughes (1962) and Campbell *et al.* (1973).

Apterous and alate pea aphid performance at the different temperatures was assessed by constructing life tables, using age-specific fecundity ( $m_x$ ) and age-specific survival ( $l_x$ ) for each age interval ( $x$ ) using both a real-time (24 hours or 1 day) and a physiological time scale (24 day - degrees C). The physiological time period of 24 day-degrees above  $t$  (lower threshold temperature for development) was arbitrarily chosen because it is simple and understandable, and it can be used as a standard against which other animals can be compared. The instar period (Hughes, 1963), although it has biological meaning, was not used in this particular analysis because it would have complicated matters needlessly.

From these data the intrinsic rate of increase,  $r_m$ , was calculated from the equation  $\sum e^{-r_m x} l_x m_x = 1$  by iterative substitution of the values of  $r_m$ . All calculations were made on a programme written in FORTRAN IV language for use in the Simon Fraser University IBM 370/155 computer. Once  $r_m$  was known the following statistics were calculated: the gross reproductive rate (GRR); the net reproductive rate ( $R_0$ ); the finite rate of increase ( $\lambda$ ); the generation time ( $T$ ); and the doubling time (DT) (Andrewartha and Birch, 1954; Messenger, 1964).

### 3. Results.

a) *Development of nymphal stages.* The duration, in days, of the developmental periods of the immature stages of both apterae and alatae of *A. pisum* at the different constant temperatures are summarized in Table II. The duration of the first three instars of apterae and alatae at each temperature was essentially the same. However, fourth instar apterae and

TABLE II. Developmental periods (in days) of apterous and alate forms of the pea aphid, *A. pisum*, reared on alfalfa (var. Vernal) at four constant temperatures, 50 - 70% RH, and a diel cycle of 18 L/6 D hours (accuracy of measurements: ranges  $\pm$  0.08 days and  $\pm$  1.0°C).

Temperature (° C)	Nymphal Instars				Pre-reproductive Period	
	I*	II*	III*	IV Apt	IV Al	Apterae Alatae
26.1	Mean	1.17a	1.22a	1.76b	—	1.18a
	SE	0.02	0.03	0.07		0.04
	n	17	17	10		10
19.7	Mean	1.89b	1.74b	2.23f	2.91c	1.49a
	SE	0.04	0.04	0.03	0.05	0.05
	n	42	42	22	20	22
14.8	Mean	3.09c	2.85c	3.48h	5.26d	2.32f
	SE	0.07	0.03	0.06	0.13	0.04
	n	23	23	9	11	9
10.3	Mean	5.10d	5.04d	7.94e	11.94g	5.29d
	SE	0.05	0.04	0.10	0.56	0.07
	n	21	21	9	11	9
						6.12de
						0.35
						11

\* No significant difference was found between apterous and alate nymphal development; therefore, data were combined. Means sharing the same letter were not significantly different at  $p = .05$  (t-test).



TABLE III. Regression equations, coefficients of determination, lower threshold temperature for development, developmental periods (in day-degrees C) for instars I to III, and time-to-adult of apterous and alate *A. pisum*.

Details	Regression equation*	Coefficient of determination (r <sup>2</sup> )	Temperature threshold t (° C)	Development period K in Day-degrees (° C) above t
Mean for each of the first three instars**	$y = -0.22421 + 0.04035 T$	0.95	5.56	24.78
Time-to-adult Apteræ***	$y = -0.05075 + 0.00913 T$	0.98	5.55	109.53
Time-to-adult Alatae***	$y = -0.04676 + 0.00841 T$	0.97	5.56	118.90

\* Regression equation  $y = a + bT$ , where  $y$  is the developmental rate  $1/D$ ;  $D$  = developmental period in days;  $T$  = temperature (° C);  $t = -a/b$  when  $y = 0$ ;  $K = 1/b$ ;  $a$  and  $b$  are constants.

\*\* Values (summarized in Table II) for the first three instars were used; apterae and alatae included.

\*\*\* Values for the four developmental instars added; i.e. from time of birth to ecdysis into adult stage.

alatae took an average of 40% and 80%, respectively, longer than the mean duration of the first three instars at each temperature.

The developmental periods for the first three instars (Table II) (i.e. taken individually) and the "time-to-adult" (i.e. the first four instar periods added together) were converted to reciprocals, and from these regression equations were calculated (Table III). From these equations the temperature threshold ( $t$ ) and the developmental periods ( $K$ ) were calculated (Table III). The mean thermal constants for nymphal development are given in Table IV. The lower threshold temperature for development was  $5.56^{\circ}\text{C}$  for both apterous and alate forms of the pea aphid collected at Kamloops. The total apterous and alate pre-reproductive periods (from birth to first larviposition) was 133.7 and 150.8 day-degrees, respectively. Using a physiological time scale was the only means of comparing the total pre-reproductive periods between apterae reared at constant laboratory temperatures and those reared under fluctuating temperatures in field cages (Fig. 4A). The apterae reared in field cages took an average of 12.3 days (Table V) or 134.0 day-degrees<sup>1</sup> above  $5.56^{\circ}\text{C}$  to develop from birth to first larviposition. The apterous pre-reproductive period of 133.7 day-degrees predicted from laboratory data compared well with 134.0 day-degrees calculated under fluctuating field cage temperatures. These data suggest that alternating and constant temperatures by and large had the same effect on aphid development.

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<sup>1</sup> Accumulated field day-degrees were calculated by using the formula  $\Sigma(T-t)D$  where  $T$  = average daily temperature calculated from 2-hourly recordings (daily temperature range must be above  $t$ ), and  $t$  = lower temperature threshold of aphid development;  $D$  = 1 day. Other methods used are described in Chapter VI.

TABLE IV. Mean thermal constants for nymphal development of the pea aphid, *Acyrthosiphon pisum*, on alfalfa (var. Vernal), from Kamloops, B.C., 1972.

Details	Mean N1,2,3	N4 Apt.	N4 Al.	Total Pre-reproductive Period	
				Apterae	Alate
Day-Degrees Above 5.56°C	24.8	34.6	44.6	133.7	150.8
Relative Length of Instar Periods	1.0	1.4	1.8	5.4	6.1

N = Nymphal instar.

Figure 4. (A) Mean daily temperatures recorded in field rearing cages between 20 June and 3 August, 1972. Means calculated from 2-hourly readings. Vertical lines represent the daily temperature ranges.

(B) Survival and mean fecundity rates for apterous *A. pisum* in field cages between 20 June and 3 August, 1972 (n = 28).

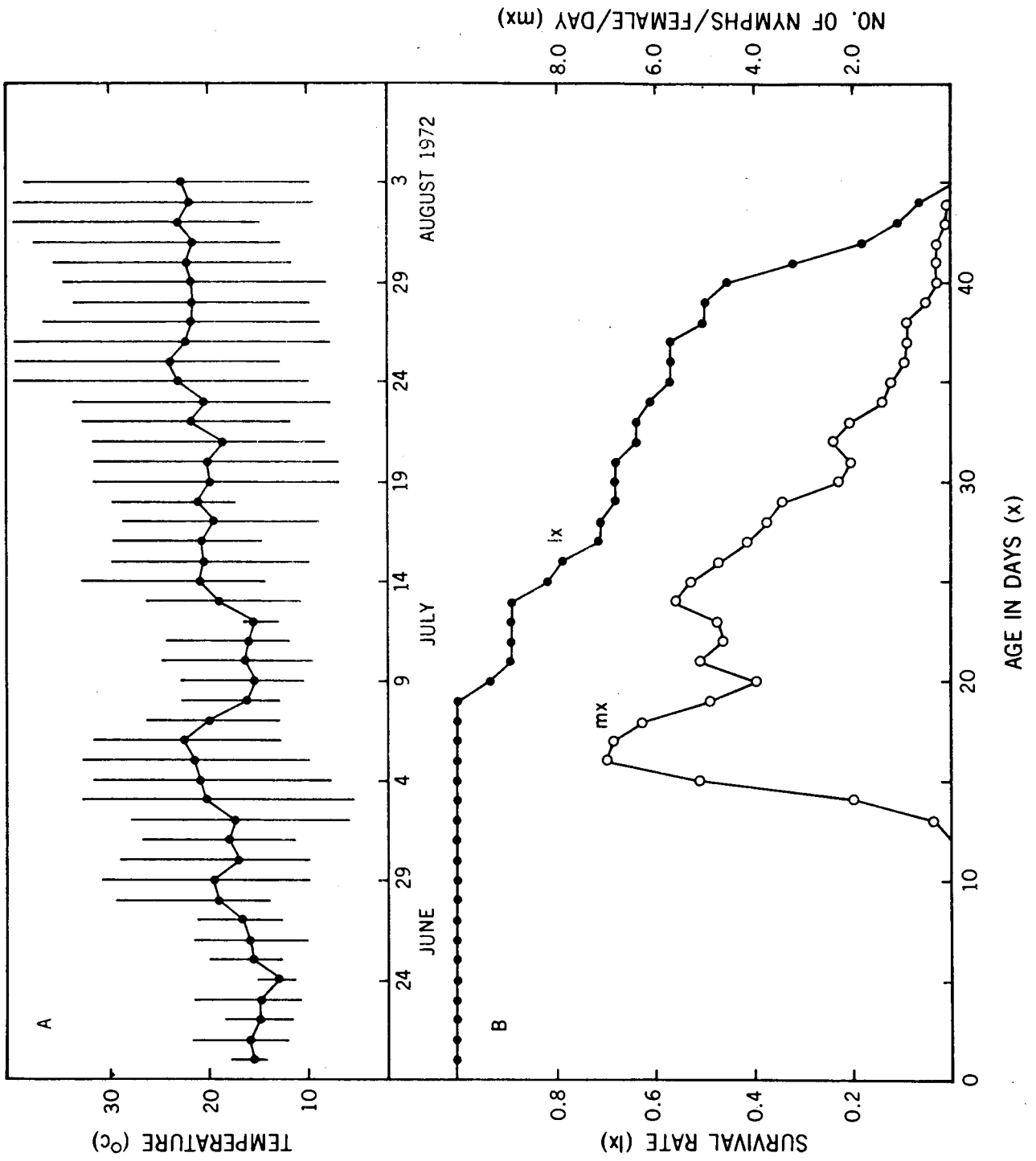


TABLE V. Some biological characteristics of adult apterous and alate *A. pisum* at various constant and alternating temperatures; all measurements in days.

Temperature (° C)	n	Total		Reproductive Period*	Post-reproductive Period*	Longevity to 50% Mortality	Days to 50% Progeny Born
		Pre-reproductive Period*	Reproductive Period*				
<i>APTERAE</i>							
27.8	10	7.4 ± .27	11.6 ± 1.31	3.5 ± 0.91	24	11	
26.1	10	6.6 ± .09	12.4 ± 1.86	4.4 ± 1.26	25	11	
19.7	22	9.0 ± .06	19.4 ± 0.86	9.8 ± 1.16	40	16	
14.8	9	14.5 ± .10	31.1 ± 0.84	9.9 ± 2.29	55	26	
10.3	9	28.3 ± .17	52.3 ± 1.25	4.2 ± 0.64	86	48	
Alternating (in field)**	28	12.3 ± .13	18.3 ± 1.41	2.4 ± 0.36	37	21	
<i>ALATAE</i>							
19.7	20	10.1 ± .06	22.9 ± 1.09	7.1 ± 1.35	41	18	
14.8	10	16.5 ± .11	27.2 ± 2.07	10.3 ± 2.12	55	28	
10.3	11	32.7 ± .87	47.7 ± 2.89	7.9 ± 2.03	88	50	

\* Mean and ± 1 SE.

\*\* See temperatures in Fig. 4A.

Apterae exposed to a constant 27.8°C took 7.4 days for their total pre-reproductive period, which was 0.8 days less than apterae exposed to 26.1°C (Table V). Constant temperatures above approximately 26°C were detrimental to pea aphid growth, resulting in a slowing down of development. The upper temperature threshold for pea aphid (when no growth occurs) is probably between 27 and 30°C for both apterae and alatae. Siddiqui and Barlow (1973) also considered the constant temperatures of 30°C to be outside the favourable range of development for the pea aphid.

b) *Longevity*. The longevity was defined as the number of days to 50% mortality of the aphid population at each temperature regime (Table V). Longevity values were obtained from the age-specific survival ( $l_x$ ) shown in Figs. 5, 6A, 7A. Aphid longevity was greatest at 10.3°C and shortest at 27.8°C. This shows that temperature and longevity (or survival) were inversely related. As the temperature increased, longevity of the pea aphids decreased, reaching a minimum at the highest temperature to which they were exposed, 27.8°C. On the average, apterae lived one to two days less than alatae (Table V).

Apterae exposed to alternating field temperatures had a mean longevity of 37 days (Fig. 4B, Table V), which suggests that the overall average field temperature was perhaps slightly above 20°C.

At every temperature regime most aphids lived until they reached their highest fecundity ( $m_x$ ) rates; i.e. there was little mortality during the main reproductive period (Figs. 4 to 7). Mortality was slightly higher, however, for apterae at a constant temperature of 27.8°C and for the reproductive period of apterae in field cages experiencing fluctuating temperatures to a maximum of 40°C (Fig. 4A, B).

Figure 5. (A) Survival and (B) fecundity rates of apterous *A. pisum* at constant temperatures of 10.3, 14.8, 19.7, and 26.1°C, 50 - 70% RH, and a diel cycle of 18 L/6 D hours.



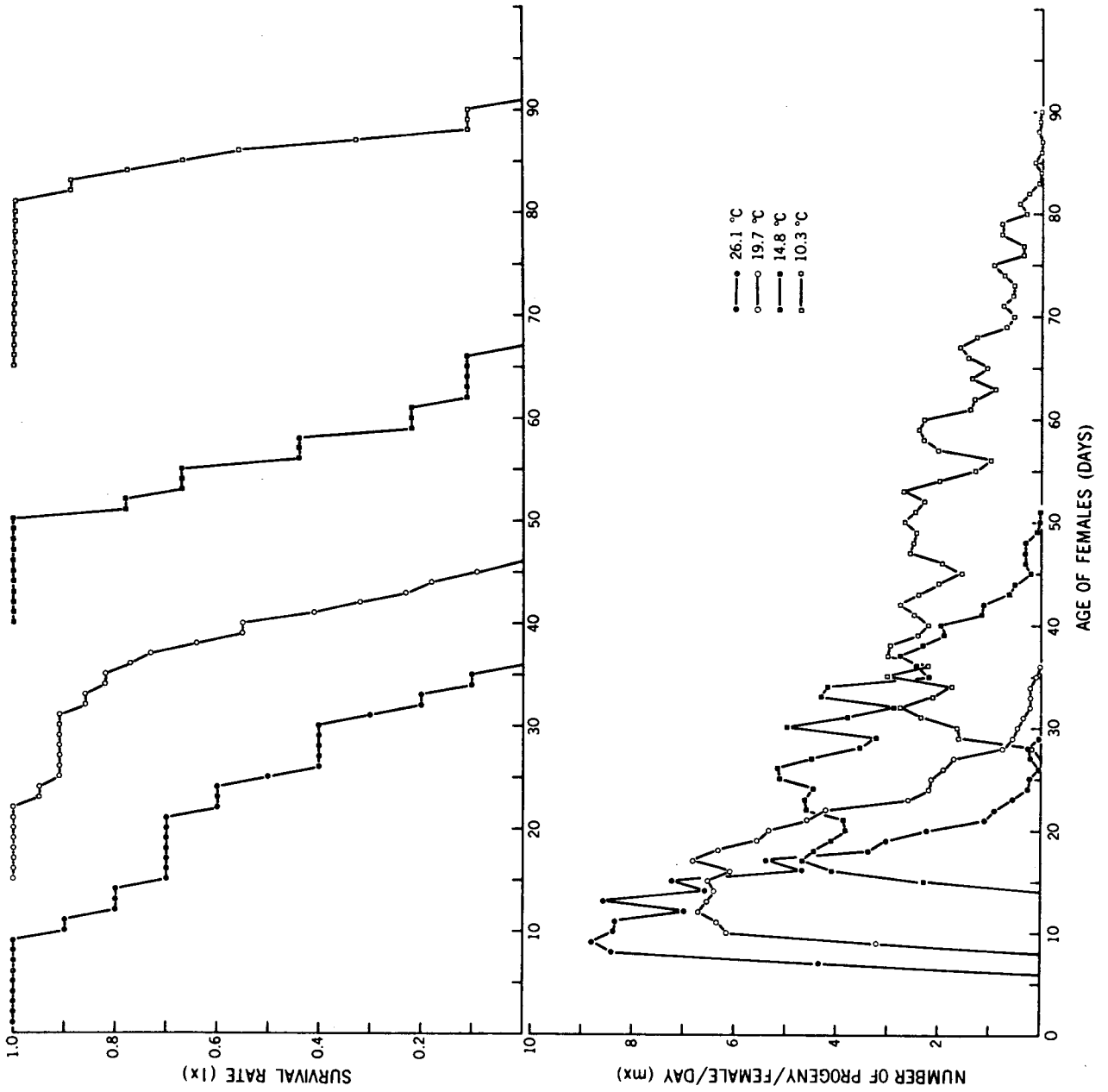


Figure 6. Survival and fecundity rates of apterous *A. pisum* at a constant temperature of 27.8°C, 50 - 70% RH, and a diel cycle of 18 L/6 D hours.

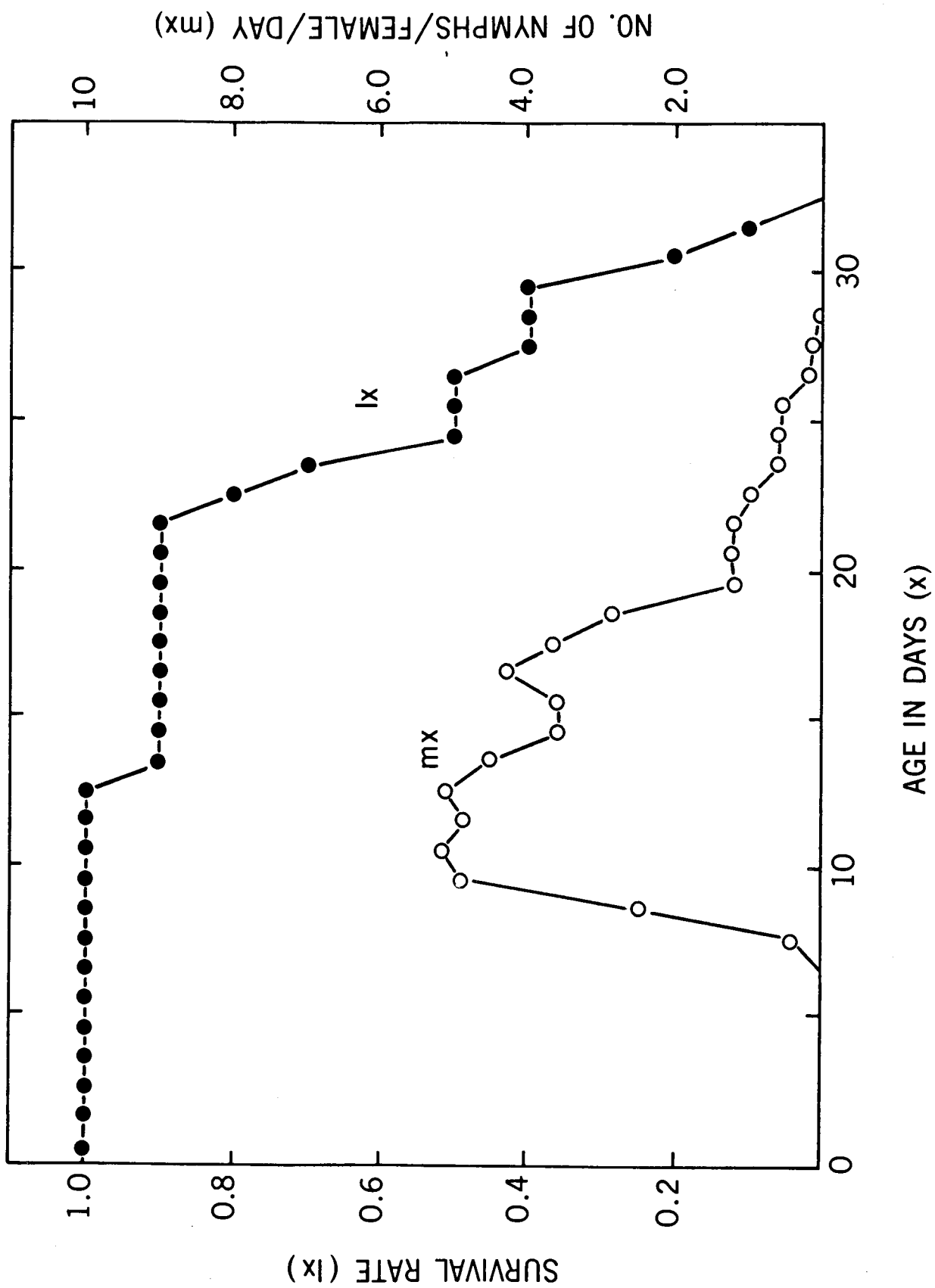
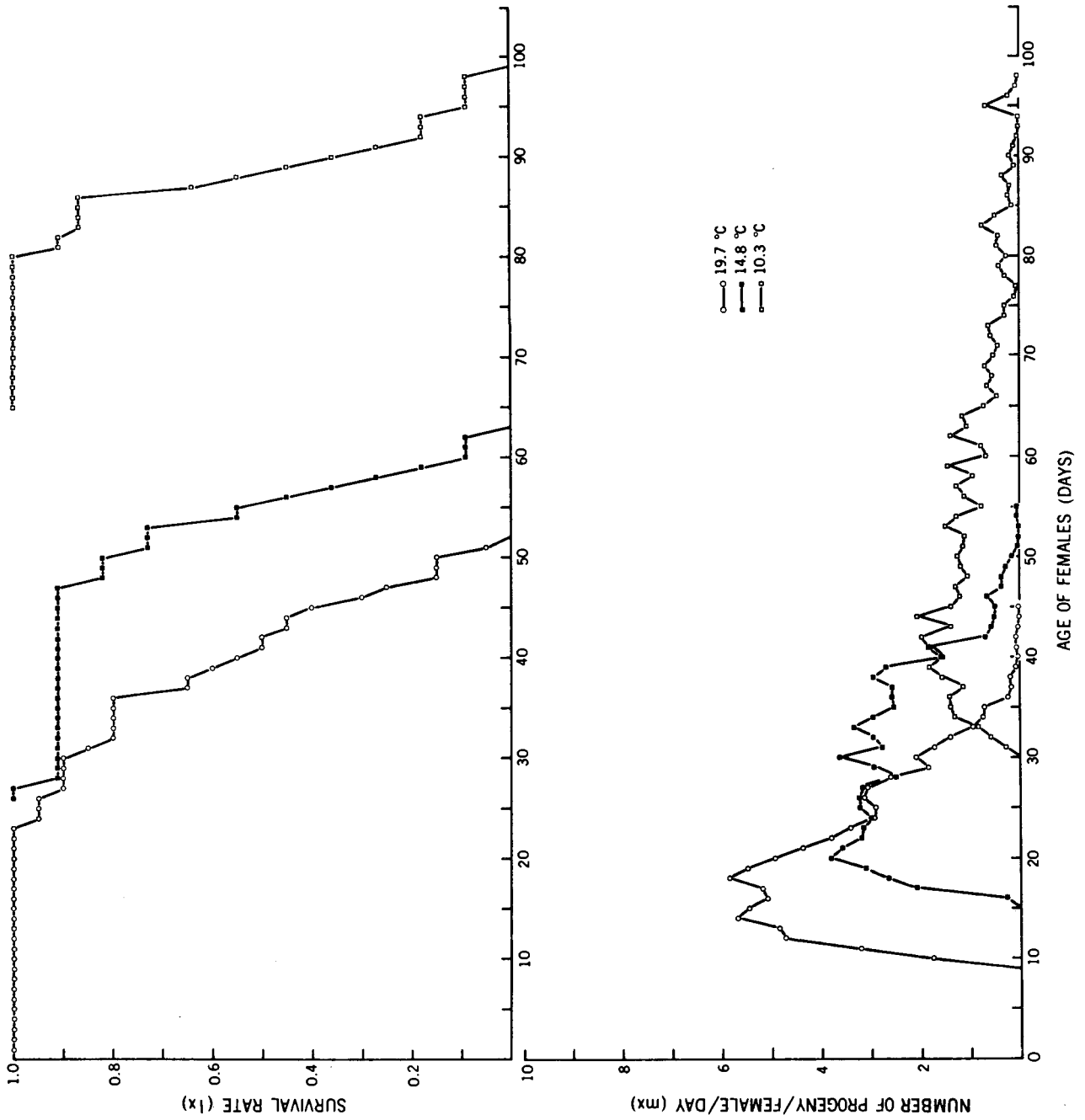


Figure 7. (A) Survival and (B) fecundity rates of alate *A. pisum* at constant temperatures of 10.3, 14.8, and 19.7°C, 50 - 70% RH, and a diel cycle of 18 L/6 D hours.



c) *Reproduction.* The pattern of reproduction per day of adult *A. pisum* was characterized by a rapid rise to peak reproduction with the largest number of births occurring during the first third of the reproductive period. This was followed by a gradual decrease in the number of births until reproduction ceased. The reproductive period was longer than the combined pre-reproductive and post-reproductive periods (Table V). The temperature to which the aphid is exposed can affect the fecundity ( $m_x$ ) pattern in both shape and magnitude (Figs. 4 to 7). Similar patterns of reproduction have been reported by Murdie (1969), Frazer (1972), Harrison and Barlow (1972), and Siddiqui and Barlow (1973) for the pea aphid. Birth rates increased with higher temperatures with maximum mean progeny of 9 ♀/♀/day produced for apterae at 26.1°C (Fig. 6B).

Progeny production started earlier in apterae than in alatae (Table V). Alatae produced fewer progeny per day than apterae at all constant temperatures. However, the pattern of reproduction was the same for apterous and alate pea aphids (Figs. 6B and 7B). Table VI summarizes for each test temperature the various reproductive and demographic characteristics of *A. pisum*. The maximum mean total fecundity of apterae was 100.8 ♀/♀/generation at 14.8°C (Fig. 8), but there was no significant difference in fecundity between 14.8, 14.7, and 26.1°C. Murdie (1969b) found 15°C to be the most favourable temperature for reproduction of apterous *A. pisum*, and Kenten (1955) found maximum reproduction in *A. pisum* to be at 19 to 20°C. At 14.8°C, all young were born before any mortality of adults occurred, making GRR equal to  $R_0$  (Table VI). In the alatae the maximum mean total fecundity ( $R_0$ ) was 86.3 ♀/♀/generation at 19.7°C. Why the optimal temperature for  $R_0$  was higher for alatae than apterae is not known; there is insufficient data for comparison (Table VI

TABLE VI. Reproductive and demographic characteristics of apterous and alate *A. pisum* reared at different constant temperatures and alternating field temperatures on *Medicago sativa*

L. (var. Vernal). Calculations are made on calendar time basis.

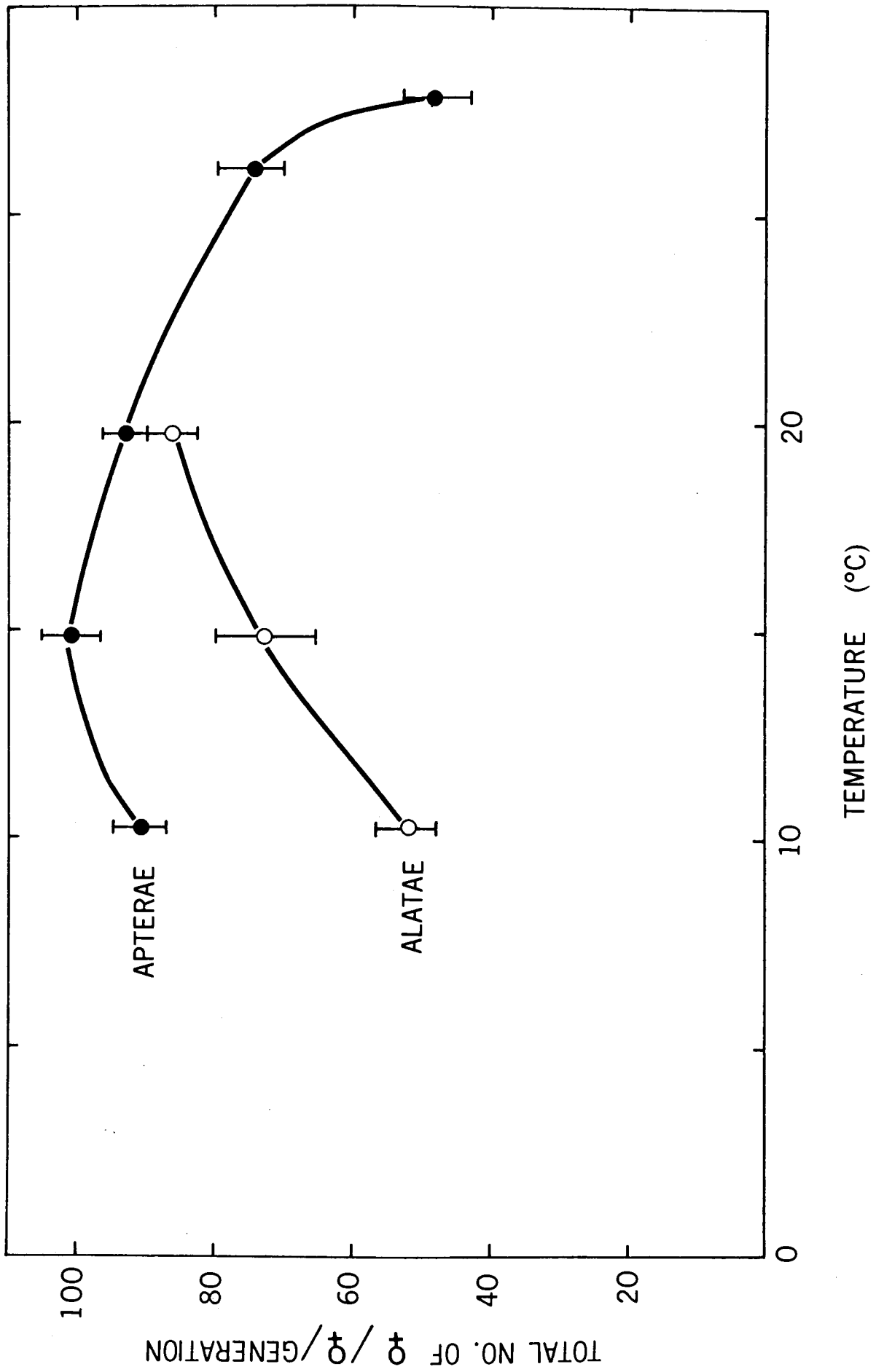
Temperature (° C)	n	Total Mean Fecundity* (Mean ± 1 SE)†	Gross Reproductive Rate (GRR)*	Net Reproductive Rate (R <sub>0</sub> )*	Intrinsic Rate of Increase (rm)**	Finite Rate of Increase (λ)**	Generation Time (Days) (T)	Doubling Time (Days) (DT)
<i>APTERAE</i>								
27.8	10	48.3 ± 5.0a	51.5	48.3	0.320	1.377	12.12	2.166
26.1	10	74.6 ± 4.4b	89.9	74.6	0.420	1.522	10.27	1.630
19.7	22	93.0 ± 3.4ce	94.1	93.0	0.330	1.391	13.74	2.100
14.8	9	100.8 ± 4.6c	100.8	100.8	0.205	1.228	22.50	3.381
10.3	9	91.2 ± 3.5ce	92.2	91.2	0.105	1.111	42.98	6.601
<i>ALATAE</i>								
19.7	20	86.3 ± 3.8ef	89.0	86.8	0.277	1.320	16.00	2.500
14.8	11	72.8 ± 7.2bf	76.8	72.8	0.175	1.191	24.50	3.961
10.3	11	52.0 ± 4.3a	53.8	52.0	0.085	1.089	46.48	8.155

\* In ♀/♀/generation; \*\* in ♀/♀/day; \*\*\* see temperatures in Fig. 4A.

† Means sharing same letters are not significantly different at p = .05 (t-test).

Figure 8. Total mean fecundity (in ♀/♀/generation) for apterous and alate *A. pisum* at different constant temperatures. The vertical lines correspond to  $\pm 1$  Standard Error.





and Fig. 8).

Figure 9 shows the accumulated values of  $l_x m_x$  for apterae exposed to various temperature regimes on a physiological time scale of 24 day-degrees above 5.56°C. This enables a comparison between apterae exposed to fluctuating temperatures with those exposed to constant temperatures (Fig. 9). The mean  $l_x m_x$  predicted from the combined constant temperature data was found to agree closely with the reproductive pattern of apterae under fluctuating field temperatures (Fig. 9).

d) *Intrinsic rates of increase.* Values of the intrinsic rate of increase ( $r_m$ ) were computed on a 24-hour basis (Table VI) and on a physiological time scale of 24 day-degree periods above 5.56°C (Fig. 10). The demographic data computed from  $r_m$  are given in Table VI. The  $r_m$  values calculated on a daily basis show a curvilinear relationship when plotted against constant temperatures (Fig. 10). The values approximate a straight line between 10 and 20°C in apterae and alatae, but at higher temperatures the  $r_m$  values decelerate and drop to .32 at 27.8°C. The  $r_m$  values for the alates are lower than those for apterous viviparae at the corresponding temperatures. The highest  $r_m$  value attained for Kamloops *A. pisum* apterae reared on alfalfa was 0.42 at 26.1°C. It is assumed that the upper constant temperature limit where  $r_m$  would reach zero is close to 30°C.

The  $r_m$  values calculated on a physiological time scale give different curves compared to those calculated on a daily time scale (Fig. 10). Values of  $r_m$  (.520) for apterae and (.430) for alatae were observed between constant temperatures 10.3 and 19.7°C, suggesting that this (constant) temperature range is physiologically optimal for pea aphid reproduction. Higher temperatures reduced  $r_m$  values.

Figure 9. A comparison of apterous *A. pisum* female fecundities ( $l_x m_x$ ) exposed to various constant and alternating field temperatures on a physiological time scale of 24 day-degree periods above 5.56°C. The predicted mean  $l_x m_x$  was calculated from fecundities exposed to all constant temperatures.

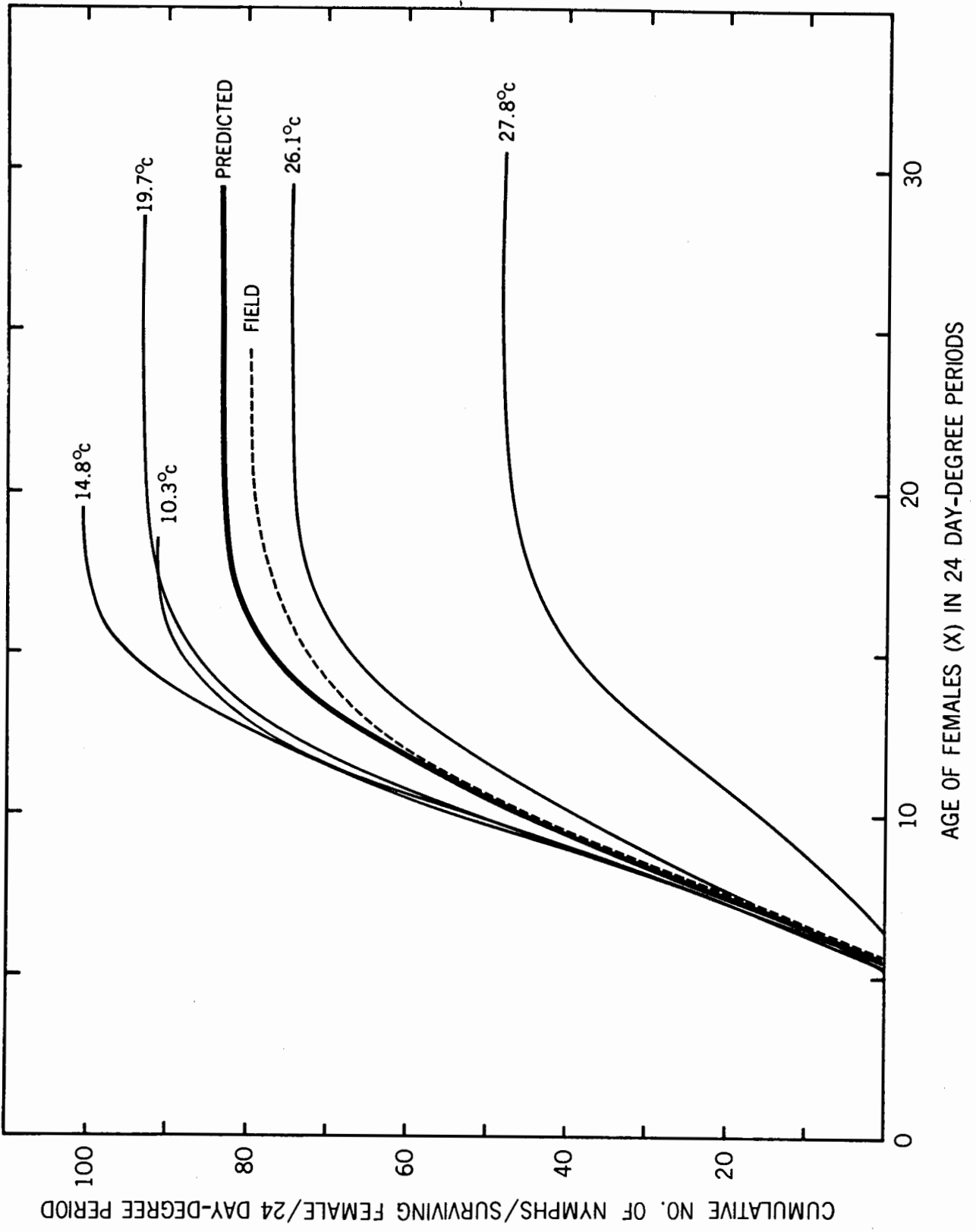
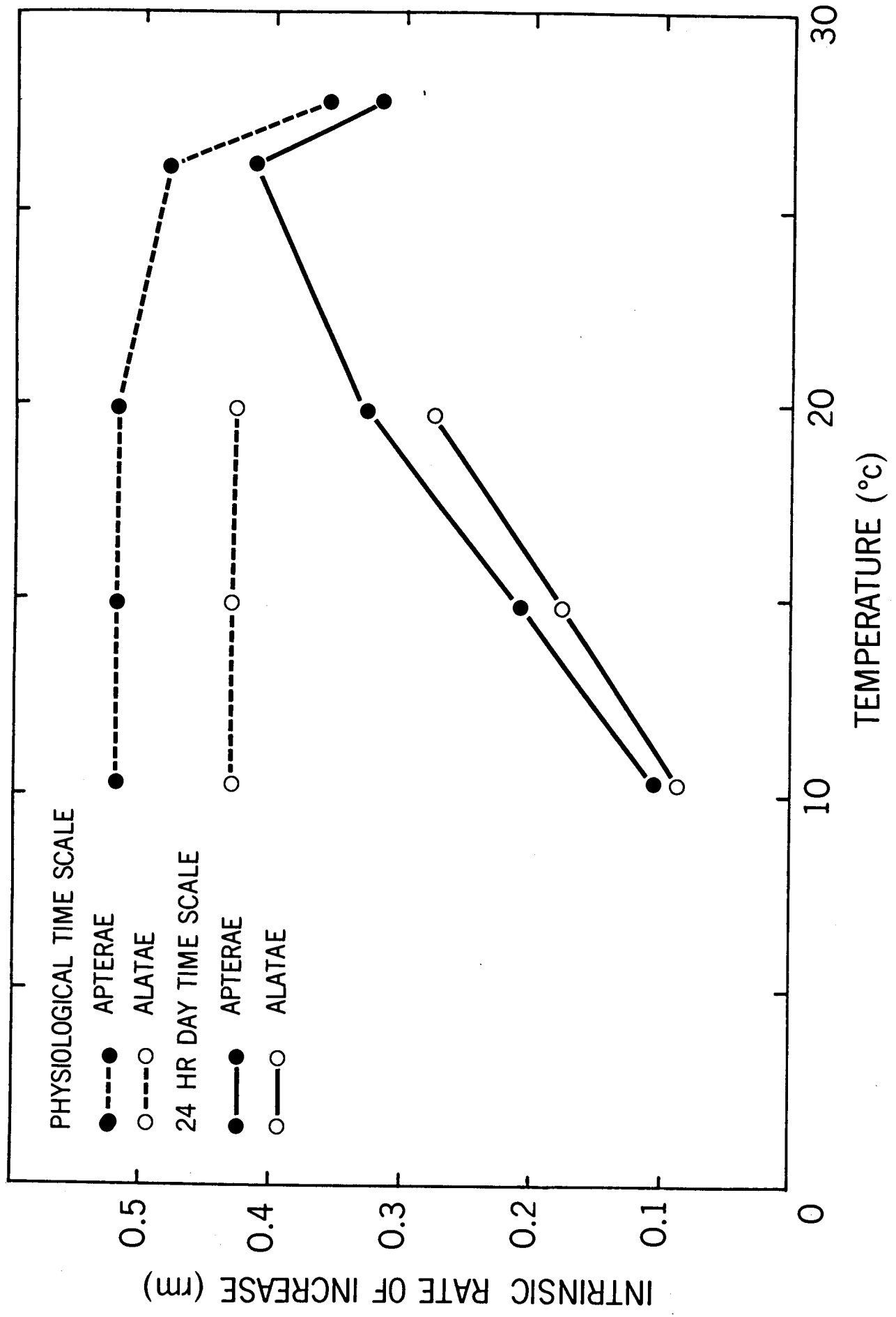


Figure 10. The intrinsic rate of increase of apterous and alate *A. pisum* in relation to constant temperature. Values of  $r_m$  are shown for age intervals (x) of 1 day (ordinary time) and periods of 24 day-degrees above 5.56°C (physiological time).



To be certain that the 24 day-degree period did not make  $rm$  values insensitive to changes in reproductive rates, the physiological age interval ( $x$ ) was reduced from 14 to 5 day-degrees above  $5.56^{\circ}\text{C}$ . This change decreased the  $rm$  values relative to each other; i.e. all  $rm$  values between  $10.3$  and  $19.7^{\circ}\text{C}$  were of equal value. Changing  $t$ , the lower temperature threshold, from  $5.56^{\circ}\text{C}$  to  $4$  and  $8^{\circ}\text{C}$  drastically changed the  $rm$  values to  $.46$  and  $.65$ , respectively, for apterae at  $10.3^{\circ}\text{C}$ . Similar  $rm$  increases or decreases were observed when  $t$  was changed in calculating  $rm$  for apterae exposed to other selected constant temperatures; however, these  $rm$  values were non-linear between  $10.3$  and  $19.7^{\circ}\text{C}$ . The linear relationship of  $rm$  when  $t = 5.56^{\circ}\text{C}$  compared with the linear relationship of  $rm$  calculated on a real time scale (Fig. 10) between  $10.3$  and  $19.7^{\circ}\text{C}$  is evidence that  $5.56^{\circ}\text{C}$  is a reliable estimate of the lower threshold temperature for pea aphid reproduction at Kamloops.

4. *Discussion.* The development of apterous pea aphids required an average 134 day-degrees above  $5.56^{\circ}\text{C}$  from birth to reproduction at both constant and alternating temperatures. These results suggest that differences in the developmental rate of the Kamloops pea aphid caused by alternating or constant temperatures (if any) were not significant. In contrast, Siddiqui and Barlow (1973) found that under optimal alternating laboratory temperatures pea aphids developed faster. In this study, it is possible that temperatures above  $25^{\circ}\text{C}$  (Fig. 4A, B) may have retarded aphid development, thus compensating for the faster aphid development at fluctuating optimal temperatures. The main problem in the present study is not whether or not alternating temperatures increase aphid development rates over those at constant temperatures. Rather, the problem is to determine the critical

amount of time above 25°C to which the pea aphid is exposed that will be detrimental to the aphid's development, survival, and reproductive rates. This information, unfortunately, was not obtained in the present work.

Kenten (1955), Murdie (1964a, b), Harrison and Barlow (1972), Siddiqui and Barlow (1973) all reported that prolonged exposure to high constant temperatures, such as 25°C or above, was detrimental to pea aphid development and survival. In this study development was decelerated at 27.8°C compared to lower temperatures, and  $r_m$  values also decreased at temperatures above 25°C. Indeed, the upper constant temperature limit for development was estimated by Siddiqui and Barlow (1973) to probably be between 28 and 30°C. However, pea aphids probably can experience field temperature ranges above 25°C for short periods (Fig. 4A) without any harmful effects. How temperature, especially high extreme temperatures, affects "aging" and "dying" in the pea aphid is little understood. We do know that high temperatures can be deleterious to the animal's physiology by affecting somatic tissues (Lees, 1959; Murdie, 1969b), thus affecting embryos in the parent's body and delaying recovery in the next generation (Harrison and Barlow, 1972). Yet little is known of how high temperatures indirectly affect aphids through the changing physiology of the host plant. For example, alfalfa resistance to the pea aphid changes with changes of temperature (Isaak *et al.*, 1963).

Pea aphids in the Kamloops alfalfa fields do not experience deleterious high temperatures except during late July to mid-August. It is during this period that aphid populations are drastically reduced due to harvesting of the second crop and the subsequent hot and dry weather (Chapter V). During the early and late part of the growing season when pea aphid populations



are in a normal growth stage, they experience normal fluctuating temperatures within the optimal range. In other words, detrimental hot temperatures generally did not occur during the critical periods of aphid population growth. Thus, in this study we will assume that all alternating field temperatures above the lower temperature of development are optimal for the pea aphid (given adequate plant availability) during development, reproduction, and survival.

The  $rm$  values which were calculated from both the predicted and field cage  $l_x m_x$  values on a physiological time scale were found to be the same, i.e. 0.500. This indicates that we have reasonably accurate data on the reproductive capacity of the Kamloops pea aphid reared at near optimal environmental conditions where all extrinsic mortality agents have been excluded.

5. *Summary.* Apterous and alate forms of the pea aphid, *Acyrtosiphon pisum* (Harris), were exposed to a series of constant temperatures in the laboratory and actual fluctuating temperatures in field cages to evaluate the temperature limits and optimal conditions for their development, survival, and reproduction. The regression equations describing the relationship between the rate of development and the constant temperature for some developmental stages are given. The lower temperature threshold for development of the immature stages was  $5.5^{\circ}\text{C}$  and the upper threshold for growth was estimated to lie between  $28$  and  $30^{\circ}\text{C}$  for both apterae and alatae, while 134 and 151 day-degrees, respectively, were required to enable completion of development (birth to deposition of first nymphs). Both apterae and alatae required an average of 24.8 day-degrees for each of the first three instar periods and 34.6 and 44.6 day-degrees, respectively, for

the fourth instar period. Fluctuating field temperatures were not found to stimulate a more rapid development, nor did they increase reproductive or survival rates of the apterae when compared with the average rates at constant temperatures. Constant temperatures above 26°C reduced aphid survival and fecundity and increased developmental periods.

Apterous and alate viviparous females reached a maximum fecundity at 15 and 20°C, respectively. Temperature and longevity were inversely related with alatae and apterae surviving approximately the same time. At 19.7°C the mean longevity was 40 days, as compared with 87 days at 10.3°C.

Age-specific fecundity and survival schedules of *A. pisum* for constant and fluctuating temperatures were determined using both real time (a 24-hour day) and a physiological time scale (24 day-degrees above 5.56°C) as two ways of measuring the age interval ( $x$ ). Mortality did not have a significant effect on the rates of increase at constant temperatures between 10 and 26°C as very few aphids died during their reproductive periods. A high mortality occurred in apterae at constant temperatures above 26°C. The reproductive period of apterae was shortened in the field cages experiencing fluctuating temperatures to a maximum of 40°C. The innate capacity for increase ( $rm$ ), computed from the life tables and a real time scale, was higher for apterae than for alatae, particularly at constant temperatures between 10 and 26°C. The highest  $rm$  value recorded was 4.04 ♀/♀/day for apterae at 26°C. The mean rate (physiological time) of cumulative progeny production for all apterae exposed to constant laboratory temperatures accurately predicted the reproductive rate of the caged apterae exposed to fluctuating temperatures in the field.

CHAPTER III  
PARASITE BIOLOGY

A. Life History

The life history and bionomics of the hymenopterous family Aphidiidae have been the subject of numerous papers and were reviewed in detail by Mackauer and Stary (1967) and Stary (1970). For this reason, only a summary of the life histories of these aphid parasites will be given. The Aphidiidae are insect parasites; the larvae are parasitic in aphids while the adults are free-living. Five aphidiid parasites are found attacking the pea aphid in British Columbia (Chapter VI). The four common parasites are *Aphidius ervi pulcher* Baker, *Aphidius ervi ervi* Haliday, *Aphidius smithi* Sharma & Subba Rao, and *Praon pequodorum* Viereck. The fifth parasite, *Monoctonus paulensis* Ashmead, was recovered only once, perhaps because it exploits the pea aphid only as a facultative host (Calvert and van den Bosch, 1972).

Females of the Aphidiidae are arrhenotokous. When unmated they lay only haploid eggs, which develop into males. When mated they lay haploid and diploid eggs, which develop into male and female adults, respectively. The sex ratio of the four main parasite species in Kamloops populations was approximately 1:1 throughout the season. The ovipositional behaviour of *A. smithi* was described by Fox *et al.* (1967). Eggs are laid in all host instars, but the second and third instars are generally preferred by *A. smithi* (Mackauer, 1973; Wiackowski, 1962). Multi- and super-parasitism occur, but only one 'solitary' parasite larva completes the development within one host (Stary, 1970). The larva feeds internally on the aphid

host and, after maturing, will pupate inside the hardened skin of the dead aphid. Before pupation the *Aphidius* parasite larva fastens the mummy to the alfalfa leaf through a slit cut in the ventral body wall and then spins a silky cocoon in the aphid skin. The *Praon* larva spins its cocoon under the mummified aphid skin; the empty aphid skin is mounted on top of the cocoon (Fig. 29). To emerge from its pupa the *Aphidius* or *Praon* parasite adult cuts a hole in the mummy with its mandibles. A female can usually oviposit as soon as she has emerged from the cocoon. It is believed that the female mates only once, usually within the first couple of days, but the male can successfully inseminate several females (Mackauer and Stary, 1967).

In Kamloops the parasites must spend a diapause period as a prepupa or pupa in the mummy to survive the severe winter weather. Parasites that survive the winter emerge within a period of two to three weeks in the spring. The spring emergence of the parasites is generally synchronized with the beginning of the spring pea aphid populations (Fig. 2). Parasites are present throughout the summer alfalfa growing season when pea aphids are available, thereby producing overlapping parasite generations.

## B. Life Table Characteristics of the Parasites

### 1. *Influence of constant temperatures on parasite development.*

a) *Introduction.* There are only a few detailed studies on the rate of development of aphidiid species: Hafez (1961) and Hughes and Gilbert (1968) studied *Diaeretiella rapae* (McIntosh); Wiackowski (1962) studied *Aphidius smithi* Sharma and Subba Rao; Force and Messenger (1965a, b) studied *Praon palitans* Muesebeck, *Trioxys utilis* Muesebeck, and *Aphelinus semiflavus*

Howard; Gilbert and Gutierrez (1973) studied *Aphidius rubifolii* Mackauer.

A laboratory experiment was performed to determine the developmental rates of four common pea aphid parasites (*A. smithi*, *A. e. ervi*, *A. e. pulcher*, *P. pequodorum*) found in the Kamloops area, exposed to four selected constant temperatures. In addition, the developmental rates of two common hyperparasite species, *Asaphes lucens* (Prov.) (Hymenoptera: Pteromalidae) and *Lygocerus niger* (Howard) (Hymenoptera: Cerophronidae), were also studied at four constant temperatures. The data obtained were used to compute the temperature coefficients for a physiological time scale (Hughes, 1963) and to interpret the field population changes (Chapters V, VI, and VII).

*b) Materials and Methods. i. Development of primary parasites.*

Mummies were collected from an alfalfa field at the Kamloops Research Station. The mummies were placed individually into gelatin capsules (size 00) and kept at room temperature until the adult parasites emerged. The emergent parasites were identified, separated according to species and sex. Female parasites were mated by introducing a male of the same species into the gelatin capsule. Once mated, each female wasp was transferred into a new gelatin capsule into which one three- to four-day-old pea aphid nymph was introduced. To prevent superparasitism, aphids were removed immediately after parasite attack and transferred to a plastic rearing cage (Mackauer and Bisdee, 1965) containing fresh alfalfa tips. At least six to ten different parasite individuals of the same species were used to parasitize aphids during periods of 30 min each. At least two rearing cages, each containing 30 to 35 aphids parasitized by the same species were placed in each of four temperature cabinets at a selected temperature. The constant temperatures selected were at 25.8, 19.7, 14.8, and  $10.3 \pm 1.0^{\circ}\text{C}$ , with

50 to 70% RH, and a diel period of 18.L/6 D hours. A total of 1,200 aphids were parasitized by the different parasite species using this method.

A convenient measurement of larval development is the "time-to-adult", which is defined as the period from oviposition to adult emergence and includes the egg, larval, and pupal periods. The F1 emergents were collected at six hour intervals during the periods of adult eclosion. The times of oviposition and adult emergence were recorded and the mean periods of time-to-adult for each temperature regime, parasite species and sex were calculated. From this data the lower temperature threshold ( $t$ , measured in ° C) and the time-to-adult ( $K$ , measured in day-degrees above  $t$ ) were calculated using the regression equation described in Chapter II. The reciprocal  $y$ , or the rate of development from egg to adult emergence, was plotted against the temperature  $T$  for each parasite species. The plot was checked for linearity. If the developmental rate showed signs of falling off at the highest temperature, this value was rejected (Campbell *et al.*, 1973).

*ii.* Development of hyperparasites. The method of measuring the larval development of the two hyperparasite species was similar to that described for the primary parasites. However, there were differences. When the hyperparasites emerged from field collected mummies, they were identified and six males and six females of the same species were placed into a rearing cage containing approximately 30 (*A. smithi* - *A. pisum*) mummies. The hyperparasites were allowed to mate and parasitize the *A. smithi* mummies for a four-hour period at room temperature. No attempt was made to prevent superparasitism. After the hyperparasites had been removed from the rearing cages, the cages, still containing the mummies, were put into the various environmental cabinets at selected constant temperatures. Subsequent

procedures were the same as described on page 48.

c) *Results.* The duration of development or the time-to-adult for the six parasite species at four constant temperatures is given in Table VII. There was no significant difference (using t-test,  $p = 0.05$ ) between the developmental periods of males and females of the same species at each temperature, permitting pooling of the data for both sexes. Temperature played an important role in influencing the development of each of the parasite species. The duration of the developmental period decreased with the increase of temperature in all parasite species. Davidson (1942) and Andrewartha and Birch (1954) suggested that a logistic curve should be used for growth data. However, the use of a linear regression equation between 10.3 and 25.9°C provided a good approximation (as shown by the high coefficients of determination,  $r^2$ ) of the relationship between temperature and the rate of development expressed as a reciprocal of time (Table VIII). There was some curvature in the slope for the developmental rates of *A. smithi* and *A. e. pulcher* at 25.9°C; therefore, these values were not used (Campbell *et al.*, 1973) in calculating the regression equations (Table VIII). From these equations the temperature thresholds  $t$  and development periods  $K$  were calculated (Table VIII).

The exotic parasites, *A. smithi* and *A. e. ervi*, and the indigenous *A. e. pulcher* have a similar threshold temperature of 6.1 to 6.2°C. *P. pequodorum*, however, had a higher threshold of 6.9°C. The threshold value of the hyperparasite *L. niger* was 6.5°C, slightly higher than that of most of the primary parasites, while the value of *A. lucens* was 8.07°C. The time-to-adult was lowest in *A. smithi* (178.6 day-degrees) and highest in *A. lucens* (233.1 day-degrees).

TABLE VII. Mean periods of time-to-adult (in days) of four primary parasites and two secondary parasites of the pea aphid, reared at four constant temperatures (accuracy of measurements: ranges  $\pm 0.12$  days;  $\pm 1.0^\circ\text{C}$ ).

Temperature ( $^\circ\text{C}$ )	<i>A. smithi</i>			<i>A. e. ervi</i>			<i>A. e. pulcher</i>			<i>P. pequodorum</i>			<i>L. niger</i>			<i>A. lucens</i>					
	25.9	Mean	9.87	10.08	10.50	10.53	9.41	13.29	SE	0.08	0.02	0.02	0.01	0.03	0.04	n	44	50	35	47	39
19.7	Mean	13.05	14.39	13.57	15.30	15.00	19.30	SE	0.10	0.02	0.02	0.02	0.03	0.07	n	49	64	54	16	2	73
14.8	Mean	21.92	23.03	22.48	26.71	25.45	37.69	SE	0.08	0.03	0.04	0.02	0.04	0.19	n	79	58	63	5	36	54
10.3	Mean	42.23	50.91*	41.87	59.29	42.69	—	SE	0.23	0.09	0.08	0.17	0.10	n	81	33	40	13	50		

\* Reared at a constant temperature of  $9.8^\circ\text{C}$ .



TABLE VIII. Regression equations, coefficients of determination, lower threshold temperatures of development, and developmental time-to-adult of four primary parasites and two hyperparasites of the pea aphid.

Species	Regression Equation*	Coefficient of Determination		Temperature Threshold t (° C)	Developmental Period K in Day-Degrees (° C)
		(r <sup>2</sup> )	(r <sup>2</sup> )		
Aphidiidae					
<i>Aphidius smithi</i> **	$y = -0.03451 + 0.00560T$	0.98	0.98	6.17	178.6
<i>A. e. ervi</i>	$y = -0.03079 + 0.00508T$	0.99	0.99	6.06	196.8
<i>A. e. pulcher</i> **	$y = -0.03230 + 0.00532T$	0.98	0.98	6.06	187.9
<i>Praon pequodorum</i>	$y = -0.03447 + 0.00501T$	0.99	0.99	6.88	199.6
Ceraphronidae					
<i>Lygocerus niger</i>	$y = -0.03534 + 0.00543T$	0.97	0.97	6.51	184.1
Pteromalidae					
<i>Asaphes lucens</i>	$y = -0.03462 + 0.00429T$	0.93	0.93	8.07	233.1

\* Regression equation  $y = a + bT$ , where  $y$  is the developmental rate 1/D; D = developmental period in days;

t =  $-a/b$  when  $y = 0$ ; K = 1/b; a and b are constants.

\*\* Developmental rates at highest temperature 25.9°C not included because not on straight line.

2. *Primary parasite reproduction and longevity.* The data on parasite fecundity and longevity are based on unpublished experiments (M. Mackauer, pers. comm.). The fecundity and longevity of the four aphidiid parasites is summarized in Table IX. There were no differences in the mean longevity of females between the four species, ranging from 4 to 13 days with means between 6.4 and 7.7 days. There were, however, differences in the mean total number of eggs laid between parasite species. *A. smithi* had the highest mean fecundity of 774 eggs laid (range 321 to 1,812), while *A. e. ervi* laid a mean of 567 eggs (range 102 to 1,011), *A. e. pulcher* 316 eggs (range 90 to 597), and *P. pequodorum* 199 eggs (range 84 to 369).

3. *Discussion and Summary.* The optimum temperature range for development was probably between 10 and 25°C for most parasites. However, at 25.9°C the development rate of *A. smithi* and *A. e. pulcher* fell off. Fox *et al.* (1967) also found constant temperatures above 25°C to be detrimental to the development of *A. smithi*.

The temperature requirements of the parasites were generally higher than those of their hosts. The threshold temperature for the primary parasites *A. smithi*, *A. e. ervi*, and *A. e. pulcher* was approximately 6.1°C and that of *P. pequodorum* was 6.9°C, while that of the host, the pea aphid, was 5.56°C. The primary parasite time-to-adult ranged from 179 to 200 day-degrees, while that of *A. pisum* was only 110 day-degrees. The temperature requirement of one hyperparasite, *L. niger*, was only slightly higher than that of some of its hosts. However, the second hyperparasite, *A. lucens*, had the highest threshold and time-to-adult of all the parasites; i.e. 8.1°C and 233 day-degrees, respectively. A low threshold permits the parasites to appear early in the spring. Because the primary parasites have a

TABLE IX. Mean total number of eggs laid per female; mean adult longevity of four primary parasite species reared at  $20.5 \pm 0.5^\circ\text{C}$ ,  $55 \pm 3\%$  RH, and a diel period of 16 L/8 D hours. Hosts used were three- to four-day-old nymphs of the pea aphid, *A. pisum* (data courtesy of Dr. M. Mackauer).

Species	Fecundity*	Adult Longevity* (days)
<i>Aphidius smithi</i>	774 $\pm$ 86.1b	7.3 $\pm$ 0.73a
<i>Aphidius e. ervi</i>	567 $\pm$ 56.0b	7.7 $\pm$ 0.69a
<i>Aphidius e. pulcher</i>	316 $\pm$ 38.4b	6.4 $\pm$ 0.39a
<i>Praon pequodorum</i>	199 $\pm$ 18.5b	6.9 $\pm$ 0.65a

\* Means and  $\pm 1$  SE (n = 20);

Means followed by letter 'a' are not significantly different (p = .05), while means followed by letter 'b' are significantly different (p = .05) (t-test).

threshold that is slightly higher than that of their host, they appear together with the first aphids in spring or shortly thereafter. Further, one would expect that the hyperparasite *L. niger* would appear at about the same time as its primary parasite hosts, and *A. lucens* would be delayed. This was confirmed from the field data shown in Chapter VI.

Although the laboratory data on the reproduction and development of the four primary parasites is useful as it makes possible a comparison of their life table characteristics, our knowledge of parasite biology is still incomplete. Information on the longevity and searching behaviour of parasites in the field is scant and not reliable. Mackauer and van den Bosch (1973) point out that under situations of stress such as at low host density, *A. smithi* females will not lay their full complement of eggs in the laboratory. Gilbert and Gutierrez (1973) have shown that *A. rubifolii* may lay only about 80 of its potential of 400 eggs in the field. Differences in parasite survival, searching behaviour, and dispersal rates may all be important factors in increasing or decreasing a parasite's effectiveness in laying its full complement of eggs. However, the use of the present life table data, put on a physiological time scale, will be helpful in the interpretation of the field data in Chapter VI and the construction of the model in Chapter VII.

## CHAPTER IV

## THE EFFECT OF PARASITISM ON APHID REPRODUCTION AND DEVELOPMENT

A. Introduction

Unlike aphidophagous predators which eat and destroy their prey soon after prey location, aphid parasites lay one or several eggs into the aphid body, leaving the endoparasitic larva to consume its host. During the early stages of parasite development the aphid continues to grow and may even reproduce.

A number of workers (Arthur, 1944; Fox *et al.*, 1967; Hafez, 1961; Stary, 1970) observed that if aphids are parasitized at an early age, they become mummified before reaching maturity and cannot reproduce. However, when older instars or adult aphids are being parasitized the aphid can reach maturity and reproduce before succumbing to parasitism. None of these authors has considered in detail the effect of parasitism on host fecundity and population growth.

The following experiment was conducted to investigate the effect of parasitism by *Aphidius smithi* Sharma & Subba Rao on the fecundity and developmental rates of the apterous and alate forms of *Acyrthosiphon pisum* (Harris). The effect of parasitization of different host ages on the rate of aphid population growth is considered.

B. Materials and Methods

Alfalfa tips, pea aphid adults, and *A. smithi* mummies were collected when needed from an alfalfa field near Kamloops, B.C., during the months of June, July, and August, 1972. This assured that the experimental animals performed as closely as possible to their counterparts in the field.

Two alfalfa tips were placed into individual 9.5 cm diameter plastic rearing cages (Mackauer and Bisdee, 1965) (Fig. 3). All alfalfa tips were replaced weekly. Care was taken to insure that all extraneous insects (e.g. insect predator larvae and eggs) were removed before using the field-collected tips.

To obtain a large number of pea aphids of a known age adult aphids collected from the field were allowed to produce progeny on alfalfa in plastic rearing cages in the laboratory. Every four hours any progeny produced were transferred with a camel's hair paintbrush into a new container with two alfalfa stems and allowed to develop to the required age. The ages of apterae and alatae to be parasitized are shown in Figs. 11A and B. Because alate nymphs could not be distinguished from apterous nymphs before the third nymphal instar, only third instar alatae or older were used.

Field collected *Aphidius* mummies were placed into individual gelatin capsules (size 00) and checked daily for adult emergences. Newly emerged *A. smithi* males and females were transferred to large wooden cages that contained a supply of honey and a bouquet of alfalfa stems with a small number of aphids (to relieve any parasite oviposition pressure). When required, 20 to 30 female parasites were transferred into individual gelatin capsules. Individual aphids of known age were also introduced into the gelatin capsules. The parasites were allowed to oviposit into the aphids only once, insuring that no superparasitism could occur.

Parasitized aphids were placed individually into a rearing cage containing an alfalfa tip and examined daily; the number of nymphs deposited, aphid deaths, and mummification were recorded. All progeny produced were

removed after each daily count. The aphid stage when mummification occurred and the mean total fecundity of each age group of parasitized apterae and alatae were recorded. Aphids that did not show any signs of parasitism after eight days were discarded and not used in the life table calculations (see below).

All cultures were maintained at  $19.7 \pm 0.5^\circ\text{C}$ ,  $70 \pm 5\%$  RH, and a diel period of 18 L/6 D hours. Control data of the development, fecundity, and survival rates of unparasitized apterous and alate pea aphids reared at  $19.7^\circ\text{C}$  are given in Chapter II.

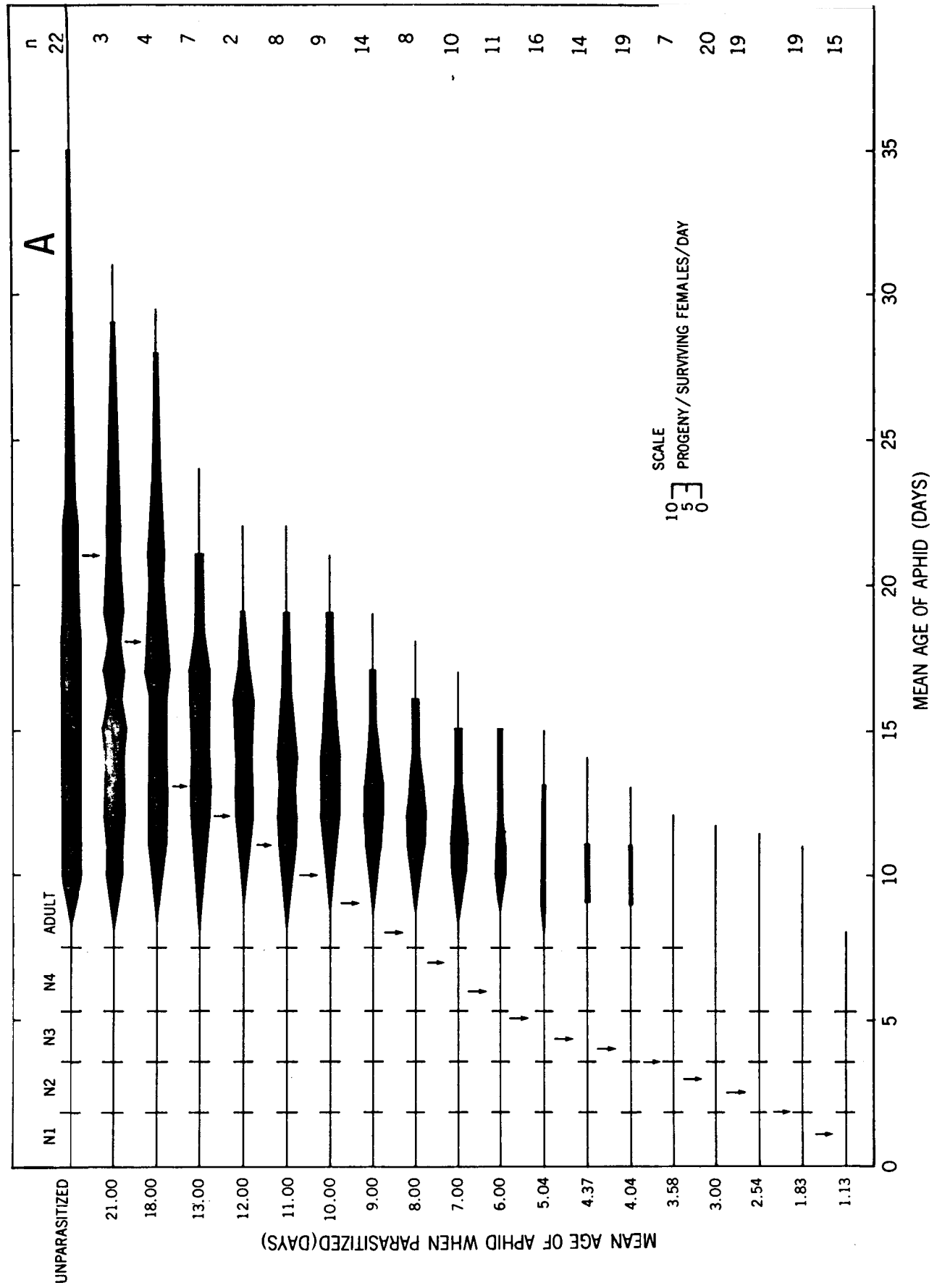
Aphid population performance was assessed by constructing life tables and calculating the intrinsic rate of increase ( $r_m$ ) and other demographic data (see Chapter II).

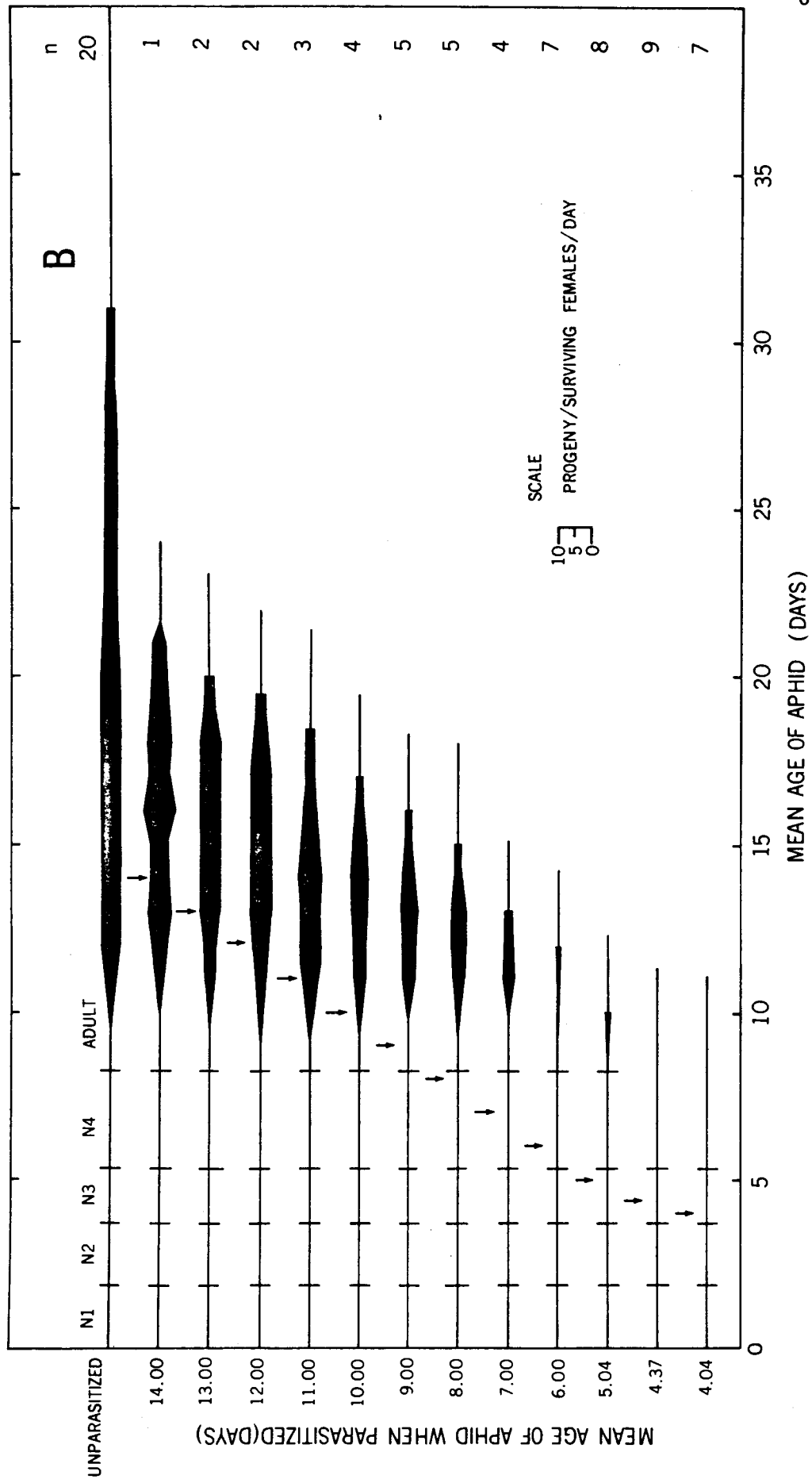
### C. Results

1. *Effect of parasitism on aphid development.* Parasitized apterous or alate *A. pisum*, irrespective of the beginning of parasitism, could still develop and moult until it reached the fourth instar or the adult stage before mummifying. If an apterous host was parasitized before it was three days old, i.e. as a first or second instar (Fig. 11A), mummification took place in the fourth instar. Third (3 to 5.8 days) or older instars, when parasitized, succumbed to parasitism in the adult stage (Fig. 11A). Because alatae have a longer fourth instar period than apterae, alatae parasitized before the middle of the third instar (4.37 days, Fig. 11B) produced fourth instar alate mummies. When third instars (5.04 days) or older aphids were parasitized, they mummified as aphids with fully developed wings.

Figure 11. The effect of parasitization on different age groups of apterous (A) and alate (B) morphs of *Acyrtosiphon pisum*, showing the approximate time of mummification and the reproductive rates of parasitized and unparasitized surviving aphids. Vertical lines indicate mean time of ecdysis of unparasitized aphids. N1, N2, N3, and N4 indicate instar periods. Arrows show mean age of aphid when parasitized. n = number of aphids that eventually mummified.







In contrast, the development of the unparasitized pea aphid is shown in Figs. 11A and B and was described in Chapter II.

2. *Reproduction of the parasitized pea aphid.* Parasitism by *A. smithi* had a significant effect on the rate of reproduction. Apterous and alate nymphs parasitized earlier than age 3.58 days (Fig. 11A) and 5.04 days (Fig. 11B), respectively, mummified before producing young. Thus aphid population growth was completely destroyed if nymphs were parasitized before the early third instar apterous or late third instar alate stages. However, a residual reproductive capacity remained in 4.04-day-old or older apterae and 5.04-day-old or older alatae (Figs. 11A and B). The later the aphid was parasitized, the greater was the mean number of progeny produced/♀/ generation (Figs. 11A, B, 12, and Tables X, XI). Progeny production usually started to drop off after the fifth day and ended seven to eight days after the beginning of parasitism (Figs. 11A, B).

Parasitized apterae tended to produce a greater mean total number of progeny and at a slightly more rapid rate than parasitized alatae (Fig. 12). If apterous or alate aphids were parasitized when 20 days old or older, the effect of parasitism on fecundity was negligible. At that time most of the nymphs that an unparasitized adult could potentially have produced had already been deposited (Figs. 11A, B, 12). Most parasitized aphids died seven to nine days after the beginning of parasitism (Figs. 11A, B).

3. *The effect of parasitism on the intrinsic rate of increase.* The intrinsic rate of natural increase,  $r_m$ , virtually summarizes in one value the observed effects of the environment on the potential growth rate of a population. A number of authors (Barlow, 1962; Birch, 1948; Force and

Figure 12. Mean total fecundity (♀/♀/generation) of each parasitized age group of apterous and alate *Acyrtosiphon pisum* reared at 19.7°C. Vertical lines  $\pm$  1 SE. Total fecundity of unparasitized apterae and alatae are also shown.

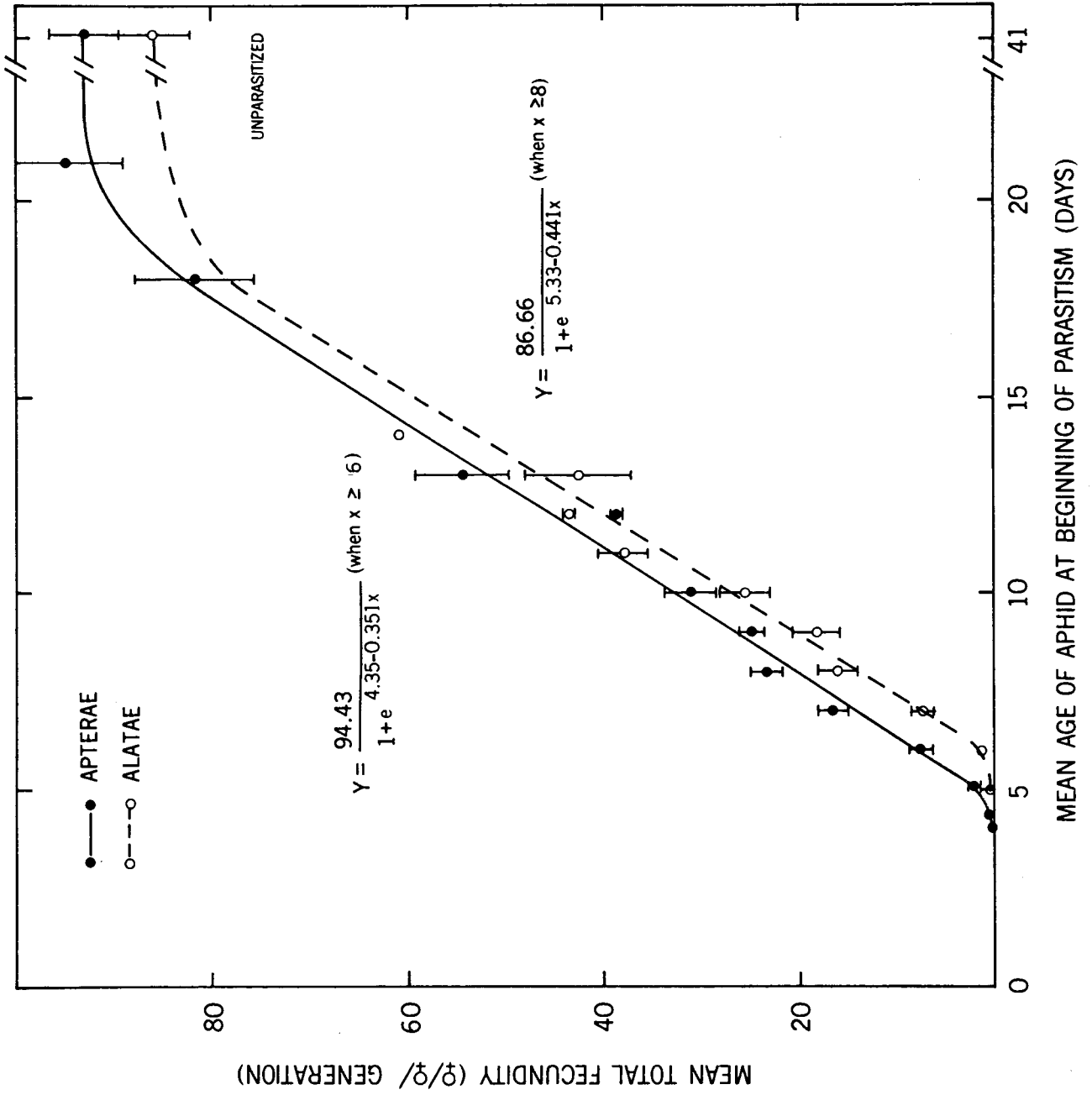


TABLE X. The effects of parasitism by *A. smithi* on the demographic and biological characteristics

of the different ages of apterous *A. pisum* (reared at  $19.7 \pm 0.5^\circ\text{C}$ ,  $70 \pm 5\%$  RH, diel period of 18 L/6 D hours, on *Medicago sativa* L., var. Vernal).

Aphid Age at Parasitization	Instar Days	n	Total Mean Fecundity*	Gross Reproductive Rate (GRR)**	Net Reproductive Rate (R <sub>0</sub> )**	Intrinsic		Finite		Doubling	
						Rate of Increase (rm)***	Rate of Increase (λ)***	Time (days)	Time (DT)		
Third	4.0	21	0.11 ± 0.07	0.11	0.11	--	--	--	--	--	--
Third	4.4	14	0.57 ± 0.31	0.72	0.57	--	--	--	--	--	α
Third	5.0	16	2.00 ± 0.58	2.00	2.00	0.070	1.073	9.902	1.073	9.902	9.902
Fourth	6.0	11	7.64 ± 1.19	8.15	7.64	0.192	1.212	10.588	1.212	10.588	3.610
Fourth	7.0	10	16.40 ± 1.39	16.47	16.40	0.252	1.287	11.100	1.287	11.100	2.751
Adult	8.0	11	23.09 ± 1.90	23.12	23.09	0.270	1.310	11.628	1.310	11.628	2.567
Adult	9.0	14	24.86 ± 1.14	25.14	24.86	0.270	1.310	11.900	1.310	11.900	2.567
Adult	10.0	9	31.00 ± 2.71	31.08	31.00	0.275	1.317	12.487	1.317	12.487	2.521
Adult	11.0	8	37.88 ± 2.44	37.89	37.88	0.295	1.343	12.319	1.343	12.319	2.350
Adult	12.0	2	38.50 ± 0.50	38.50	38.50	0.280	1.323	13.038	1.323	13.038	2.476
Adult	13.0	7	54.43 ± 4.75	54.52	54.43	0.315	1.370	12.688	1.370	12.688	2.200
Adult	18.0	4	81.75 ± 6.06	81.75	81.75	0.315	1.370	13.979	1.370	13.979	2.200
Adult	21.0	3	95.00 ± 5.77	95.00	95.00	0.330	1.391	13.799	1.391	13.799	2.100
Unparasitized (Control)		22	93.00 ± 3.36	94.05	93.00	0.330	1.391	13.74	1.391	13.74	2.10

\* Mean ± 1 SE; \*\* In ♀/♀/generation; \*\*\* In ♀/♀/day.

TABLE XI. The effects of parasitism by *A. smithi* on the demographic and biological characteristics of the different ages of alate *A. pisum* (reared at  $19.7 \pm 0.5^\circ\text{C}$ ,  $70 \pm 5\%$  RH, diel period of 18 L/6 D hours, on *Medicago sativa* L., var. Vernal).

Aphid Age at Parasitization	Instar Days	n	Total Mean Fecundity*	Gross Reproductive Rate (GRR)**	Net Reproductive Rate (R <sub>0</sub> )**	Intrinsic Rate of Increase (rm)***	Finite Rate of Increase (λ)***	Generation Doubling	
								Time (days)	Time (DT)
Third	5.0	8	0.13 ± 0.12	0.13	0.13	—	—	—	α
Fourth	6.0	7	1.43 ± 0.37	1.43	1.43	0.032	1.033	11.15	21.66
Fourth	7.0	4	7.50 ± 1.04	7.50	7.50	0.173	1.189	11.68	4.00
Fourth	8.0	5	16.00 ± 2.05	16.00	16.00	0.227	1.255	12.20	3.05
Adult	9.0	5	18.20 ± 2.31	18.20	18.20	0.233	1.257	12.49	2.98
Adult	10.0	4	25.50 ± 2.63	25.49	25.49	0.246	1.279	13.21	2.82
Adult	11.0	3	37.60 ± 2.50	37.67	37.67	0.275	1.317	13.19	2.251
Adult	12.0	2	43.50 ± 0.50	43.50	43.50	0.276	1.319	13.60	2.51
Adult	13.0	2	42.50 ± 5.50	42.50	42.50	0.260	1.297	14.42	2.666
Adult	14.0	1	61.00	61.00	61.00	0.275	1.317	14.95	2.521
Unparasitized (Control)		20	86.25 ± 3.75	89.25	86.25	0.277	1.320	16.00	2.50

\* Mean ± 1 SE; \*\* In ♀/♀/generation; \*\*\* In ♀/♀/day.

Messenger, 1964; Messenger, 1964a; Siddiqui and Barlow, 1972) discuss in detail the value of  $rm$  as a measure of the reproductive potential of an organism under a variety of experimental conditions.

In this experiment, life table data of age-specific survival ( $l_x$ ) and fecundity ( $m_x$ ) (summarized in Figs. 11A, B and in Tables X and XI) were obtained from only those aphids that died due to parasitism. The intrinsic rates of increase calculated from these data were used to provide an indication of the maximal attainable rate of increase under the specified experimental conditions. The doubling time calculated directly from  $rm$  was also used to evaluate the relative effect of parasitism on aphid population growth. The doubling time is considered to be the time in days required for an aphid population to double in numbers.

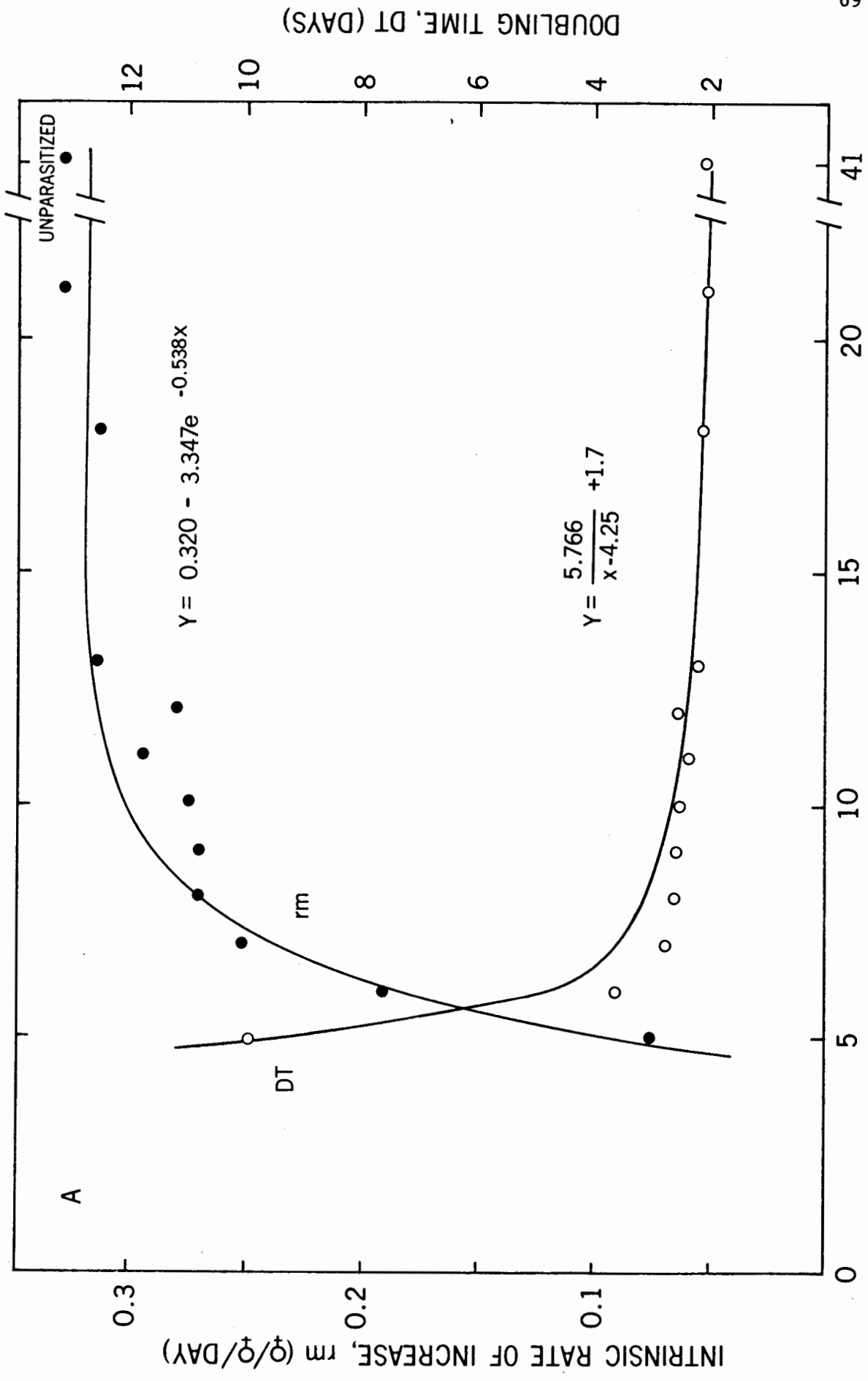
Apterous and alate pea aphids parasitized before the age of five and six days, respectively, showed zero or extremely small values for  $rm$  with the doubling time approaching infinity. This means that aphids parasitized in the first, second, or third instar periods could not contribute significantly to population growth, usually succumbing to parasitism before producing any offspring (Figs. 13A, B).

The later the aphid was parasitized, the larger the  $rm$  values became, with these values reaching the equivalent of that of a normal unparasitized aphid 15 days or older (Figs. 13A, B). Indeed, the  $rm$  levelled off to 0.330 ♀/♀/day for apterae and 0.275 ♀/♀/day for alatae when older aphids were parasitized (Figs. 13A and B).

In contrast, the doubling time of the aphid population decreased with the older aphids being parasitized. However, the DT levelled off to 2.1



Figure 13. The intrinsic rate of increase and doubling times of apterous (A) and alate (B) *A. pisum* parasitized at different ages by *A. smithi*. The  $r_m$  and DT values for unparasitized *A. pisum* are included for comparison.



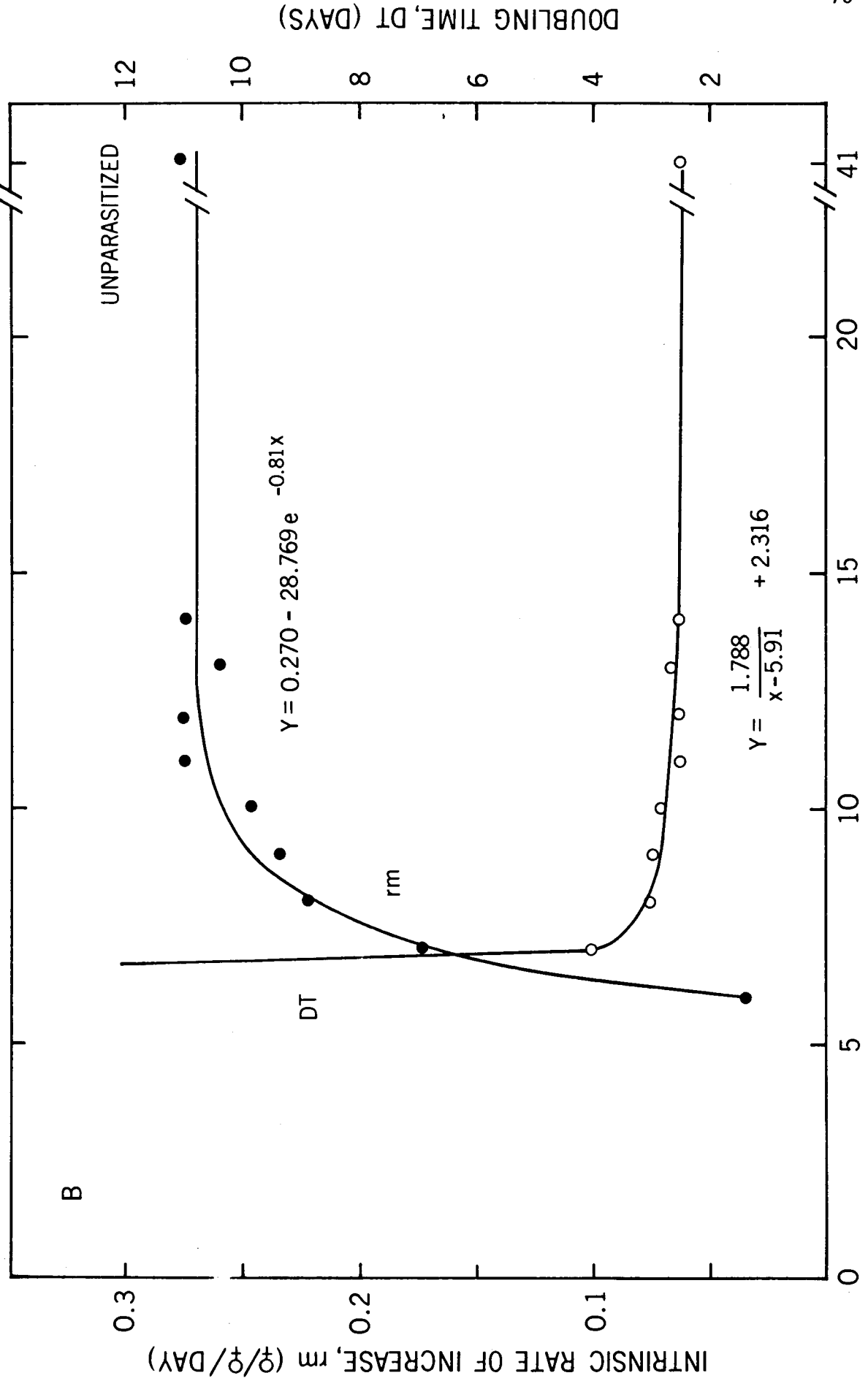
MEAN AGE OF APHID AT BEGINNING OF PARASITISM (DAYS)

INTRINSIC RATE OF INCREASE,  $r_m$  (♀/♀/DAY)

DOUBLING TIME, DT (DAYS)

UNPARASITIZED

A



B

MEAN AGE OF APHID AT BEGINNING OF PARASITISM (DAYS)

DOUBLING TIME, DT (DAYS)

UNPARASITIZED

12  
10  
8  
6  
4  
2

INTRINSIC RATE OF INCREASE,  $r_m$  (♀/♀/DAY)

DT

$r_m$

0  
5  
10  
15  
20  
41

days for apterae and 2.52 days for alatae when older aphids were parasitized (Figs. 13A, B). The above data indicate that the later aphids are being parasitized in their life, the less effect parasitism has on the aphid population as a whole.

4. *The effect of host age on the parasite's reproductive success.* The success of a parasite female in producing offspring depends on a number of factors which include host preference and host suitability. These factors were reviewed by Mackauer (1973) and Stary (1970). In this study the highest proportion of aphids that mummified were those in the second and third instars (ages 1.83 to 5.3 days) (Figs. 14A and 15A). The lowest proportion of aphids mummified consisted of adult aphids that had reached reproductive age. Parasite females were not given a choice between different aphid ages; rather, females were provided with aphids of known age, one at a time.

Female parasites are not always successful in injecting an egg into the host, even though the motions of oviposition have been observed. Aphids attacked by parasites were not dissected to determine the proportion of eggs deposited per total number of attacks made because it was important to obtain as many mummified aphids as possible to determine the effect of parasitism on aphid fecundity and development. Thus, there was no real way of knowing whether or not an egg was injected into the aphid after an attack was made. Figures 14B and 15B show the proportion of attacked aphids at different ages that did not succumb to parasitism and continued normal development and fecundity patterns. With increasing age, a higher proportion of aphids escaped parasitism.

Parasite attacks on reproductive aphids were generally unsuccessful, as few mummies were produced. These aphids either died a few days after parasite

Figure 14. The proportion of apterous *A. pisum* that (A) died before the eighth day; (B) escaped parasitism; (C) mummified, after parasite attack relative to aphid age groups.  $n$  = number of aphids exposed to parasite attack.

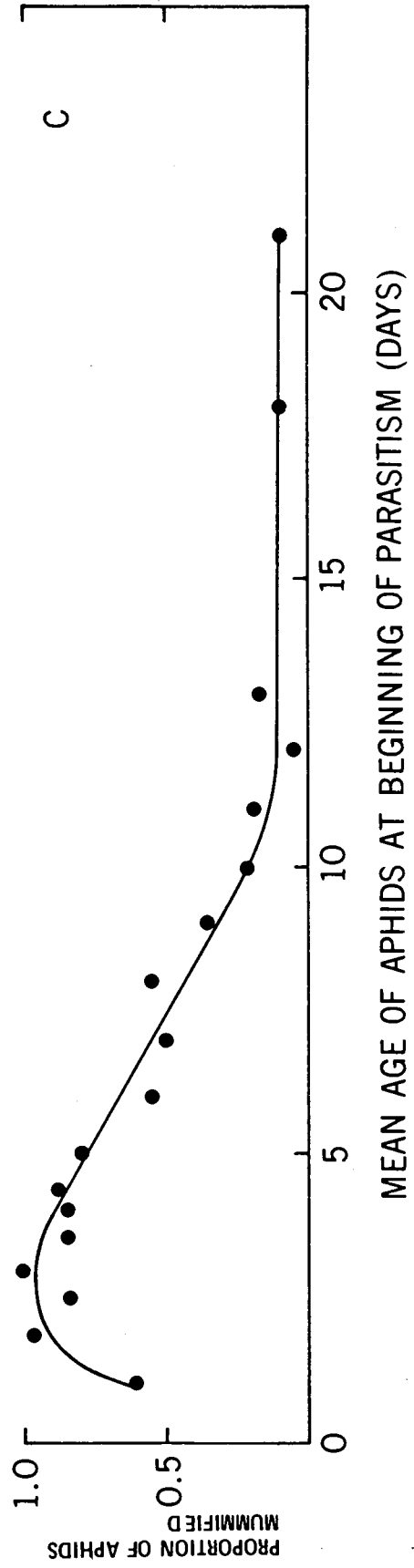
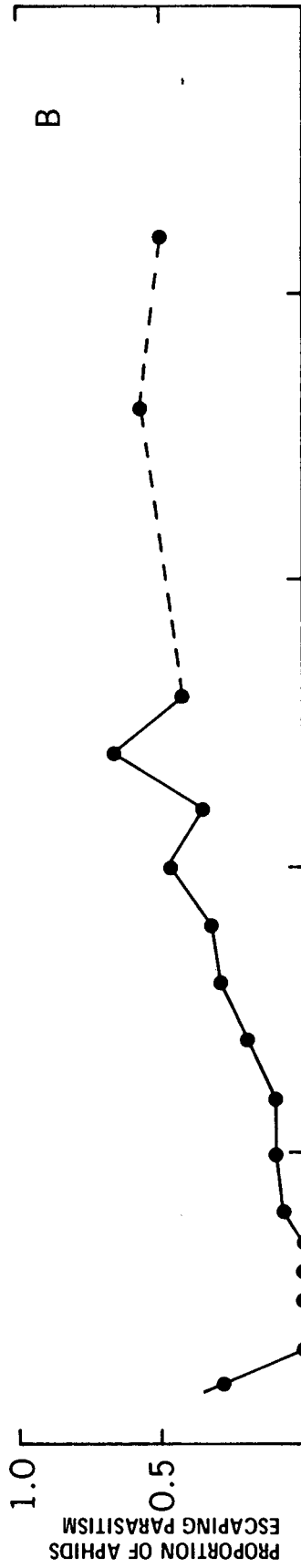
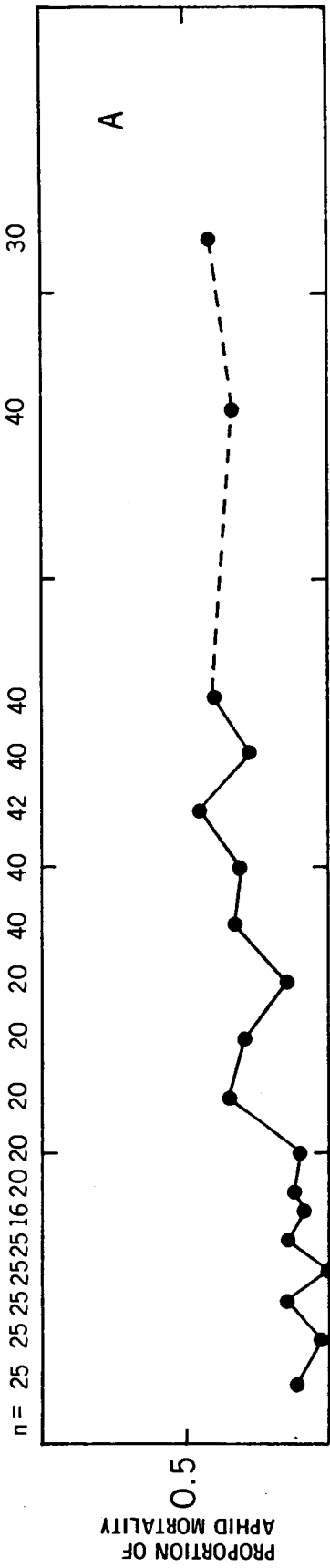
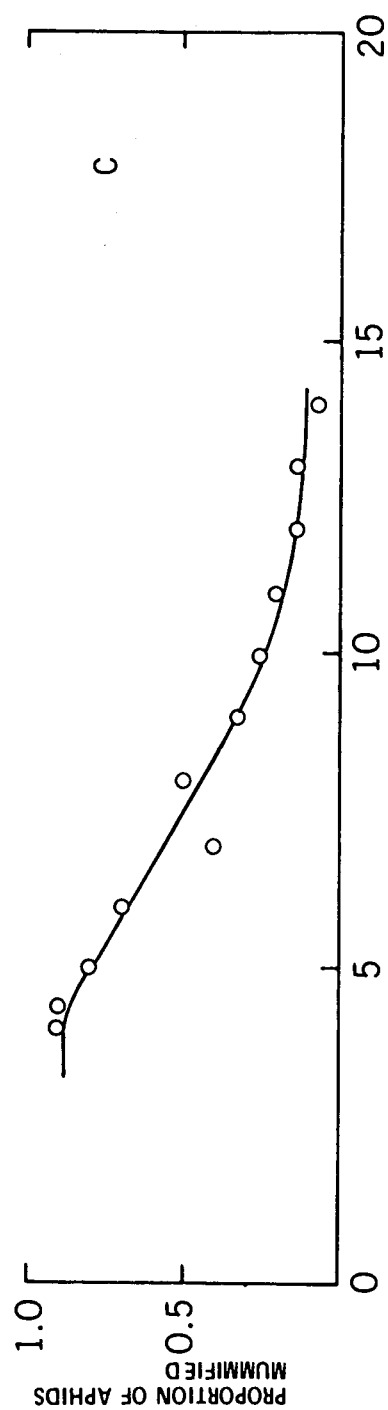
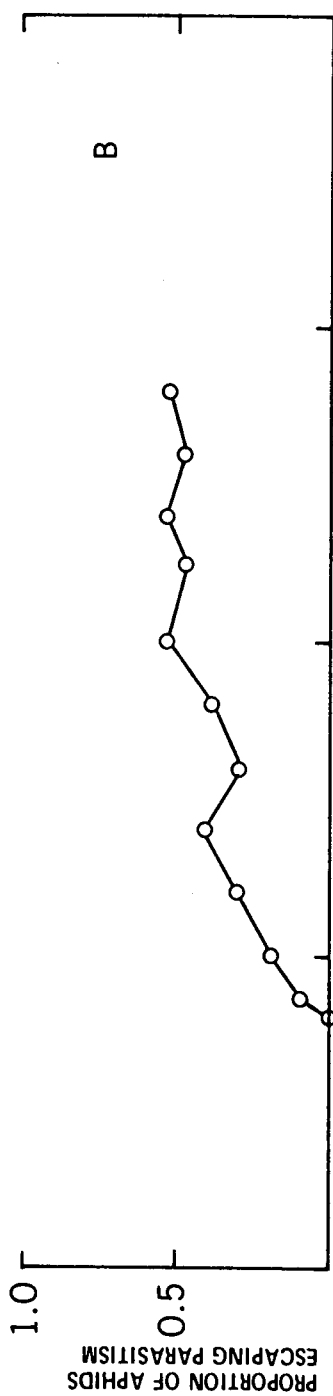
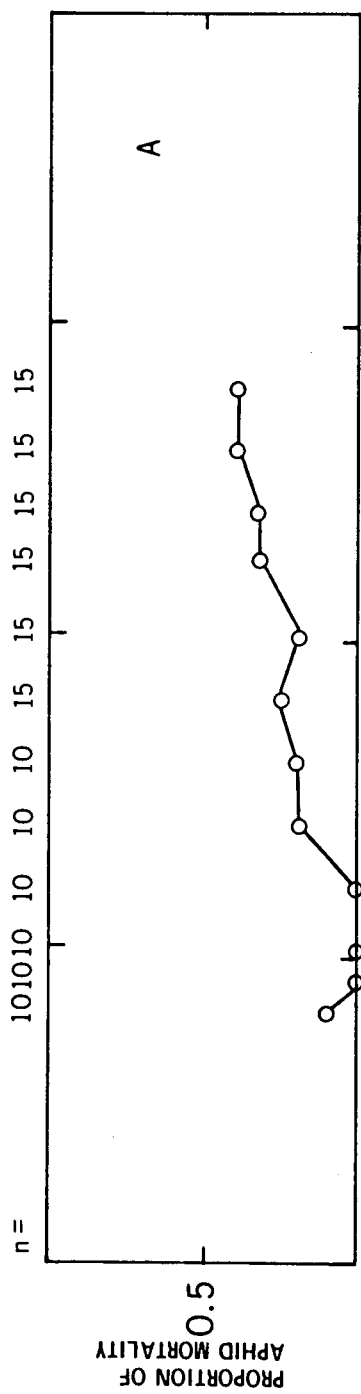


Figure 15. The proportion of alate *A. pisum* that (A) died before the eighth day; (B) escaped parasitism; (C) mummified, after parasite attack relative to aphid age groups.  $n$  = number of aphids exposed to parasite attack.





attack or escaped parasitism and achieved a normal longevity (Figs. 14, 15). The proportion of aphid mortality increased with older aphid ages being attacked. The aphids that died within eight days after oviposition (Figs. 14A, 15A) could have died from a number of causes, e.g. natural death, handling, plant resistance, or other.

#### D. Discussion

Parasitism by *A. smithi* results in the aphid's organs and tissues being slowly consumed by the developing parasite larva. Thus there is a lag period between the time of oviposition of the parasite egg and aphid death. The age of the aphid when parasitized will determine if the aphid will develop to maturity, reproduce, and contribute to aphid population growth. Generally, the pea aphid can continue to produce progeny for six to seven days after oviposition, at which time the reproductive rate drops off. The aphid can still contribute to population growth before succumbing to parasitism. This phenomenon was also observed in field collected parasitized aphids which produced up to 45 progeny before mummifying.

A number of other workers have found similar results. Hafez (1961) found that the rate of development of an aphid is influenced to a significant degree by parasitization. When first or second instars of *Brevicoryne brassicae* L. were parasitized by *Diaretiella rapae*, the duration of development was increased in comparison with that of non-parasitized aphids of the same age. The delay in development due to parasitization in higher instars and the adult stage was not (apparently) obvious or significant (Hafez, 1961). Although parasitization can result in a lengthening of an aphid instar period (Hafez, 1961), the longevity of the host is usually shorter than that of

normal unparasitized aphids. Webster and Phillips (1912) found that when aphid nymphs were parasitized before the first or second molt, both aphids and parasites failed to survive. However, Johnson (1958, 1959) noted that adult *Aphidius platensis* emerged from all stages of *Aphis craccivora* that were parasitized.

Johnson (1958, 1959) showed that parasitization of nymphs of *Aphis craccivora* by *Aphidius platensis* resulted in physiological and morphological changes compared to normal host development. These changes were the result of a premature breakdown of the host's prothoracic glands (Johnson, 1965).

Fox *et al.* (1967) found that *A. pisum* did not produce progeny if parasitized in the third instar by *A. smithi*; although, if late fourth instar and young adults were parasitized, they did give birth to young. They also found that parturition usually ended abruptly four days after the beginning of parasitism in aphids which had been parasitized when parturition had just begun.

The effect of parasitization on pea aphid reproduction in nature depends on host instar selection by the parasite female. Fox *et al.* (1967) reported that *A. smithi* females usually attacked first and second instar aphids with little hesitation but tended to hesitate and/or reject third and fourth instar nymphs and adult aphids. Wiackowski (1962) found that second and third instars of the pea aphid were preferred by *A. smithi* females, while the first and fourth instars were less frequently attacked. Mackauer (1973) showed that when *A. smithi* females were given a choice, they preferred second or older instar (i.e. 1.8 to 5.3 day old) pea aphids (Figs. 14C, 15C), while attacking first instars and pre-reproductive adults with less frequency than

second instars. In addition, the second and third aphid instars seem to be the most suitable for parasite development (Mackauer, 1973).

In this study, aphids parasitized in their early stages did not contribute to population growth. It is possible that an efficient parasite such as *A. smithi*, if it attacked only young aphids (assuming all aphids of a particular stage were found and parasitized by the searching parasite), could cause a local host population to become extinct. However, *A. smithi* does not attack exclusively any one stage. Field collected pea aphids have been shown to contain parasite eggs in all developmental and adult stages (field data). This shows that the parasite is not rigidly selective or specific in aphid instar requirements and can oviposit into older aphids, which in turn still can contribute to aphid population growth before succumbing to parasitism.

#### E. Summary

Groups of apterous and alate pea aphids differing in age from 1 to 21 days were parasitized by *Aphidius smithi* to determine the effect of parasitism on host development and fecundity. The laboratory data were intended to explain, in part, the effect of parasitism on aphid population growth rates in the field.

There was a lag period between the time of parasite oviposition (parasite larval development) and aphid death. The age of the aphid at time of parasitism determined whether or not it would develop to maturity, reproduce, and contribute to population growth. Apteræ parasitized as first or second instars (one to three days of age) developed to the fourth instar before mummification, while third or older instar apteræ (3.6 days) developed to

the adult stage. Alatae, due to their' longer fourth instar, produced fourth instar mummies when parasitized in the third or younger instar (4.4 days). When apterous and alate fourth instar or adult stages were parasitized, the aphids continued to develop and produce progeny for six to seven days after the beginning of parasitism, at which time reproduction ceased.

The intrinsic rates of increase ( $r_m$ ) were calculated from laboratory life table data. Apteræ and alatae parasitized before five and six days of age, respectively, showed infinitely small values for  $r_m$  and thus could not contribute significantly to population growth. When older aphids were parasitized, the  $r_m$  value became larger until it reached a maximum value equivalent to that of unparasitized aphids. The data indicate that the later an aphid is parasitized in its life, the less effect parasitism has on the aphid's contribution to population growth. *A. smithi* females, however, do not accept all host stages equally, but tend to select second to early third instar pea aphids more frequently than other ages. When second and third instar aphids are parasitized, they cannot contribute to population growth. Under these conditions the parasite could cause a local host population to become extinct. However, in the field the parasite is not entirely restricted to ovipositing into a given (i.e. young) aphid instar, but will also oviposit into older aphids.

## CHAPTER V

## SEASONAL DYNAMICS OF PEA APHID POPULATIONS

A. Introduction

Although there are numerous studies on the pea aphid, there are only a few works that have analysed mortality factors and pea aphid population trends throughout a growing season. Two peak curves of *A. pisum* populations occur during the growing season on alfalfa in various parts of the world (Cooke, 1963; Dunn and Wright, 1955; Hagen *et al.*, 1971; Hagen and van den Bosch, 1968; Pass and Parr, 1971; van den Bosch *et al.*, 1966). Many factors can cause fluctuations in pea aphid population levels. The individual or combined effects of physical factors such as temperature extremes, heavy rains (Dunn and Wright, 1955), and harvesting practices (van den Bosch *et al.*, 1966, 1967) can cause significant mortality in pea aphid populations. Biotic factors such as the increase in maturity of the host plant or high aphid densities may cause a reduction in aphid fecundity and developmental rates (Murdie, 1969a, b) and the production of alate offspring (Sutherland, 1969) which leads to mass migration, causing rapid population declines (Dunn and Wright, 1955). Mortality agents such as parasites, predators, and pathogens contribute to the regulation of pea aphid populations (Dunn and Wright, 1955; Cooke, 1963; Fluke, 1929; Hagen and van den Bosch, 1968; Smith and Hagen, 1966; Stary, 1969; Voronina, 1971). The characteristics of aphidophagous insects have been reviewed, e.g. for Coccinellidae by Hagen (1962), Hodek (1967), and Hagen and van den Bosch (1968); and for Syrphidae by Schneider (1969). The impact of natural enemies on aphid populations was reviewed by Hagen and van den Bosch (1968) and discussed by Hodek *et al.* (1972), Mackauer (1973), and Stary (1970).

Although indigenous hymenopterous parasites, predators (such as Coccinellids, Syrphids, and Chrysopids), and fungal and bacterial diseases undoubtedly are important mortality agents (Glendenning, 1935, 1941; Handford and Neilson, 1957), no detailed study of their impact on pea aphid populations in alfalfa fields of B.C. has been made to date.

This chapter reports on the population fluctuations of the pea aphid and the possible mortality agents causing these fluctuations during 1971 and 1972 in an alfalfa field near Kamloops, B.C. Parasitism is considered as a whole in this chapter; the relative contribution of each parasite species to aphid mortality is dealt with in Chapter VI.

#### B. Materials and Methods

1. *Study area.* An alfalfa field (approximately 2.4 acres or 0.98 ha) was studied at the Canada Department of Agriculture Field Station, Kamloops, B.C. The field was approximately 800 metres north of the Kamloops Airport weather observation site (Lat. 50°43' N; Long. 120°25' W; elevation 345.3 m above sea level).

The Middle Latitude Steppe climate at Kamloops is generally dry with a mean annual precipitation of 260.6 mm (Table XII) and is characterized by hot dry summers (mean normal for July is 20.9°C) and cold dry winters (mean normal for January is - 6.0°C).

The Kamloops climate is ideal for growing crops such as alfalfa during the summer months because the high insolation and heat are present. There is also an unlimited supply of irrigation water available from the nearby Thompson River.

Table XII. Mean monthly temperatures and precipitation for Kamloops Airport, B. C. (Lat. 50° 43' N; Long. 120° 25' W; elevation 345.3 m).\*

Month	Mean maximum temperature (° C)			Mean minimum temperature (° C)			Mean precipitation (mm)		
	Normal	1971	1972	Normal	1971	1972	Normal	1971	1972
January	-2.3	-2.0	-6.8	-9.7	-8.8	-16.1	28.7	44.2	34.5
February	3.1	2.7	0.1	-5.8	-4.7	-8.9	15.5	19.1	14.2
March	9.1	6.8	9.3	-2.1	-3.0	-1.8	8.1	12.7	24.1
April	16.2	16.6	13.0	2.4	2.3	1.2	12.4	27.9	7.1
May	21.8	22.2	22.9	6.8	7.2	7.5	19.0	23.1	14.2
June	25.2	22.3	23.3	10.8	10.4	11.5	36.3	36.0	34.5
July	29.1	29.9	28.2	12.7	12.9	12.4	25.9	15.5	18.3
August	27.6	31.2	29.2	11.8	14.4	13.1	26.9	12.4	19.3
September	22.4	20.1	18.7	7.6	7.7	6.4	20.3	13.7	14.9
October	13.8	13.3	12.2	3.0	2.6	-0.8	18.5	5.3	13.5
November	5.4	6.6	5.3	-2.0	-0.2	0.2	20.6	20.6	6.4
December	0.7	-5.7	-1.3	-5.8	-13.4	-8.1	28.2	91.2	21.8

\* Weather records from the Kamloops Weather Office, Atmospheric Environment Service, Canada Department of the Environment (Normals given are based on the period 1941 to 1970).

2. *Agro-production techniques.* The alfalfa variety Vernal (Hienrichs, 1968) was used in this study. It is one of the varieties that is least resistant to pea aphid infestations (Kindler *et al.*, 1971; Pimentel and Wheeler, 1973).

Alfalfa is usually harvested for hay three or, in very warm sunny years, four times a year in Kamloops (Fig. 1). Alfalfa, when cut at an immature stage, has a higher amino acid (Loper *et al.*, 1963) or higher protein content and thus a higher feed value than when cut later. To acquire a balance between the maximum obtainable protein content for a hay crop without causing a damaging reduction of food reserves in the roots, Hubbard and McLean (1961) suggested that alfalfa be cut when in 10% blossom. The last alfalfa harvest, in the fall, is made approximately four weeks before the first major frost. This allows the alfalfa to regrow a crown and insures an abundant food supply stored in the roots, considerably reducing the possibility of winter kill (W. A. Hubbard, pers. comm.). The alfalfa plant overwinters in its dormant branch-root system. New shoots begin to grow in late March to mid-April (Fig. 1).

The alfalfa in the study area was five years old in 1971; this is a relatively old stand. The stand was in good condition, although some dandelions (*Taraxacum officinale* Weber) and shepherd's purse (*Capsella bursa-pastoris* [L.]) were interspersed in the field. When the height of alfalfa was between 25 and 35 cm, there was a mean of 44.9 alfalfa tips per square foot ( $.0929 \text{ m}^2$ ) ( $\pm 2.8$  SE from a sample of 40 one foot squares taken randomly in the field).<sup>2</sup> Cooke (1963) considered a good stand of alfalfa to

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<sup>2</sup> Total estimated mean number of alfalfa tips in the field were  $4.7 \times 10^6 \pm 0.2 \times 10^6$  SE.



be about 50 tips/ft<sup>2</sup> in the alfalfa fields of the Blue Mountain Range of eastern Washington and Oregon.

The field was irrigated with water sprinklers at least once per crop, generally when the alfalfa was 8 to 20 cm high or during dry periods, when required.

The alfalfa crop was harvested three times each year for hay. The alfalfa was mown, allowed to dry for two to three days, raked into windrows, and baled as soon as it was properly cured. The bales were usually removed from the field a day later.

Only one chemical treatment was made during the field study. In early April, 1972, the field was fertilized with 300 lbs/acre of superphosphate (0-20-0) and then harrowed.

3. *Sampling Methods.* Three sampling methods were used at weekly intervals to estimate aphid, parasite, and predator populations on the alfalfa plants: (a) alfalfa tip sampling; (b) sweep sampling; and (c) mummy sampling. However, only the results of the alfalfa tip sampling are considered in detail in this chapter. Because of the unreliability of sweep sampling as a quantitative measure of insect populations (Turnbull, 1973), the results obtained by this method are only briefly mentioned. The method and results of the mummy sampling are described in Chapter VI.

a) *Alfalfa tip sampling.* Weekly alfalfa tip samples were made to obtain a population estimate of aphids (all stages and morphs), parasites (only immature stages), and predators (larvae, adults). The collected samples consisting of 100 alfalfa tips (each 10 to 20 cm long) were gathered in groups of 10 and placed into separate plastic bags. When aphid popula-

tions were expected to be low (i.e. in early spring), an additional 100 to 200 tips were collected. The tip sample was generally made between 8 and 10 AM (Pacific Standard Time). This insured that most insects to be collected were relatively inactive, thus lessening the chances of losing specimens. Each alfalfa tip sampled was approached slowly so that the feeding or resting insects were not disturbed. An additional precaution was taken by holding the open end of the plastic bag below the alfalfa tip while it was being picked, so that all insects would drop into the bag.

Each alfalfa tip was collected at least 7 m (5 to 10 walking steps) apart along four transient lines (18 m apart) within the entire area of the field. A 10 m margin along the edges of the field was not sampled to avoid "edge effects" (van Emden, 1965).

After the 100 alfalfa tips had been sampled, they were taken immediately to the laboratory and processed; however, if the tip sample could not be processed immediately it was placed in a cooler at 5°C to reduce aphid development, reproduction, and insect predation until processed. To process the tip sample one tip at a time was removed from a plastic bag and all aphids, mummies, and insect predators were collected from the foliage, using a camel's hair brush or a pair of fine forceps. All aphids and predators were placed into 75% ethanol; the mummified aphids were counted and placed individually into gelatin capsules for later parasite emergence and identification. The preserved aphids were separated into instars (using antennal lengths as a stage indicator; see Fig. 2 or Davis [1915]) and morphs and counted. The third and fourth instars and adult aphids were dissected to determine the frequency of parasitism by hymenopterous parasites. Aphids were considered

parasitized if they contained one or more parasite eggs or larvae. First and second aphid instars were not dissected, as they were too small for rapid dissection. Insect predators were counted and grouped into families and stages as follows: Syrphidae (larvae, pupae); Coccinellidae (larvae, pupae, adults); Chrysopidae (larvae, pupae); and Nabidae (nymphs, adults).

*i.* Some advantages and disadvantages of alfalfa tip sampling as a sampling method. A number of authors have reviewed plant clippings as a method of sampling (Cooke, 1963; Fenton and Howell, 1957; Heathcote, 1971). The tip sample is an accurate method of determining quantitatively the mean numbers of insects per alfalfa tip. I have found that the common insect predators that are known to attack and feed on the pea aphid can usually be collected if sampling is done with care. This sampling method gives a good quantitative and qualitative means of measuring aphid population age structure and predator numbers, and the frequency of parasitism. Several disadvantages of the tip sampling method are known, one of which is a tendency to slightly underestimate the insect populations per tip because some insects will drop off when sampling or be missed while sorting the insects from the foliage. Also, parasite adults are far too active and invariably fly off before they are placed into the plastic bag. Coccinellid larvae probably remain inactive on the lower regions of the alfalfa stems during the cooler time of the night and early morning, and thus there is a tendency for the alfalfa tip sample to underestimate the number of coccinellid larvae present.

*b) Sweep sampling.* Sweep samples were made to determine the relative abundance of adult parasites and the presence or absence of predators. Sweeps were made with a 38 cm diameter beating net attached to a

90 cm long handle. A sweep was taken by holding the net as far forward as possible, with the lower rim 15 to 25 cm below the top of the alfalfa in the field, and brought in a 180° arc to the left then back to the right, while the operator stepped forward one or two paces. All the sweeps were made by me to keep the sampling method as consistent as possible. A sample consisted of 100 sweeps made diagonally across the field.

The collected material was subsequently frozen (at - 10°C) for several days. The insects were sorted in a white enamel tray (40 x 30 x 2 cm) containing a mixture of water and 5% detergent.

Sweep samples do not give absolute numbers but only an indication of the relative numbers of insects in a field. The unreliability of the sweep sample technique in producing quantitative data is discussed by Fenton and Howell (1957), Coe (1963), and Heathcote (1971). For this reason the sweep sample data (Appendix 5) was used only as a "rough and ready" differentiation between high and low numbers or the presence or absence of certain aphidophagous insects in the field.

c) *Estimation of alfalfa height and blossoming.* The mean height of alfalfa in the field was estimated by randomly choosing ten stems and measuring the length of the stems from ground level to the highest tips. Only a visual estimate of the percent blossom and seed was made.

4. *Calculation of the physiological time scale.* Although calendar time was used to represent the field study results, a physiological time-scale (Hughes, 1963) was used in analysis of the field data and the computer model (Chapter VII). There are a number of ways to convert calendar time in the field to a physiological time-scale. Gilbert and Gutierrez (1973)

fitted sine curves to the daily maximum and minimum air temperatures and integrated them above the threshold temperature for development to obtain the physiological time. In this work a computer programme was written to sum the day-degrees above the threshold, using two-hourly temperatures.<sup>3</sup> The aphid and parasite species had different temperature thresholds (Table XIII); however, the different physiological time scales calculated from these thresholds were generally in constant proportion (Table XIII and Appendix 1) throughout the season. Thus the same basic time scale of a "quip" (quarter instar period) could be used for all insects. The number of quip periods throughout the season<sup>4</sup> were calculated and are used in the physiological time scales.

5. *Calculation of alate production, emigration, and immigration.* The proportion of fourth instar aphids that would develop into alatae was determined by the method of Hughes (1963) and Hughes and Gilbert (1968). A regression equation was fitted to the proportion of alatform fourth instar pea aphid nymphs against the density of aphids 15 quips previously. (It should be noted that the determination of alate production occurs in the mother in response to stimuli such as aphid density.)

Emigration of aphids was considered as alatae leaving the local population and contributing to the pre-reproductive mortality of the aphid population (Hughes, 1963). Emigration was measured by an indirect method in this study. An average fourth instar aphid takes, from the middle of i.s instar,

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<sup>3</sup> The formula  $DD = (T-t)D$  was used where: DD = sum of day-degrees above t for one day; T = temperature ( $^{\circ}$  C) for a two-hour interval; t = threshold temperature for development; D = time period 1/12 of one day.

<sup>4</sup>  $NQ = DD/Q$ , where: Q = one quip; NQ = accumulated number of quips through season.

Table XIII. The threshold temperatures for development (t), the different proportions of the physiological time scales (P), and the equivalent number of day-degrees of a quip for the pea aphid and its associated parasites and a predator.

Species	Threshold Temperature, t (° C)	Proportion P	Quip* Equivalent Day-degrees
<i>A. pisum</i>	5.56	1.00	6.19
<i>A. smithi</i>	6.10	0.95	5.87
<i>A. e. ervi</i>			
<i>A. e. pulcher</i>			
<i>P. pequodorum</i>	6.88	0.88	5.50
<i>L. niger</i>	6.55	0.92	5.69
<i>A. lucens</i>	8.55	0.78	4.83
<i>C. transversoguttata</i> **	10.0	0.68	4.22

\* Quip = quarter instar-period; One instar-period = 24.78 day-degrees (° C) above 5.56°C.

\*\* For further details see Appendix 1.

one instar period (or four quips) to mature, ecdyse, and dry its wings before emigrating (Table IV). With this information a crude emigration rate can be estimated by comparing the number of alatae per 100 alfalfa tips with the expected number of alatiform fourth instar nymphs four quips before (found by extrapolating between two alfalfa tip samples in Appendix 4). If there were fewer alatae than the calculated number of fourth instar alatiforms, emigration had taken place. If there were more alatae than the calculated number of alatiform fourth instars, immigration of alatae into the field was assumed.

6. *Calculation of the total predator equivalents.* To calculate the numbers of aphids taken by predators in the field an indirect method was used to determine the feeding rates and density of predators. Maximum feeding rate values were estimated (Table XIV, Appendices 2 and 3), and the density of the predators was obtained from the alfalfa tip samples (Appendix 4). To simplify matters a common total number of predators with one feeding rate was required. Because each predator type had a different feeding rate (Table XIV), the adjustment of the numbers of the predator types to one equivalent predator total was accomplished by using the formula  $V_p P_p$ , where:  $V_p$  is the equivalent predator voracity of a particular predator type (p) (Table XIV), and  $P_p$  is the number per 100 alfalfa tips of predator type (p).

### C. Results

The numbers and stages of the insect species found on the alfalfa tips were averaged for the whole field and are shown in Appendix 4 and Figs. 16 and 17 as mean numbers per 100 alfalfa tips. Some of the data were transformed into  $\log_{10} (n + 1)$  for illustration purposes. Subsequent discussions

Table XIV. A summary of the mean feeding rates or voracities of each predator type and the equivalent predator voracity values when compared with coccinellid larval feeding rates.

Predator (p)	Mean Feeding Rates = No. of aphids eaten per quip (F)*	Equivalent Predator Voracity (V)**
Coccinellid larvae	9.6	1.00
Coccinellid adults	14.2	1.48
Chryopid larvae	4.4	0.46
Nabid nymphs and adults	4.0	0.38
Syrphid larvae	6.1	0.64

\* Appendices 2 and 3 show how these values were calculated.

\*\*  $V = F/F_c$ , where: F = mean feeding rate of a predator; and  $F_c$  = mean feeding rate of Coccinellid larvae which is 9.6.



Figure 16. Composite diagram showing: (A) daily mean temperatures\* and total precipitation; (B) predator trends; (C) total aphid and percent parasitism trends; (D) height and period of blossom of alfalfa in an alfalfa field near Kamloops, B.C., during the summer of 1971.

\* (Means of two-hourly recordings of ambient [shaded] 1.22 m above ground temperatures taken at the Kamloops airport, Canada Department of Environment Weather Station, approx. 800 metres from the field; vertical lines are temperature ranges.)

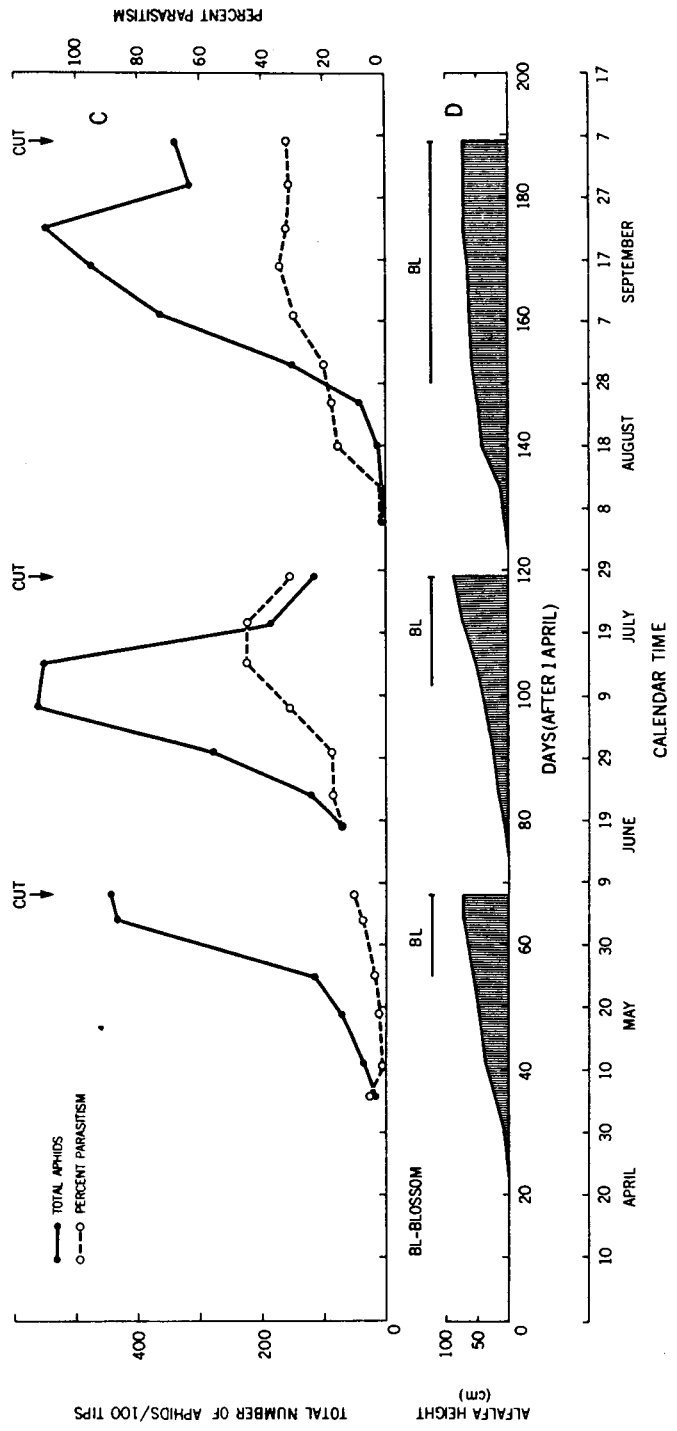
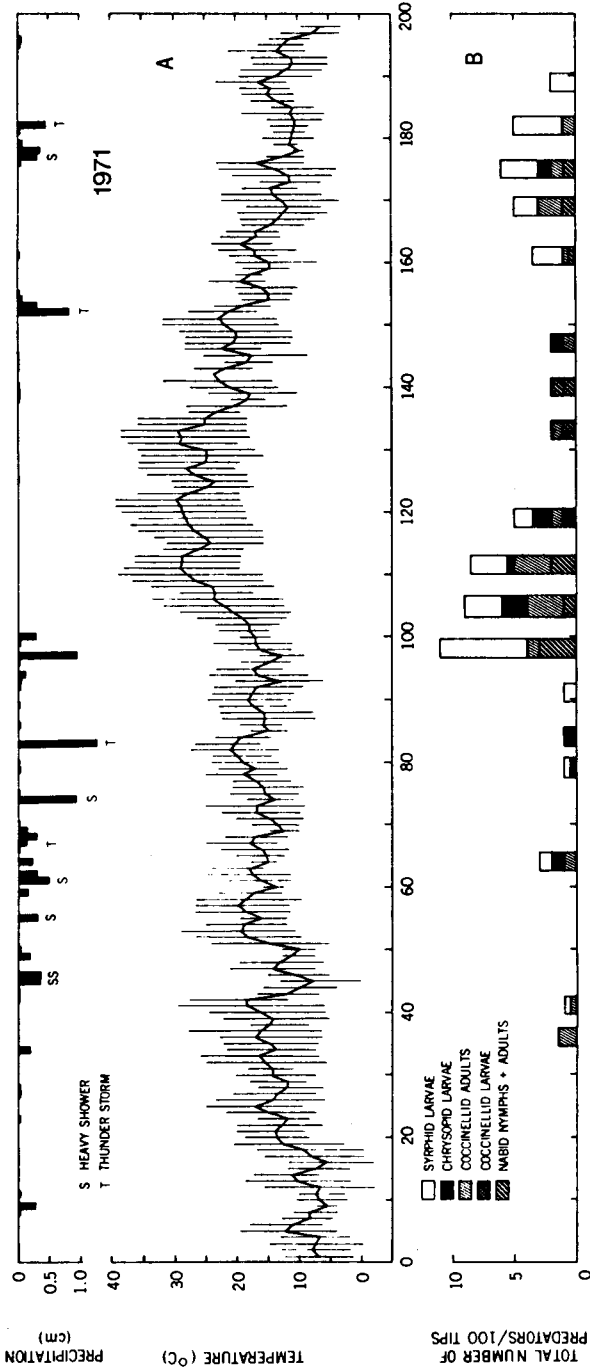
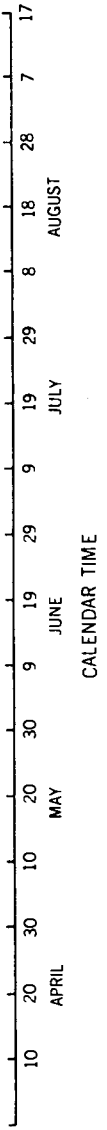
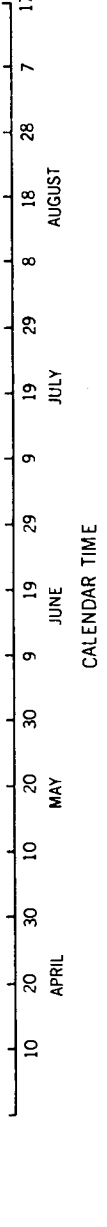
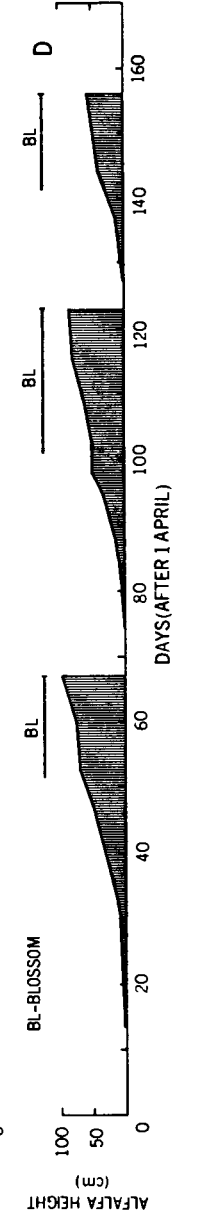
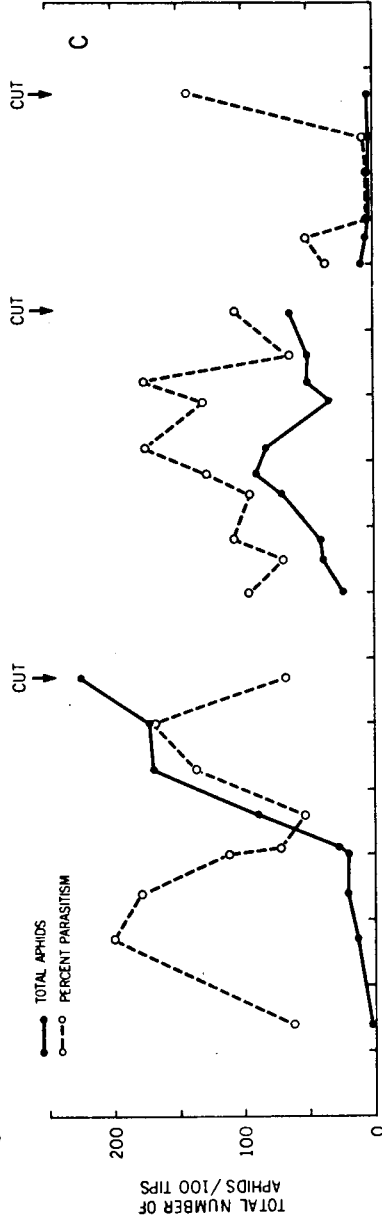
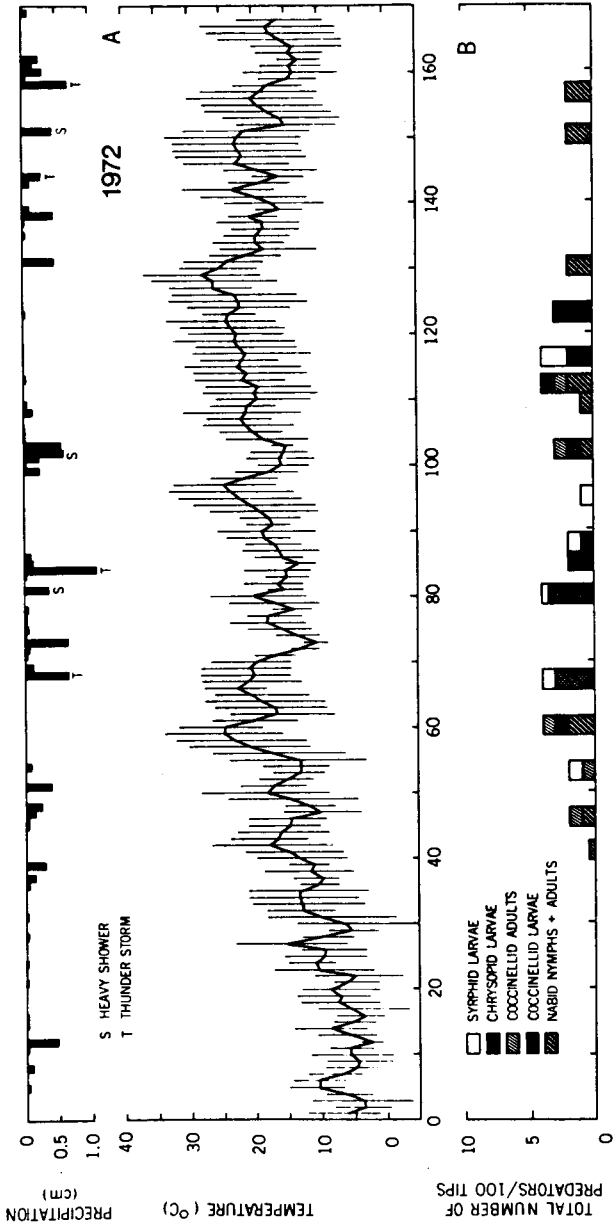


Figure 17. Composite diagram showing: (A) daily mean temperatures\* and total precipitation; (B) predator trends; (C) total aphid and percent parasitism trends; (D) height and period of blossom of alfalfa in an alfalfa field near Kamloops, B.C., during the summer of 1972.

\* (Means of two-hourly recordings of ambient [shaded] 1.22 m above ground temperatures taken at the Kamloops airport, Canada Department of Environment Weather Station, approx. 800 metres from the field; vertical lines are temperature ranges.)

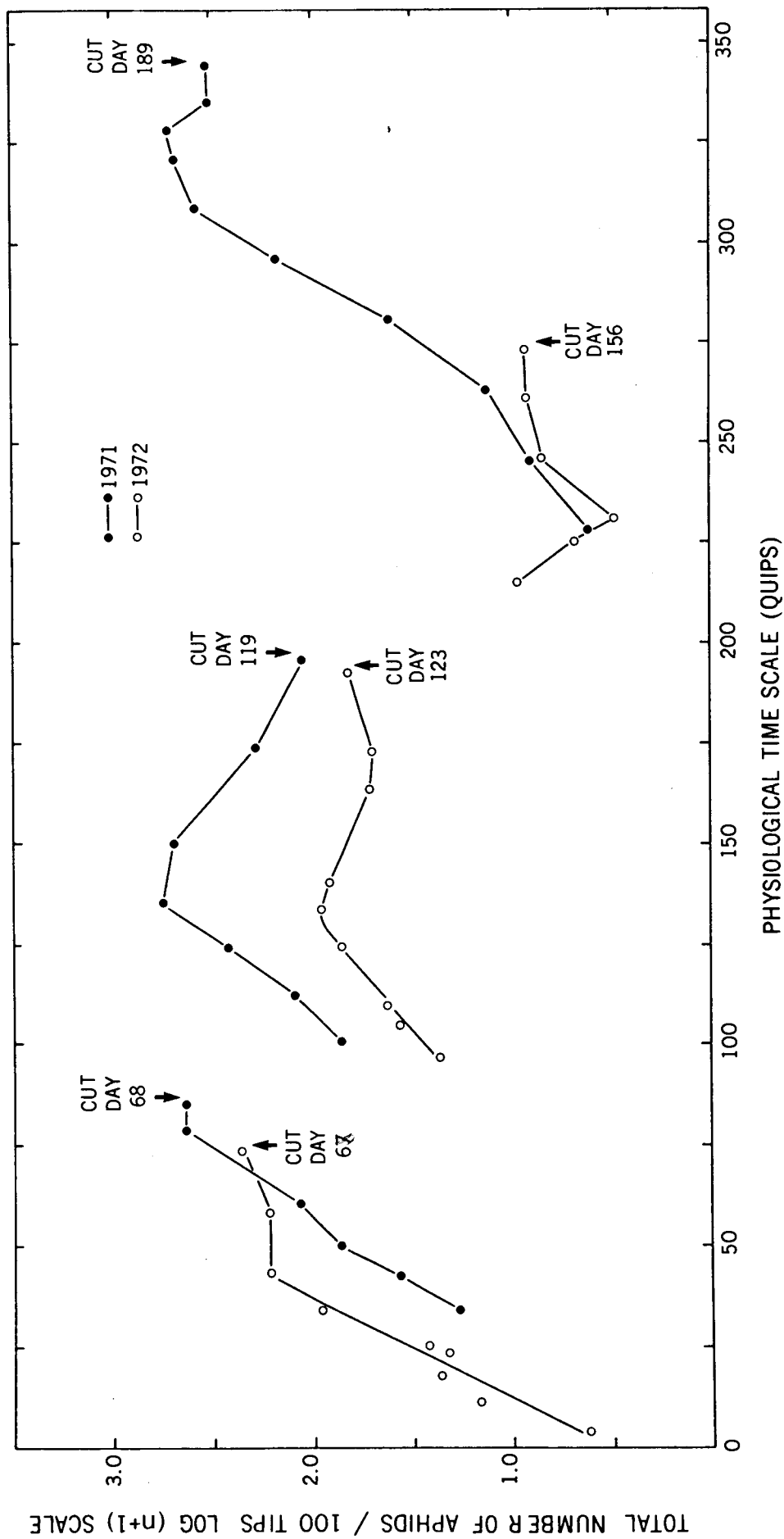


and analyses are largely based on these data.

1. *Seasonal aphid population trends.* In the spring of both 1971 and 1972 the aphid numbers increased rapidly once the first apterous progeny of the fundatrices had matured. The peak aphid population for the first crop was 443 aphids per 100 tips during 1971, twice as many as in 1972 (Figs. 16, 17). Although harvesting reduced aphid populations, the regrowth of alfalfa was usually accompanied by a rapid recovery in aphid numbers. Aphid densities usually peaked before each harvest; there were three alfalfa crops and generally three aphid population peaks per season, especially in 1971. The first crop cutting caused heavy aphid losses in both years. The highest number of aphids per 100 tips was 563 during the second crop in 1971, which declined rapidly to about 100 aphids before the crop was cut. Aphids did not reach as high a population peak in the second crop during 1972 as in 1971. In the third crop of 1971 the aphid population increased to 549 aphids per 100 tips before declining again. In 1972 the aphids were extremely rare during the third crop period.

The interpretation of pea aphid population fluctuations becomes clearer when changes in the total aphid numbers are plotted on a logarithmic scale against a physiological time scale (Fig. 18). There was more accumulated heat (in day-degrees) in 1971 than in 1972; e.g. the first harvest occurred at approximately the same time (day 68 and 67) in both years, but the total number of quips in 1971 after 1 April was greater by 11 quips than it was in 1972 (Fig. 18). However, the initial rate of increase was the same for both aphid populations in spring of 1971 and 1972. This suggests that similar processes of population increase occur at the beginning of aphid

Figure 18.  $\text{Log}_{10} (n + 1)$  of the total number of pea aphids per 100 tips plotted on a physiological time scale (after 1 April), from an alfalfa field near Kamloops, B.C., during 1971 and 1972. (1 quip = 6.2 day-degrees above 5.56°C.)



TOTAL NUMBER OF APHIDS / 100 TIPS LOG (n+1) SCALE

PHYSIOLOGICAL TIME SCALE (QUIPS)

population growth, even though initial aphid densities may be different.

In spring, 1971, aphid numbers reached a plateau shortly before the alfalfa harvest; while during spring, 1972, a plateau was reached 20 quips prior to the harvest. The plateau in both years coincided with the mass emigration of alates from the field (Fig. 20).

The initial increase and peaking of aphid numbers in the second crop of both years closely parallel each other, although there was a much lower aphid density in 1972. Aphid densities were very low in the third crop, 1972, and remained low until the alfalfa was cut (Fig. 17C). In contrast, there was a steady rate of increase in the third crop of 1971, similar to the other two crops of that year, before the aphid numbers declined in the late fall (Figs. 16C, 17C, 18).

2. *Possible factors causing aphid population changes.* a) *Weather.*

Kamloops climate restricts aphid population growth to the summer months (April to October). During the late autumn and winter the temperatures are too cold for either plant or aphid growth (Table XII). The summer of 1971 was generally warmer than that of 1972 (Table XII, Figs. 16, 17), especially during April, July, and August. Heavy rain and winds up to 50 mph occasionally occurred during both summers, especially during thunderstorms (Figs. 16 and 17). The mechanical effect of heavy rain and strong wind gusts during prolonged bad weather in 1971 (days 175 to 185) and 1972 (days 103 to 110) may have caused the aphid population to decrease (Figs. 16, 17). In general, however, the effect of heavy rains or wind on aphid populations may have been detected more readily by more frequent sampling.

Weather effects on aphid populations were especially important during the period of one week after hay harvesting. The process of harvesting caused a reduction in aphid numbers. However, the mild weather after the



first cut in both years apparently allowed the survival of many aphids (Figs. 16, 17, 18), which began reproducing on the new alfalfa growth. Many parasite adults and Coccinellid larvae were also observed to survive this period (casual observations). In contrast to the first cuts, the weather was hotter and drier after the second crop cuts. Very few surviving aphids, parasites, and predators were left to reproduce on the subsequent new alfalfa growth, perhaps having been killed immediately after the second cut, in both years, by the hot dry weather (Figs. 16, 17, Appendix 4). Aphid recolonization of the field for the third crop occurred when immigrant alates flew in from other plant hosts or alfalfa fields.

b) *Harvesting.* Mowing left a 7 to 15 cm stubble and the cut alfalfa drying on the ground for one to two days. This microclimate afforded some shelter for insects and induced a rapid regrowth of the plants. However, the drying and removal of cut alfalfa deprived the remaining aphids of food, except for the regenerating young shoots, causing high aphid mortality.

The mowing operation is often combined with raking to reduce leaf loss in the cut crop. However, in the study field the mowing, raking, and baling operations were performed separately, causing considerable leaf loss from the hay harvest. The leaves settled on the ground in the field, allowing any mummies which were attached to these leaves to remain in the field. In addition, the effect of leaving the alfalfa to dry in windrows for several days allowed some parasitized aphids to mummify on the stubble or on the ground, thus reducing parasite mortality due to harvesting.

c) *Plant aging.* The field evidence did not show whether or not maturation or the quality of the alfalfa plant affects pea aphid development or reproduction. A simple laboratory experiment showed that there were no differences in the development or total mean fecundity of apterae reared on pre-bud and bloom stages of alfalfa cut from the field and kept in tap water at 19.7°C (procedure as in Chapter II). The data were not considered adequate, however, to draw any definite conclusions nor to report in detail here. Sutherland (1969a) reported that the aging of the alfalfa plant (i.e. the flowering stage) may increase alate production.

d) *Emigration.* Figure 19 shows the relationship between aphid density and alate formation in the first alfalfa crop for both years. In this study no attempt has been made to analyse the possible mechanisms that influence alate formation. However, Sutherland (1969a, b) has shown aphid density and plant age can affect pea aphid alate production.

Figures 20A and B compare the number of alatae observed in the alfalfa tip samples with the calculated number of alatiform fourth-instar nymphs moulting four quips previously. These graphs give an indirect indication of alate production and emigration in the field for both years. If there were more alatiform fourth-instars present than alatae, it was assumed that the difference in numbers was the result of alatae that emigrated away from the field. The largest production of alatiform fourth instar nymphs occurred during the first crop in both 1971 and 1972. The large number of alates in crop 3, 1971, was comprised mainly of winged sexuals (Fig. 20A, Appendix 4).

The large production of alatiform progeny in the first crop is shown in Figs. 19 and 20. Emigration from the alfalfa field could be considered

Figure 19. The relationship between pea aphid density and the proportion of winged progeny (fourth instars) in alfalfa tip samples of *A. pisum* during the first alfalfa crop period, 1971, 1972.

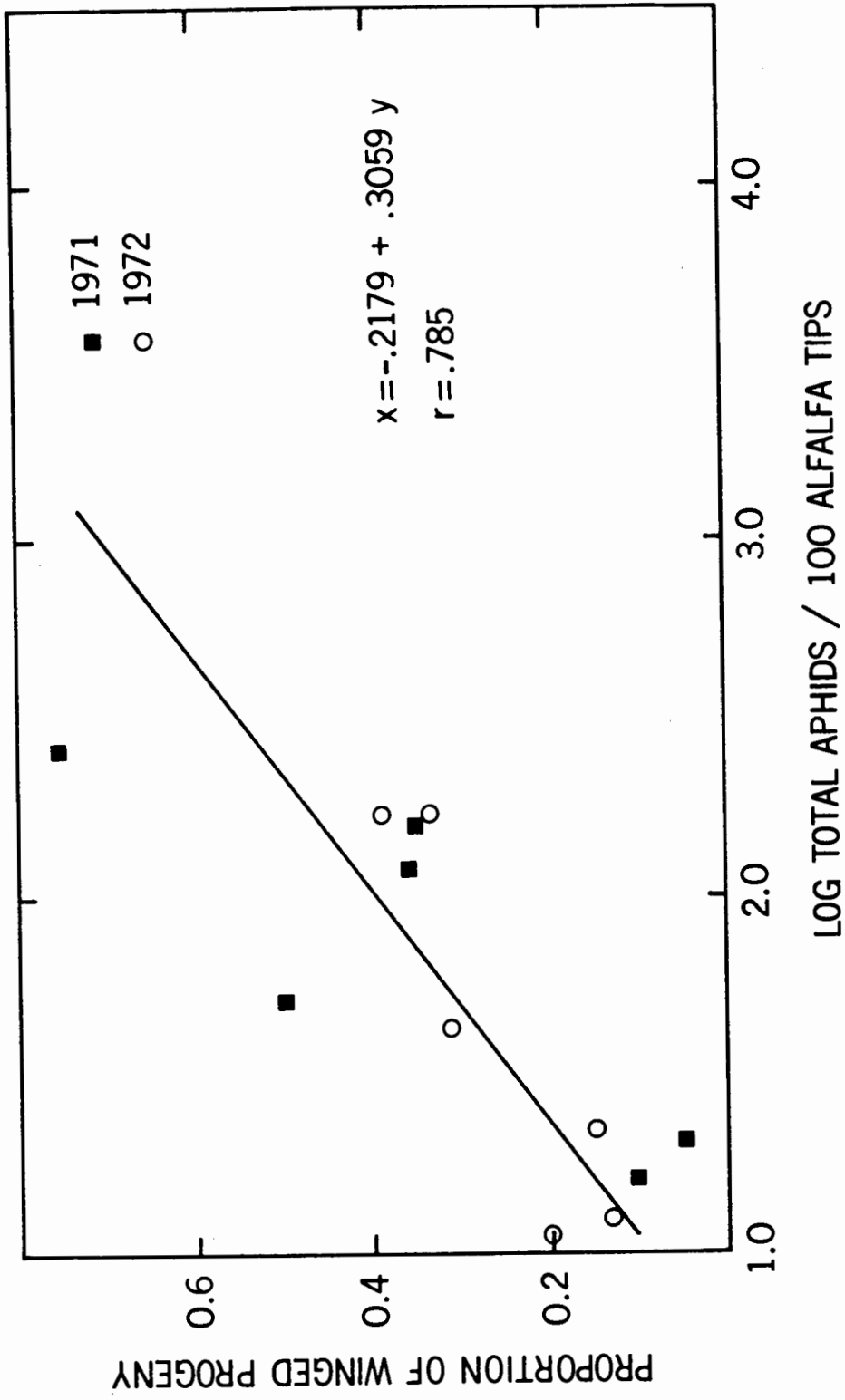
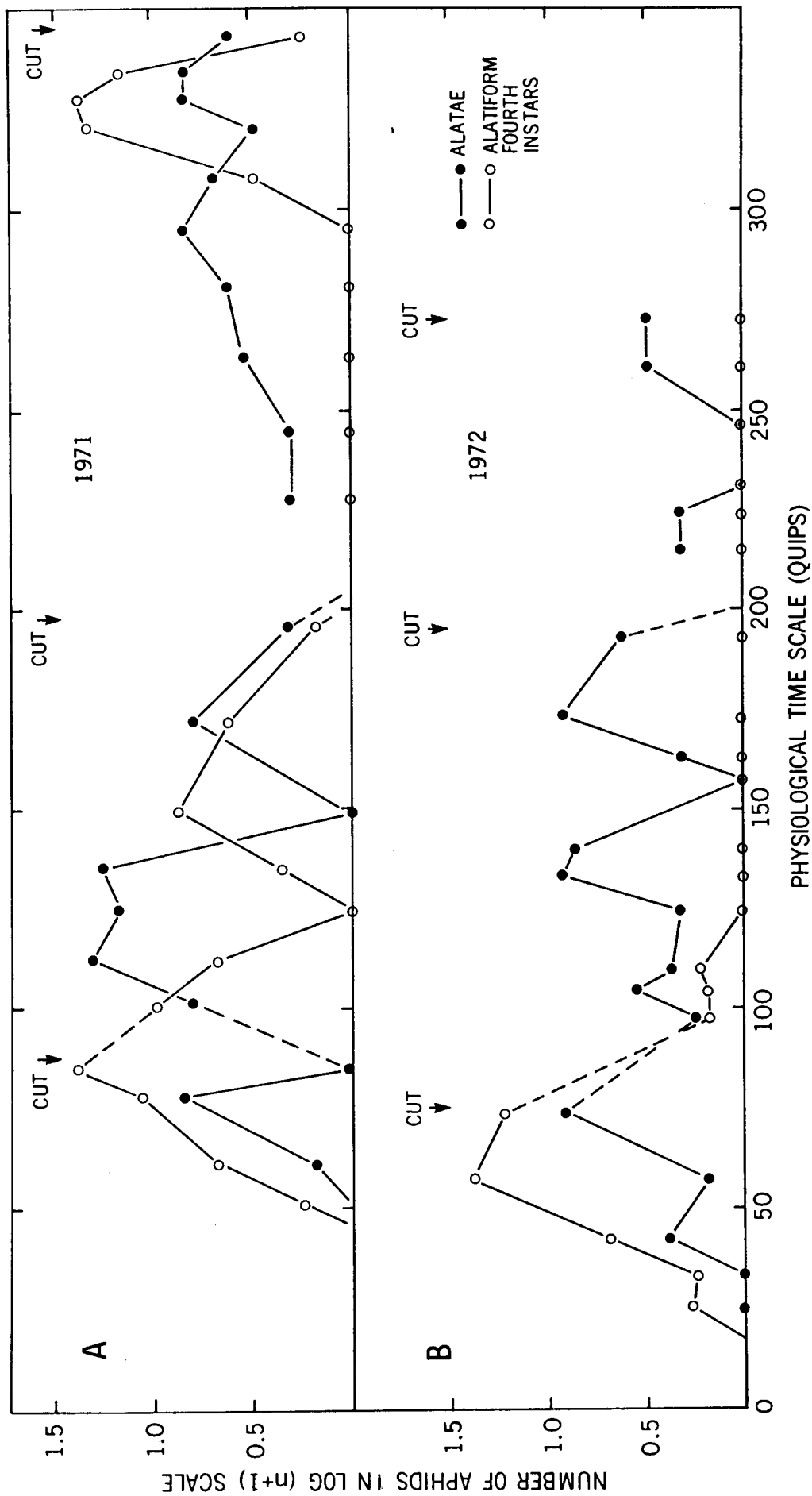


Figure 20. Comparison of the number of alatae found in the alfalfa tip samples with the expected number of alate fourth-instar nymphs of *A. pisum* moulting four quips previously, presented on a physiological time scale (A) 1971 and (B) 1972. (1 quip = 6.2 day-degrees above 5.56°C)



a mortality factor, as the loss of reproductive adults reduced aphid population growth at least temporarily, especially just before the first cuts in both years (Figs 18, 20). Mass emigration of alatae occurred just before the first crop was cut in 1971 (Fig. 20A) and 15 quips before the first cut in 1972 (Fig. 20B). This pre-reproductive mortality (Hughes, 1963) may have caused the reduction in aphid population growth just before the crop was cut in 1971 (Fig. 18, quips 77 to 85; Fig. 16C, days 65 to 70) and in 1972 (Fig. 18, quips 45 to 55; Fig. 17C, days 52 to 60). However, once new apterous progeny matured and began reproducing the aphid population resumed an upward trend (see day 60 and 67 in Appendix 4, Fig. 17C).

Alate production declined after the first cut in both years (Figs. 20A, B). Any fourth instar alatae found in the field samples immediately after the first cut were probably progeny of apterae surviving from the first cut and reproducing during the early alfalfa recovery.

In the second and third crops there was a lag period between the arrival of the first immigrant alates and before their apterous progeny could start producing offspring during the second and third crops (Appendix 4, Figs. 20A, B). However, it really was not until high aphid densities were reached that alate offspring were produced in abundance. During 1971 the aphid population quickly increased in density, reaching a peak during quips 125 to 150 (Fig. 18), while fourth instar alate production also increased (Fig. 20A) and declined along with the aphid population decline. In contrast, during the second crop in 1972 aphid populations did not increase to as high a density as in 1971 (Fig. 18). Indeed, fourth instar alate production in the field was non-existent after quip 125 for the rest of the 1972 season (Fig. 20B).

e) *Immigration.* Flights of alatae immigrating into the field probably started just before the first crop of alfalfa was cut. However, there was no way of knowing the degree of immigration during the first crop, as there were more alatiform fourth instars produced in the field than the total of alatae present four quips later (Figs. 20A, B). After the first cut there were large numbers of immigrant alatae observed in the samples collected during quips 100 to 140, 1971 (Fig. 20A). High numbers of immigrant alatae and the survival of aphids from the previous crop were important in producing a rapid aphid population growth rate during the second crop, 1971 (Figs. 20A, 18, 16C, and Appendix 4). In contrast, there were very few alatae observed in the early alfalfa regrowth period of the second crop, 1972 (Fig. 20B). As a consequence of low alate immigration and few aphids surviving from the previous crop, aphid population growth was slow in the second crop, 1972 (Figs. 20B, 17, 17C, and Appendix 4). Although there were two peaks of alate numbers later in the second crop (Fig. 20B) and although these aphids contributed to minor aphid population increases (Fig. 18), these increases were insignificant.

The contribution of immigrant alatae was extremely important in deciding the density levels that pea aphid populations would reach subsequent to a harvesting in the field. The effect of immigrant alatae on the population trends was amply demonstrated by comparing the number of immigrants and population growths in the second and third crops of 1971 and 1972 (Figs. 16C, 17C, 20A and B). The larger the number of immigrant alatae colonizing a field, the greater the aphid population natality and the higher densities to which the population peaked.



The importance of immigrant alatae recolonizing alfalfa fields is clearly shown in the early part of the third crop during both years. After the second crop cut during both years, the weather was very hot and dry (Figs. 16A and 17A), which caused the mortality of practically the whole aphid population. In 1971 low numbers of healthy alatae were found in the field samples of the early third crop (Fig. 20A); no other adult morph (i.e. apterae) were found until day 147 (Appendix 4, Table 4.1). The data indicate that only after the recolonization of the alfalfa field by immigrant alatae and the development of their progeny did adult apterae reappear in the field (see the instar and morph distribution between days 128 and 147 in Appendix 4, Table 4.1). In contrast, although there were immigrant alatae entering the field during the early third crop, 1972 (Fig. 20B, Appendix 4, Table 4.2), they were few in number and of poor quality (i.e. showed low reproductive potential). Consequently, due to the low number of immigrant alatae, the aphid population did not adequately recover and remained at a low density until the alfalfa was harvested in early September, 1972 (Figs. 17C, 18).

f) *Disease*. The incidence of fungal disease in pea aphid populations was negligible in the present study. Thus, mortality due to pathogens was not considered as limiting to the pea aphid in the field studied.

However, fungus epizootics can occur in the Kamloops area. I have observed up to 10% fungus infection of a pea aphid population when the population reached densities of over 2,000 aphids/100 tips in another field in Kamloops during July, 1971.

g) *Parasitism*. In this chapter, parasitism is considered only in terms of its general contribution to the mortality of pea aphid populations. Internal parasitism of the pea aphid is one of the few selective mortality agents that can be measured using a direct approach (Kiritani and Dempster, 1973) in quantitatively evaluating parasite effectiveness in the control of pea aphid populations. Once a parasite female has oviposited into an aphid, the latter is "marked" for the rest of its life. Unlike predators that leave no trace of having eaten their prey, the parasite larva is detectable in a living aphid.

All ages of parasites were generally evenly distributed in all of the aphid stages dissected (third instar nymphs to adults). The percent parasitism of the third, fourth nymphal instar, and adult followed the same trends throughout each season. Thus, the parasitism rate was considered as an overall percentage for each field sample:

$$\% \text{ parasitism} = \frac{\text{total parasitized}^5 \text{ third instars or older aphids}}{\text{total live aphids (third instar or older)}} \times 100$$

The percent parasitism of pea aphid populations was higher during most of the 1972 growing season than in 1971 (Figs. 16C, 17C, 21). During 1971 parasitism rates were low in early spring, reaching a high of 10% before the first cut; they then increased steadily to slightly more than 45% in the second crop and stabilized at 31 to 34% in the third crop period (Figs. 16C, 21). In contrast, during 1972 parasitism fluctuated from 20 to 80% in the spring and from 25 to 70% in the second and third crops (Figs. 17C,

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<sup>5</sup> An aphid with more than one parasite immature was still counted as one parasitized aphid.

Figure 21. A comparison of the parasitism rates of pea aphid populations on a physiological time scale during 1971 (A) and 1972 (B).

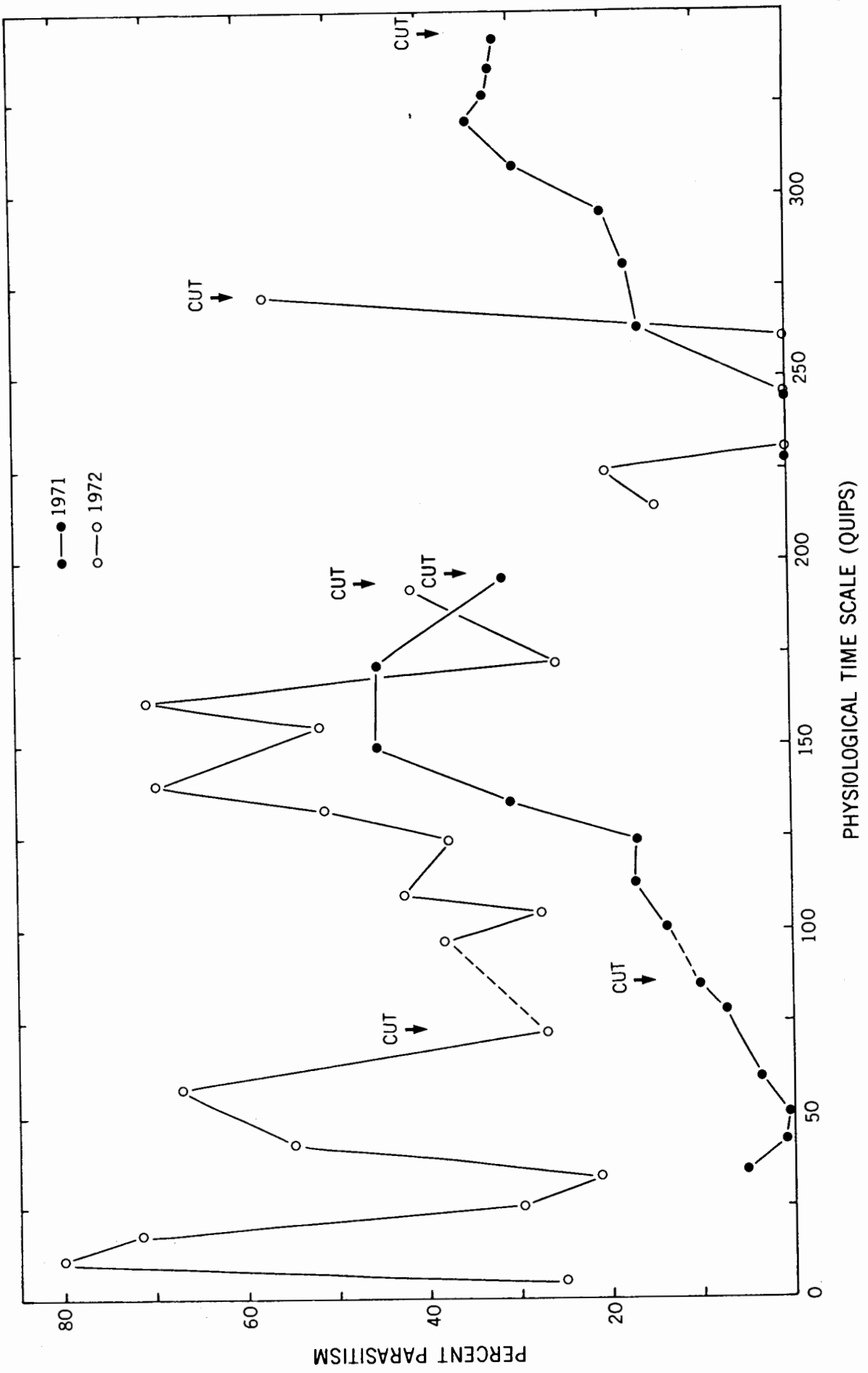
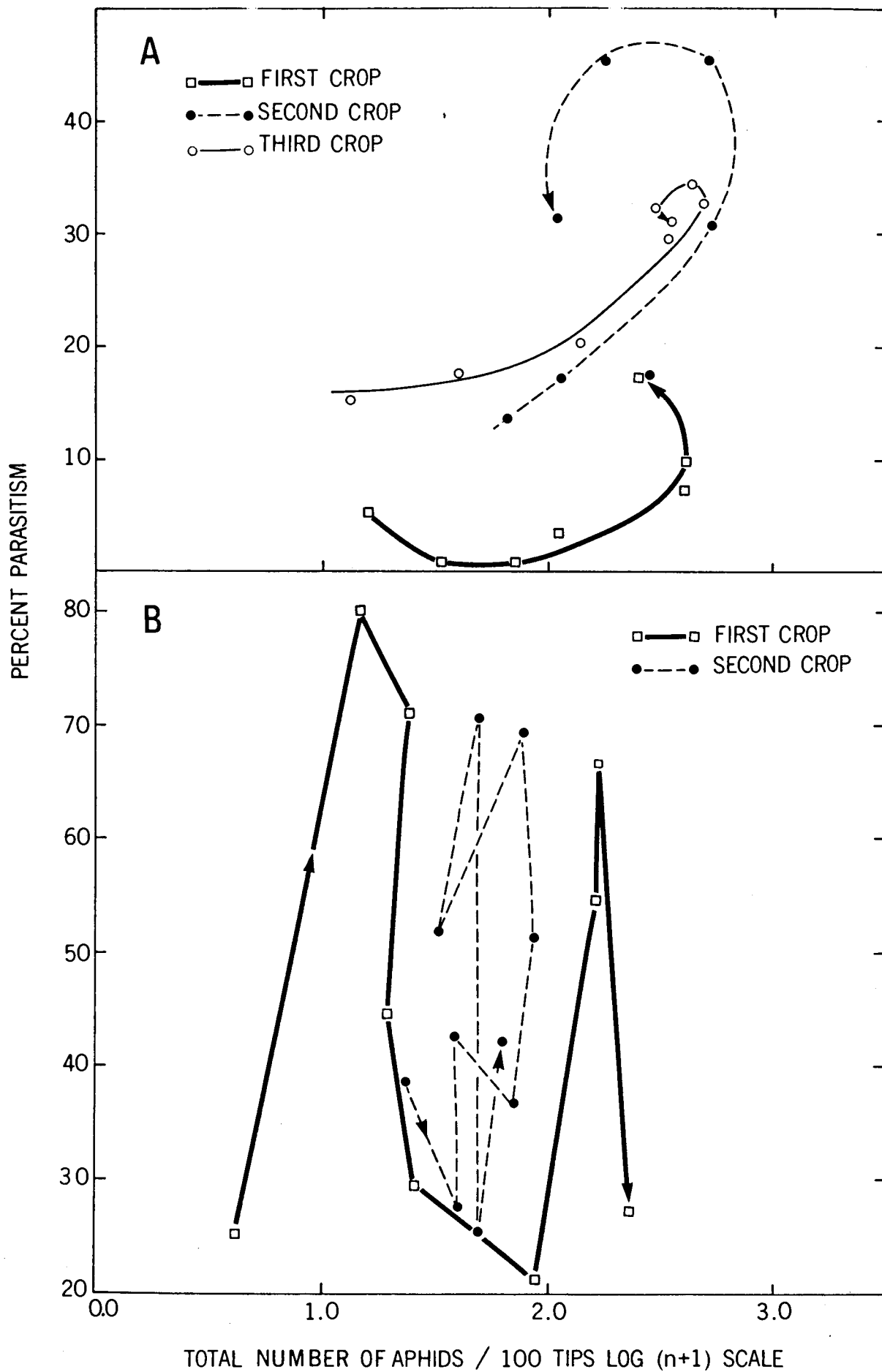


Figure 22. Time trends\* in the relation between percent parasitism and the number of aphids during each crop in 1971 (A) and 1972 (B).

\* (Each point along a line represents a subsequent sampling occasion.)



22). On days 14 and 27, during 1972, most parasite adults had emerged from their diapausing mummies (see Appendix 5 for total number of parasite adults collected in sweep samples). The mass parasite emergence during spring, 1972, coincided with the appearance of the fundatrix generation (Appendix 4), giving a very high parasite to aphid ratio<sup>6</sup> which resulted in competition for hosts among parasite females and super and/or multiparasitism; up to four parasite eggs or larvae per aphid were recorded. This was the only period during which superparasitism was recorded.

Figures 22A and B show the relationship between the parasitism rates and changes in aphid population densities in each crop for both years. There was a delayed density dependent relationship between parasitism rates and changes in aphid numbers for each of the three crops during 1972 (Fig. 22A). The disruptive effect of the harvesting of each crop (at arrow) on the aphid-parasite interrelationships can be seen (Fig. 22). There was a time lag probably due to slower parasite than aphid developmental rates, resulting in an increase of parasitism even after aphid numbers declined (Fig. 22A). The curve for the third crop, in 1971 (Fig. 22A), became increasingly smaller, suggesting aphid and parasite populations had generally stabilized (Figs. 16C, 21, 22A). It should be noted that this occurred in late fall when temperatures were low, slowing up aphid and parasite development.

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<sup>6</sup> Similar results were found in "spot checks" of sweep and alfalfa tip samples in two other alfalfa fields 10 to 20 miles away from the study area on day 14, 1972. Over 80% parasitism and 16 parasites/100 sweeps were recorded.

In contrast, the relationships between the parasitism rate and changes in aphid numbers during 1972 were different from those in 1971 (Figs. 22A, B). The percent parasitism of aphids seemed to be independent of changes in aphid density for both the first and second crops during 1972 (Fig. 22B). There were two peaks in the rate of parasitism as the aphid population increased during the first crop (Figs. 21, 22B). The probable reasons for there being no density dependent association between parasites and aphid population growth during the first crop, 1972, were: (1) the large numbers of parasite adults emerging from diapause in early spring causing a high parasite to aphid ratio; (2) a "generation effect" causing two discrete<sup>7</sup> generations of parasites to develop during the spring. In the second crop, 1972, there was probably a density dependent response of parasites to aphid population growth. However, this response was probably masked by factors such as: (1) low aphid population growth rate; and (2) a generally high parasite to aphid ratio due probably to immigration of parasite adults from other fields. (Unfortunately no data were collected to show adult parasite dispersal patterns.) The harvesting practices also probably had an obscuring effect on the parasite-aphid relationships.

*h) Predation.* Ladybird beetle adults and larvae (Coccinillidae) and hoverfly larvae (Syrphidae) were the main aphid predators found in the alfalfa tip samples (Appendix 4, Figs. 16B, 17B). Lacewing larvae (Chrysopidae) and nabid nymphs and adults (Nabidae) were present in smaller numbers.

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<sup>7</sup> The phenomenon of discrete generations of parasites occurring in spring was confirmed by the simulation model (Chapter VII); however, as the season progressed the overlapping of parasite generations became maximum.



The following is a list of the common and more important predator species associated with the pea aphid found in the alfalfa field near Kamloops, B.C.: *Coccinella transversoguttata richardsoni* Brown, *Cycloneda polita* Casey, *Hippodamia convergens* Guerin-Meneville, *H. quinquesignata* (Kirby) (Coleoptera: Coccinellidae); *Chrysopa carnea* Stephens (Neuroptera: Chrysopidae); *Nabis alternatus* Parsh (Hemiptera: Nabidae); *Scaeva pyrastris* (Linn) (Diptera: Syrphidae).

The total predator equivalents (Appendix 3) are presented on a physiological time scale in Fig. 23. Using these totals one can multiply the numbers by 9.6 (which is the mean feeding rate of Coccinellid larvae or the voracity equivalent) to obtain the maximum number of aphids that could have been eaten. This method is crude, but it does give a rough estimation of aphid mortality due to predation. Although there were generally more predators found in the field samples during 1971 as compared with 1972 (Fig. 23), there was a higher predator to aphid ratio in 1972 than in 1971 (Figs. 16, 17). Most of the common predator types were present in the alfalfa field from early May to October (Figs. 16B, 17B) (see also sweep samples of 1972, Appendix 5).

Syrphid larvae were most abundant when aphid numbers were high (Fig. 16B), showing a density dependent response to changes in aphid population levels (Figs. 24A, 16B). However, there were more predators in the first crop in 1972 than in 1971 (Fig. 23). Coccinellid adults were the first to reproduce during the first crop, 1972, and many Coccinellid larvae survived the first harvest to pupate 10 to 15 days later (Figs. 17B, 23).

There seemed to be a density dependent association with the total number of predators and aphids in each crop during 1971 and the first crop

Figure 23. A comparison of the total predator equivalents for 1971 and 1972 on a physiological time scale.

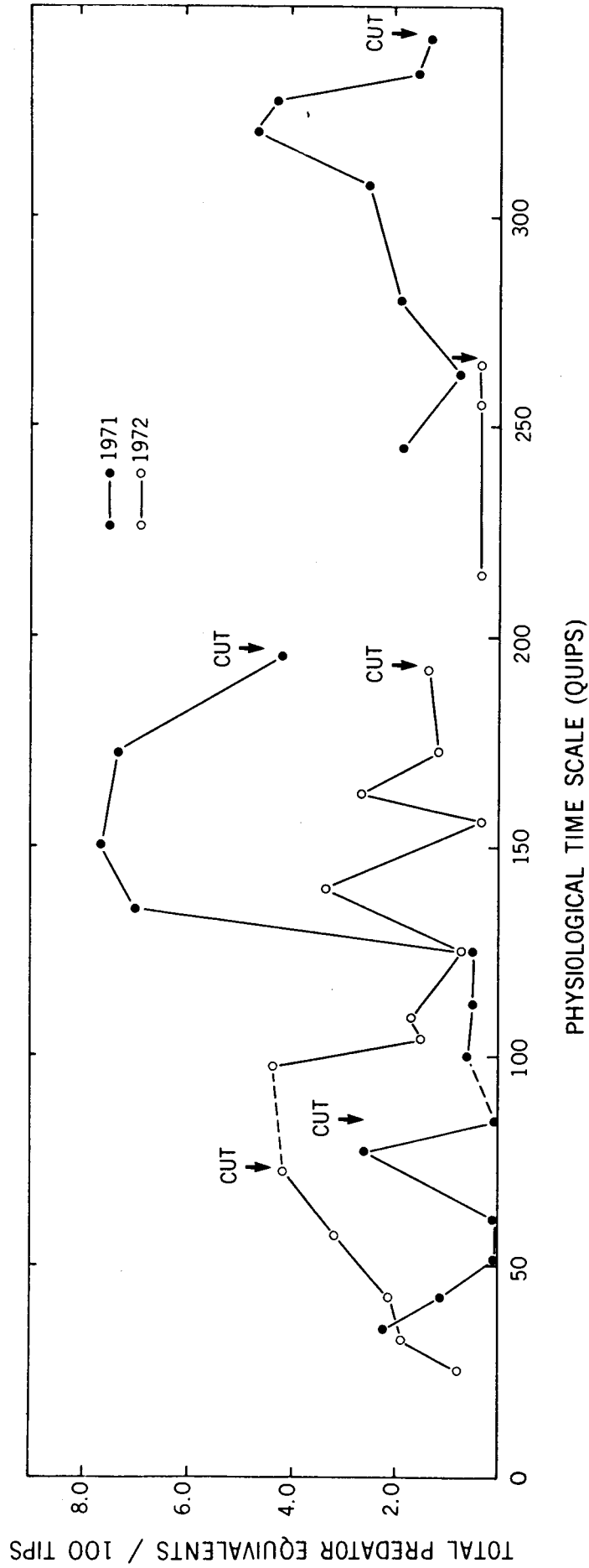
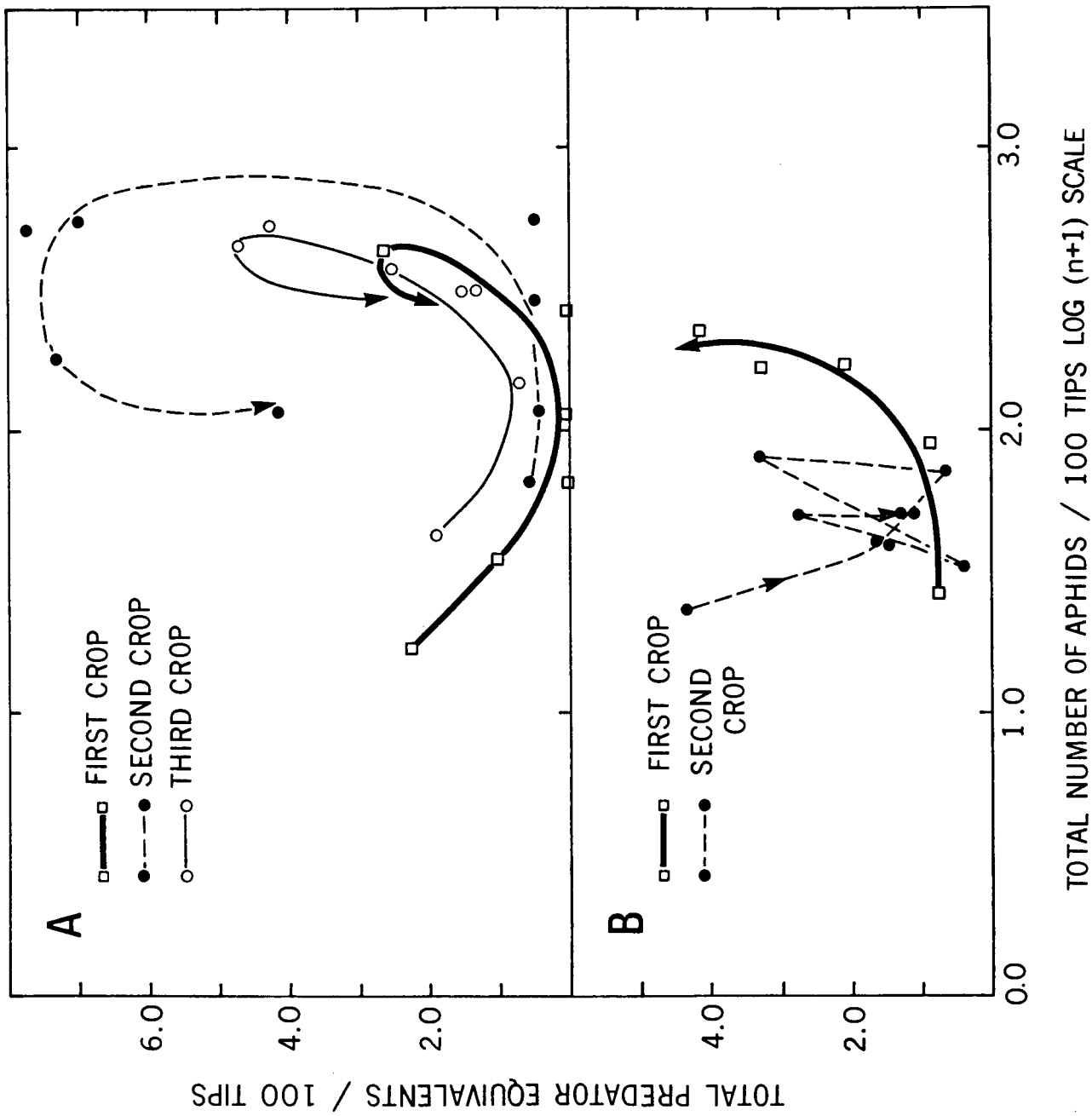


Figure 24. Time trends\* in the relation between total predator equivalents and the number of aphids during each crop in 1971 (A) and 1972 (B).

\* (Each point along a line represents a subsequent sampling occasion.)



in 1972 (Fig. 24), although no such association was observed during the second crop in 1972.

#### D. Discussion

Numerous factors can cause fluctuations in aphid numbers. Factors such as weather, emigration, disease, parasites, and predators have been discussed by many workers (Cooke, 1963; Dunn and Wright, 1955; Pass and Parr, 1971; Stary, 1968; van den Bosch *et al.*, 1966). Prior to the mid-1950's little was known of the effect of predators and parasites on pea aphid populations in North America. Smith and Hagen (1966) reported on populations of *A. pisum* and *Therioaphis trifolii* and their parasites, predators, and pathogens in California. They concluded that Coccinellids were extremely important factors in the biological control of these aphids on alfalfa, especially during spring and fall. Cooke (1963) studied the pea aphid on alfalfa and peas in the Blue Mountain area of eastern Washington and Oregon. He concluded that, although Coccinellid and Syrphid larvae were the most "valuable" predators of the pea aphid, "their activities usually come too late to check an incipient (aphid) outbreak". As a result of such studies a number of hymenopterous parasites were introduced into North America to supplement the impact of indigenous parasites (see Chapter I and Mackauer, 1971). Recent studies have shown the introduced hymenopterous parasite *A. smithi* to be an effective mortality agent of the pea aphid in California (van den Bosch *et al.*, 1966) and in Kentucky (Pass and Parr, 1971).

In this study there were a number of interrelated factors which determined the general level to which aphid densities would rise and fall before the hay harvest. Perhaps the most important factors were those that influenced

the initial numbers and age structure of the aphid population at the beginning of each crop, because it was these initial values that influenced aphid population growth rates.

Alfalfa is a perennial host plant for the pea aphid; however, harvesting has a disruptive effect which causes heavy aphid mortality, especially when accompanied by hot dry weather. The surviving aphids are especially vulnerable to the vagaries of the weather immediately after a harvest, until sufficient alfalfa regrowth has occurred to supply adequate shelter. If the weather is generally mild during alfalfa recovery, some aphids survive and reproduce, contributing to a rapid aphid population growth. In addition, the contribution of the immigrant alatae to the recolonization of harvested alfalfa fields is an important factor in influencing the initial numbers and aphid population growth rates. The "rain" of these dispersing alatae probably depends on the many "source" alfalfa fields in the Kamloops area.

Any aphid colony or colonies within an alfalfa field can produce alatae that contribute to the alate "rain", although the production of alatae is influenced by a number of factors. Sutherland (1969a, b) reported that more alate offspring were produced when pea aphids fed on mature plants or were exposed to the tactile stimulation of other aphids at higher aphid densities. It should also be noted that there is probably an intrinsic factor (Sutherland, 1970) which may cause pea aphids to be more sensitive to producing a higher proportion of alates during some periods compared to others. In Kamloops the first few pea aphid generations of the early spring were probably more sensitive to environmental stimuli than the pea aphid generations

occurring during the rest of the summer. The highest proportion of alatae produced in Kamloops occurred during early spring, 1971, when aphid densities were usually not as high as during the rest of the season. The most evident emigration of alatae in both years occurred as the alfalfa matured in late May to early June. Cooke (1963) also found the heaviest pea aphid flights occurred during spring in the Blue Mountain region of Oregon and Washington. In this study, alate emigration flights after the main spring dispersal occurred only during the later periods of the second and third crops when higher aphid densities probably induced alate production.

During both 1971 and 1972 the incidence of fungus disease was extremely low and probably had little effect on pea aphid populations. In contrast, the aphidophagous parasites and predators were important mortality agents of the pea aphid. The aphidiid parasites were generally more effective in reducing aphid numbers than the insect predators. As will be seen from the following discussion, the effect of timing of parasitism or predation on the initial numbers of aphids was important in the natural control of the pea aphid population.

Although there was a larger number of parasites and predators during 1971 than in 1972, the ratio between the number of parasites (or predators) and aphids was higher in 1972 as compared to 1971 (Appendix 4). The lower parasite to aphid ratio was reflected in the parasitism rate of the aphid population, which reached a maximum of only 45% in 1971, compared to 70 to 80% in 1972 (Fig. 21). High parasitism rates of pea aphid populations have been recorded by other authors. Up to 69% and over 80% parasitism of the pea aphid by *Aphidius smithi* have been reported by Pass and Parr (1971) and



van den Bosch *et al.* (1966), respectively.

Although the predators could have helped to destroy the newly arrived immigrant alatae, the predators were low in numbers (Fig. 16B). Only when the aphid population had reached higher densities did predator numbers also increase, becoming more effective in reducing aphid population growth. Parasites also showed a lag in response to aphid population growth (Figs. 16C, 21A). Parasites are not particularly effective in reducing the initial population growth "explosion" caused by immigrant alatae; i.e. if healthy alate adults were parasitized as soon as they arrived in a field, the alatae could still reproduce and contribute to aphid population growth (Chapter IV).

In contrast, during early spring, 1972, a large number of parasites emerged from diapausing mummies to coincide with the fundatrix generation. This mass emergence caused a very high initial parasitism of up to 80% of the aphids. Stary (1969) also reported high percent parasitism of fundatrices of *A. pisum* by *Aphidius e. ervi* during early spring in alfalfa fields of Czechoslovakia. Van den Bosch *et al.* (1964) observed the parasite *Trioxys complanatus* freshly emerged from diapause reduced a springtime outbreak of *Therioaphis trifolii* with heavy parasitization, although parasitization was low during the rest of the season. Gilbert and Gutierrez (1973) found that the effectiveness of the parasite *Aphidius rubifolii* in controlling *Masonaphis maxima* was dependent on the performance of its first generation in spring.

In this study, the early spring high parasitism rates of the reproductive aphids probably helped to reduce aphid population growth for the rest of the 1972 season. Spot checks of two other fields in the Kamloops area during the spring and summer showed similar low aphid population levels and high

parasitism rates. With the generally reduced aphid populations throughout the Kamloops area during 1972, the alate "rain" was probably also reduced. Thus, with the combined effect of the first harvest, which removed a considerable number of aphids, and a lack of alate immigrants after the first cut, the aphid population never was able to recover rapidly. Relatively high numbers of predators and parasites surviving the first cut because of the mild weather (Figs. 17A, B) also reduced the chance of the surviving aphid population to contribute to rapid aphid population growth.

The higher parasite or predator to aphid ratio may have contributed to the lack of a density dependent association between parasites or predators and aphid numbers in the second crop, 1972 (Figs. 22B, 24B). In contrast, parasites and predators showed a density dependent response to aphid population changes during 1971 (Figs. 22A, 24A). Van den Bosch *et al.* (1966) and Pass and Parr (1971) found the parasite *A. smithi* to exhibit a density dependent response to pea aphid growth; however, many factors could mask this response. Van den Bosch *et al.* (1966) found weather conditions, agricultural practices, and competition from fungus disease to obscure *A. smithi*'s density dependence. Pimentel and Wheeler (1973) found no density-dependent association between parasitism and the numbers of pea aphids on various alfalfa varieties; they did not attempt to explain their results. In this study the reasons for the lack of parasite density dependent association with aphid numbers during 1972 are not completely clear. The effect of discrete generations during the spring and the probable mass immigration of parasites from other fields accompanied by a low number of immigrant alates may have produced a high parasite to aphid ratio, thus causing low aphid population

growth rates and a lack of parasite density dependent response to changes in aphid numbers.

Parasites were generally a more important mortality factor than predators in affecting pea aphid numbers (see also Chapter VII). Parasites probably seldom overwhelm pea aphid populations as they did in this study during 1972; however, parasites along with other mortality agents such as predators (Coccinellidae, Syrphidae, Chysopidae) could exert a considerable regulatory influence on pea aphid populations. Indeed, the combined effects of harvesting, weather, and aphidophagous insects probably keep pea aphid populations in the alfalfa fields of the Kamloops area well below economic threshold levels during most years. Outbreaks of pea aphid populations could easily occur in local areas when there is a high initial aphid infestation and rapid aphid population growth due to high survival rates of reproductive adult apterous aphids from the previous crop. This aphid population growth may be enhanced by large numbers of immigrant alates entering the area and initially low parasite and/or predator responses.

The duration and harshness of a winter probably determines the number of aphids and parasites and the time when they appear in early spring. Indeed, the winter conditions may well determine the initial aphid and parasite numbers and the ultimate densities at which they will peak during the summer.

#### E. Summary

The population trends of the pea aphid, *Acyrtosiphon pisum*, and its mortality agents were studied in an alfalfa field near Kamloops, B.C. Samples of 100 alfalfa tips were collected weekly during the summer months

of 1971 and 1972; the numbers and stages of aphid, parasite, and predators collected were recorded. Both calendar time and a physiological time scale were used to analyse the field data. Pea aphid populations usually reached a peak in numbers for each of the three alfalfa crops with the highest peak occurring in the second crop during 1971, which reached 563 aphids per 100 alfalfa tips.

The disruptive effect of harvesting considerably reduced aphid populations, and subsequent weather conditions influenced aphid recovery. Mild weather after the first crop in both years allowed rapid aphid recovery, while hot dry weather after the second crop of both years decimated aphid and parasite populations. Aerial migration was clearly essential to pea aphid recolonization of an alfalfa field, especially after a hay harvest and subsequent hot dry weather. The numbers of parasitized and unparasitized aphids surviving from the previous crop and the numbers of immigrant alatae were important in determining the density levels at which the pea aphid population would peak.

High wind velocities and heavy precipitation rates decimated aphid numbers on several occasions, but usually only after aphid populations had already reached peak levels.

The main production of alatae and mass emigration occurred during the later period of the first crop in both years. However, smaller emigration flights did occur during the later periods of the second and third crops in 1971. Emigration of alatae was not considered an important mortality factor; although when mass dispersal occurred during the spring, aphid population growth was reduced.

Among natural enemies the hymenopterous parasites appeared to be the most important mortality factor of pea aphid populations in Kamloops; up to 80% parasitism was recorded. The parasites showed a delayed density dependent response to the increase of pea aphid populations. However, the density dependent response could be masked by an increase of the parasite to aphid ratio probably caused by a large number of immigrant parasites, or by early spring parasite emergents from diapausing mummies, or by harvesting practices.

High parasitism rates of the early spring generation, especially of the fundatrix generation in 1972, were important in slowing down initial aphid population growth and contributing to low aphid numbers for the rest of the season.

Aphidophagous predators belonging to the Coccinellidae, Syrphidae, Chrysopidae, and Nabidae were found to respond to aphid population increases.

## CHAPTER VI

## THE DISTRIBUTION AND SEASONAL DYNAMICS OF THE PARASITES

A. Introduction

There are very few studies on the population dynamics of the pea aphid that have considered the effects of primary and secondary parasite species in the field. The influence of primary and secondary parasitism on aphids was reviewed by Hagen and van den Bosch (1968), and that of secondary parasitism by Gutierrez (1968) and Sullivan (1969). Hagen and van den Bosch (1968) considered it difficult to determine the impact of primary parasites on aphid populations, especially when the study of the secondary parasites added to the already complex problem.

Chapter V analysed the impact of parasitism on the pea aphid in relation to other mortality factors. The purpose of this chapter is to show the relative contribution of each parasite species, especially of the exotic *Aphidius smithi*, to the overall parasitism of the pea aphid. To achieve this purpose the following aspects were studied: (1) the distribution and relative abundance of the parasite species in southern B.C.; (2) the changes in seasonal abundance of each parasite species near Kamloops during 1971 and 1972; and (3) the effect of hyper-parasites on primary parasite abundance during this period.

B. Materials and Methods

The distribution and relative abundance of the primary parasites of the pea aphid throughout southern British Columbia was determined in surveys during late July to early August of 1971 and 1972. In addition, seasonal changes in parasite abundance were monitored in an alfalfa field

at the Canada Department of Agriculture Research Station, Kamloops, B.C., on a weekly basis during the summers of 1971 and 1972. To measure yearly changes of the parasite complex between 1969 and 1972 additional samples were taken during July and August in another alfalfa field about 100 metres east of the main study field.

Over 20,000 mummies were collected and examined from the samples taken throughout southern B.C. and the two fields in Kamloops during 1971 and 1972.

Mummified aphids containing advanced parasite larvae or pupae were collected in the field. Samples were taken by walking through a field collecting alfalfa leaves to which mummies were attached. The leaves and mummies were then placed into half-pint cardboard containers. The sampling time usually was one hour. All sampling times were recorded. Mummy counts are expressed in numbers collected per unit effort or per one hour period of searching.

Mummy samples were taken to the laboratory, and mummies were categorized into: previously emerged; attacked by Coccinellid adults or Chrysopid larvae (Figs. 29A, B); with or without wings; and *Aphidius* or *Praon* mummies (Figs. 28A, C). *Praon* and *Aphidius* mummies were placed into separate containers and stored at room temperature. Emerged parasites were collected and put into alcohol at one to two-day intervals. When all parasites had emerged, the primary parasites were identified as to sex and species according to criteria given by Mackauer and Campbell (1972) and Mackauer and Finlayson (1967). The secondary parasites were determined as to genus and species, using the criteria given by specimens previously

identified by Dr. M. Mackauer and Dr. C. M. Yoshimoto. The total number of each parasite species and the unemerged mummies were counted and recorded.

To obtain further information on mummy characteristics and parasite associations over 3,000 mummies were taken from various samples and individually reared in gelatin capsules (size 00). The emergent parasite species and the characteristics of the emergence hole on the mummy were noted.

To assess the damage caused to a mummy by an insect predator, various predator types were placed in gelatin capsules containing mummies (see also Appendix 2).

To enable the recognition of parasite species emergence patterns from mummy samples taken at various stages of pea aphid population growth and decline, emergences of each parasite species were daily recorded from mummy samples taken at the beginning and end of crop 2 in 1971.

## C. Results

1. *The parasite complex in southern British Columbia.* This section reports on a survey which was made during 1971 and 1972 to observe the distribution and relative abundance of the exotic and indigenous parasites of the pea aphid throughout southern B.C. Most of this section (pages 131 to 141) is quoted directly from Campbell and Mackauer (1973).

Table XV shows the primary and secondary parasites associated with the pea aphid in alfalfa fields throughout southern B.C. (See also Appendix 6).

a) *The parasites of the pea aphid.* In southern B.C. the pea aphid is attacked by three native and two exotic aphidiid parasites. Two of the native parasites, *Praon pequodorum* Viereck and *A. ervi pulcher* Baker, are relatively common throughout the area (Table XV). The third, *Monoctonus*



Table XV. The pea aphid-parasite complex in the alfalfa ecosystem in southern British Columbia.

Secondary Parasites	Primary Parasites	Phytophagous Host	Host Plant
HYMENOPTERA			
Cerophronidae <i>Lygocerus niger</i> (Howard)			
Cynipidae <i>Charips</i> spp. (possibly 3 species)	Aphididae * <i>Aphidius smithi</i> Sharma and Subba Rao		
Encyrtidae <i>Aphidencyrtus aphidivorus</i> (Mays)	* <i>Aphidius ervi ervi</i> Haliday	Aphididae <i>Acyrtosiphon pisum</i> (Harris)	<i>Medicago sativa</i> L. Alfalfa
Pteromalidae <i>Asaphes lucens</i> (Prov.) <i>Asaphes vulgaris</i> Walker <i>Coruna clavata</i> Walker <i>Fachyneuron siphonophorae</i> Ashmead	<i>Aphidius ervi pulcher</i> Baker <i>Praon pequodorum</i> Viereck <i>Monoctonus paulensis</i> Ashmead	Pea aphid	

\* Deliberately introduced species.

*paulensis* Ashmead, was recovered only once, perhaps because it exploits the pea aphid only as a facultative host (Calvert and van den Bosch, 1972). The two introduced parasites are *A. e. ervi* and *A. smithi*, which invaded and became established in large areas of southern British Columbia following their release into the northwestern United States (Mackauer and Campbell, 1972).

b) *Distribution and relative abundance of parasites.* The four common parasites (as mentioned above) were found throughout the area surveyed. The parasites, however, differed significantly in relative abundance, suggesting that climate may have influenced the abundance, distribution, and performance of the exotic species.

i. *The Interior of southern British Columbia.* The Interior includes the area between longitude 121°30' and 115° W (Fig. 25). The area which is typified by the Lower Thompson and Okanagan River Basin has a Middle Latitude Steppe type climate with very hot and dry summers and generally cold and dry winters (Fig. 26A). The total annual precipitation is approximately 25 cm. The Columbia and Kootenay River basins to the east are relatively cooler and wetter than the Okanagan.

*Aphidius smithi* was the most abundant pea aphid parasite throughout the Interior during 1971 and 1972 (Figs. 25, 27). In the hottest and driest areas, such as the Okanagan between Summerland and Osoyoos (Fig. 25, Nos. 7, 8), *A. smithi* comprised over 90% of the parasite-mix. At sampling sites north of latitude 50° N and towards the eastern border of distribution, the relative abundance of *A. smithi* declined gradually to a low of 45 to 70%. The reduction in numbers of *A. smithi* in these "marginal" areas was compensated for by a corresponding increase of either *P. pequodorum* or *A. e.*

Figure 25. Distribution and relative abundance of four hymenopterous parasites of the pea aphid in southern British Columbia during June to August, 1971. (Small circles = 1 to 300 mummies per man hour of collection time; medium circles = 301 to 600 mummies per hour; large circles = 601 to 1,000 mummies per hour.) (From Campbell and Mackauer, 1973.)

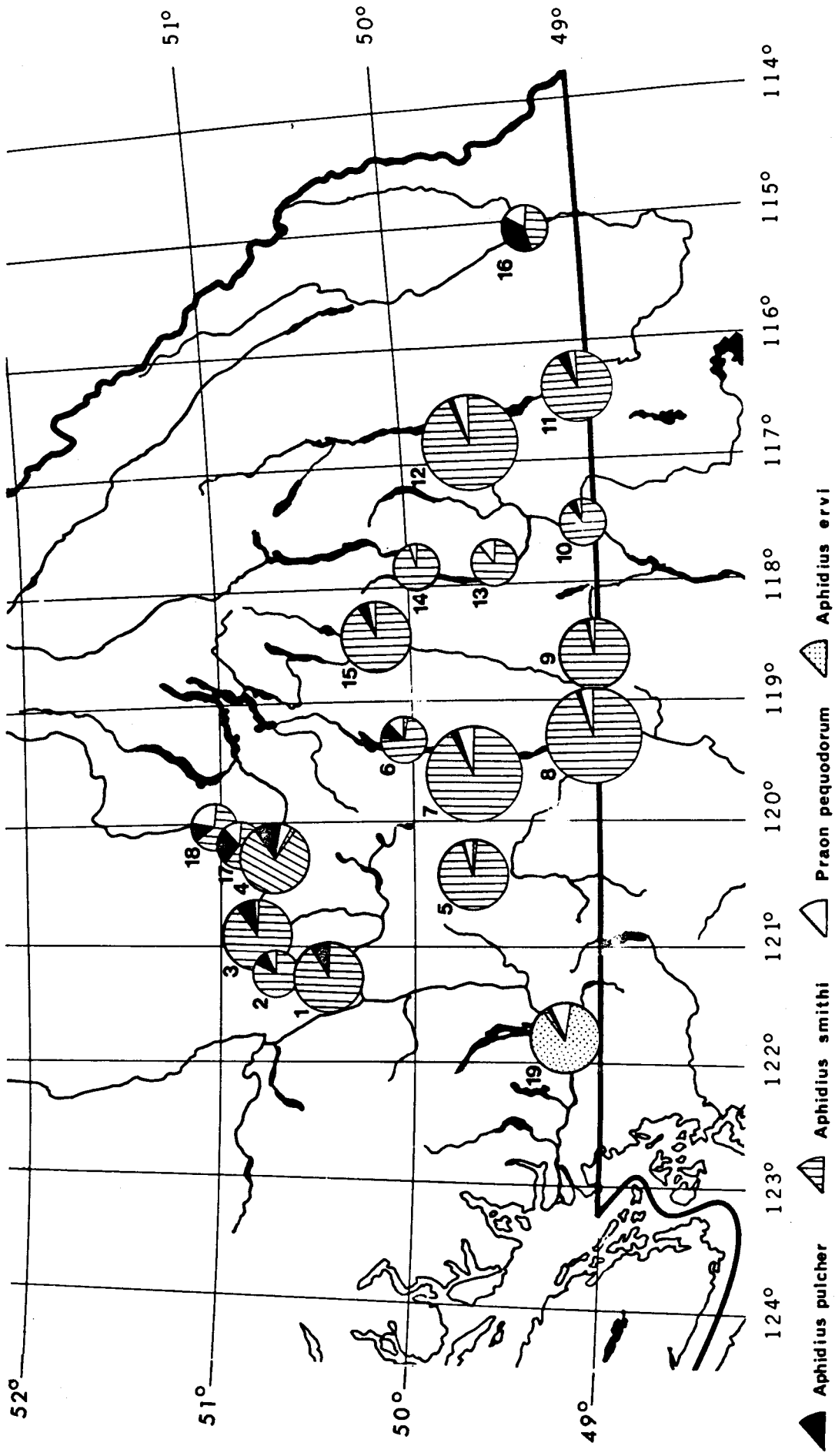
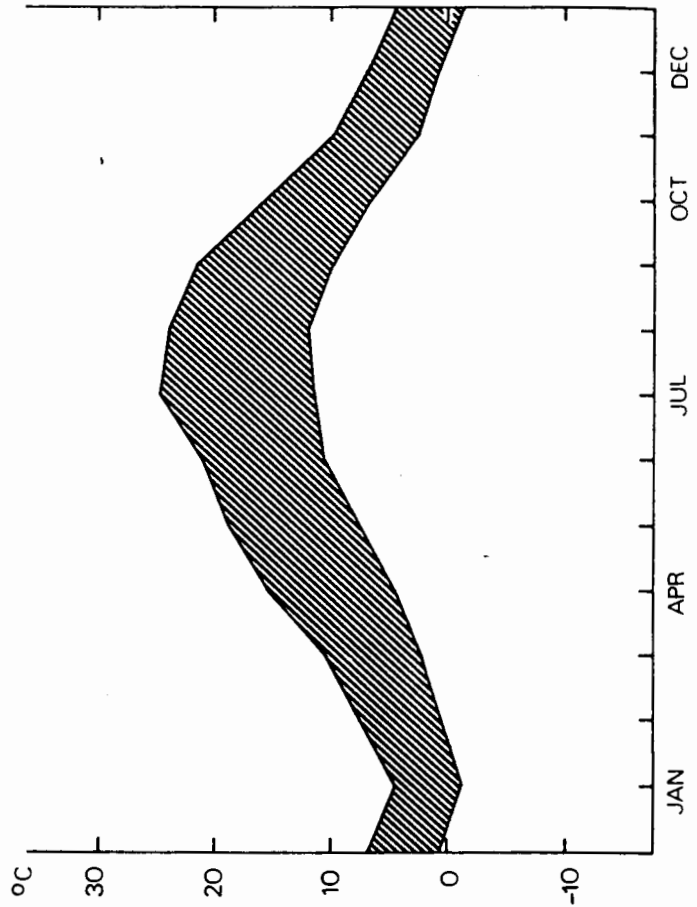
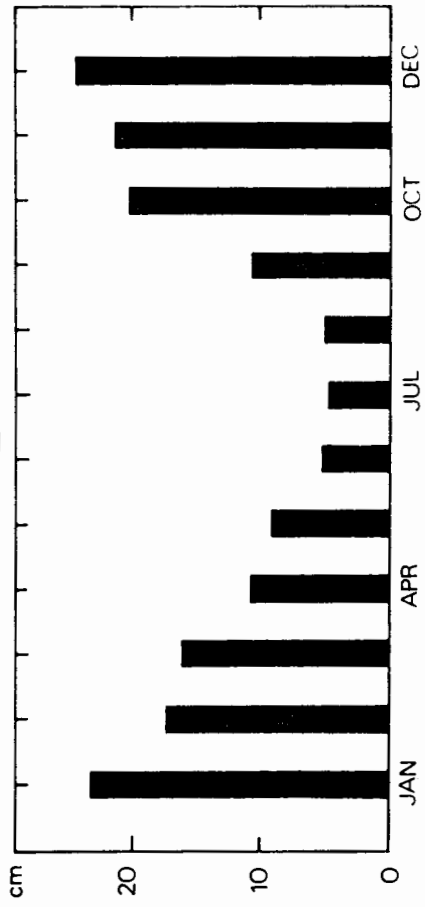


Figure 26. Climatographs of (A) Kamloops, B.C., and (B) Chilliwack, B.C., giving mean total precipitation (above) and mean maximum and minimum temperatures (below). (Data from Temp. PPT Tables, Publ. Atmos. Environ. Serv. Govt. Canada. Based on a 30-year period, 1941 to 1970.) (From Campbell and Mackauer, 1973.)

**B**



**A**

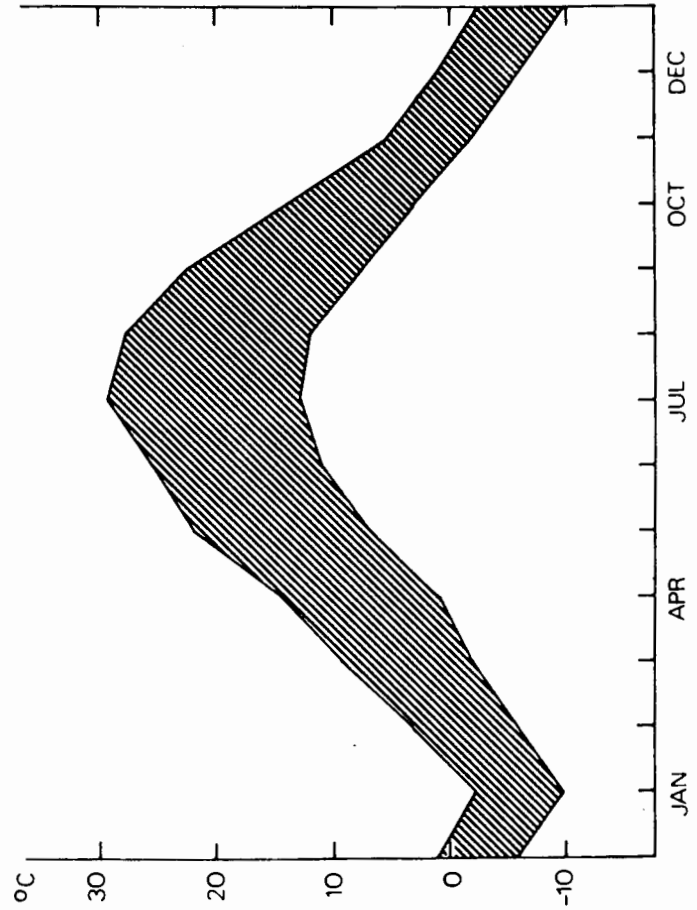
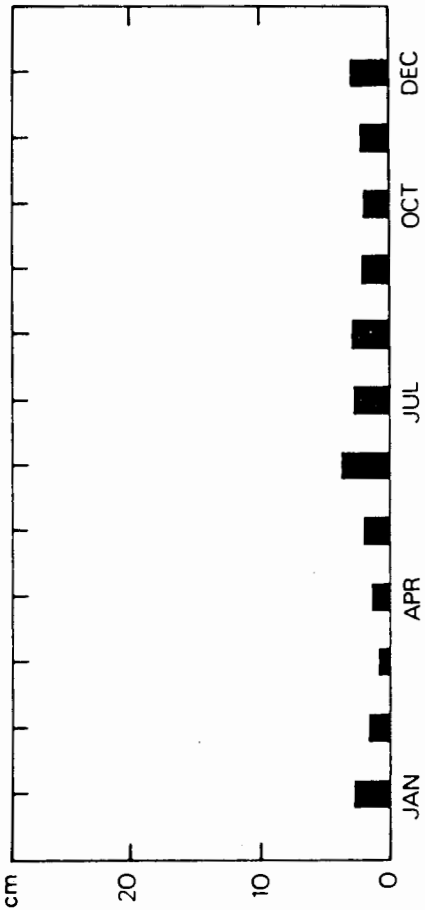
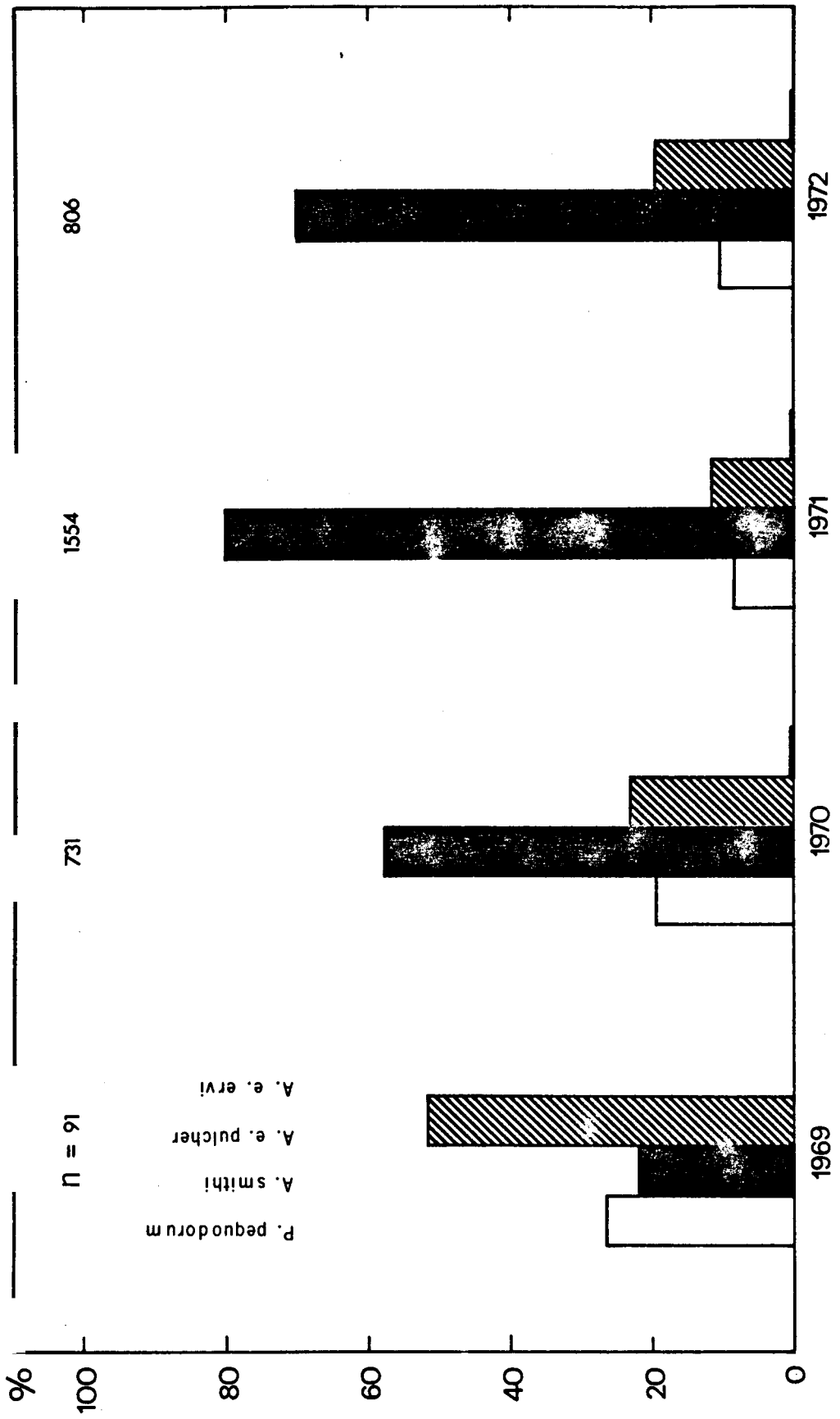


Figure 27. Changes in the relative abundance of four hymenopterous parasites of the pea aphid in an alfalfa field 100 metres east of main study field at Kamloops, B.C., between 1969 and 1972. Sample total (n) based on emerging primary parasites. (From Campbell and Mackauer, 1973.)





*pulcher*, depending on locality and seasonal conditions. The second introduced parasite, *A. e. ervi*, while present in the Interior, was not a significant constituent of the parasite complex.

*ii.* The Lower Fraser River Basin. The area west of longitude 121°30' W (Fig. 25) has a Marine West Coast climate, i.e. relatively wet and mild summers and winters with the average total annual precipitation ranging between 100 and 180 cm (Fig. 26B).

The most abundant pea aphid parasite in the Lower Fraser River Basin was *A. e. ervi*. Samples taken near Chilliwack in 1971 and 1972 (Fig. 25, No. 19) contained slightly more than 80% of this species, with *P. pequodorum*, *A. e. pulcher*, and *A. smithi* collectively contributing the remaining 12 to 18% of the total. The parasite complex and the relative abundance of *A. e. ervi* at additional collecting sites near Vancouver (Frazer and Gilbert, pers. comm.) and in northern Washington State were similar to the data for Chilliwack. For example, a sample taken near Burlington, Wash., in 1970 contained 69.1% *A. e. ervi*, 15.4% *A. e. pulcher*, 7.7% *A. smithi*, and 7.8% *P. pequodorum*.

*c) Changes in the parasite complex.* Changes in the relative abundance of each parasite species at Kamloops between 1969 and 1972 are shown in Fig. 27. In 1969 (and probably earlier) *A. e. pulcher* was numerically the most important pea aphid parasite. In 1970 it was displaced from this position by the invading *A. smithi*, which presumably had colonized the area sometime between 1966 and 1968. The increase in relative abundance of *A. smithi* from 22% in 1969 to 80% in 1971 had the greatest impact on the native *A. e. pulcher*, which decreased in abundance from 51.6 to 11.5%.

The impact of *A. smithi* on *P. pequodorum* was less dramatic, reducing the percent contribution of *P. pequodorum* from 26.4 to 8.2% during the period.

*Aphidius e. ervi* was recovered at Kamloops for the first time in 1970. It constituted 0.3 and 0.1% of the total number of primary parasites in 1971 and 1972, respectively. There is no information on the relative impact of the species on the parasite complex in the Lower Fraser Valley Basin prior to 1971.

2. *The seasonal dynamics of parasites near Kamloops.* a) *Mummy characteristics.* The different composition of the mummy samples changed throughout the alfalfa growing season in both 1971 and 1972 (Figs. 30, 31). Because mummies were cemented to the substrate there was a tendency for the accumulation of old emerged mummies (Figs. 28A to 28F) from one generation to the next, leading to an apparent increase of parasites in the field. This "graveyard" effect was well demonstrated in the mummy samples collected throughout the season; the previously emerged mummies increased in numbers as each alfalfa crop matured (Fig. 30). Indeed, the highest proportions of previously emerged mummies were observed at the end of the second and third crops during 1971 and the second crop in 1972 (Figs. 31A, B). The weighted mean percent of previously emerged mummies collected in the samples was 14.9% and 8.3% for 1971 and 1972, respectively (Table XVI).

Practically all samples contained some mummies that failed to emerge. The causes of unemerged mummies were probably due to a number of factors: (a) handling; (b) death due to natural causes, e.g. parasite adult unable to complete emergence (Fig. 29E); (c) excessive hyperparasite attack (Fig. 29C); and (d) parasite larva leaving mummy before completing cocoon (Fig. 29D).

Figure 28. Emergence holes made by primary and secondary parasites on pea aphid, *Acyrtosiphon pisum*, mummies.

- (A) *Aphidius smithi* mummy of the pea aphid; typical *Aphidius* sp. round emergence hole on dorsum of mummy.
- (B) *Aphidius ervi ervi* mummy of the pea aphid; typical *Aphidius* sp. emergence hole with lid attached.
- (C) *Praon pequodorum* mummy with dead alate pea aphid skin above cocoon; emergence hole is also shown.
- (D) *Monoctonus paulensis* mummy of the pea aphid; typical emergence hole on the apical portion of the mummy, postero-lateral view.
- (E) *Lygocerus niger* emergence hole in an *Aphidius* sp. - pea aphid mummy.
- (F) *Asaphes lucens* emergence hole in an *Aphidius* sp. - pea aphid mummy.

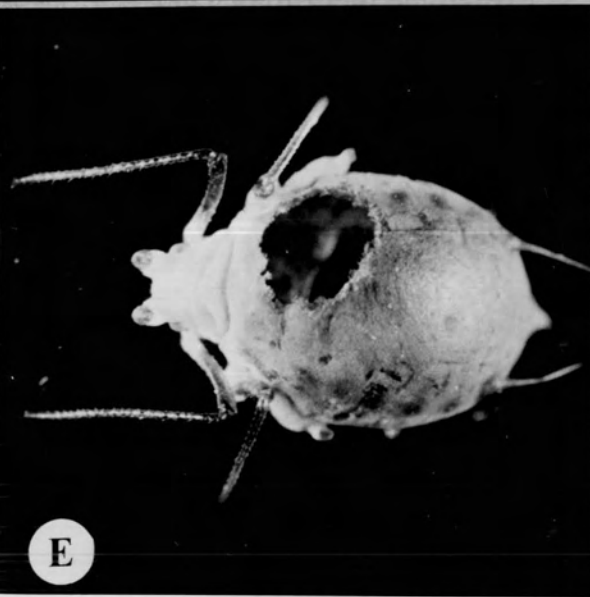
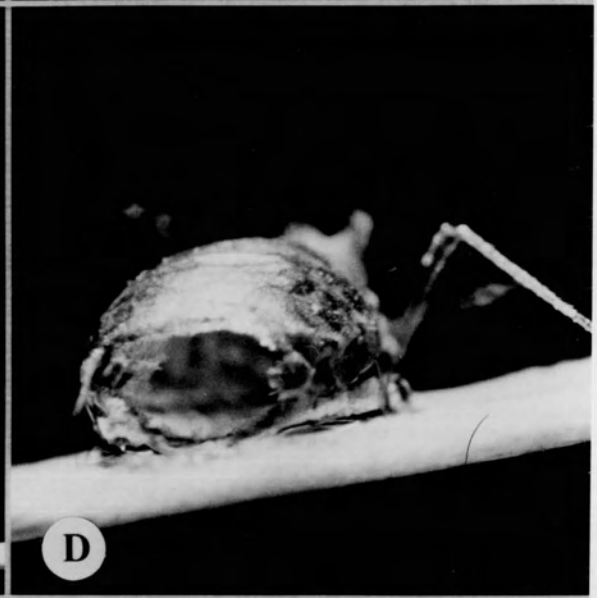
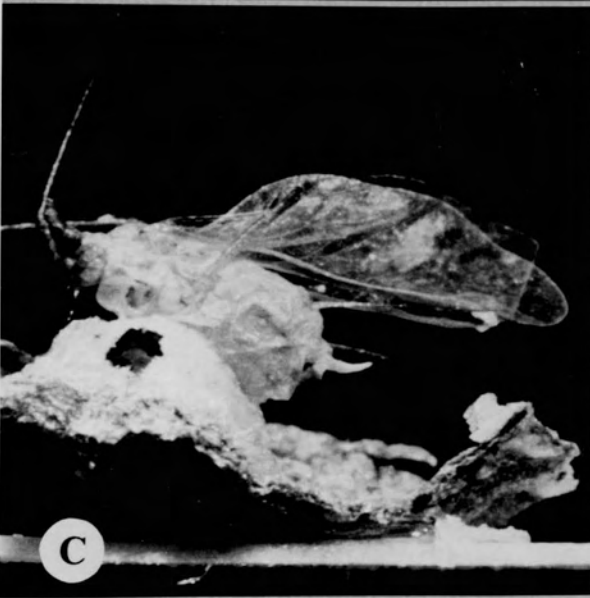
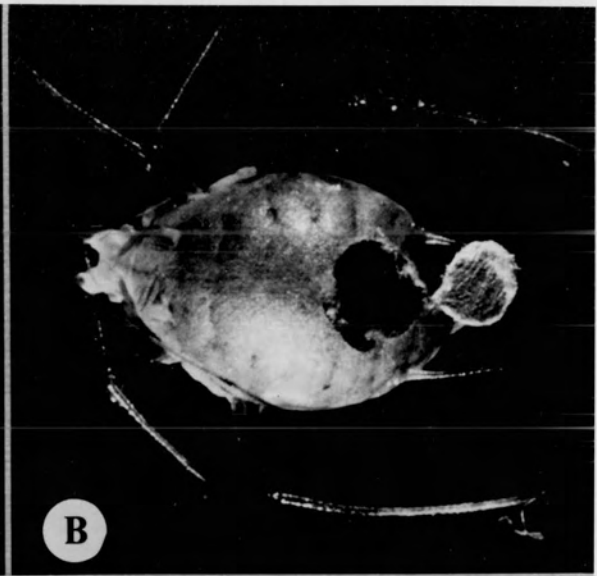
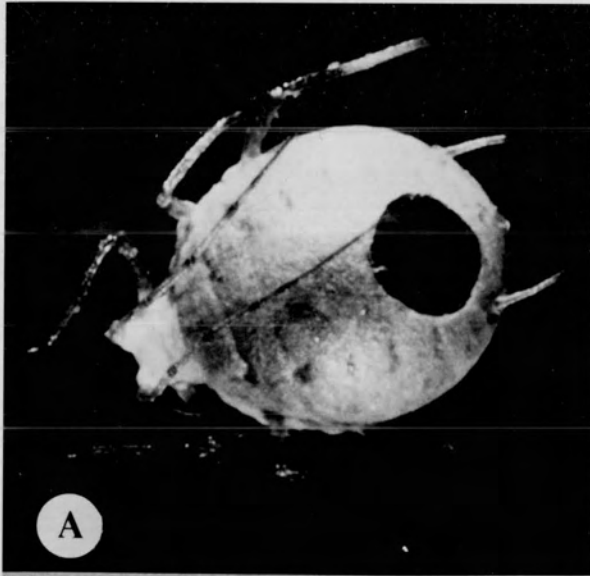


Figure 29. The effect of entomophagous predators and other factors on pea aphid, *Acyrtosiphon pisum*, mummy characteristics.

- (A) *Aphidius* sp. - pea aphid mummy attacked by a *Coccinella transversoguttata* adult. Note dark stained edges of hole caused by Coccinellid adult "digestive juices".
- (B) *Aphidius* sp. - pea aphid mummy attacked by a *Chrysopa carnea* third instar larva. Note hole caused by penetration of Chrysopid mandible.
- (C) *Aphidius* sp. - pea aphid mummy with multiple "drill" holes probably caused by secondary parasites.
- (D) Pea aphid skin, but without parasite cocoon causing the skin to be translucent. Mature parasite larva probably left or removed from aphid skin before completion of its silk cocoon.
- (E) *A. smithi* adult unable to successfully complete emergence from mummy which died in half-emerged position.
- (F) Pea aphid attacked by fungus (probably *Entomophthera* sp.) and could be mistaken for an *Aphidius* sp. mummy.

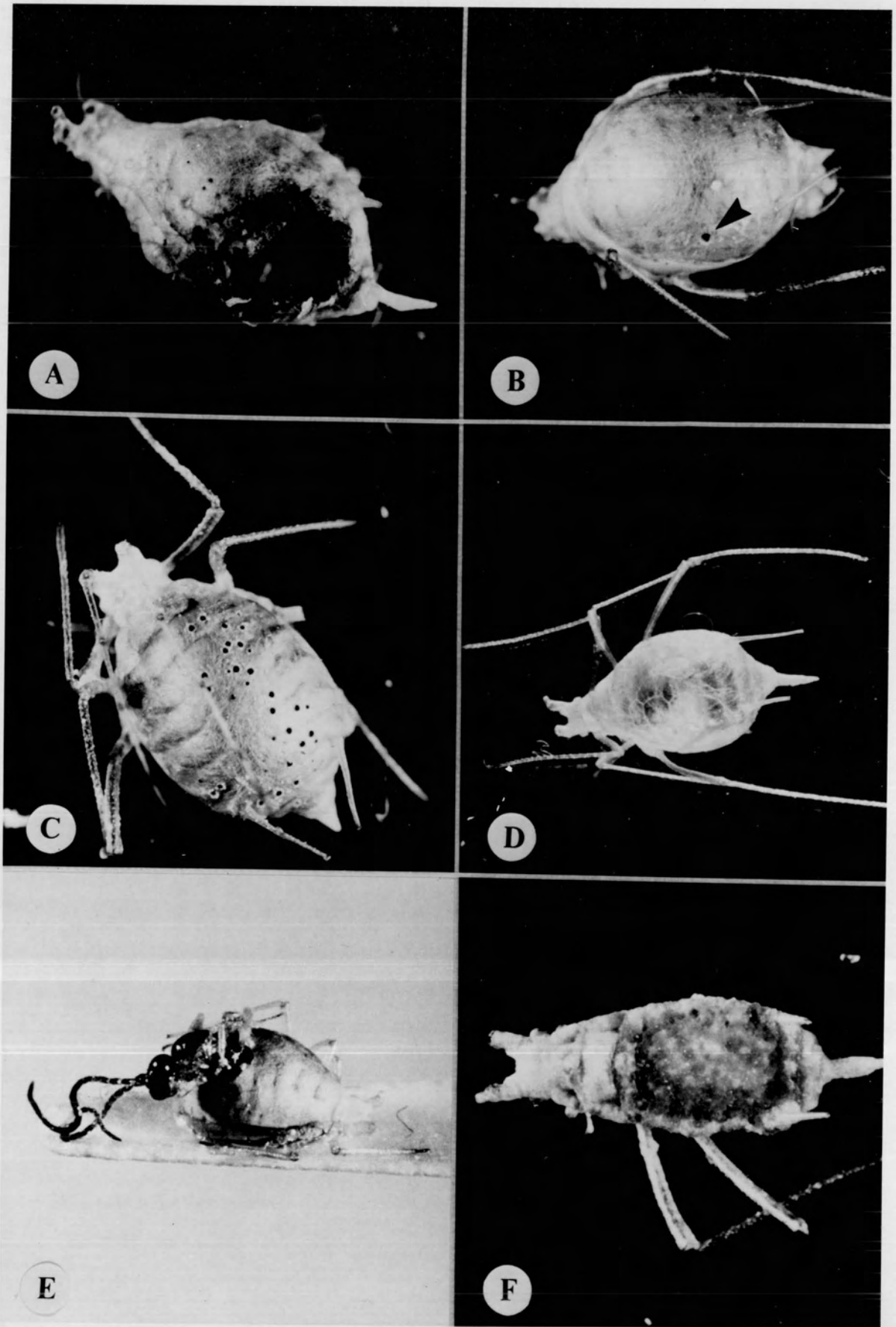
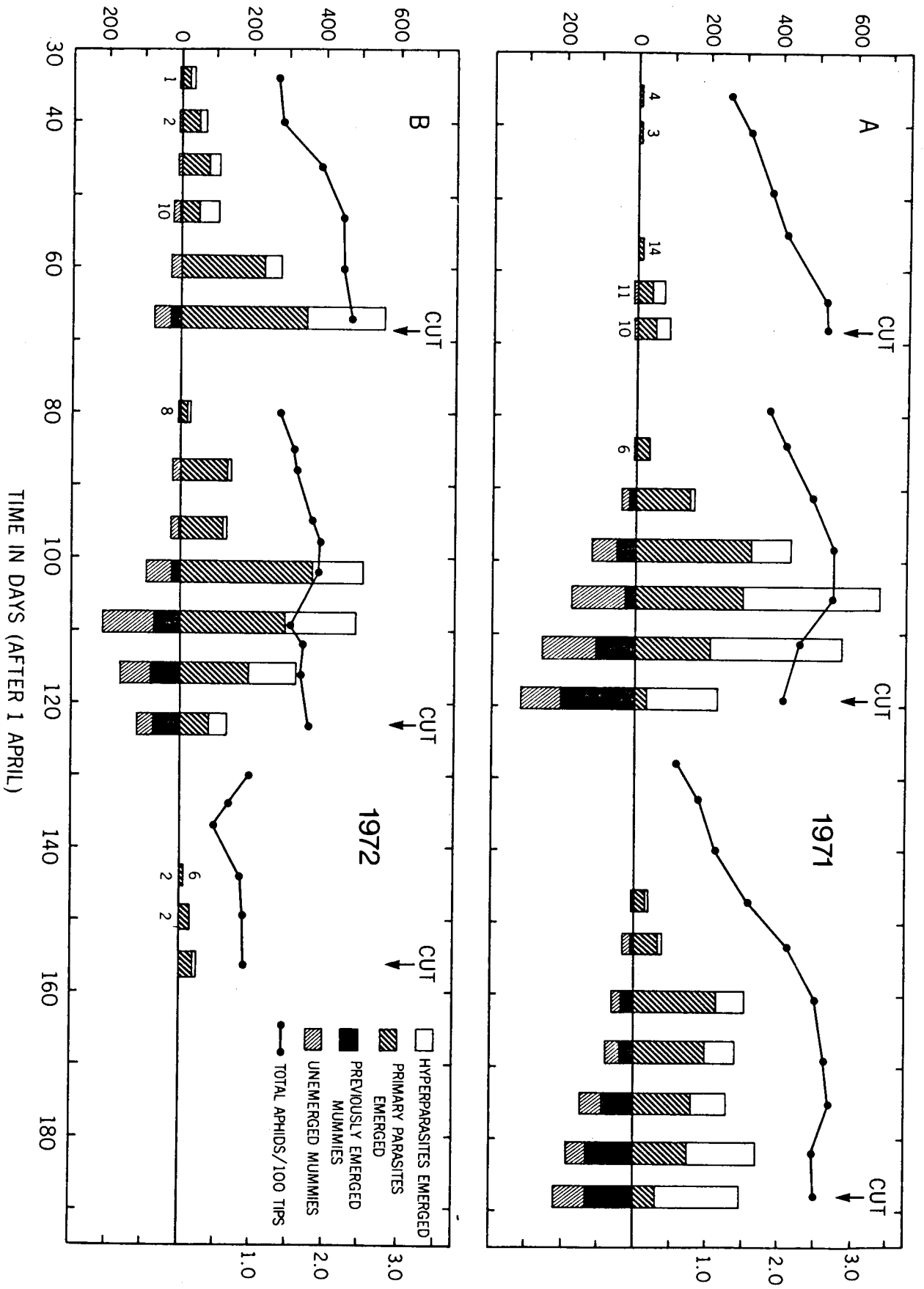


Figure 30. Seasonal changes in the composition of the mummy samples measured as totals per hour (total aphid population trends from alfalfa tip samples are also shown) for (A) 1971 and (B) 1972. (Numbers near histograms are numbers of mummies collected per hour lower than or equal to 14.)

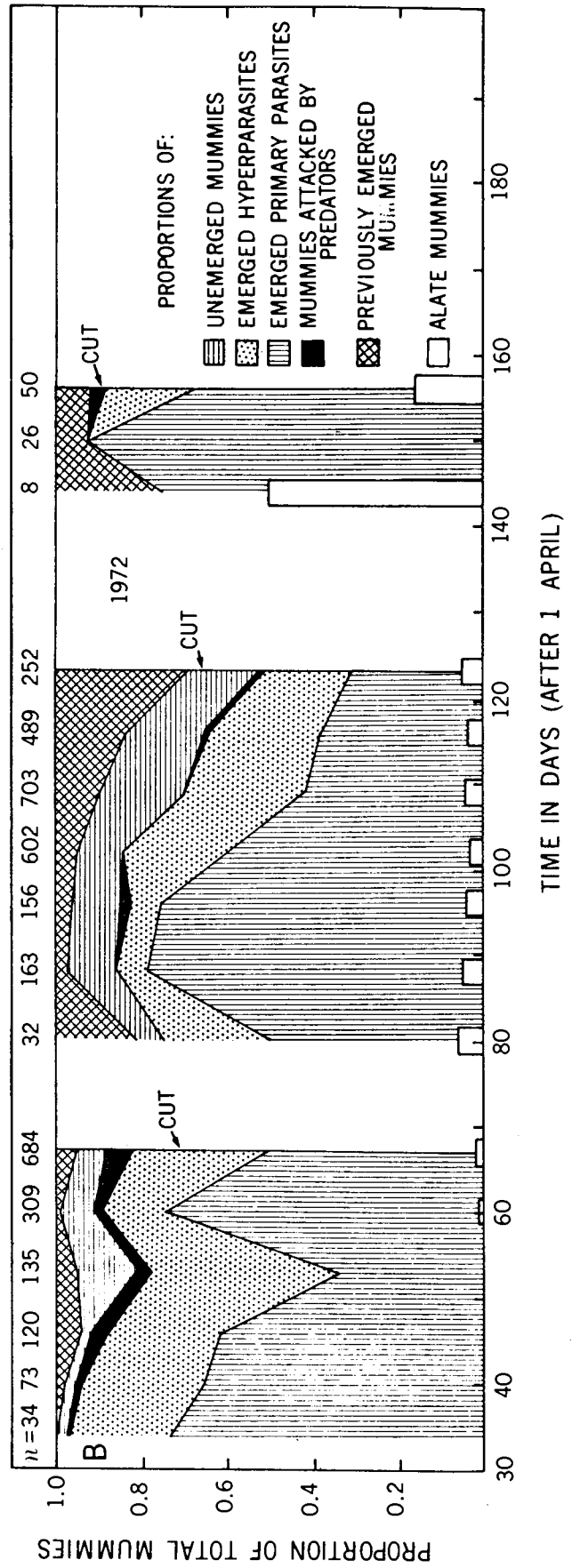
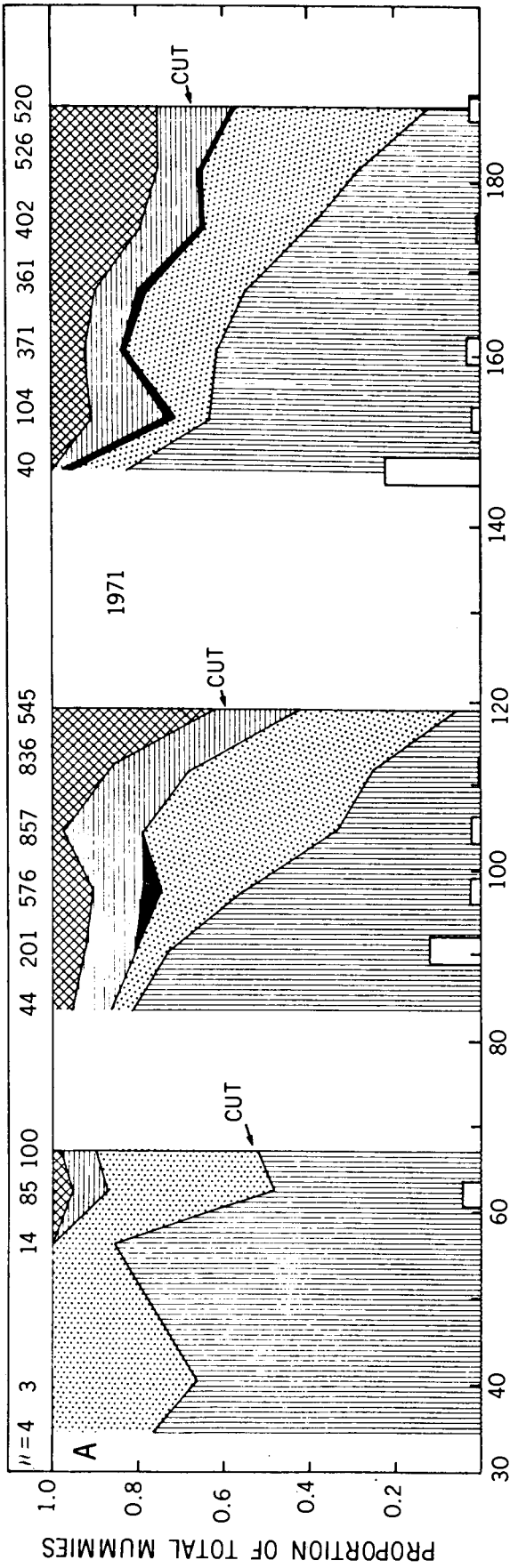
TOTAL NUMBER OF MUMMIES / HOUR



TOTAL NUMBER OF APHIDS / 100 TIPS LOG(n+1) SCALE



Figure 31. Seasonal changes of the proportions in the composition of the mummy samples during (A) 1971 and (B) 1972. Sample totals (n) are based on total number of mummies collected per hour.



The proportion of unemerged mummies generally remained constant during both 1971 and 1972 (Figs. 30, 31), with an overall mean proportion of 0.13 in all mummy samples collected in the study field ( $\pm 0.01$  SE,  $n = 30$ , range 0.00 to 0.21).

Al Rawy *et al.* (1969), Stary (1966), and Wheeler *et al.* (1968) reported that predators belonging to the families Coccinellidae, Chrysopidae, and Nabidae attacked and fed on pea aphid mummies. In this study, only a small proportion of the mummies collected throughout the two years had been attacked by predators (mean 0.01 to 0.02, ranging from 0.00 to 0.06) (Fig. 31). These mummies had been attacked by Coccinellid adults and Chrysopid larvae (Figs. 29A, B) (see also Appendix 2).

Usually less than 0.05 of the mummies collected consisted of alate aphids (Figs. 28C, 31). However, during some periods high proportions of alate mummies were noted, especially in the early third crops of both years (Fig. 31). It is assumed that some of the immigrant alatae were probably parasitized prior to colonizing the field.

The mean percentages of parasites emerging from the total mummy samples in 1971 and 1972 were 77.2 and 69.7%, respectively (Table XVI). From 9,424 mummies collected in the main study area during 1971-72, a total of 6,857 or 72.7% primary and secondary parasites emerged.

Changes in the total number of primary parasite emergences from the mummy samples generally corresponded with increases and decreases of the aphid populations (Fig. 30).

Table XVI. Totals (n) and weighted mean percentages (%) of previously emerged and unemerged mummies, mummies attacked by predators, and emerged adult parasites from mummy samples taken near Kamloops, during 1971, 1972.

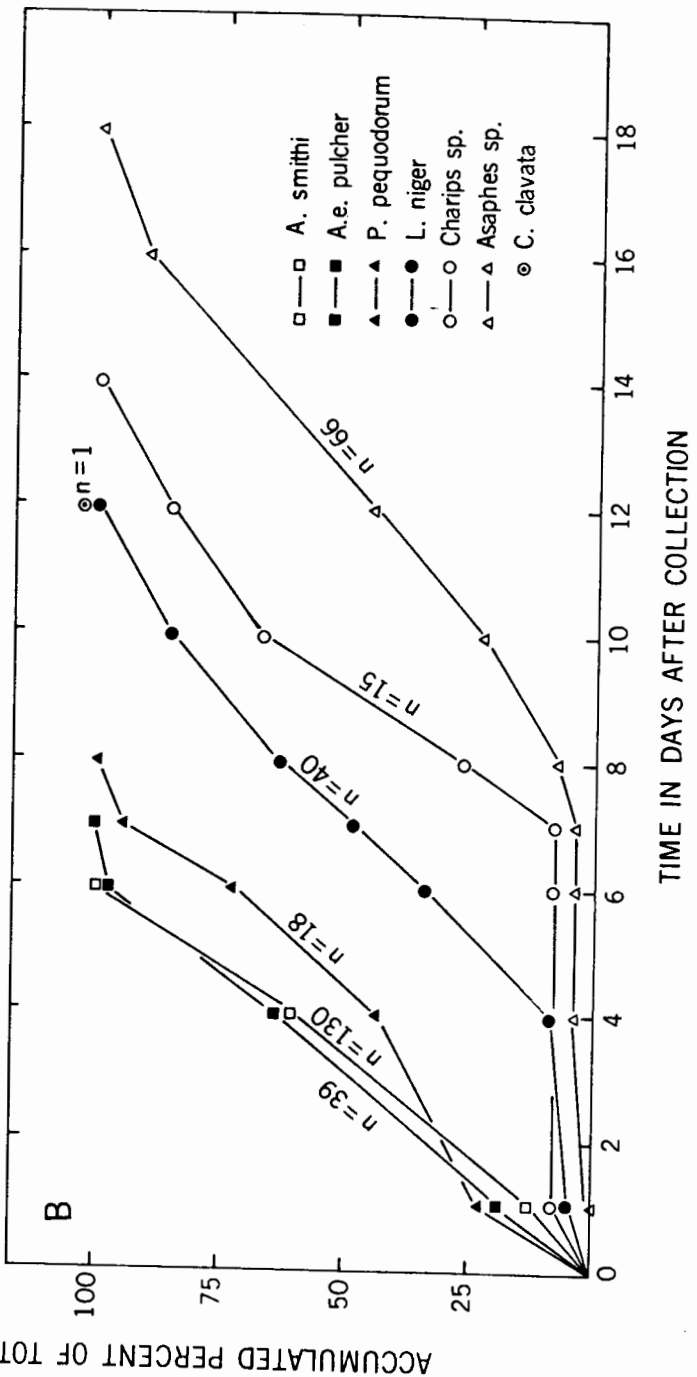
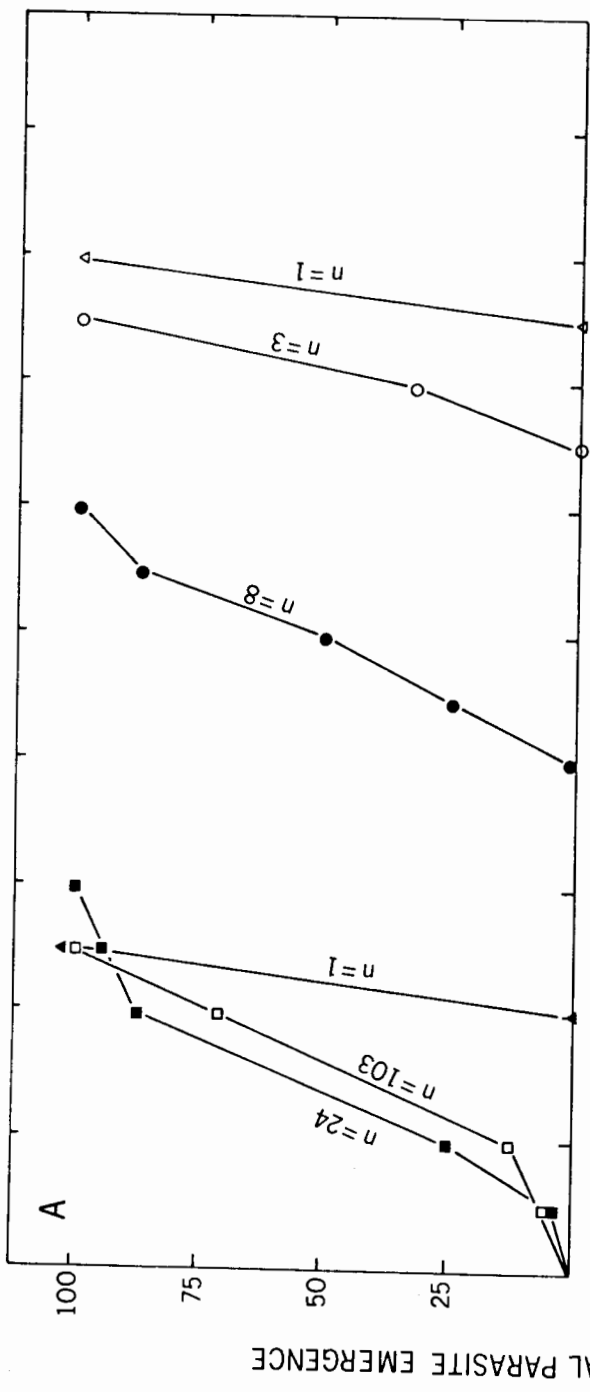
Mummies	1971		1972	
	n	%	n	%
Previously emerged	832	8.3	318	14.9
Attacked by predators	42	1.8	69	0.8
Unemerged	820	12.7	486	14.6
Total primary and secondary parasite emergences	3895	77.2	2962	69.7
Total	5589	100.0	3835	100.0

With an increase in viable mummies collected from the field, there was a corresponding increase in the total number of hyperparasite emergences (Fig. 30). Indeed, as the alfalfa crop matured and aphid population declined, the proportion of primary parasite emergences decreased and the proportion of hyperparasite emergences increased (Figs. 30 and 31).

Detailed daily observations of parasite emergences from mummy samples revealed that the emergence patterns of parasites changed with the maturation of an alfalfa crop (Fig. 32). Primary parasites emerged distinctly earlier than the hyperparasites in mummy samples collected during the early second crop in 1972 (Fig. 32A). In contrast, the mummies collected later in the same crop produced an overlapping of primary and hyperparasite emergences (Fig. 32B).

The typical pattern of hyperparasite emergence in the mummy samples shown in Fig. 32A revealed 50% of *L. niger* emerged 4.5 days earlier than 50% of *Charips* sp. and 5 days earlier than the *Asaphes* sp. The pattern of emergence in Fig. 32A seems to indicate the presence of discrete hyperparasite generations. However, the mummy sample collected on day 116 from the study field (Fig. 30B) shows a different pattern of hyperparasite emergences (Fig. 32B). The order of parasite species emergence is similar, but there is an overlapping of emergence within the hyperparasite species; i.e. young hyperparasite immatures as well as pupae were collected in the mummy sample at the same time. Thus, the period of hyperparasite emergences was longer during the later part of the crop (Fig. 32B) than in the early crop growth (Fig. 32A).

Figure 32. Daily parasite emergence patterns showing the accumulated percentages of parasites emerging from two mummy samples taken from an alfalfa field near Kamloops on (A) day 88 (27/June/1972) and (B) day 116 (25/July/1972) (see Fig. 30B for total sample sizes). The total number (n) of each parasite species that emerged is shown. (Room temperature 20 to 24°C.)



b) *Primary parasites*. The relative abundance of the primary parasite species found in the study field near Kamloops during the summers of 1971 and 1972 are shown in Table XVII and Figs. 33, 37B, 38B. *Aphidius smithi* was the most abundant primary parasite, contributing 80.9% in 1971 and 75.6% in 1972 to the total number of primary parasite emergences (Table XVII). *A. e. pulcher* was the second most abundant parasite (12.6% in 1971 and 19.3% in 1972), while *P. pequodorum* contributed 6.0 to 4.7% of the total primary parasite population in 1971 and 1972, respectively. *A. smithi* "orange" mutant and *A. e. ervi* were rarely found near Kamloops, constituting 0.5% of the total parasite population. Differences in the relative abundance of primary parasites between the main study field and the field 100 m east of the study field during 1971 and 1972 were small (Fig. 27 and Table XVII).

Fluctuations in relative parasite percentages in the second and third crops of both years were probably due to sampling error or incomplete overlapping of parasite generations during early alfalfa growth (Fig. 33). The change in parasite species composition was especially evident during the early spring in both years (Fig. 33). *A. e. pulcher* was the most abundant parasite in the first sample taken in 1971 and 1972; however, *A. smithi* soon became more abundant than *A. e. pulcher*. There were two peaks in *A. e. pulcher* and *A. smithi* abundance during the first crop of both years (Fig. 33), but these peaks did not coincide. The data suggest that *A. e. pulcher* adults emerged slightly earlier than *A. smithi* adults from diapause. Because *A. e. pulcher* and *A. smithi* have approximately the same heat requirements for development (Chapter III), an earlier appearance of



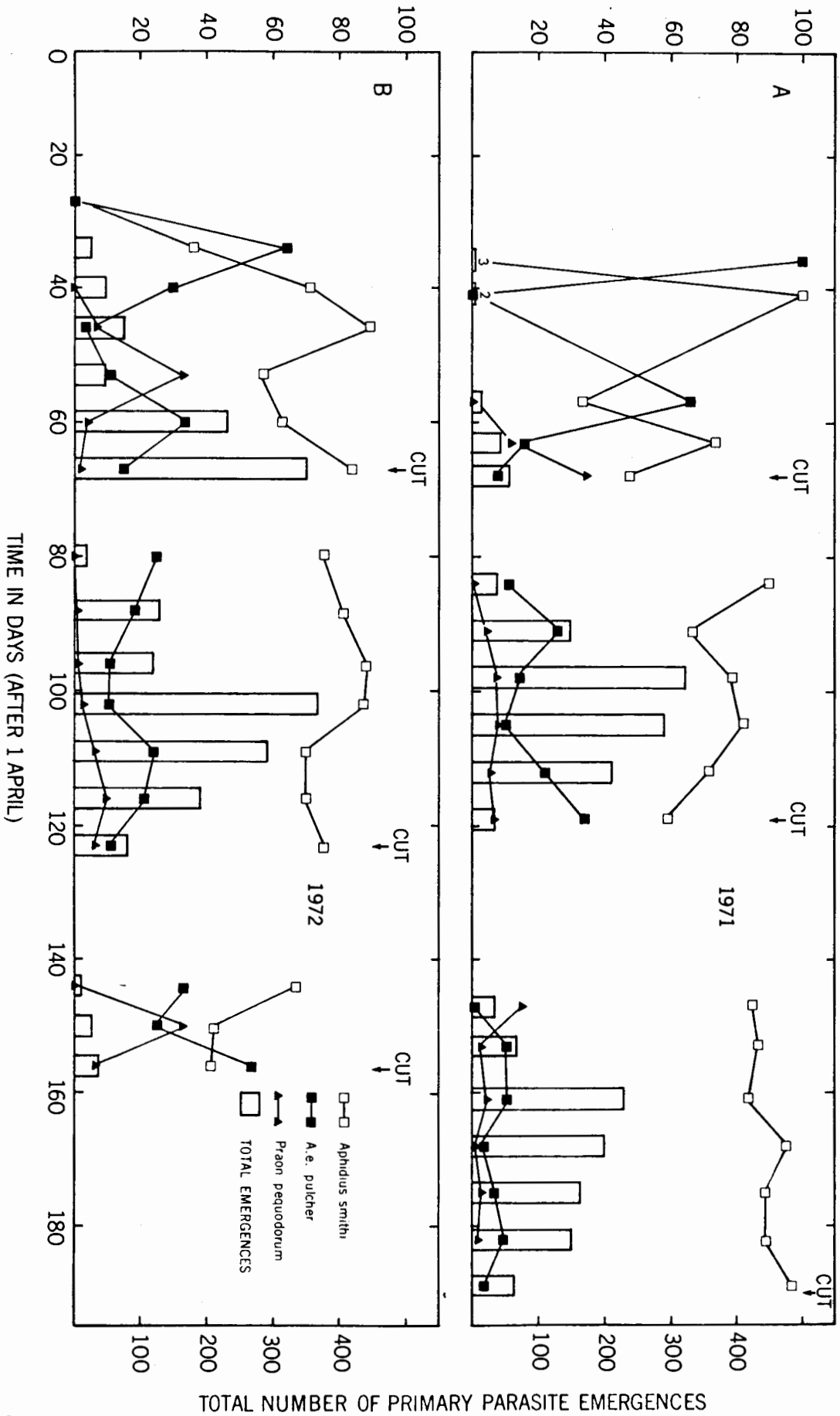
Table XVII. The mean relative abundance of primary parasites, expressed as percentages of total primary parasite emergences from all mummy samples collected during 1971 and 1972 from the main study field at Kamloops.

	1971		1972	
	n	%	n	%
<i>A. smithi</i>		80.9		75.6
<i>A. e. pulcher</i>		12.6		19.3
<i>P. pequodorum</i>		6.0		4.7
Others*		0.5		0.4
Total	2042	100.0	2015	100.0

\* Other parasites include *A. smithi* "orange" mutant and *A. e. ervi*.

Figure 33. The seasonal relative abundance of primary parasites, expressed in percentages of total primary parasite emergences from mummy samples collected during (A) 1971 and (B) 1972, in an alfalfa field at Kamloops.

PERCENT OF TOTAL PRIMARY PARASITE EMERGENCES



*A. e. pulcher* adults would result in an earlier appearance of *A. e. pulcher* mummies (Fig. 33). Sweep samples confirm the staggered appearance of the adults of both parasite species in early spring (Appendix 5).

The assumed correlation between heat requirements and mummy appearance is further strengthened when comparing the higher temperature threshold (6.9°C) of *P. pequodorum* with the lower threshold (6.1°C) of *A. e. pulcher* and *A. smithi*. *P. pequodorum* adults appeared about two weeks after the other parasites in the sweep samples (Appendix 5). As a consequence of the late *P. pequodorum* emergence from diapause, *Praon* mummies did not start appearing until day 32 in 1971 and day 16 in 1972 (Fig. 33). Indeed, because of the slower developmental rate of *P. pequodorum* only one peak of abundance (i.e. one generation) occurred in the first crop of both years.

The changes in relative peak abundance for each of the parasite species during the first crop were probably due to a discrete generation effect. However, as the season progressed, overlapping parasite generations occurred and, in response to aphid population increases, the superior fecundity (Chapter III) (and probably searching capacity) of *A. smithi* helped it to become more abundant than the other two parasites (Fig. 33).

The weighted mean sex ratios of each parasite species emerging from the mummy samples throughout each season in 1971 and 1972 are shown in Table XVIII. There were generally slightly more females than males of each species in both years.

c) *Secondary parasites*. Additional information was obtained on secondary parasite emergences from the mummy samples. However, it is not within the scope of this thesis to analyse in detail the secondary parasite

Table XVIII. Weighted mean sex ratios of three primary parasites emerging from mummies sampled near Kamloops during 1971 and 1972.

Species	Sex ratio*		Overall mean
	1971	1972	
<i>A. smithi</i>	.53 ± .01 (1652)	.58 ± .01 (1524)	.55 ± .01 (3176)
<i>A. e. pulcher</i>	.55 ± .03 (258)	.58 ± .03 (389)	.57 ± .02 (647)
<i>P. pequodoru.</i>	.64 ± .01 (123)	.44 ± .05 (94)	.55 ± .01 (217)

\* Mean sex ratio ± 1 SE; numbers in brackets are the total parasite emergences of each parasite species from 18 samples for 1971 and 16 samples for 1972.

(or hyperparasite) population dynamics. Only a brief analysis was made to determine: (1) the overall effect of hyperparasitism as a mortality factor of primary parasites; and (2) the relative abundance of each hyperparasite species. Some relevant information on hyperparasite development and seasonal abundance is summarized. For detailed studies and literature reviews on hyperparasites attacking pea aphid parasites, see Gutierrez (1968) and Sullivan (1969).

The proportion of hyperparasitism generally increased as the alfalfa crop matured (Figs. 30, 31). Figure 34 shows the proportion of total parasite emergences from the mummy samples that yielded primary parasites on a physiological time scale. The figure, in other words, shows the proportion of primary parasites that survived the activity of the hyperparasites in the field. Little was known on the exact population interrelationships between each hyperparasite and primary parasite species. If there was any hyperparasite specificity towards a particular primary parasite species, this was not detected because all hyperparasite species emerged from both *Aphidius* and *Praon* mummies. Thus the most realistic way of showing hyperparasite activity in the simulation model (Chapter VII) was to use the equations (Table XIX) describing the overall survival rates of primary parasites as shown in Fig. 34.

The hyperparasite species found to attack parasitized pea aphids are listed in Table XV. More secondary parasites were collected in 1971 than in 1972 (Fig. 30 and Tables XX, XXI). *Asaphes lucens* and *Lygocerus niger* were the most abundant secondary parasites during each season in both years (Table XXI). *L. niger* appeared earlier than *A. lucens* in early spring

Figure 34. Proportion of primary parasites surviving hyperparasitism (or proportion of total parasite emergences producing primary parasites) in the mummy samples on a physiological time scale. (one quip or KA = 6.2 day-degrees above 5.56°C). Each numbered straight line is described by an equation in Table XIX.

PROPORTION OF PRIMARY PARASITES  
SURVIVING HYPERPARASITISM

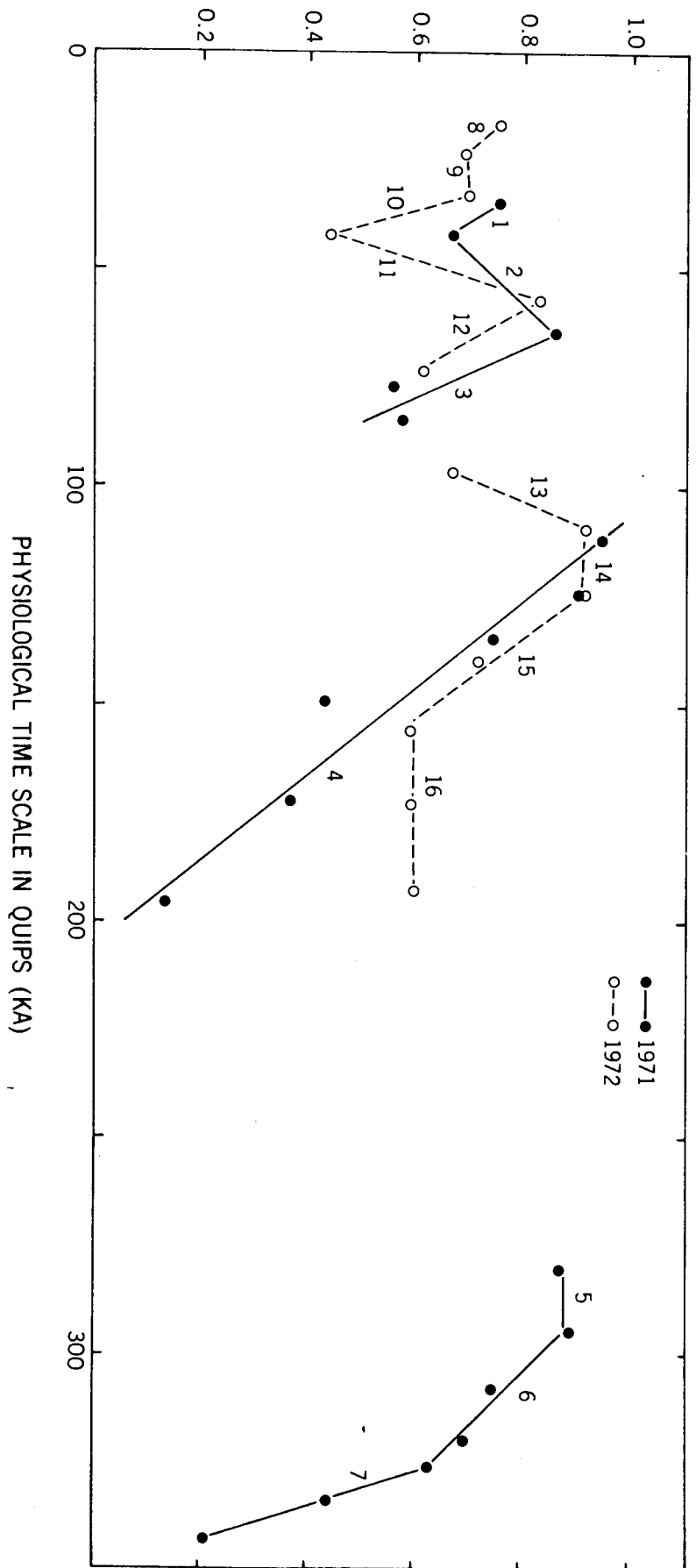




Table XIX. Proportion of primary parasites surviving hyperparasitism.  
 Numbered equations represent the straight lines shown in  
 Figure 34.

Equation No.	Time period (KA)	Equation	Correlation coefficient (r)*
1971			
1	34 - 42	HYPER = 1.170 - 0.0124 KA	
2	43 - 65	= 0.294 - 0.0085 KA	
3	66 - 85	= 1.856 - 0.0158 KA	
4	112 - 196	= 2.080 - 0.0101 KA	0.96
5	281 - 295	= 0.880	
6	296 - 327	= 0.319 - 0.0070 KA	0.97
7	328 - 344	= 9.089 - 0.0259 KA	0.99
1972			
8	17 - 23	= 0.945 - 0.0111 KA	
9	24 - 33	= 0.694	
10	34 - 42	= 1.652 - 0.0289 KA	
11	43 - 57	= -0.659 + 0.0262 KA	
12	58 - 73	= 1.585 - 0.0133 KA	
13	97 - 109	= -1.357 + 0.0208 KA	
14	110 - 124	= 0.914	
15	125 - 156	= 2.149 - 0.0101 KA	
16	157 - 193	= 0.593	

KA = Physiological time in quips (equivalent to horizontal axis in Figure

HYPER = Proportion of primary parasites surviving hyperparasitism during  
 season on physiological time scale.

\* Correlation coefficients shown when four or more values were used to  
 calculate regression equations.

(Figs. 35, 37A, 38A), probably because of *L. niger*'s lower temperature developmental threshold (6.55°C) compared to *A. lucens*' threshold (8.55°C). Indeed, *L. niger* was the first hyperparasite to emerge from most of the mummy samples (Fig. 32). Because *Charips* sp. adults can parasitize earlier stages of primary parasites (Gutierrez, 1968), *Charips* sp. usually appeared first in the early stages of the alfalfa growth, especially in the second and third crops, 1971 (Fig. 35A). However, as more mummies accumulated in the field an increasing proportion of *Asaphes lucens* appeared in the mummy samples. Because of the ability of *Asaphes* sp. to parasitize primary parasites and other secondary parasites (Sullivan, 1969), there was invariably an increase in the number of mummies containing *Asaphes lucens*. At the end of each crop in both years, when a large number of mummies were collected, the highest proportion of hyperparasite emergences were of *A. lucens* adults (Figs. 35, 37A, 38A).

#### D. Discussion

Most of the following section (pages 165 to 171) is quoted directly from Campbell and Mackauer (1973).

1. *Exotic parasite dispersal and establishment.* As already mentioned, *A. e. ervi* and *A. smithi* were liberated against the pea aphid in the northwestern United States between 1961 and 1964 (Halfhill *et al.*, 1972). Both species subsequently spread across the border into Canada, where they became important natural enemies of the aphid.<sup>8</sup> Various factors such as climate,

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<sup>8</sup> The only pea aphid parasites released in western Canada were ca. 13,000 specimens of the Orange phenotype of *A. smithi*, which were liberated in 1972 near Kamloops for experimental purposes.

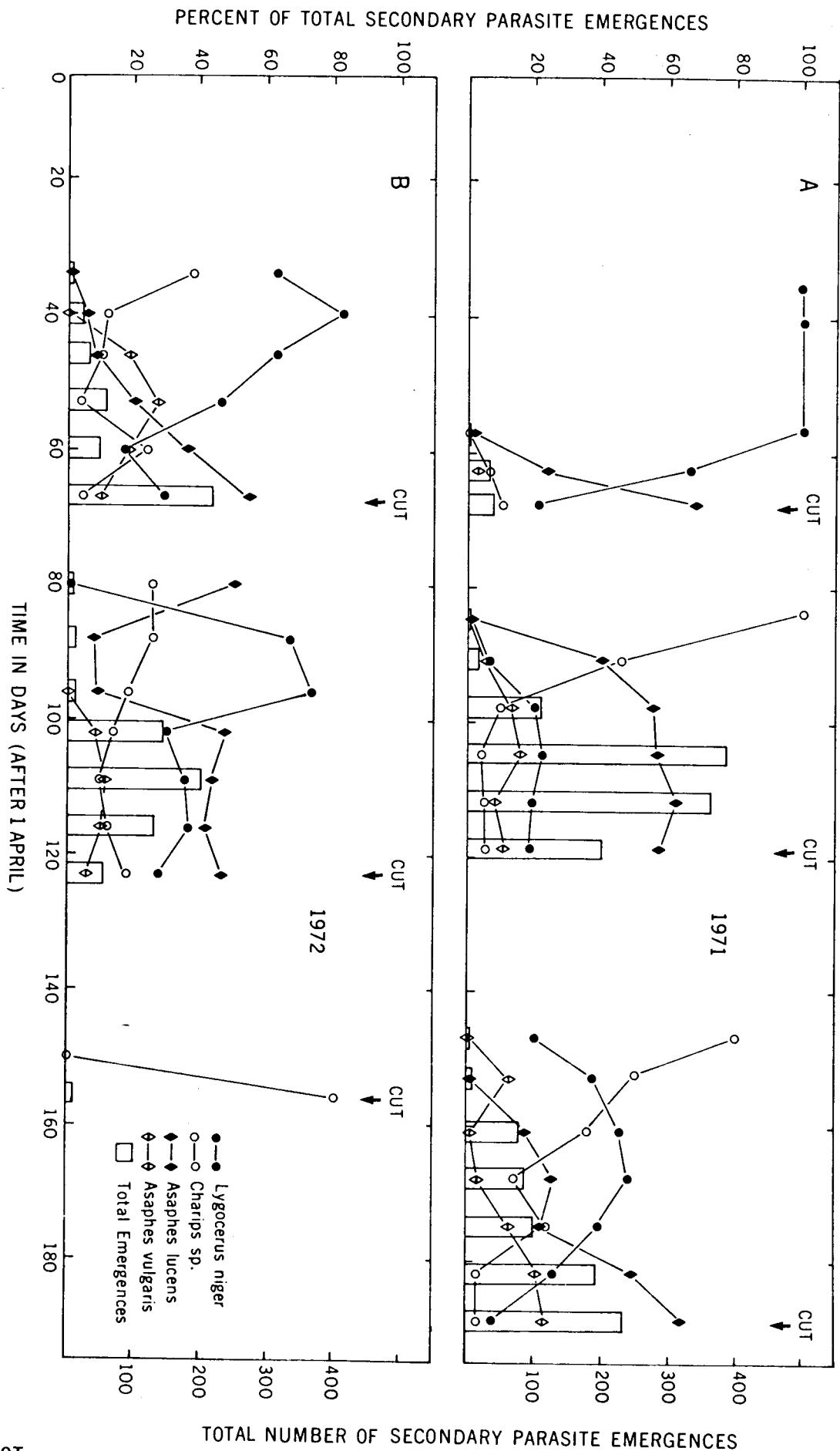
Table XX. Mean percentages of total primary and secondary parasite emergences from mummy samples collected in study field during 1971 and 1972.

	1971		1972	
	n	%	n	%
Primary parasites		52.4		68.1
Secondary parasites		47.6		31.9
Total	3895	100.0	2962	100.0
No. of mummy samples	18	-	16	-

Table XXI. Mean relative abundance of secondary parasites, expressed as percentages of total secondary parasite emergences from all mummy samples collected during 1971 and 1972 from the main study field at Kamloops.

	1971		1972	
	n	%	n	%
<i>Lygocerus niger</i>		23.6		34.7
<i>Charips</i> sp.		8.4		11.3
<i>Asaphes lucens</i>		52.0		41.1
<i>Asaphes vulgaris</i>		13.1		10.9
<i>Pachyneuron siphonophorae</i>		1.8		-
<i>Coruna clavata</i>		1.1		2.0
Total	1853	100.0	947	100.0

Figure 35. The seasonal relative abundance of the more common secondary parasites, expressed in percentages of total secondary parasite emergences from mummy samples collected during (A) 1971, (B) 1972, in an alfalfa field at Kamloops. (N.B. *Pachyneuron siphonophorae* and *Coruna clavata* are not shown because they were rarely observed in the samples.)



physical environment, and the availability of suitable hosts, among others, affected the rate of spread and the degree of success of establishment, if any, of the colonizing species.

The data in the present study indicate that the exotic parasites invaded southern British Columbia and spread along two main routes from release sites in Washington State (and Idaho). One route was along the Okanagan and Columbia River systems into the Interior. Halfhill *et al.* (1972) first observed *A. smithi* in 1965 in southern Washington State, near Walla Walla. The first report of the parasite occurring in British Columbia was also in 1965 from Christina Lake, in the Columbia River Basin close to the Canada-United States border (Mackauer and Finlayson, 1967). Further northward expansion by the invading parasite was affected by a reduction in agricultural land. While the pea aphid occurs throughout most of southern British Columbia, it is reasonably abundant only where alfalfa and clover are grown commercially for hay, silage, or seed production. Other host plants, such as sweetclover, are common components of the ruderal flora; however, these plants usually do not support sufficiently numerous aphid colonies to enable the development of large parasite populations. Dispersal, it was shown by Johnson (1969), is a density dependent phenomenon. When parasite abundance is low, both the dispersion within a species' general area of distribution and the probability of dispersal over large areas or across ecological barriers tends to be reduced. It is, therefore, not surprising that *A. smithi* required between one to three years to spread 200 to 300 km from the border area to Kamloops, in the Interior. The estimation of the rate of spread in this largely forested area is based on

the finding that *A. smithi* was well established in the vicinity of Kamloops in 1969, having arrived perhaps one or two years earlier.

The second route of entry was along the coast from northwestern Washington into the Vancouver area and from there east into the Lower Fraser River Basin. It would appear that *A. e. ervi* spread mainly through the cool and wet coastal area, although the parasite's appearance at Winfield and at Kamloops (Fig. 26, Nos. 6, 4) suggests that it also entered through the river valleys running from the Interior of southern British Columbia to Washington State. Human transport may have aided in the invasion of the Lower Fraser River Basin by the exotic parasites, in particular by the transportation of parasitized aphids and mummies on baled alfalfa hay from the Interior to dairy and cattle farms near the coast.

2. *Distribution of exotic parasites.*<sup>9</sup> On the basis of laboratory experiments Mackauer (1971) concluded that *A. smithi* was superior to *P. pequodorum*, *A. e. ervi*, and *A. e. pulcher* in searching behaviour, fecundity, and developmental time. This assessment was not generally confirmed by the field performance of *A. smithi*. Open releases of the parasite over large areas of the United States, eastern Canada, and Hawaii resulted in economic control of the pea aphid only in California (Hagen and Schlinger, 1960; Hagen and van den Bosch, 1968). Although the parasite became established in Hawaii (Davis and Krauss, 1962), Mexico (Clancy, 1967), and in the northwestern United States (Halfhill *et al.*, 1972), there is no evidence suggesting that these colonizations had any long-term effect on pea aphid

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<sup>9</sup> Most of this section (pages 171 to 173) is quoted directly from Campbell and Mackauer (1973).



abundance. Releases in the eastern United States (Angalet and Coles, 1966) and Canada (Mackauer, 1971), while resulting in the temporary establishment of the parasite, apparently failed as control measures. Following its discovery in southern Ontario in 1964 (Mackauer and Bisdee, 1965), the parasite's relative abundance had increased to approximately 53% by 1966; however, during the next four years the impact of *A. smithi* declined drastically from 23% in 1968 to 0.3% in 1970 (M. Mackauer, pers. comm.). Mummy samples collected during 1972 in Prince Edward County, Ontario, did not contain any representatives of this parasite but, instead, included specimens of *A. e. ervi*.<sup>10</sup>

Comparing the performance of *A. smithi* in southern British Columbia directly with that of the European *A. e. ervi* suggests that the usefulness of both parasites as biological control agents is restricted by certain factors. Both *A. smithi* and *A. e. ervi* successfully colonized areas of North America that differed in important elements from the countries of origin. In addition, the presence of several native (and presumably well-adapted) parasites and hyperparasites did not prevent the colonization. Direct competition between parasite species, however, apparently did not play an important role in determining local abundance. This is surmised from the relative infrequency in the field of super- and/or multiparasitism, except when aphids were rare in early spring.

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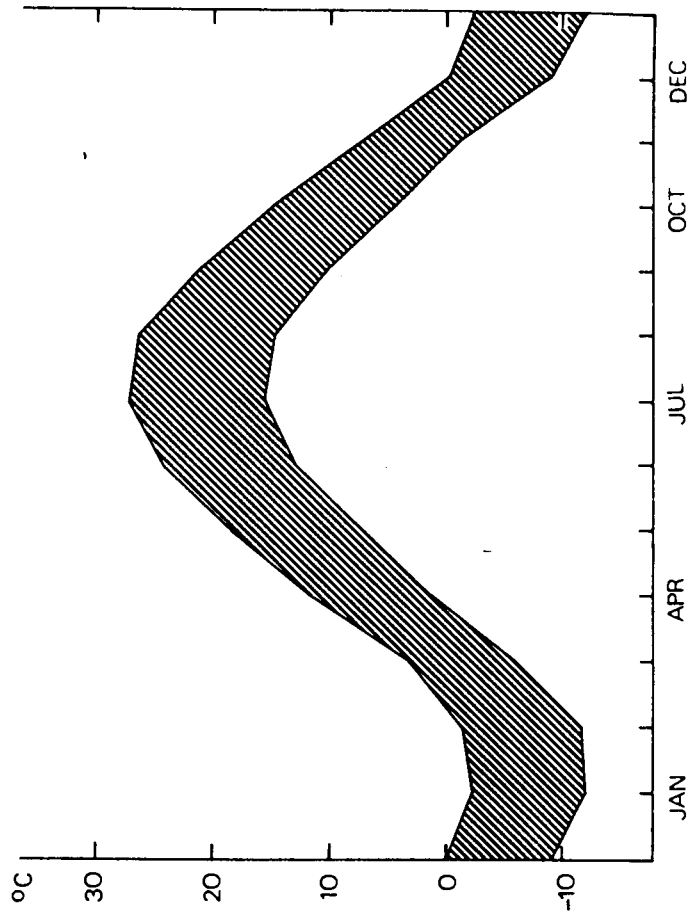
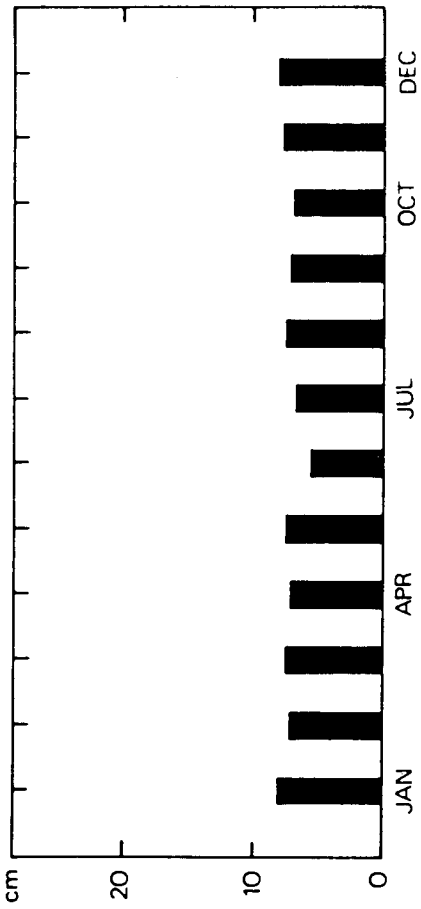
<sup>10</sup> The parasite *A. e. ervi* was liberated in the eastern United States between 1959 and 1968 (R. J. Coulson, pers. comm. to Dr. M. Mackauer). This is the first record of its establishment in eastern North America.

A comparison of the climatographs (Figs. 26 and 36) of major release and study areas suggests that climate was a major factor among the variety affecting establishment and abundance of the exotic parasites. For example, in British Columbia *A. smithi* became the chief parasite of the pea aphid in the Steppe climate of the Interior region (Fig. 26A). The parasite also performed well in the valleys of central and coastal California (Fig. 36A) which are climatically similar to the Okanagan Valley, indicating that *A. smithi* tolerates (and probably is adapted to) a hot and dry climate. *Aphidius smithi*, so far, has performed very poorly under the relatively mild and wet climatic conditions of the Lower Fraser River Basin (Fig. 26B), to which conditions, apparently, the European *A. e. ervi* is well adapted. The hypothesis regarding the role of climate gains further support by reference to Fig. 36B, which shows that south-central Ontario has, on the average, a relatively humid summer climate with considerable precipitation throughout the year. Although low winter temperatures persist for a long period in Ontario, there is no significant difference in the average minimum winter temperatures between, e.g., Belleville and Kamloops. In fact, *A. smithi*'s poor performance in eastern Canada strongly argues that it is precipitation (possibly in combination with temperature) rather than an assumed inability to survive low winter temperatures in diapause (Hagen and Schlinger, 1960) that limits the parasite's potential distribution and control ability.

3. *Seasonal dynamics of parasites.* As the aphid population increased the rate of parasitism increased (Chapter V), and there was a corresponding increase in the total number of mummies collected in field samples (Fig. 30).

Figure 36. Climatographs of (A) Bakersfield, California; (B) Belleville, Ontario, giving mean total precipitation (above) and mean maximum and minimum temperatures (below). (Data from Temp. PPT Tables, Publ. Atmos. Environm. 1970 Serv. Govt. Canada; and Climates Calif. State, U.S. Dept. Commerce, rev. 1966) (From Campbell and Mackauer, 1973.)

**B**



**A**

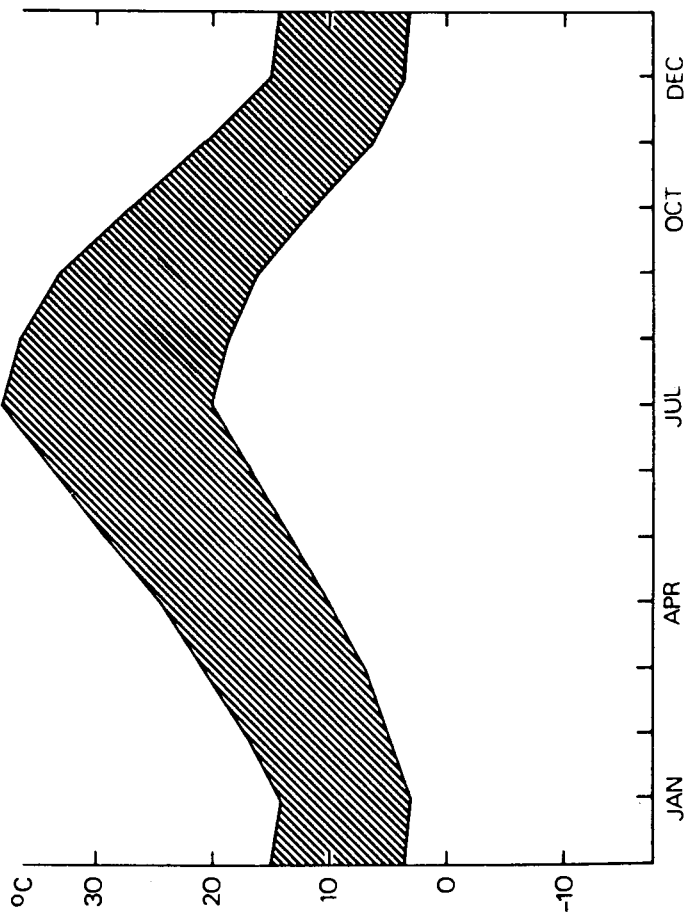
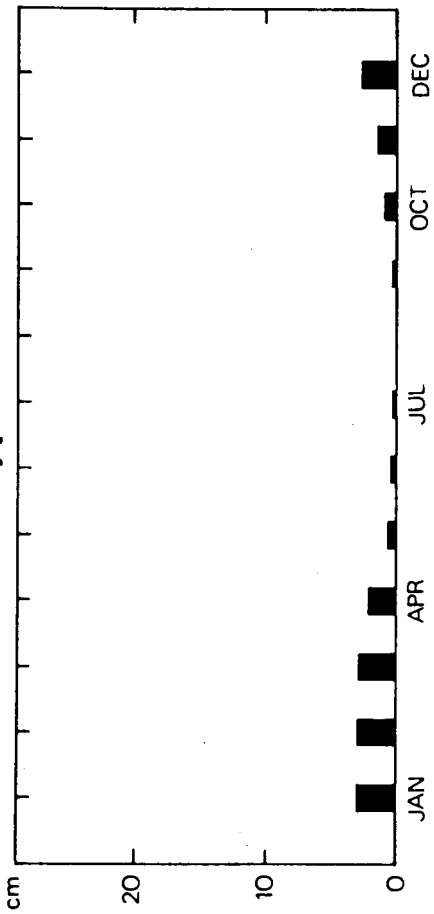


Figure 37. Total emergences (logarithmic scale) of (A) secondary parasites, (B) primary parasites from mummy samples taken from an alfalfa field near Kamloops, B.C., during 1971.

TOTAL NUMBER OF EMERGENCES LOG (n+1) SCALE

PRIMARY PARASITES

SECONDARY PARASITES

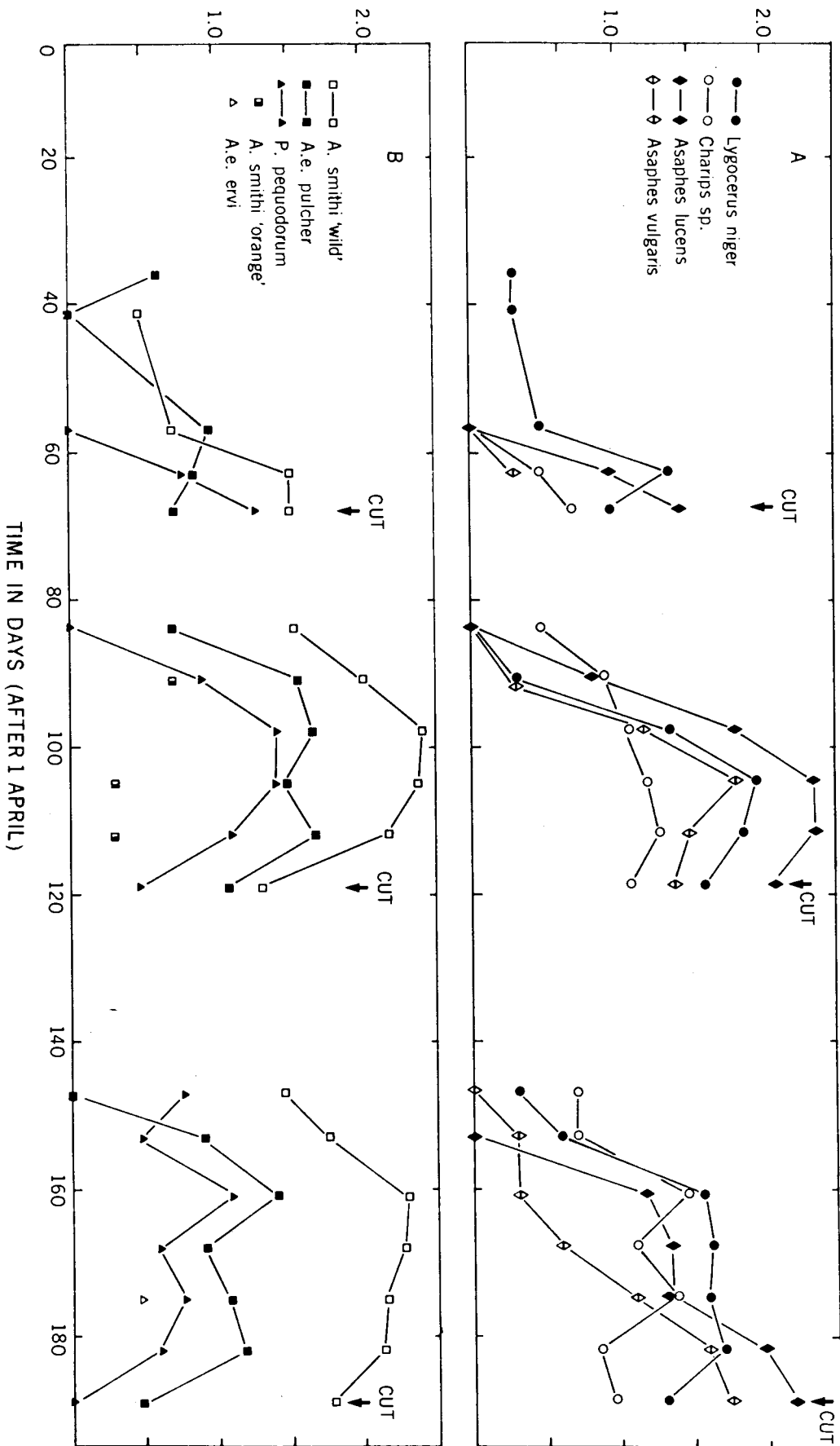
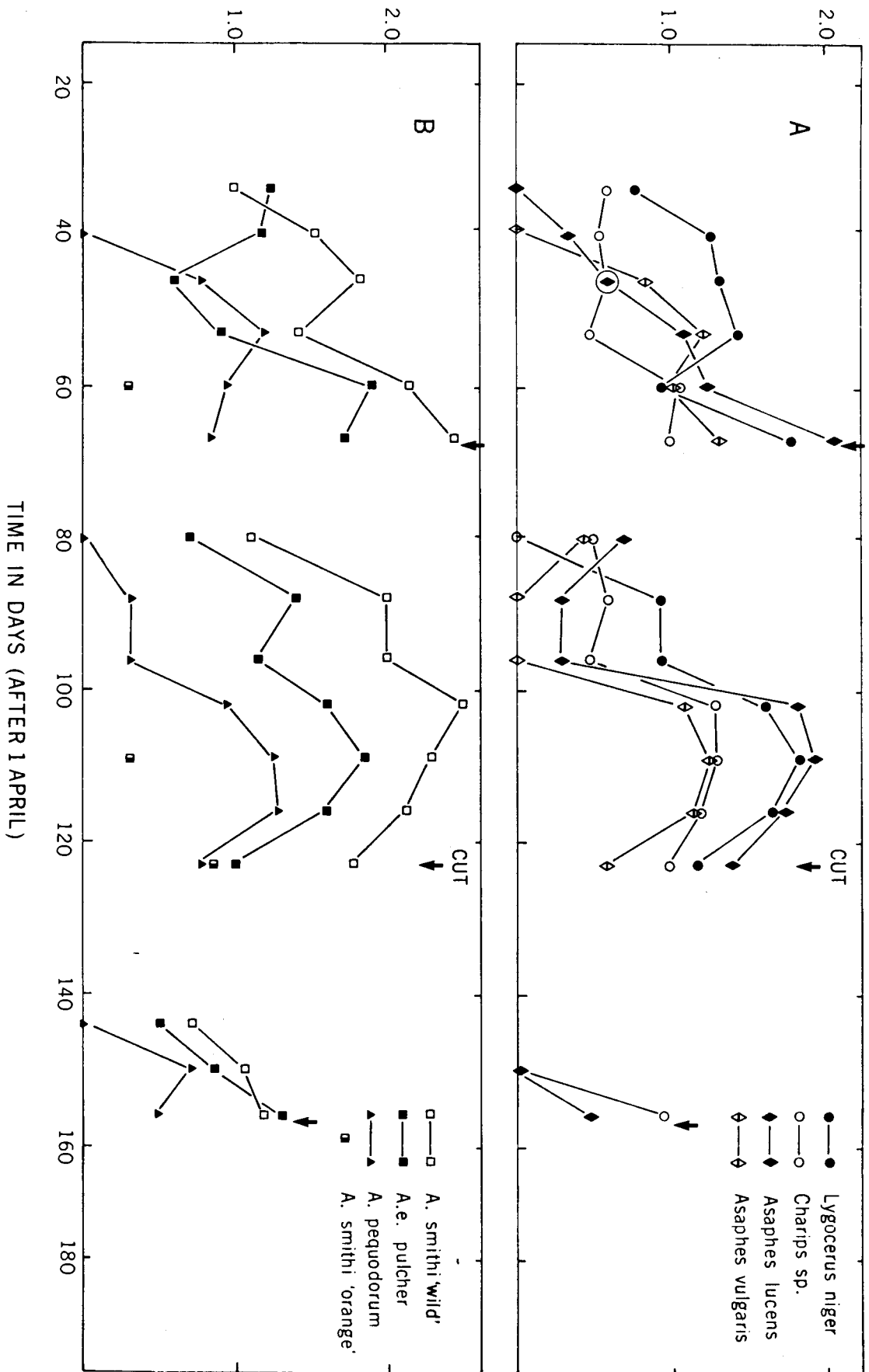


Figure 38. Total emergences (logarithmic scale) of (A) secondary parasites, (B) primary parasites from mummy samples taken from an alfalfa field near Kamloops, B.C., during 1972.

TOTAL NUMBER OF EMERGENCES LOG (n+1) SCALE  
 PRIMARY PARASITES                      SECONDARY PARASITES





This was due to the accumulation of emerged mummies in the field. This "graveyard effect" could probably be misleading when considering parasite effectiveness in controlling the aphid. In contrast, when the aphid population grew or declined there was a corresponding increase and reduction in the parasitism rate and a lag period in the increase and decrease in numbers of primary parasites emerging from the mummies (Fig. 30). These observations generally confirm the density dependent action of the parasites, which was noted in Chapter V. However, it would be difficult to engage in any accurate calculations associating aphid densities with mummy collections or parasite emergences because of the complicating action of hyperparasites (Fig. 30). All three primary parasite species responded to aphid density increases proportionally, or in a density dependent manner, especially during the second and third crops, 1971 (Figs. 33, 37B, 38B).

*A. smithi* contributed the highest to aphid parasitism at 80.9 and 75.6% during 1971 and 1972, respectively, while *A. e. pulcher* (12.6 and 19.3%) and *P. pequodorum* (6.0 and 4.7%) contributed less than *A. smithi* to overall parasitism of the pea aphid during 1971 and 1972. *A. smithi* was the main contributor to the high rates of parasitism (two peaks) in the first crop of spring, 1972 (Fig. 33B and Figs. 17C, 21).<sup>11</sup> *A. smithi*'s higher fecundity and developmental rates than those of the indigenous parasites (Chapter III) seem to have contributed to *A. smithi* becoming the most abundant

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<sup>11</sup> N.B. Mean physiological time between mean mummy stage and immature parasite stage is 14 to 16 quips. Aligning peak *A. smithi* abundance from first crop mummy samples in Fig. 33B with peak percent parasitism rates 14 to 16 quips earlier in Fig. 21 (use Fig. 17C as a help to convert calendar time to physiological time) gives a close agreement of curves.

parasite in the study field, practically for the whole of the growing season during 1971, 1972.

Because *A. e. ervi* occurred at very low numbers at Kamloops, it was not considered in the final analysis of the parasite dynamics.

The pattern of secondary parasite emergences (Fig. 32) was influenced by (1) development time and (2) stage of primary parasite that is preferred for ovipositioning by the hyperparasite. For example, *L. niger* has a lower temperature developmental threshold (8.55°C) than *Asaphes lucens* (6.55°C) (Chapter III). Gutierrez (1968) showed that *Charips* sp. generally attacked primary parasite larvae before aphid mummification. *Lygocerus* sp. generally attacked primary parasite larvae in the early mummy stages (Spencer, 1926), while *Asaphes* sp. could attack mummies containing either the primary parasite (mature larva or pupa) or a secondary parasite (egg to pupa) of another species or its own species (Sullivan, 1969). The majority of *Charips* sp. emerged later than *Lygocerus* adults (Fig. 32), indicating that although *Charips* attacked an earlier developmental stage of primary parasite, it probably had higher heat requirements than *Lygocerus*.

There were three main extrinsic mortality factors acting on the mummy stages of primary parasites that were measured: (1) predation; (2) harvesting; and (3) hyperparasitism. In general, predation of mummies was not appreciable. A maximum predation value of approximately 6% of the total mummies collected was recorded in early spring, 1972, due mainly to an abundance of adult Coccinellids in the field.

The harvesting of alfalfa was the main mortality factor of primary parasite mummies, decimating the mummy population in the field. Only a

few mummies usually remained attached to the stubble or on leaves that had dropped off after the dry alfalfa was raked, baled, and removed. Harvesting also has the effect of (1) reducing the potential reservoir of hyperparasites and (2) removing emerged mummies. Van den Bosch *et al.* (1966, 1967) and Pass and Parr (1971) also recorded harvesting as being an important mortality factor of parasites. By removing the mature alfalfa, the subsequent new alfalfa growth allowed aphid and parasite populations to increase and reach densities similar to those experienced in the earlier crop.

The importance of hyperparasites as mortality factors of primary parasites is influenced by the environment and the aphid and parasite host species involved. Many authors (Evenhuis, 1964; George, 1957; Hafez, 1961; Paetzold and Vater, 1966; Way *et al.*, 1969) have found that the effectiveness of the aphidiid parasite, *Diaeretiella rapae*, in controlling the cabbage aphid, *Brevicoryne brassicae*, was more or less limited by the activity of hyperparasites. Hafez (1961) reported 69 to 80% and Paetzold and Vater (1966) over 90% hyperparasitism of mummies collected during a growing season. In contrast, Shands *et al.* (1965) found hyperparasitism did not have an appreciable nor a consistent effect on primary parasites that attacked potato-infesting aphids in Maine. Hyperparasitism ranged from 22 to 42% during the period of 1952 to 1961 (Shands *et al.*, 1965).

There are only two field studies on the pea aphid that recorded the effect of hyperparasites on primary parasites. The first was by Stary (1966), who found an average of 33% hyperparasitism of *A. e. ervi* in red clover fields in western Bohemia during 1956. The main hyperparasite

species were *Alloxysta scutellata*, *Còruna clavata*, *Asaphes vulgaris*, and *Lygocerus* sp. He found that hyperparasite percent infestation was especially great at the end of an aphid outbreak, when primary parasites had already reached higher density levels. In the second study, Gutierrez (1968, 1970) found an average of 33% hyperparasitism of a large primary parasite complex (which consisted of *A. smithi*, *P. pequodorum*, *Ephedrus* sp., *Trioxys* sp., and several *Aphelinus* spp.) attacking *A. pisum* and *Therioaphis trifolii* (the spotted alfalfa aphid) in alfalfa fields of California during 1966. The parasite complex is more complicated in California (because of the additional presence of *T. trifolii* and its parasites) than at Kamloops,<sup>12</sup> making a direct comparison of parasitism rates difficult. However, in some alfalfa fields where Gutierrez found mostly *A. smithi* mummies, *Lygocerus* sp. (63%) was the most abundant of all hyperparasites emerging, with *Asaphes lucens*, *Charips vitrix*, *Aphidencyrthus aphidivorus*, and a few other species being less abundant. Gutierrez (1968) suggested that repeated harvesting of alfalfa probably had an inhibiting effect on both primary and secondary parasites.

In this study, the mean hyperparasitism rate of mummies was 47.6 and 31.9% in 1971 and 1972, respectively. *Asaphes lucens* and *Lygocerus niger* were the most abundant of the hyperparasites attacking the primary parasites in Kamloops (Table XXI, Figs. 37A, 38A). These mean hyperparasitism rates are similar to those reported by Stary (1966) and Gutierrez (1970), as

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<sup>12</sup> Only one other aphid species, the pink form of *Macrosiphum euphorbiae* Thomas, was found at very low densities in the alfalfa field. No parasite species that attack the pea aphid were found to attack *M. euphorbiae*.

reported above. However, the mean annual hyperparasitism rate does not reflect the seasonal changes in hyperparasite numbers. Indeed, hyperparasites showed a density dependent response to the increase in parasitized hosts similar to that shown by the primary parasites to the pea aphid numbers. Hyperparasitism was low early in each crop but as the number of parasitized hosts increased so did the number of hyperparasites (Figs. 30, 35, 37A, 38A). Hyperparasites did not seem to affect the primary parasite numbers, especially during the growth phase of the aphid and parasite populations. Up to the point of peak host populations there was between 15 and 40% hyperparasitism (Figs. 30, 34). Thus, about 85 to 60% of the primary parasites emerged from mummies surviving hyperparasitism (Fig. 34), which was probably sufficient to maintain parasite population growth. But after host populations peaked, the rate of hyperparasitism sometimes increased rapidly to 70 and 85% (Fig. 34). This increase was probably due to a decrease in the number of parasitized hosts (Figs. 30, 37, 38) rather than to an increase in the abundance of hyperparasites.

In other words, hyperparasitism is probably not an important mortality factor to primary parasites that are in surplus supply. Hyperparasites probably do not limit primary parasite numbers when the impact of primary parasites on pea aphid populations (i.e. during the aphid population growth phase) is most crucial. Thus, hyperparasites take care of some of the overabundance of primary parasites when the latter are not needed to help reduce growing aphid populations. There are probably enough primary parasites emerging (even with 60 to 70% hyperparasitism) to respond to any renewed aphid population growth. Moreover, the alfalfa harvesting generally

removed the hyperparasite buildup at the end of each crop growth, giving primary parasites the chance to respond rapidly to aphid population growth in the following crop.

#### E. Summary

A survey of the pea aphid parasites was made by taking mummy samples in alfalfa fields throughout southern British Columbia. In addition, the population trends of these parasites were monitored by taking mummy samples in an alfalfa field near Kamloops during the summers of 1971 and 1972.

The indigenous parasites, *Aphidius ervi pulcher* and *Praon pequodorum*, and the exotic parasites, *A. smithi* and *A. e. ervi*, were found throughout southern B.C. *A. smithi* was the numerically dominant parasite under hot dry climatic conditions in the Interior of B.C., while *A. e. ervi* was numerically dominant under the relatively wet and mild climatic conditions of the lower Fraser Valley. It is suggested that the effect of wet or humid climate reduces *A. smithi*'s potential to control the pea aphid.

A total of 9,424 mummies was collected at weekly intervals (of one hour duration) in an alfalfa field near Kamloops, B.C., during the summers of 1971 and 1972. Only 72.7% of the parasites emerged (n = 6857) from the total mummies collected. More primary parasites emerged from the mummies than hyperparasites; 52.4% of 3,895 emergences in 1971 and 68.1% of 2,962 emergences in 1972 were primary parasites. During 1971 and 1972, 2,042 and 2,015 primary parasites emerged from the samples, respectively, of which *A. smithi* (80.9 and 75.6%) was the most abundant, while *A. e. pulcher* (12.6 and 19.3%) and *P. pequodorum* (6.0 and 4.7%) were less abundant.

Low spring temperatures influenced the development of the various parasite species differently. *Aphidius smithi* and *A. e. pulcher* develop at lower temperatures than *Praon pequodorum* and were therefore relatively more abundant in early spring. Discrete generations caused changes in the abundance of parasite species during the first spring crop. However, increased temperatures in summer and parasite responses to aphid population growth produced overlapping generations and an average contribution of 70 to 80% by *A. smithi*, 13 to 20% by *A. e. pulcher*, and 5 to 10% by *P. pequodorum* to aphid parasitism rates during the second and third crops.

Predation of mummies by Coccinellid adults and Chrysopid larvae was not significant, with a mean loss ranging from 0.8 to 1.8% during both years and a maximum of 6.0% coinciding with Coccinellid adult abundance in the spring of 1972. Harvesting, however, was an important mortality factor, decimating mummies at the end of each crop.

Of the total number of mummies that yielded emergents, 47.6 and 31.9% yielded hyperparasites in 1971 and 1972, respectively. *Asaphes lucens* (52.0 and 41.1%) and *Lygocerus niger* (23.6 and 34.7%) were numerically the most abundant hyperparasites in 1971 and 1972, respectively. Hyperparasites did not limit the parasite population growth phase, as during this period hyperparasitism of parasitized aphids rarely exceeded 15 to 40%. However, after aphid and parasite populations had peaked, hyperparasitism sometimes increased rapidly to 70 to 85%. This was probably due to a decreased number of parasitized hosts rather than to an increase in hyperparasite abundance.

CHAPTER VII  
THE PEA APHID-PARASITE MODEL

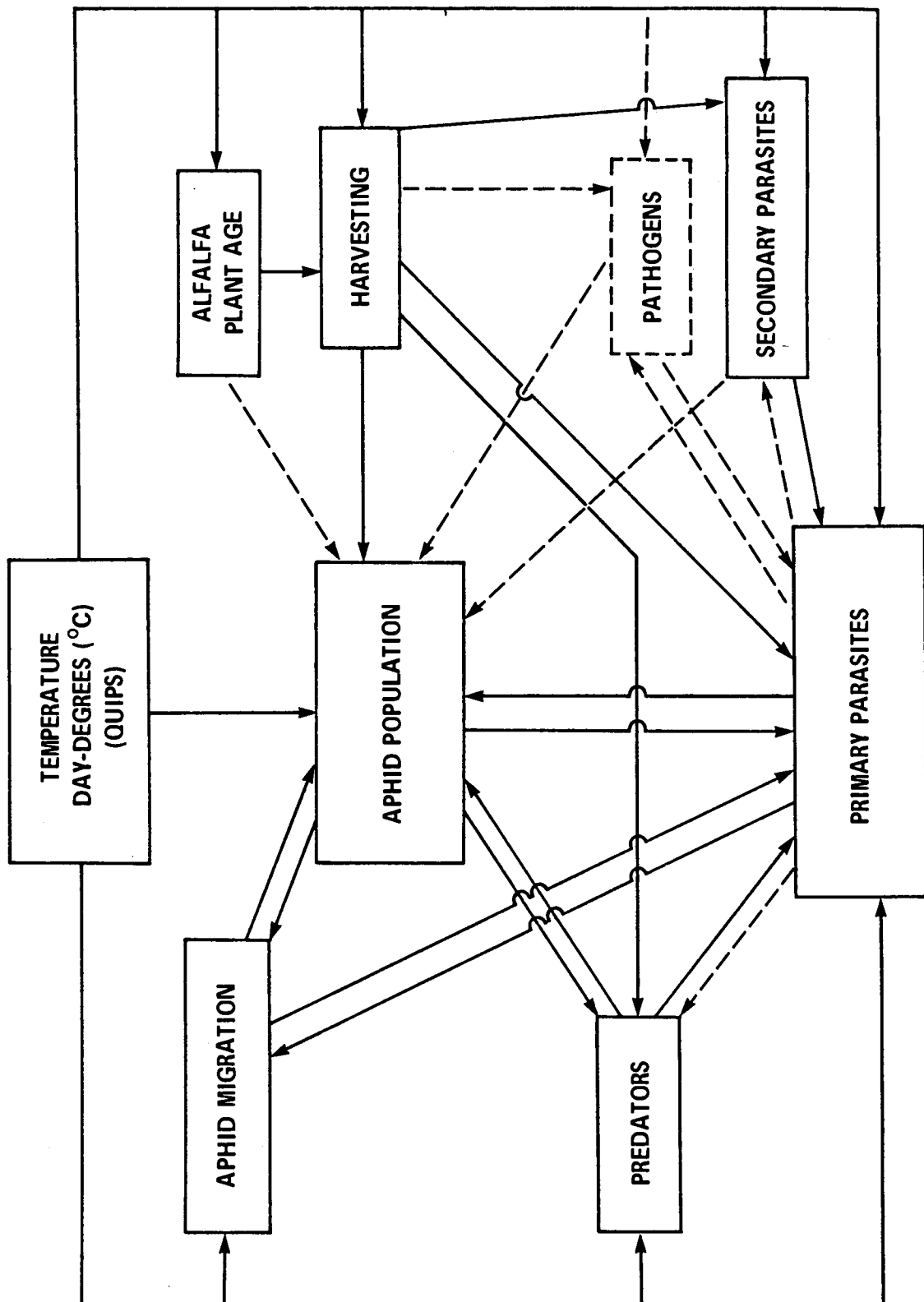
A. Introduction

The methods of analysis which are suitable for the study of the population dynamics of insects having discrete generations, such as the "key factor" analysis (Morris, 1959; Varley and Gradwell, 1960), are generally inapplicable to insects with overlapping generations (Varley and Gradwell, 1970). Only recently have first attempts (Hughes and Gilbert, 1968) to analyse aphid populations using computer models been made.

This chapter synthesizes all the relevant data obtained from the laboratory and field studies in a computer simulation model in an attempt to understand more fully pea aphid-parasite population dynamics in an alfalfa ecosystem. The model is an extension of the methods used by Hughes and Gilbert (1968), Gilbert and Hughes (1971), and Gilbert and Gutierrez (1973). The analysis is essentially descriptive, using known biology and life table characteristics of both the aphid and its three parasite species to calculate aphid and parasite population trends. Where detailed information was lacking on hyperparasite and predator biology, their activity was estimated from field data based on the field study made in Kamloops during the years 1971 and 1972. The model was built after all the data had been collected; thus, it is essentially a retrospective analysis organizing the data described in the preceding chapters into a workable simulated life system (Fig. 39).



Figure 39. General flow diagram of Kamloops alfalfa pea aphid-parasite model. (Solid lines are direct relationships; dotted lines are probable relationships which are not used in the model.)



## B. Materials and Methods

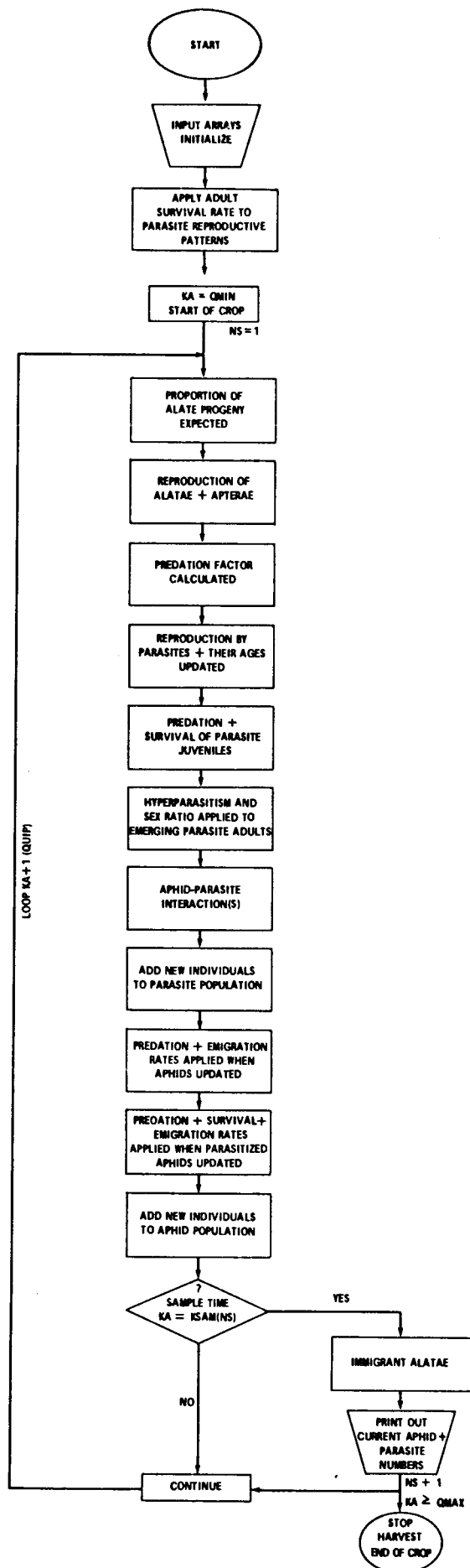
1. *Description of the Model.* The model (Appendix 7, Fig. 40) was written in basic FORTRAN IV language for use in the Simon Fraser University IBM 370/155 computer. The model is essentially deterministic as only averages were used, i.e. no estimation of biological variability was incorporated. It approximates continuous biological processes by a step by step calculation.

All data used in the model were obtained or calculated from the laboratory and field data presented in the preceding chapters. Some of the assumptions used were derived from the data and information obtained by other authors and are indicated as such. All values from the alfalfa tip samples (Appendix 4) were divided by 100 to give the average number of aphids, parasites, and predators per one alfalfa tip. Although the model represents an average alfalfa tip in fractional numbers, there should not be any difficulty in considering these population trends as occurring in an average alfalfa field.

The various input parameters used are incorporated in the model in the form of DATA statements. A glossary of the symbols and terms accompanying the basic model is shown in Appendix 7.

a) *The time-step length.* Real time in the field was converted into a physiological time scale (as described in Chapter V) of day-degrees above 5.56°C to remove the effects of temperature changes. Although the pea aphid and parasite developmental rates were different (threshold temperatures ranged from 5.56 to 6.88°C), the different physiological time scales calculated from the threshold temperatures were generally in constant

Figure 40. Flowchart of a digital computer programme to perform repeated simulations of a pea aphid-parasite biological system. Time is measured on a physiological time scale ( $KA = 1$  quip) during one alfalfa crop at Kamloops, B.C.



proportion during the growing season (Chapter V and Appendix 1). Thus, one basic time scale for all the insect species could be used. The model step length or basic time unit used was one "quip" (or a quarter-instar period) (Hughes and Gilbert, 1968; Gilbert and Gutierrez, 1973). It was calculated from pea aphid development periods in Chapter II (Tables IV and XIII). The model iterates at one-quip-period at a time. The various subscripts in the model denote time; i.e. (KA) is the physiological time in quips after the first of April, while (I and J) are ages of the insects measured in quips.

The various input parameters and values are initialized in the programme. One main DO-LOOP simulates the aphid-parasite-predator interactions over the season at one quip at a time (Fig. 40).

b) *The run length.* The model life system is limited in time to the average alfalfa growing season. Once the alfalfa starts growing in early April, it is capable of supporting the pea aphid fundatrices and adult parasites which emerge from diapause soon afterwards. In autumn (early October) the first heavy frosts kill the alfalfa top growth and the non-diapausing aphids and parasites. Thus the model can run during one season for about 340 quips. However, due to the disruptive effects of the harvesting and to changeable weather conditions, it was difficult to predict the number of aphids and parasites surviving from one crop to another. It was more convenient to initialize the appropriate number of aphids and parasites at the beginning of each crop and allow the model to run for one crop period, which could be up to 130 quips, rather than for the whole season.

The initial values of aphid and parasite numbers to start the programme were obtained from the first alfalfa tip samples of each crop. The initial

parasite species composition was obtained from the first mummy sample. The age and numbers of the parasites were backtracked by the appropriate number of quips to when the first alfalfa tip sample of the crop was taken.

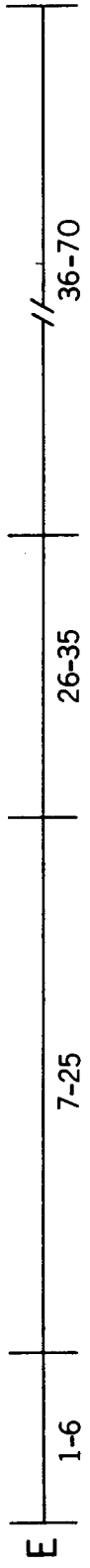
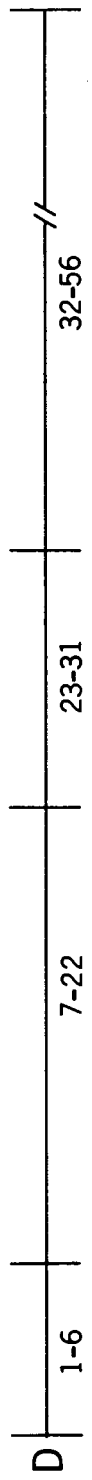
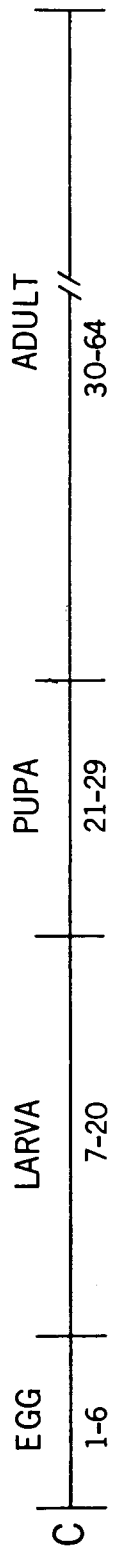
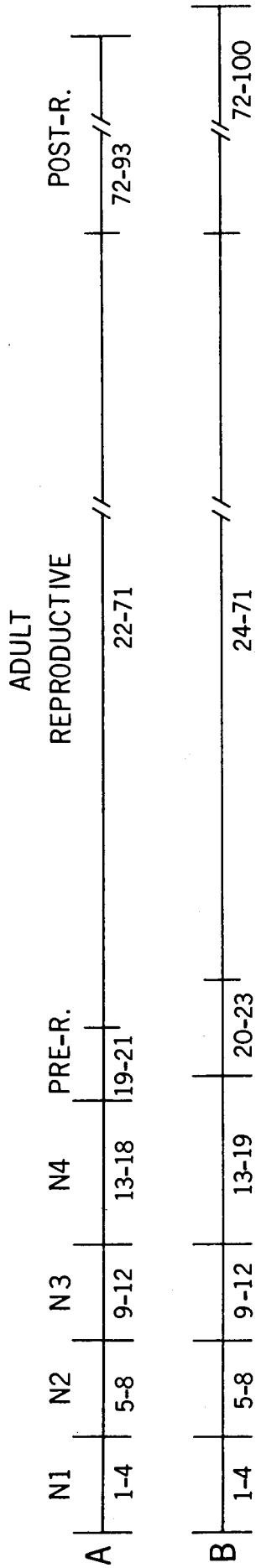
The model was set to print predicted calculations of aphid and parasite numbers at the appropriate periods when actual field samples were taken. Thus predicted values could be compared with the observed population trends.

*c) The pea aphid biology. i. Fundatrices.* All aphids were considered to be viviparous parthenogenetic females that were either winged (alatae) or wingless (apterae). In early spring the stem mothers (fundatrices) hatch from overwintering eggs and are the first pea aphids to feed on the alfalfa plant. In the model, the fundatrices were treated as apterae; because there was no data available on the biology of the fundatrices, they were assumed to have reproductive and developmental rates similar to that of apterous virginoparae.

*ii. Aphid development.* The mean duration of the various life stages of apterous and alate pea aphids are shown in Fig. 41. These data were calculated from the laboratory experiments described in Chapter II. The apterous and alate first, second, and third nymphal instar periods are four quips each, while the apteriform fourth instar takes six quips and the alatform fourth instar seven quips. The total pre-reproductive period takes 21 quips for apterae and 23 quips for alatae. The laboratory and field cage observations show that adult apterous and alate pea aphids can live for 75 and 81 quips, respectively. Unless killed by extrinsic mortality factors (such as parasitism), the apterous and alate aphids die of old age

Figure 41. The mean duration of the life stages of (A) apterous and (B) alate morphs of *Acyrtosiphum pisum* and its associated parasites, (C) *Aphidius smithi*, (D) *A. e. pulcher*, and (E) *Praon pequodorum*, on a physiological time scale. Age in quips: 1 quip = 6.2 day-degrees above 5.56°C. (N = nymphal instars; Pre-R = Pre-reproductive period; Post-R = Post-reproductive period.)





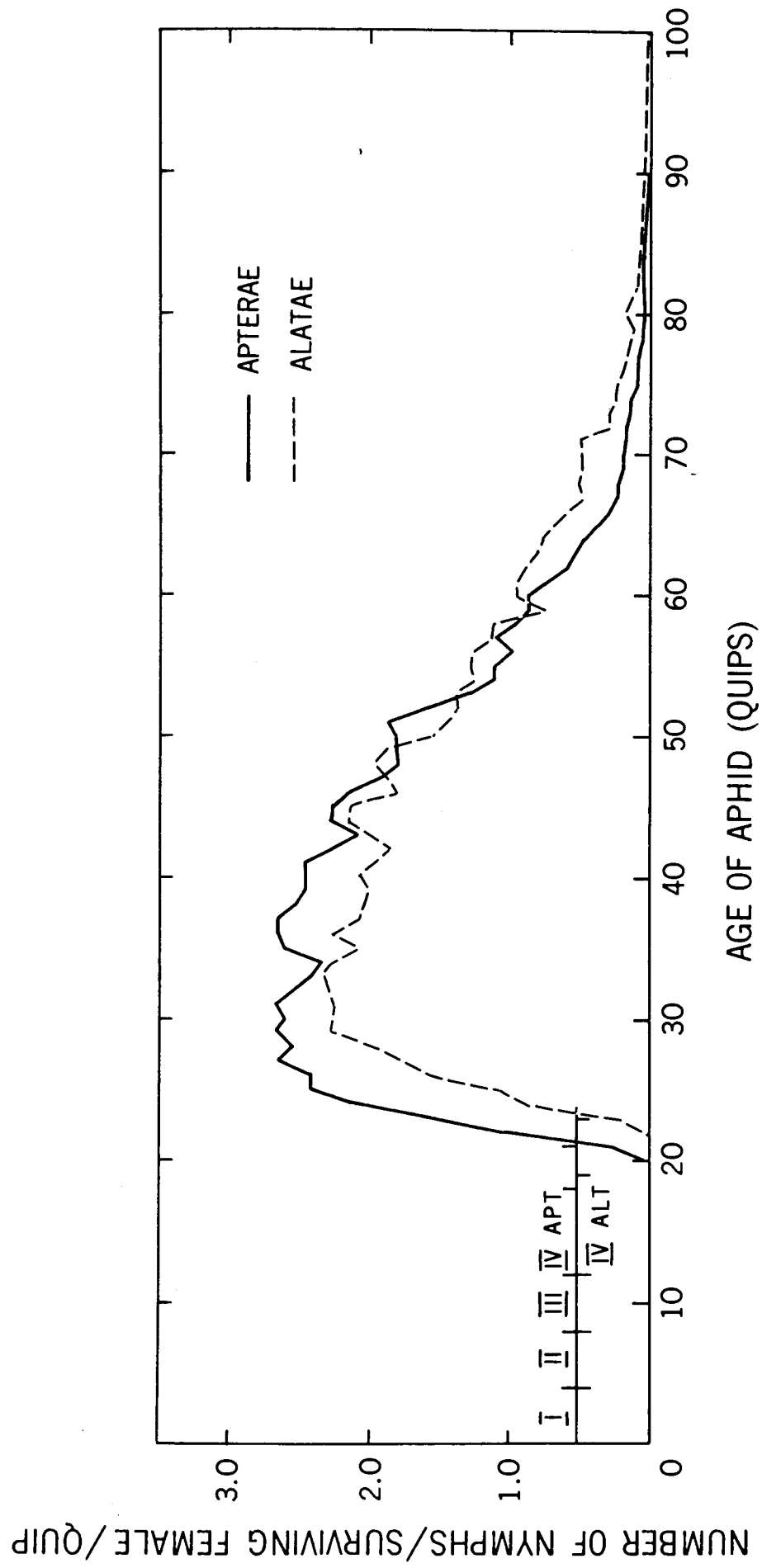
at quip 93 and 100, respectively. The two categories of aphid APTRA and ALATE give the current numbers of apterae and alate of known age (I) quips. The programme initializes these values with PSTART and ASTART which are read into APTRA and ALATE, respectively (line 33, Appendix 7) as the number of aphids of known age and morph at the beginning of a crop or the beginning of the programme run.

*iii.* Reproduction of the unparasitized aphids. Unparasitized aphid reproduction is achieved by multiplying together the current numbers of reproductive adults of age I with the age-specific pattern of reproduction of apterae and alatae called REPAP and REPAL, respectively (Fig. 42 and line 94 in Appendix 7). The predicted number of progeny produced by the fecund aphid age group is added to working sums A and AX in a DO-LOOP. The progeny AX produced by adult apterae can mature into alate or apterous morphs, but the progeny A produced by adult alatae can only mature into apterous adults. The total new progeny produced can not be added to the aphid population until (1) the progeny of parasitized aphids have been calculated (see next section), (2) the proportion of new progeny destined to be alatae have been calculated, and (3) the aphids in the population have been "updated" or increased in age by one quip. Thus, the newly produced progeny are not added to the aphid population until later in the model (line 222, Appendix 7) (Fig. 40).

*iv.* Development and reproduction of the parasitized aphids.

*General Statement.* Aphids that have been parasitized can continue to develop and produce progeny. However, to make parasitized adult apterae and alatae reproduce in the model requires a different

Figure 42. Mean age-specific pattern of reproduction and development of apterous and alate pea aphids, *A. pisum*, on a physiological time scale as used in the model. (1 quip = 6.2 day-degrees above 5.56°C) (roman numerals represent nymphal instars).



procedure (or "bookkeeping" method), although the simple principle of multiplying the current number of aphids capable of reproduction with the age specific reproductive pattern is still used. Parasitized apterae and alatae from ages 21 to 33 quips, containing parasite immatures from age 1 to 12 quips, remain fecund. Thus the total number of apterae or alatae in each age group with parasites aged 1 to 12 quips are summed with the working sums SP and SPAL from the PARA and PARAL matrices, respectively (line 100, Appendix 7). Once the number of reproductive parasitized aphids is known, the appropriate age specific reproduction is applied and the total progeny produced added to AX and A (line 102, Appendix 7).

*Detailed Statement.* Because parasitized aphids continue to develop and can reproduce, a record of these aphids had to be kept in a two-way table. PARA(I,J) and PARAL(I,J) were set up as two (41 x 20) matrices to keep a record of the number and ages of parasitized apterae and alatae, respectively. The numbers of parasitized aphids of ages I quips (i.e. 1 to 41) are recorded with parasite ages of J quips (i.e. 1 to 20) in these two matrices.

Although more than one parasite egg can be laid in an aphid, only one parasite adult will finally emerge from the mummy. The matrices PARA and PARAL assume a ratio of one parasite to one aphid. Although the numbers of each age of aphids parasitized were recorded in the matrices, the same numbers and ages of juvenile parasites in these aphids are divided into the correct proportions of each parasite species and recorded in the vectors SMITH, PULCH, PRAON. This means that the total numbers of parasite juveniles of each age are recorded in both the matrices PARA and PARAL and in these

vectors. The same survival rates and aging (or updating) are applied to both the vectors and matrices to keep the correct values in parallel.

Because the interrelationship of only *A. pisum*/*A. smithi* was studied (Chapter IV) and as no information is available on the effect of *A. e. pulcher* and *P. pequodorum* on pea aphid reproduction, we will assume in this study that all parasite species have the same effect on *A. pisum* reproduction as did *A. smithi* immatures.

To obtain data on the reproduction of parasitized aphids without complicating the computer programme the following method was used. Instead of using the age-specific fecundity patterns of parasitized aphids as noted in Chapter IV, the fecundity patterns of unparasitized aphids, REPAP and REPAL (which were already incorporated in the model), were used. The ages of the aphids when parasitized (X) and the total number of progeny produced (Y) before succumbing to parasitism were obtained from Chapter IV and are shown in Table XXI. The unparasitized apterous and alate pea aphid fecundity patterns (Fig. 42 or REPAP and REPAL in Appendix 7) were then consulted. By comparing the accumulated total progeny produced by a parasitized aphid (Y) with that of an unparasitized aphid (e.g. REPAP), the age of an unparasitized aphid producing the equivalent total progeny compared to a parasitized aphid (Y) could be determined (see Z in Table XXI). If the fecundity pattern of an unparasitized aphid is used to describe the fecundity of a parasitized aphid, a common cut-off point must be found. That is, it was found that at whatever age an aphid was parasitized it took approximately 12 quips for the parasite larva to stop aphid reproduction (i.e. using unparasitized fecundity patterns) (see (X-Z) in Table XXI).

TABLE XXI. The total progeny produced by parasitized aphids and the equivalent ages of unparasitized aphids producing the same total number of progeny (see text for explanation).

Aphid age when parasitized Days	Quips (X)	Mean total progeny produced per parasitized aphid (Y)	Age of unparasitized aphid producing equivalent total progeny as in Y (Z)	Equivalent period for unparasitized aphids (quips) before reproduction ceases (X-Z)
<i>APTERAE</i>				
4.0	9.22	0.11	20.5	11.27
4.4	9.88	0.57	21.5	11.30
5.0	11.51	2.00	22.3	10.98
6.0	13.69	7.64	25.0	11.30
7.0	15.98	16.40	28.5	12.52
8.0	18.26	23.09	31.0	12.73
9.0	20.55	24.86	31.5	10.95
10.0	22.83	31.00	34.5	11.67
				Mean 11.62*
				SE ± 0.24
<i>ALATAE</i>				
5.0	11.51	0.12	22.5	10.98
6.0	13.70	1.25	24.5	10.80
7.0	15.98	9.23	28.0	12.01
8.0	18.26	17.37	32.0	13.70
9.0	20.55	20.20	33.0	12.40
10.0	22.80	26.60	36.0	13.20
				Mean 12.20*
				SE ± 0.48

\* No significant difference between means ( $p = .05$ ) (t-test).

Using this method the reproductive pattern of a parasitized aphid is not exactly the same as that of a healthy unparasitized aphid. The difference is in the rate of progeny production; i.e. when the parasite matures, the fecundity of the parasitized aphid is cut off abruptly. The method produces results that are less accurate than when using the actual fecundities of the parasitized aphids; however, the accuracy lost is well within experimental error. The above method has the advantage of reducing the complexity of the computer programme and increases the efficiency of the programme running.

v. Proportion of alate progeny produced. The proportion of young aphids produced by apterae which develop into winged adults is called PROP. The value of PROP is determined by the population density affecting the adult apterae at time KA (line 86 in Appendix 7). PROP is expressed as a simple regression line calculated from the field data in Chapter V for each crop. The value of PROP is later applied (line 221 in Appendix 7) to the newly born progeny (AX) of the apterae and then added to the aphid population.

vi. Emigration and immigration of unparasitized and parasitized alatae. In the model all alate (ALATE) produced emigrated at age 21 quips. In the field probably a little over 80% of the alates produced that reached maturity emigrated from the field (Chapter V). The remaining 20% mature alates remained in the field, probably due to either parasitism or an inability to fly.

Migrant alatae have to be over the age of 21 quips to be able to fly (Fig. 41). However, as alatae mature their wing muscles autolyse, causing



the aphids to lose their ability to continue flying (Johnson, 1953). Thus, alatae are given an arbitrary three quips from age 21 in which to disperse or migrate from other fields and arrive in the study field at age 24 quips, after which they cannot fly.

It was not possible to distinguish between adult alatae that remained in the field after their birth and those that immigrated into the field from other areas. In order to eliminate the problem of deciding which alatae were resident or immigrant, it was assumed (for the purpose of the model) that all alatae found in the alfalfa tip samples were immigrants. To obtain the current number of adult reproductive alates in the model, the number of alatae found per tip in the alfalfa tip samples (Chapter V) were read into ALATE (24) at the appropriate sample time periods using ALIMM. The adult alatae of all other ages occurring previously to these additions were removed. Thus, all alatae produced in the field emigrate at age 21 quips and begin to reproduce normally. The numbers of immigrant unparasitized alatae at each sample period are stored in ALIMM and added to ALATE (24) at the appropriate KA time period.

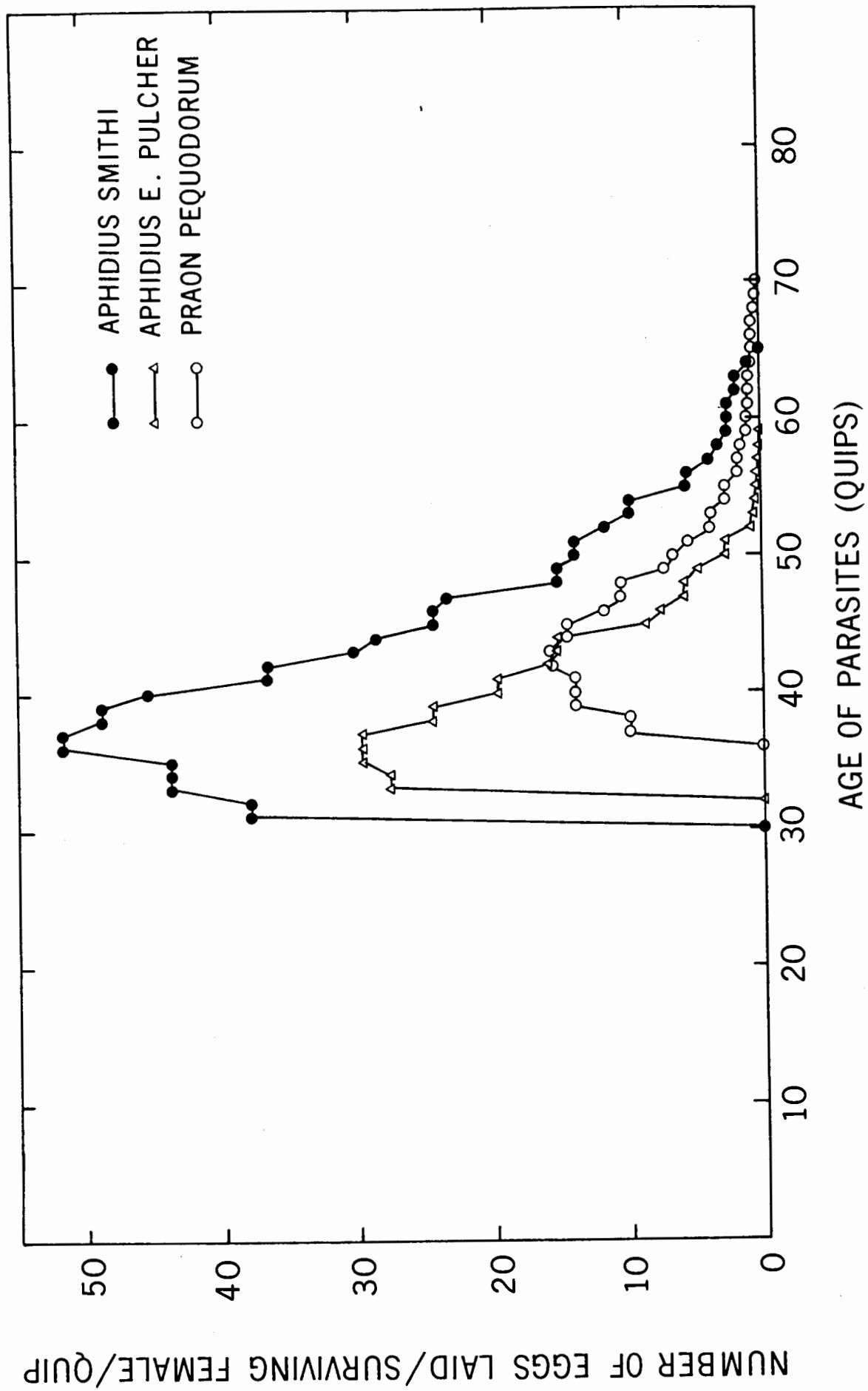
Parasitized alatae are treated in a slightly different way. All parasitized alatae of age 21 emigrate with the exception of those alatae that contain parasites aged 11 quips or older. Only alatae of age 21 with parasite immatures of ages 1 to 10 quips can emigrate. The juveniles of all three parasite species are assumed to have an equal chance of emigrating within the bodies of the alatae. Immigration of parasitized alatae is performed by recording the number of parasitized alatae (data from alfalfa tip samples) in PLIMM and entering these data into the PARAL(I,J) matrix at the appropriate sample time during KA (line 238, Appendix 7).

The numbers of immigrant parasitized alatae of age 24 (I) quips with parasites ages 4 to 13 (J) quips are evenly distributed into the matrix PARAL and each parasite species vector (line 239, Appendix 7).

d) *Parasite biology.* i. Parasite development. The average life history of each parasite species is shown in Fig. 41. The total development time from the deposition of an egg to parasite emergence was 30 quips for *Aphidius smithi*, 32 quips for *A. e. pulcher*, and 36 quips for *Praon pequodorum* (Fig. 41 and Chapter III). The data in Chapter III showed that the adults of *A. smithi* could survive up to 35 quips, *A. e. pulcher* for 25 quips, and *P. pequodorum* for 35 quips under laboratory conditions. The duration of individual egg, larval, and pupal stages of each parasite species were estimated from rough laboratory observations. On that basis the three parasite species categories SMITH, PULCH, PRAON were set up. These categories give the current number of each parasite species of known ages I quips. The categories are initialized with predetermined values in SMST, PUST, PRST (line 39, Appendix 7).

ii. Parasite reproduction. The reproductive patterns of each of the three parasite species are shown in Fig. 43. The original data (Dr. M. Mackauer, unpublished data) were calculated on a physiological time scale, using the specific heat developmental requirements (Chapter III) to produce the required age-specific reproductive patterns of each parasite species. The vectors RESM, REPU, REPR incorporate the laboratory reproductive and survival rates ( $m_x l_x$ ) as shown in Fig. 43 in the model for *A. smithi*, *A. e. pulcher*, and *P. pequodorum*, respectively (lines 10-12, Appendix 7).

Figure 43. Mean age-specific pattern of reproduction of three primary parasites on a physiological time scale (1 quip = 6.2 day-degrees above 5.56°C).



Parasite reproduction is achieved by multiplying the actual number of each parasite species of age (J) by the age-specific fecundity pattern (Fig. 43). The total possible number of eggs that can be laid for each of the three parasite species are then summed in TSM, TPA, TPR (lines 118-120, Appendix 7). These values are the potential number of eggs that each parasite species is trying to lay. The actual number of eggs laid is determined later in the programme (see section on aphid-parasite interaction).

*iii. Parasite survival. Immatures.* From the experimental data in Chapter IV aphids were found to be successfully parasitized between ages 3 to 22 quips. There was a lower proportion of successful mummification of aphids that were parasitized at an older age than for those parasitized at an earlier age (Fig. 14). To compensate for a lower proportion of aphids mummifying after being attacked at older ages and to apply a natural mortality factor to parasite immatures, an indirect method was used. All aphids attacked by parasites between ages 3 and 22 quips are assumed to be successfully parasitized. However, not all of these parasitized aphids will live or reach the mummy stage. By applying an arbitrarily chosen constant survival rate SK (which is equal to 0.97) to all parasitized aphids of age I for each seasonal time interval KA, the desired mortality rate of parasite immatures and their host aphid is calculated. This survival rate imposed on the parasite larvae makes the output results more realistic in terms of aphid-parasite field densities.

*Adults.* The survival of adult parasites in the field in terms of loss due to natural mortality, emigration, weather, and other factors were not measured in the field. However, an adult survival rate

was required to make parasite numbers and reproduction more realistic. Thus, adult survival was arbitrarily modified by introducing a per-quip survival rate for adult parasites, PASU. Parasite reproduction was modified by applying PASU to the original reproductive values expressed in RESM, REPU, REPR to new survival-reproductive ( $l_x m_x$ ) rates and assigned to RPSM, RPPU, RPPR, respectively. The application of PASU in effect changes the time pattern of egg laying by reducing the number of eggs laid/female/quip (lines 50-52, Appendix 7).

The value of PASU, 0.25, was chosen empirically. It reduces the mean total fecundity of 774 eggs per female of *A. smithi*, 316 of *A. e. pulcher*, and 199 of *P. pequodorum* (as observed under laboratory conditions) to 193.5, 79.0, and 49.75 eggs per female, respectively. This is a completely artificial estimation, expressing a biological effect in the field which is known to exist but was not measured.

It is possible that there is a difference in the emigration rates of each of the parasite species. For instance, *A. smithi* probably has a higher emigration rate than *P. pequodorum*. However, at present there is no evidence or data to quantify differential emigration; thus, an equal overall survival rate (PASU) was applied to all three species at the same time.

*iv.* Hyperparasitism and sex ratio of the primary parasites. A simple method to describe the mortality of primary parasites from hyperparasitism was used. The survival rates of the primary parasites from hyperparasite activity, HYPER, over a physiological time scale were measured directly from the mummy samples collected during each growing season in 1971 and 1972 at Kamloops. HYPER is expressed by equations which are solved

when (KA) the time of season is known; the equations are shown in Table XIX (and in lines 133-157, Appendix 7). All hyperparasite species are lumped together. It is assumed that each primary parasite species has an equal chance of being attacked by the hyperparasites. This assumption may not be entirely correct, as in the field some hyperparasite species may show specificity towards one or a few parasite species (Gutierrez, 1970). HYPER is applied as a survival rate at the appropriate time in the season to the numbers of parasites emerging from the mummies. Although a hyperparasite will take longer to emerge from a mummy than a primary parasite, this is not important because we are only interested in the actual number of primaries which will emerge (i.e. the mummies containing hyperparasites are eliminated as a mortality factor at the time of primary parasite emergence).

The sex ratio of each parasite species was calculated from the overall mean proportion of females emerging from all the mummy samples collected in the field (Table XVIII) during both years. The sex ratios are applied at the time of parasite emergence. Thus all parasite adults in the model are assumed to be females which have been mated at the time of emergence.

e) *Predation.* Predators were considered as a general mortality factor of parasite and aphid populations. From the field samples the numbers of the more important predators were obtained (Chapter V), while the overall predator voracities and developmental rates were determined from the laboratory studies and the literature (Appendices 2 and 3). To reduce the number of predator data statements in the model to a minimum, all predator types were converted to one total of equivalent predator numbers

according to their voracities (Chapter V, Fig. 23). All predator numbers were expressed in terms of the Coccinellid larval feeding rate of 9.6 aphids/quip, and the converted observed predator numbers were read into PRED(KA). The total demand for aphids or "voracity" by the predators for each time step KA is the product of the feeding rate (i.e. 9.6 aphids/quip) and the equivalent total number of predators observed in the field sample. All predators were assumed to search at random for aphids (Bänsch, 1966; Dixon, 1959; Murdoch and Marks, 1973; Schneider, 1969). The total predator demand for aphids is made proportional to the total number of aphids available to be eaten. The zero term of a Poisson distribution is used to determine the proportion of aphids escaping predation (Hughes and Gilbert, 1968). This proportion allows the predators to respond to changes in aphid numbers. The calculation of the predation factor is by no means an accurate representation of what actually happens in the field situation. However, this crude estimation of the predation rate utilizes all the relevant information that is available. Then the predation factor PREDN (line 104, Appendix 7) is applied to both parasitized and unparasitized aphids of all ages. If a parasitized aphid dies from predation, the parasite within the aphid also dies. The calculated predation rates are probably of sufficient magnitude to produce aphid and parasitized aphid mortality rates similar to those occurring in the field.

f) *Aphid-parasite interaction.* TSM, TPU, TPR are the total number of eggs which the total number of each parasite species, *A. smithi*, *A. e. pulcher*, and *P. pequodorum*, respectively, are trying to lay during the current time-step (KA). They were calculated (in the parasite repro-



duction section) from the numbers of adult parasites of various ages, SMITH(I), PULCH(I), PRAON(I), and their appropriate fecundity patterns, RPSM, RPPU, and RPPR, respectively. The total numbers of aphids in the current time step (KA) which are susceptible to parasite attack are:

(1) apterae and alatae (TN) between the ages 3 to 22 quips, and (2) newly parasitized aphids with parasite eggs of age 1 quip (TNP) (line 168, Appendix 7).

The parasite demand for aphids is made proportional to the total aphid population (TN, TNP) which can be parasitized. Because there is no specific information available on the searching behaviour of these parasite species in the alfalfa field, it is assumed that all three parasite species search for and find aphids at random. Thus the proportion of aphids which escape parasitism is determined as the zero term of a Poisson distribution (Hughes and Gilbert, 1968) (lines 170-172, Appendix 7). SSM, SPU, and SPR are the survival rates of the aphid population after being attacked by *A. smithi*, *A. e. pulcher*, and *P. pequodorum*, respectively. The rest of the programme section (lines 173-178, Appendix 7) uses these survival rates to calculate the numbers of new aphids parasitized, aphids surviving parasitism, and the new individuals of each parasite species to be added to the aphid and parasite population.

g) '*Aging*' or *updating of aphids and parasites*. For each time step (KA) the programme advances the parasitized and unparasitized apterae and alatae and the three parasite species by one unit of age or by one quip. The method used starts with the oldest age-groups and works downwards, using a direct loop (e.g. controlled by lines 191-198, Appendix 7) instead of

a DO statement. The programme then adds the newly born aphids from the calculated aphid reproduction to the youngest age group ( $I = 1$ ). The appropriate proportion of young alates and apterae are entered by using the previously calculated value of PROP (lines 221-223, Appendix 7).

The rest of the programme essentially consists of bookkeeping; updating the aphids and applying the various mortality factors or survival rates, such as predation and emigration and adding new aphid progeny (previously calculated) to the appropriate vectors or matrices (Fig. 40).

The DO-LOOP iterates over a number of time-steps (KA) (Fig. 40) until the maximum value of KA is reached, when the programme terminates.

*h) Print-out.* At the end of each iteration in the programme, if the time in the season KA is equal to the time of a field sample, an IF statement directs the programme to print out the current predicted aphid and parasite population values (Fig. 40). The observed immigrant alatae are also added to the aphid and parasite population at this time.

Each aphid stage and morph is totalled and printed out. Only the third instar or older aphids that are parasitized are shown (to correspond to observed field data dissections). Only parasite juveniles older than 3 quips are considered because very young parasite eggs of 1 to 3 quips probably were not detected with accuracy in the field samples.

The following is a list of the data provided in the print-out:

1. Total number of aphids.
2. Numbers of each aphid stage and morph.
3. Proportion of first instar aphids to become alatae.
4. Total number of parasite larvae.

5. Total number of parasite mummies.
6. Proportion of parasitism; parasite larvae and/or mummies included.
7. Species composition of parasites from the total number of mummies.
8. Proportion of aphid population mortality due to predation.

### C. Results

When the model was first run, it gave unrealistic answers, and the predicted population trends of both the aphid and parasites did not compare well with the observed field data. After a number of adjustments in the "scaling" of the initial input parameters and assumptions, the model began to produce reasonably realistic population predictions. Table XXIII gives an example of the type of print-out produced by the model. The table compares the actual aphid and parasite numbers observed in the alfalfa tip samples with the predicted values from the model for the period of the first crop during 1972. The predicted values generally agree with the observed changes in aphid and parasite numbers and stages. The following sections give an account of the adjustments made to the model and the important characteristics of the model's simulation of an aphid-parasite system.

1. *Input Parameters.* a) *Aphids.* The initial values (i.e. aphid numbers and age structure) used in the model were obtained from the first sample of each crop. In the model, for crop 1, 1972, it was found that some additional adult apterae had to be added to the initial values (Table XXIII) to produce the desired population growth rate. This suggests that there was a sampling error or some inconsistency in the field samples, as

TABLE XXIII. ACTUAL FIELD DATA COMPARED WITH PREDICTED DATA FOR CROP 1, 1972.

CROP I	FIELD DATA FROM ALFALEA TIP SAMPLES																				
	APHIDS/TIP					PARASITES/TIP					PREDATORS										
	NI	N2	N3	AP4	AL4	APT	ALT	TOTAL	TOTAL LARVAE	TOTAL MUMMIES	PER1	PER2	PER3	PER4	PER5	PER6	PER7	PER8	PER9	PER10	
4	0.016	0.012	0.004	0.000	0.000	0.000	0.000	0.032	0.001	0.000	0.250	0.250	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
11	0.050	0.016	0.004	0.000	0.000	0.000	0.000	0.136	0.032	0.000	0.800	0.800	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
17	0.132	0.064	0.012	0.020	0.000	0.024	0.000	0.252	0.035	0.000	0.714	0.714	0.360	0.640	0.000	0.000	0.000	0.000	0.000	0.000	0.000
25	0.072	0.048	0.048	0.056	0.008	0.024	0.000	0.256	0.040	0.000	0.294	0.294	0.710	0.289	0.000	0.000	0.000	0.000	0.000	0.000	0.000
33	0.587	0.117	0.040	0.040	0.007	0.103	0.020	0.890	0.040	0.003	0.211	0.224	0.892	0.041	0.068	0.018					
42	0.600	0.365	0.360	0.140	0.065	0.160	0.015	1.705	0.405	0.150	0.547	0.556	0.565	0.109	0.326	0.021					
57	0.170	0.260	0.440	0.455	0.300	0.085	0.005	1.715	0.860	0.145	0.669	0.703	0.626	0.335	0.035	0.032					
73	1.095	0.255	0.265	0.220	0.110	0.245	0.070	2.260	0.245	0.165	0.269	0.381	0.836	0.147	0.017	0.041					

CROP I	PREDICTED DATA FROM MODEL																			
	APHIDS/TIP					PARASITES/TIP					PREDATION									
	NI	N2	N3	AP4	AL4	APT	ALT	TOTAL	TOTAL LARVAE	TOTAL MUMMIES	PER1	PER2	PER3	PER4	PER5	PER6	PER7	PER8	PER9	PER10
4	0.016	0.012	0.004	0.001	0.000	0.006	0.000	0.039	0.000	0.002	0.000	0.182	0.182	0.000	0.000	0.000	0.000	0.000	0.000	0.000
11	0.082	0.024	0.013	0.009	0.000	0.006	0.000	0.133	0.12	0.022	0.000	0.809	0.809	0.000	0.000	0.000	0.000	0.000	0.000	0.000
17	0.126	0.045	0.071	0.018	0.000	0.012	0.000	0.272	0.22	0.041	0.001	0.412	0.418	0.367	0.633	0.000	0.000	0.000	0.000	0.000
25	0.033	0.031	0.118	0.086	0.006	0.026	0.000	0.299	0.24	0.036	0.007	0.154	0.180	0.981	0.019	0.060	0.061			
33	0.224	0.037	0.016	0.021	0.007	0.089	0.001	0.396	0.26	0.020	0.012	0.148	0.220	0.803	0.161	0.036	0.096			
42	0.483	0.327	0.131	0.024	0.007	0.055	0.016	1.029	0.39	0.068	0.003	0.289	0.298	0.594	0.142	0.263	0.045			
57	0.506	0.346	0.325	0.260	0.172	0.208	0.029	1.856	0.47	0.242	0.013	0.243	0.253	0.778	0.189	0.033	0.033			
73	3.105	2.106	1.237	0.434	0.414	0.542	0.104	7.901	0.66	0.305	0.062	0.112	0.131	0.888	0.099	0.013	0.012			

N = NYMPHAL INSTARS; AP + APT = APTERAE; AL + ALT = ALATAE; PER1 = PROPORTION PARASITE LARVAE/ TOTAL APHIDS (9 QUIPS OR OLDER); PER2 = PROPORTION OF PARASITE LARVAE + MUMMIES/TOT APHIDS + MUMMIES; PER3 = PROPORTION OF EACH PARASITE SPECIES/TOTAL NUMBER OF MUMMIES; SMITH = A.SMITHI; PULCH = A.E.PULCHER; PRAON = P.PEQUODORUM; PROP = PROPORTION OF ALATE PROGENY

they did not detect all adult aphids in the field at quip 4 but did at quip 11 (Table XXIII). The model says that aphid nymphs at quip 4 could not have developed into adults until after quip 11. It should be noted that the adult aphids in quips 4, 11, 17 (shown as apterae in Table XX) are actually fundatrices. Indeed, if we reject the possibility of a sampling error, the model suggests that the immature fundatrices probably have a lower developmental temperature threshold and could develop faster than immature virginoparae during the spring.

In most runs of the model, however, the use of the aphid numbers and age structure of the first samples of each crop as initial values to predict aphid population growth were generally quite adequate (Fig. 46).

The predicted number of alate fourth instars generally agreed with the observed values (e.g. see AL4 and PROP in Table XXIII). In the model, most alatae reaching maturity emigrated from the field. However, if the model was changed so that no alatae were allowed to emigrate and/or there was an increase in the number of immigrant alatae, the model would predict a tremendous aphid population increase. Any detailed simulations of the effect of changes in alate production and migration on aphid and parasite populations (such as described by Gilbert and Hughes, 1971) were not considered to be in the scope of this thesis.

b) *Parasites*. The initial parasite numbers used were reasonably accurate in predicting the percent parasitism rates actually experienced in the field. Although the actual initial numbers and ages of parasite immatures could be calculated from the alfalfa tip samples, it was difficult to decide which initial density of parasite adults should be used. In

addition, some adults of each parasite species had to be present at the start of the programme run to prevent the occurrence of wild fluctuations in parasite numbers. However, no accurate estimation of adult parasite density from the field samples data was available. To overcome this problem an indirect approach was used. An arbitrary estimation of the number of parasite adults was used so that the correct percent parasitism rates of at least the first and second sample periods in the crop were obtained. Equal numbers of adults of each parasite species were always used as initial values, although the adult ages of each parasite species were varied occasionally (lines 19 to 21, Appendix 7). This method worked well for most runs (e.g. Table XXIII).

Table XXIII shows that the predicted percent parasite species composition of the total mummies generally agreed with the observed values. The changes in parasite species abundance (discussed in detail in Chapter VI) during the spring were attributed to discrete generations occurring as shown in the model (Table XXIII). In the later crops there were generally more *A. smithi* mummies being produced. This suggested an overlapping of generations which was achieved in the model by having a large number of all stages of adults and immatures being produced at the same time. In the field the discrete generation effect was probably continually diffused (especially early in each crop) by the continual dispersal of parasite adults from one alfalfa field to another. Although I have no data to support this assumption, van den Bosch *et al.* (1966) have found large numbers of *A. smithi* females moving from one field to another.

c) *Predators*. The same predation rate was applied to both parasitized and unparasitized aphids. Aphid mortality due to predation ranged from 0.0 to 30% (e.g. Table XXIII) of the total aphid populations throughout both years, which was generally not as high as the parasitism rates which on occasion reached over 80% of the aphid population. The combination of both predation and parasitism rates were important in reducing aphid populations.

When the predation rate was extremely severe, there were few aphids and an overabundance of predators such as in crop 1, 1972, and the first few samples of crop 3, 1971. In these cases the observed equivalent predator totals in combination with the high feeding rates of 9.6 aphids/quip and low aphid densities caused the aphids to go extinct. Under these circumstances it was obvious that the model overestimated predator activity. The actual number of predators per tip, as determined by the field samples, could not be changed as the observed field data were assumed to be reasonably accurate. Rather the feeding rate of the Coccinellids was probably overestimated. Thus, the feeding rates were reduced from 9.6 to 2.0 aphids/quip to achieve a realistic aphid population trend. It should be noted that when there were high aphid densities and high predator numbers (e.g. crops 2 and 3 in 1971), the aphid population managed to survive without requiring any changes to predator voracity.

It is surprising that the Coccinellids reproduced in the field during spring, 1972, when there were low aphid numbers, while the Coccinellids did not reproduce in spring, 1971, when there were higher aphid numbers (Appendices 4, 5). Indeed, the effect of the predators on the aphid popula-

tion is little understood, especially when considering factors such as the searching behaviour of the various predator species and their ability to feed on alternative prey when aphid numbers are low in the field.

2. *Parasite survival and reproduction.* One of the problems of "scaling", or obtaining predicted aphid and parasite population values that correspond to the observed field data, was deciding on the correct reproductive capacity of the parasites. If the parasites were allowed to lay their full complement of eggs, the aphid populations were unable to cope with such high mortality pressures and became extinct. Thus, a low survival rate (PASU) was applied to the parasite reproductive rates (Fig. 44) to reduce parasite pressure on the aphid population.

By applying various survival rates (PASU) to the parasite reproductive rates (Fig. 44) and observing the changes in aphid population numbers, the correct value of PASU could be estimated. To illustrate this method of "scaling" I have used the same input values and parameters already described for crop 1, 1972 (Table XXIII and Appendix 7). The only values changed were the parasite survival rates starting at 0.05 and incremented by 0.05 up to 1.0. The criterion used for parasite success in suppressing the aphid population was the total number of aphids per tip at the end of the crop. The effect of changing PASU on the aphid population at the end of the crop 1, 1972, is shown in Fig. 45. (N.B. Consider only the curve described as "partial discrimination" in Fig. 45 for the present; parasite discrimination is discussed later in this section.) With an increase in the survival rate there is an increase in the parasite reproductive capacity (Fig. 44), causing higher mortality in the aphid population (Fig. 45). When PASU



Figure 44. A comparison of the total fecundity of three parasite species of the pea aphid when a survival rate (PASU) is applied to the parasite adult reproductive rates.

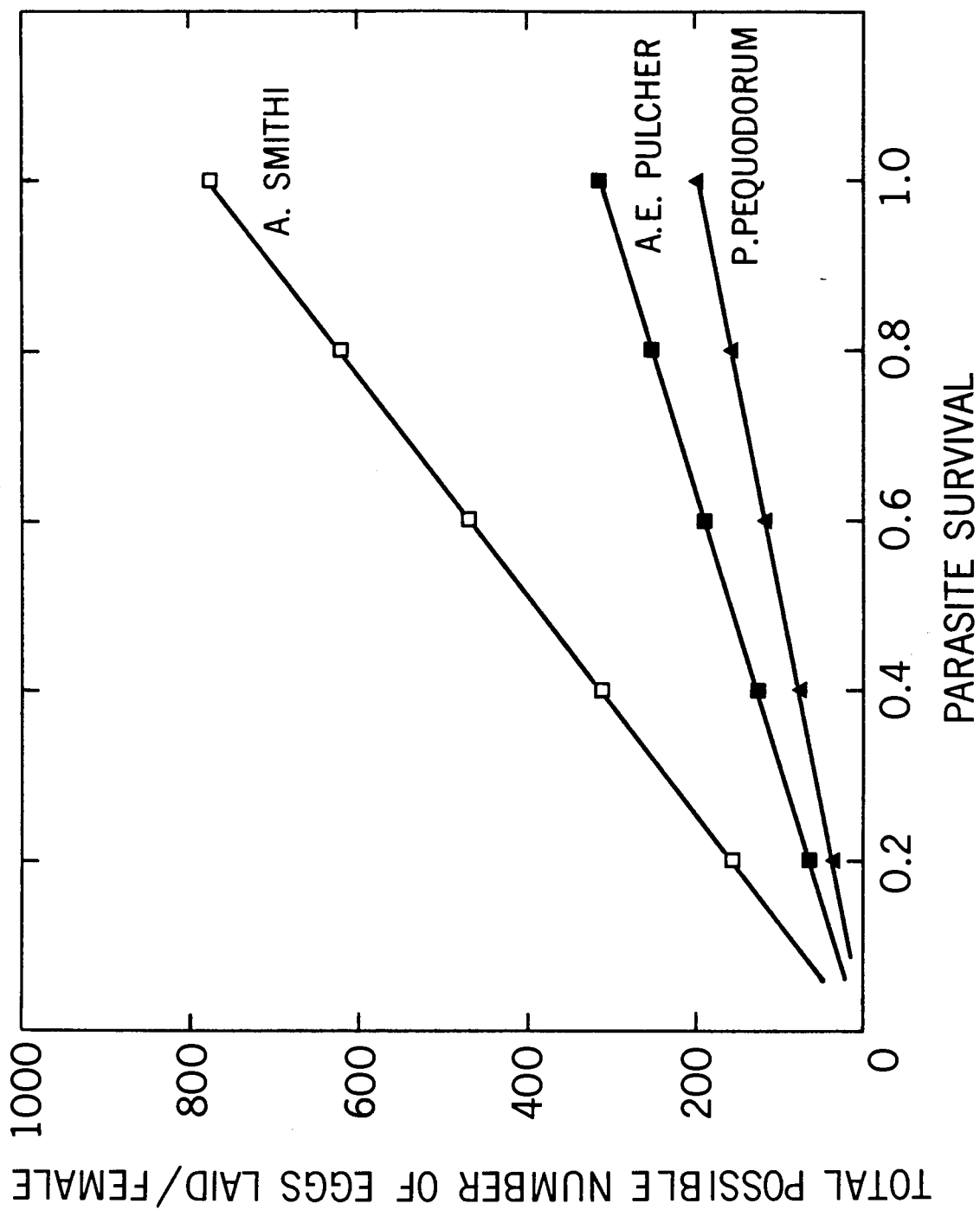
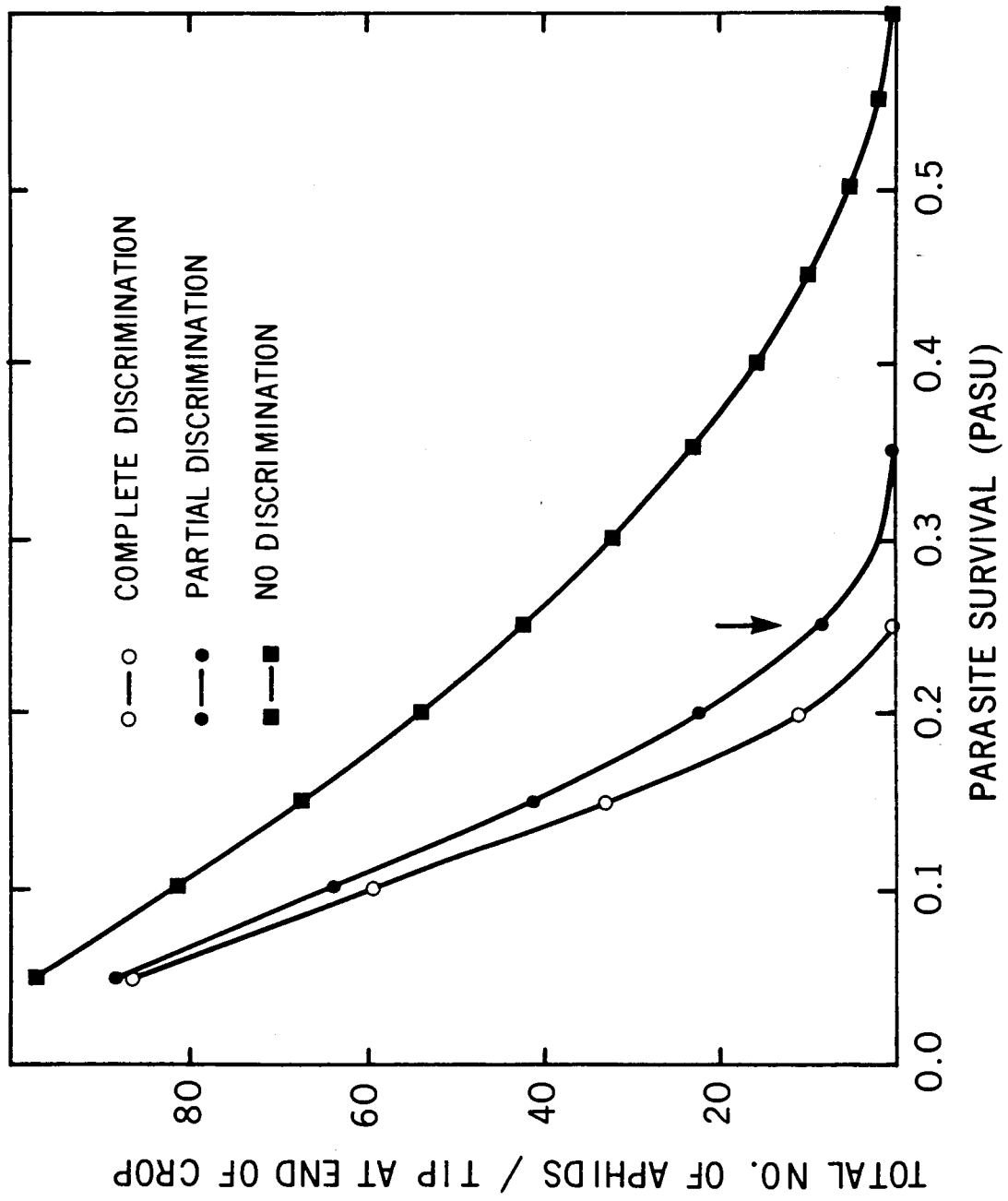


Figure 45. The effect of changing the parasite survival rates (PASU) on the total aphid population at the end of crop 1, 1972. (All initial values used are shown in Table XXIII and Appendix 7.) Complete discrimination = only unparasitized aphids of age 3 to 22 quips attacked by parasites; partial discrimination = only unparasitized and parasitized (parasite age 1 quip) aphids of age 3 to 22 quips attacked; no discrimination = all aphids, whether parasitized or not, attacked. Arrow denotes the value PASU (0.25) which was used to obtain the total aphid population (i.e. 7.9 aphids/tip) at the end of crop 1 (or quip 73) in Table XXIII.



reaches 0.35 the parasites become too fierce, causing the aphid population to become extinct at the end of the crop.

The value of 0.25 for PASU (see arrow in Fig. 45) was found to be the best parasite survival rate to approximate the predicted number of parasite and aphid individuals with the observed data (Table XXIII). In nature, however, this high mortality of parasites may not be a death rate as such, but rather may mean that the parasite females (1) have a high dispersal rate; (2) waste time searching for hosts; or (3) are unsuccessful in their attacks after host location (discussed further in a later paragraph). Also, Mackauer (1973) has suggested that parasite females may waste eggs by ovipositing into unsuitable hosts.

Comparing the effect of PASU (i.e. 0.25) on the reproductive rates of the different parasite species reveals that although *A. smithi* is contributing far less of its potential number of eggs, it still contributes more eggs than *A. e. pulcher* and *P. pequodorum* (Fig. 44). *A. e. pulcher* would require a 0.63 survival rate and *P. pequodorum*, that of 1.00, to produce as many eggs as *A. smithi* at a survival rate of 0.25. Indeed, by starting all parasites at equal numbers and allowing the model to run for a whole season (350 quips) (without harvesting disruptions and assuming continual aphid population growth), it was found that although the differences in parasite developmental rates caused proportional changes in numbers of the three parasite species, the differences in fecundity were by far the most important factor in making *A. smithi* the dominant parasite.

Although multi- and super-parasitism was not common in the field during 1971 and 1972, it did occur during spring 1972 when there were a large

number of parasites and few aphids. When more than one parasite egg is laid in an aphid, it is the oldest parasite immature, especially if it is more than 1 quip older than the others, that eventually matures and emerges as an adult; the younger parasite immatures are eliminated by the oldest parasite larva (M. Mackauer, pers. comm.). Thus, multi- or super-parasitism essentially results in a wastage of parasite eggs as only one adult emerges.

In most runs of the model it was assumed that the parasites partially discriminate between parasitized (aphids with parasites of age 1 quip) and unparasitized aphids between the ages 3 and 22 quips. Figure 45 shows what happens to the aphid population at the end of crop 1, 1972, when PASU changes and when parasites are completely discriminatory or, alternatively, do not discriminate at all between parasitized or unparasitized aphids. (N.B. Parasites that do not discriminate can attack all aphids in the population, but only unparasitized aphids between ages 3 and 22 quips can be parasitized and produce offspring successfully.) Parasites that can completely discriminate were more efficient in utilizing their available eggs and were more "fierce" on the aphid population than the parasites that only partially discriminated (Fig. 45).

Parasites that attacked all aphids indiscriminately and laid eggs into them did not reduce the aphid population as rapidly as those parasites that could discriminate (Fig. 45). Although parasites that attacked all aphids wasted many of their eggs in aphids that had already been parasitized or that were unsuitable (i.e. younger than 3 quips or older than 22 quips [Chapter IV; Mackauer, 1973]), these parasites could still reduce the aphid

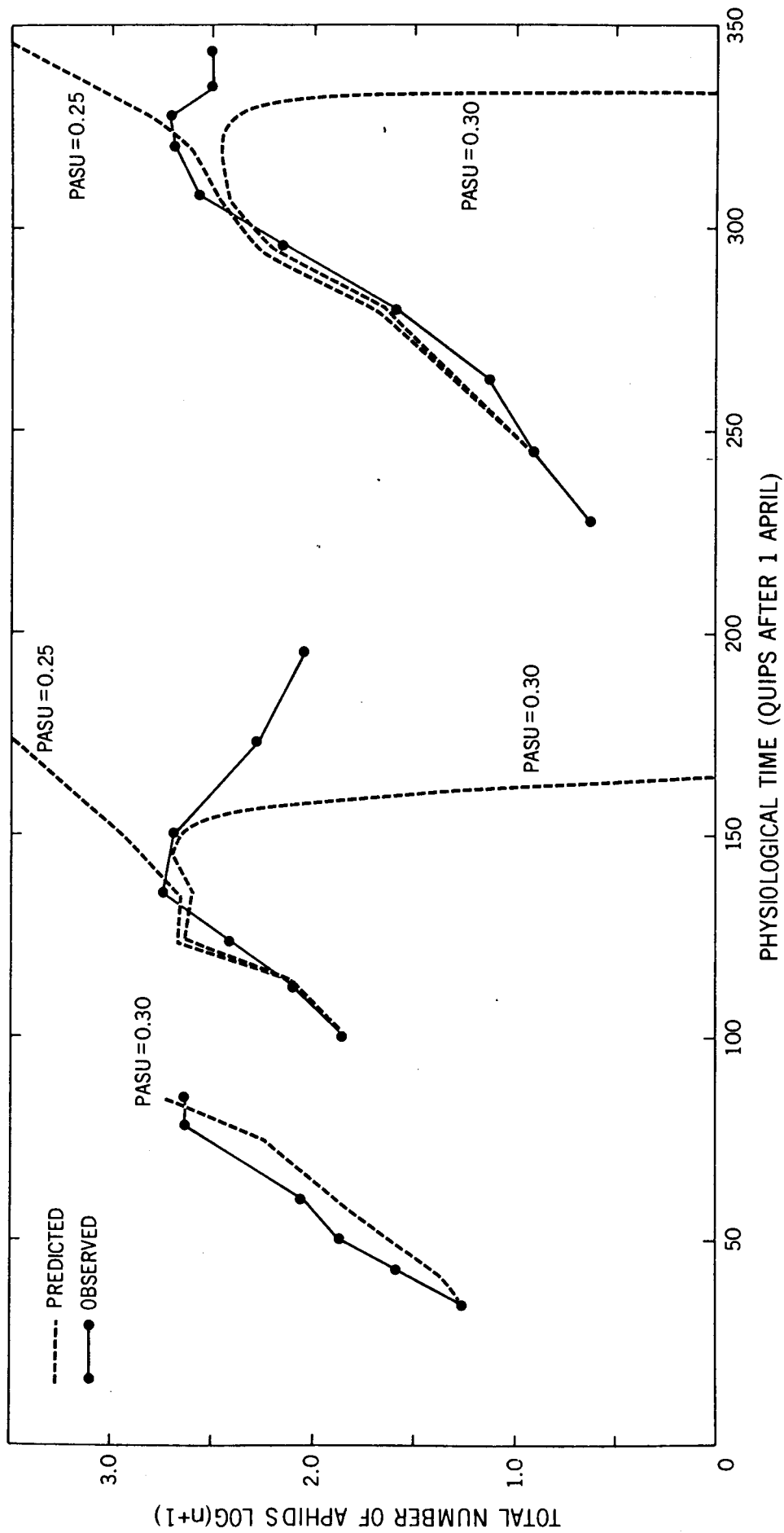
population to extinction without utilizing their full complement of eggs (i.e. when PASU = 0.6, Fig. 45). Indeed, to obtain the same level of control of the aphid population at the end of crop 1, 1972, by parasites that do not discriminate as compared to those parasites that partially discriminate (when PASU = 0.25), the survival rate (PASU) would have to be 0.465 (Fig. 45). By increasing the reproductive rate (or PASU) the parasites that do not discriminate essentially compensate for the egg wastage in unsuitable hosts.

3. *Prediction of the aphid population trends.* Figure 46 shows the predicted curves of the total aphid population and observed population trends in the field during 1971. The predicted growth phase of the aphid population generally agrees with the observed aphid population increases. However, when the aphid density tends to level off, the model predicts that two possibilities exist. The first is that aphid mortality due to parasitism can cause the aphid population to crash to such a low level that the aphid population will not recover. The second is that there are just enough aphids maturing to the reproductive stage in the population to overcome the control imposed by the parasites (and predators) and cause the aphid population to resume uncontrolled growth.

By changing the parasite survival rate (PASU) between values 0.3 and 0.25 (an even finer adjustment can be made), the number of eggs that the parasites will lay is also changed and in turn the number of aphids that survive is changed (Fig. 45). The model is sensitive to changes in parasite survival which affect the value of the exponent, i.e. the zero term of a Poisson distribution. Changing the value of the exponent by .01 can

Figure 46. A comparison of the predicted aphid population trends with those observed in the field samples. (PASU = proportion of adult parasite survival.)





make the difference between an aphid explosion or an aphid population to go extinct. Perhaps the main reason for this is the lack of a feed-back in the model between the parasites and aphids.

The model predicts that the parasites can cause the aphid population growth to stop and decline rapidly to a point where the aphids cannot recover; while in fact, in the field situation the aphid population can be reduced by parasites, but the decline is neither as rapid nor do aphids reach such low densities. Thus, the results of the model become suspect in any further analysis of prediction. Until the correct parameters which help to stabilize the system are found one cannot expect to use the model to predict the number of parasites or predators required to "control" the aphid population.

#### D. Discussion

In the present study the model described the parasite-aphid population interactions as realistically as the available data permitted. As in many population models described to date, there are a large number of components which are included, but also many that are omitted. This model is reasonably faithful in describing the life table characteristics such as the developmental and reproductive features of the aphid and parasites involved. However, the model is deficient in a number of features of the pea aphid-parasite life system which would help to make the model a useful predictive tool. Perhaps the more important components which are missing are those that determine the initial aphid and parasite numbers in the spring (i.e. the effect of weather on the overwintering insects) and the parameters of aphid-predator and aphid-parasite behavioural interactions which help to

stabilize the system.

The zero term of a Poisson distribution alone was found to be inadequate to explain aphid-parasite interactions in this model. The formula was found to be adequate in other models (Hughes and Gilbert, 1968; Gilbert and Gutierrez, 1973) because the parasite species involved did not really affect aphid mortality, let alone "control" the aphid populations. Hughes (1963) found that *Diaeretiella rapae* only parasitized up to a maximum of 20% of *Brevicoryne brassicae* populations at any one time in Australia. Indeed, *B. brassicae* reached peak densities of over 4,000 per plant, and it was only due to intraspecific controls that the cabbage aphid population tended to stabilize (Hughes and Gilbert, 1968). In this study, pea aphid populations reached maximum densities of only 5.6 aphids per stem (i.e. approximately 224 aphids per plant if one assumes about 40 stems per plant), and parasitism rates reached values of over 80%. Both the field study and the model suggest that certain parasites can "control" aphid populations, but the mechanism by which this "control" is achieved is not as yet known.

It is assumed in the model that all parasites search for aphids in the field at random (see Rogers, 1972). However, the model does not explain why parasites cannot find all aphids in the field. The model assumes that the aphids that survive after each iteration have an equal chance of being parasitized in the next iteration. However, in the field these assumptions probably do not apply (see below). The equations to describe these interactions are thus unavoidably simplistic. Indeed, the exponent used in this study to describe parasite searching is similar to Thompson's (1924)

formula<sup>13</sup> which assumes: (1) random attack; (2) parasites can always find their hosts, but are limited by their egg supplies; and (3) the whole outcome of searching behaviour of the parasites depends on a single constant (i.e. the number of eggs laid by a parasite) (Rogers, 1972). Hassell and Rogers (1972) discuss the recent advances in the development of mathematical models that describe insect parasite searching behaviour. They show that recent models have included additional parameters to describe insect parasitism: (1) the functional response to host density (Holling, 1959, 1966); (2) the response to changes in host distribution (Hassell, 1966); and (3) the response to other parasites (i.e. the interference component) (Hassell and Varley, 1969). It should be remembered, however, that these are not population models as such, but rather components useful within main host-parasite models.

Hassell and Rogers (1972) have used the above different responses in simple population models to analyse their effect on the stability of host-parasite interactions. They found "of these responses only aggregation of the parasite population in regions of high host density and interference between the searching parasites" contributed to the stability of these host-parasite interactions. It is unfortunate that, in this study, a more precise measurement of the adult parasite density in the field was not obtained, because the "interference"<sup>14</sup> component could have been incorporated

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<sup>13</sup>  $H_{ha} = H (1 - e^{-\frac{H_a}{H}})$  where:  $H$  = number of hosts;  $H_a$  = GP or number of attacks on  $H$  hosts by  $P$  parasites;  $H_{ha}$  = number of hosts parasitized by  $P$  parasites;  $P$  = number of parasites;  $G$  = eggs laid per parasite.

<sup>14</sup> The interference component in Hassell and Varley's (1969) model can be easily tested from field data, provided that the adult parasite density and the percentage of parasitized hosts are known.

in the model. Although an "interference" component may have contributed to the stability of the host-parasite interactions, it may not necessarily have improved the accuracy of the model's predictions.

The exact features which allow a parasite and its host population to fluctuate within upper and lower limits without both parasite and host becoming extinct are still not completely understood. Mackauer (1973) has shown that *Aphidius smithi* females prefer for oviposition second or older instars of the pea aphid, although the second instar appears to be the optimally suitable host. He suggests that by having a "tolerable degree of flexibility in host selection the probability of persistence is increased" in a parasite such as *A. smithi*. The apparent stability in aphid-parasite interactions may well be the result of the parasites not having a rigidly narrow specialization in the selection of host stages, but rather a flexible host selection with the ability to absorb minor host changes (Mackauer, 1973).

One possible explanation for the model not achieving some degree of stability during the aphid-parasite interactions is that some aphids may have a smaller chance of being parasitized than other aphids and some aphids may escape parasitism even after being attacked. In this study changes in aphid distribution were not studied. However, Forsythe and Gyrisco (1963) found that the spatial pattern of pea aphid populations was generally contagious in spring and late summer but randomly distributed in mid-summer. They found that "the presence of parasitized and alate aphids had little apparent effect on the aphid spatial pattern form." In contrast, Tamaki *et al.* (1970) have shown that *A. smithi* could cause the dispersal and re-

duction of colonies of pea aphids in a greenhouse situation. The pea aphids disturbed by *A. smithi* females moved greater distances than those that dispersed naturally. The disturbed aphids assumed a random dispersal pattern rather than the expected clumped distribution around the original plant. Although parasitization was the main cause of the reduction of aphid colony size, Tamaki *et al.* (1970) found that the harassment of the aphids by the parasite adults also caused the aphids to leave the host plants, thus increasing mortality. Thus, the parasites could cause aphid mortality by disturbing the aphids without actually parasitizing them. In this case the parasite acts as a predator by effectively killing the aphid before the aphid can reproduce.

I have observed that the pea aphid, especially in the fourth instar and adult stages, can be active and easily disturbed; while the first, second, and third instars are usually less agile or mobile, increasing their chances of being parasitized. Indeed, in encounters with predators or parasites the pea aphid can exhibit escape responses such as walking away or dropping off the alfalfa plant.

Detailed accounts of active avoidance of enemies of aphids have been made by several authors. Dixon (1958) and Russell (1972) have shown that various aphids, especially the nettle aphid, *Microlophium evansi* (Theobald), and the sycamore aphid, *Drepanosiphum platanooides* (Schrank), avoid capture by predators by exhibiting various escape responses (e.g. walking, swiveling, or dropping, or actively defending themselves by kicking). Recently, Kislow and Edwards (1972) found that certain aphids, including the pea aphid, release small amounts of repellent odour from the siphunculi.

Apparently the odour repels the nearby aphids from one another, causing the aphids to be spaced out evenly over the host plant. The repellent odour of *A. pisum* has been identified as trans- $\beta$ -farnesene (Bowers *et al.*, 1972). Nault *et al.* (1973) call the "odours" that volatilize from the cornicle droplets alarm pheromones because they alert nearby aphids of the danger of predators. Whether parasite attack can cause the alarm pheromones to be produced by the pea aphid has not been determined as yet.

The parameters that measure the above parasite-host behavioural interactions may explain the changes in pea aphid and parasite distribution and density in the field. Indeed, it is suggested that the parasite-host interactions will be stabilized in the model when these critical parameters (and the kinds of functions that connect them) have been found.

In retrospect, the exercise of modelling the pea aphid-parasite system has been a valuable tool in the organization and clarification of ideas and data. By testing various input parameters and biological assumptions (e.g. the effect of various parasite survival rates on aphid population trends and the function to describe parasite searching), the model has helped to place research efforts in perspective. Starting to build the model at the beginning of the project would have been more helpful than producing the model after all the field and laboratory data had been collected. A simulation model can only be as good as the biological data that is fed into it. Thus, it is an excellent tool in showing where one's lack of knowledge really lies, as well as suggesting areas for further research. This model suggested that any further studies on pea aphid-parasite populations should include the parasite searching parameters.

described by Holling (1959), Hassell (1966), Hassell and Varley (1969), Hassell and Rogers (1972), and Readshaw (1973). These parameters should be studied or applied to field conditions so that a realistic "scaling" of the parasite-host interactions can be achieved. In addition, peculiar to the pea aphid-parasite system are the behavioural host-parasite interactions (discussed above) that can continually change host-parasite densities and distributions, which also should be included in any new pea aphid-parasite model.

#### E. Summary

A computer model has been developed which simulates reasonably accurately the pea aphid and parasite population growth and age structures up to peak population levels. However, the model was unable to simulate population changes during the season when the pea aphid and parasite populations were not reproducing rapidly; i.e. the model was unable to predict the decline in aphid population numbers to levels actually experienced in the field. The model was helpful in placing particular research results in perspective and proposing areas for further research such as parasite searching and dispersal behaviour, as well as the effect of aphid and parasite behavioural interactions that may cause changes in pea aphid distribution and abundance in the field.



CHAPTER VIII  
GENERAL DISCUSSION

This thesis presents information on the biology and population dynamics of the pea aphid and its associated parasites at Kamloops, B.C. Since the exotic parasites *Aphidius smithi* and *A. e. ervi* became established in British Columbia (Mackauer and Campbell, 1972) during the late 1960's, they have become the numerically dominant parasites in the southern interior of British Columbia and in the lower Fraser Valley, respectively. *Aphidius smithi* colonized the alfalfa fields around Kamloops, probably during 1967 or 1968, where it became the most abundant parasite, contributing about 70 to 80% of the total parasitism rates of pea aphid populations. Judging from reports on the contribution of *A. smithi* to the successful biological control of the pea aphid in some parts of California (van den Bosch *et al.*, 1966; Hagen *et al.*, 1971) which have hot dry summer weather similar to that of Kamloops, it is likely that *A. smithi* will continue to be as abundant (and perhaps as effective) in Kamloops as it has been in California.

Although parasites were considered to be among the major contributing factors to the biological control of the pea aphid in Kamloops, the exact mechanisms by which this effectiveness is being achieved are still not completely understood. Indeed, we can only speculate, at present, about the processes that are important in allowing both aphid host and parasite to persist in the alfalfa ecosystem. For instance, if a parasite, such as *A. smithi*, were to lay its full complement of eggs in the field, local pea aphid populations would probably go extinct. However, the simulation model suggests that *A. smithi* deposits only about 193.5 (or 0.25) of a total mean

complement of 774 eggs in the field. 'Gilbert and Gutierrez (1973) deduced that *A. rubifolii* lays only about 80 (or 0.20) of a total complement of 400 eggs in the field. Mackauer (1973) suggests three possible reasons why either not all eggs are being deposited or some are being wasted, i.e. adult parasites: (1) "do not survive long enough to reach their potential fecundity"; (2) "spend considerable time in searching from one colony to the next"; or (3) "oviposit into unsuitable hosts". Another possibility may be that a large proportion of parasites disperse from one field to another. The emigration of parasites from one field may be greater than the gain by immigration from other fields during some periods, resulting in a net loss of parasites in a particular area. Van den Bosch *et al.* (1966) have shown that large numbers of *A. smithi* females do move from one field to another. Little is known about the causes for parasite dispersal except that it may happen when aphids become scarce (Way, 1966) or when parasite interference may cause parasites to migrate away from areas of high parasite densities.

In this study, there was no attempt to manipulate natural enemies in an effort to maintain pea aphid populations at a low density. Indeed, the degree to which pea aphid populations are controlled at Kamloops seems to depend on a delicate balance of a large number of regulatory forces interacting at different times during the season. The most important determinants of aphid density were climate and the timing of the harvests along with the prevailing weather conditions immediately following the harvests. The synchronization of aphid and parasite emergence from diapause in spring helped to modify aphid population trends for most of the growing season.

Additional modifying factors which determined the level to which pea aphid densities would rise were the numbers of aphids surviving from the previous crop and the number of immigrant alatae entering the field early in the alfalfa growth phase. Both the pea aphid and its parasites seem to be well suited to the alfalfa ecosystem mainly because of: (1) their high reproductive capacity enabling rapid population increases during the alfalfa growth period; and (2) their ability to disperse, as winged adults, from one field to another, especially prior to hay harvesting.

At Kamloops, although there may occur the occasional pea aphid population explosion that will damage an alfalfa crop, these explosions probably occur infrequently and only in localized areas. The presence of parasites, such as *A. smithi*, along with other entomophagous predators, usually will keep the pea aphid at reasonably low densities at Kamloops. Attempts to manipulate entomophagous insects, especially by inundative releases of *A. smithi* (Halfhill *et al.*, 1973), in an area such as Kamloops where alfalfa is grown mainly for hay, would be justified only if periods of pea aphid population explosions could be accurately predicted. One way of attempting such predictions would seem to be by constructing a more complete model of the alfalfa-pea aphid-parasite system.

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## APPENDIX 1. Calculation of Equivalent Quips

To find the relative number of day-degrees utilized by each parasite species for development in the field compared to those utilized by the pea aphid, the following equations were used:

$$P = DDP/DDA \quad . . . (1)$$

$$EQ = QUIP \times P \quad . . . (2)$$

where: DDA = The accumulated day-degrees above  $t$  experienced by the pea aphid over a time period.

DDP = The accumulated day-degrees above  $t$  experienced by a parasite or predator species over a time period.

EQ = "Equivalent quip" is the equivalent amount of day-degrees utilized by another insect compared to the quip measured for a pea aphid.

P = Mean proportion of heat utilized by a particular insect compared to the heat utilized by the pea aphid under the same field temperatures. (P generally is constant throughout the season; see Table 1.1.)

QUIP = Physiological time scale of 6.195 day-degrees above  $t$  required for the pea aphid to develop a quarter of an instar period.

$t$  = Lower temperature threshold for development.

This method provides a simple way of dealing with the problem of putting a number of species with unequal heat requirements onto the same physiological time scale. Other methods that could have been used, although perhaps slightly more accurate, would have considerably increased computer

time and expense.

The following Table 1.1 illustrates the values used in the calculations.

TABLE 1.1. The number of day-degrees above the thresholds of each insect species experienced at Kamloops, B.C., in 1972. The relationships between the amount of heat utilized by each species compared with the pea aphid is given as a proportion (P) and in equivalent quips (EQ).

Time Periods in Days After 1 April, 1972	Accumulated Day-degrees Above t For:		
	<i>A. pisum</i>	<i>A. smithi</i> *	<i>C. transversoguttata</i>
16 - 21	30.5	28.3 (.93)**	-
22 - 30	64.4	60.2 (.94)	-
30 - 40	96.0	90.7 (.95)	83.3 (.86)
50 - 60	119.0	113.6 (.95)	105.9 (.89)
70 - 80	108.1	102.8 (.95)	94.9 (.87)
90 - 100	102.2	96.7 (.95)	89.0 (.87)
120 - 130	214.8	209.4 (.97)	201.6 (.94)
130 - 140	186.8	177.4 (.95)	166.0 (.89)
Mean P	(1.0)	(.947)	(.888)
"Quips" or EQ (day-degrees t (° C)	6.196	5.867	5.502
	5.56	6.10	6.88
			10.00

\* Also applicable to *A. e. ervi* and *A. e. pulcher*; \*\* Values of P are given in brackets.



## APPENDIX 2. Some Notes on Predator Biology

Introduction

The biology and bionomics of various aphidophagous predators have been reviewed by Hagen and Sluss (1966), Hagen and van den Bosch (1968), Hodek (1966, 1967), and Schneider (1969). This section reports on some laboratory experiments performed on the feeding and development of some common insect predators associated with the pea aphid at Kamloops. Additional data from the literature to determine the general voracities of four predator groups of the Coccinellidae, Chrysopidae, Nabidae, and Syrphidae are reported in Appendix 3.

Methods

Gravid females of *Coccinella transversoguttata richardsoni*\* Brown, *Nabis alterantus*\*\* Parsh, and *Chrysopa carnea*\*\*\* Steph. were collected in the field for egg laying purposes. Eggs deposited in the laboratory were placed individually into glass shell vials (2 x 5 cm) plugged with cheese cloth. At least five vials containing eggs of one of each predator species were placed into three constant temperature cabinets (maintained at 25.8, 19.7, and  $14.8 \pm 0.5^{\circ}\text{C}$ ; 50 to 70% RH; and a diel of 18 L/6 D hours). When the eggs hatched, the immature predators were supplied with third to fourth instar pea aphids. The aphids were counted and transferred daily into clean new vials, along with the predators and two fresh alfalfa leaves. The aphids added each day were nearly always more than the predators could

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\* Coleoptera: Coccinellidae.

\*\* Hemiptera: Nabidae.

\*\*\* Neuroptera: Chrysopidae.

consume. All aphids, whether completely eaten or partially eaten, were recorded as consumed. The data obtained gave developmental rates and maximum feeding rates of these three predator species at three constant temperatures.

An additional experiment was performed to observe if these three predators and *Hippodamia convergens* Guerin-Meneville\* would feed on parasitized aphids. Twenty of each predator species were placed individually into gelatin capsules containing a pea aphid per capsule (as follows: five gelatin capsules contained unparasitized aphids and served as a control; five capsules contained aphids with parasite eggs or larvae; and ten capsules contained mummies of *A. smithi*). The capsules were kept at room temperature of  $20 \pm 2^\circ\text{C}$ . After 24 hours the aphids and mummies that were consumed were recorded.

### Results

Tables 2.1, 2.2, and 2.3 summarize the data obtained from the predation experiments. Because of a malfunction of two incubators the experiments to determine the feeding and developmental rates for *C. carnea* and *N. alternatus* were not completed.

The development rates for *C. transversoguttata* were used to calculate the threshold temperature of development, which was found to be  $10^\circ\text{C}$  (Table 2.2). All predators tested were found to feed on unparasitized and parasitized aphids (Table 2.3); however, Coccinellid larvae and the adults and nymphs of *N. alternatus* did not feed on the mummified aphids.

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\* Coleoptera: Coccinellidae.

TABLE 2.1. Mean feeding rates of three predator species at three constant temperatures.

Temperature (° C)	Mean Number of Aphids Eaten per Day by			
	<i>C. transversoguttata</i> Larvae*	Adult*	<i>Nabis alternatus</i> Nymphs and Adult**	<i>Chysopa carnea</i> Larvae***
25.8	21.3 (.43)****	46.5 (.61)	15.0 (.30)	11.9 (.30)
19.7	22.1 (.73)	28.6 (2.35)	5.1 (.4)	—
14.8	14.5 (1.10)	14.8 (2.15)	—	—

\* n = 5

\*\* n = 6

\*\*\* n = 3

\*\*\*\* Figures in brackets are  $\pm 1$  SE.

TABLE 2.2. Developmental periods (in days) of *Coccinella transversotuttata* and *Nabis alternatus* at three constant temperatures.

Species	Temperature (° C)	n	Egg	Mean Developmental Periods in Days					Egg-adult**
				N1	N2	N3	N4	Pupa	
<i>C. transversotuttata</i>	25.8	5	2.8 (.08)*	3.3 (.08)	2.0 (.00)	1.0 (.03)	5.0 (.00)	4.4 (.24)	18.6 (.23)
	19.7	5	5.0 (.00)	4.0 (.00)	2.6 (.39)	3.8 (.20)	7.4 (.50)	8.4 (.50)	31.3 (.77)
	14.8	5	10.0 (.00)	11.0 (.32)	6.2 (.20)	7.6 (.24)	11.6 (.68)	16.6 (.24)	63.0 (1.05)
<i>N. alternatus</i>	25.8	6	5.8 (.78)	2.2 (.08)	1.4 (.01)	2.2 (.03)	4.1 (.24)	6.5 (.31)	20.6 (1.00)
	19.7	5	9.2 (.95)	3.5 (.07)	2.3 (.01)	3.3 (.04)	6.7 (.09)	10.4 (.80)	33.0 (2.00)

\* Figures in brackets are  $\pm 1$  SE.

\*\* The relationship between temperature and the rate of development of *C. transversotuttata* is shown in the regression equation  $y = -35.6 + 3.46 T$ , where:  
 $y$  = rate of development 1000/D,  
 $D$  = period of development in days,  
 $T$  = temperature; the lower threshold temperature for development ( $t = -a/b$  when  $y = 0$ ) was found to be 10°C.

$N$  = larval or nymphal instars.  
 $n$  = number of individuals measured.

TABLE 2.3. Some predators found in alfalfa fields near Kamloops, B.C., that were observed to feed on unparasitized and parasitized pea aphids in the laboratory.

Species	Stage	<i>A. pisum</i> with		
		Unparasitized	Parasite Egg or Larva	<i>A. smithi</i> Mummy
<i>Hippodamia convergens</i> *	larva	+	+	-
Guerin-Meneville	adult	+	+	+
<i>Coccinella transversoguttata</i> *	larva	+	+	-
<i>richardsoni</i> Brown	adult	+	+	+
<i>Nabis alternatus</i> **	nymph	+	+	-
Parsh	adult	+	+	-
<i>Chrysopa carnea</i> ***	larva	+	+	+
Stephens				

+ All aphids or mummies eaten.

- No mummies eaten; parasite adults eventually emerged from mummies.

\* Coleoptera: Coccinellidae

\*\* Hemiptera: Nabidae

\*\*\* Neuroptera: Chrysopidae.

## APPENDIX 3. Calculation of Predator Equivalents

Although predation has not been studied in depth for this thesis, it was nevertheless an important mortality factor of aphid populations in the field. The effect of predators on aphid populations was more difficult to assess than that of the parasites. While parasitism could be measured directly in terms of percent parasitization, predation involved the aphids being usually completely consumed, leaving no easy measure of aphid mortality.

Van Emden (1966) outlined the main factors to be taken into account in determining predator effectiveness. These factors are predator voracity (a function of appetite, activity, and predator abundance), synchronization with the aphid, and the aphid's reproductive rate. The latter two factors were determined from field and laboratory data. However, a crude estimation of predation or "predator voracity" was necessary to aid in the analysis of the field data.

The literature was searched for additional information to supplement the results described in Appendix 2. The search revealed that among many studies on predator feeding rates only few (if any at all) used the same predator and/or prey species as encountered in the present and under similar conditions. To insure that the data obtained from the literature were compatible with those obtained in this study, a number of conversions and assumptions had to be made. The main assumption was that all predators studied had the same lower temperature threshold of development of 10°C; thus differences in predator feeding rates due to different experimental temperatures could be adjusted. The main conversion was that of changing

the numbers of aphids of different stages or species to the numbers of pea aphids of third to fourth instars eaten per day. This conversion was based on the relative biomass (in dry weights) of each aphid used to feed the predators.

The conversions were as follows:

- Third to fourth instar pea aphids (P3) with a mean dry weight of 0.4778 mg (range 0.1891 to 0.6666 mg)\* were used as prey in this study.
- Hagen and Sluss (1966) found pea aphid adults (PA) to weigh 1.23 mg in their predation studies. They also found that 1 PA were equal to 4.44 spotted alfalfa aphids (SAA) (*Therioaphis trifolii* [Monell]) in biomass.
- To find a conversion factor or an equivalent weight or biomass of third to fourth instar pea aphids (P3) with the aphids used by Hagen and Sluss (1966), the following assumptions were made:

If                      1 PA = 4.44 SAA,  
 then                    1 P3 = 1.23/0.48 = 2.57 PA,  
 and                      1 SAA = 0.58 P3

- The biomass of *T. trifolii* (SAA) used in Hagen and Sluss (1966) was assumed to be the same as that of *T. maculata* in Simpson and Burkhardt (1960).
- To convert feeding rates to common equivalents, the formula

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\* Courtesy of Mr. C. Cloutier.

$$F = \frac{MCQ}{D(T - t)}$$

was used when:

F = No. of third to fourth instar pea aphids eaten per quip.

M = Mean number of third to fourth instar pea aphids eaten per day.

Q = "Quip" = 4.22 day-degrees above 10°C (Appendix 1).

C = Conversion factor that converts numbers of aphids (from other studies) into third to fourth instar pea aphid equivalents.

D = Time units (usually one day).

T = Constant mean temperature at which experiment was conducted (° C).

t = Lower threshold temperature of development (° C).

Table 3.1 shows the mean equivalents of aphids eaten per quip by the various predator types. To find a relationship between the voracity of each predator type relative to the other, the term "equivalent predator voracity" was arbitrarily chosen:

$$V = \frac{F}{F_C}$$

where:

V = Equivalent predator voracity.

F = Mean number of third to fourth instar pea aphids eaten per day.

F<sub>C</sub> = Mean number of third to fourth instar pea aphids eaten per day by Coccinellid larvae = 9.6; considered a constant so that other predator voracities could be related to this constant of 9.6 aphids/quip.



TABLE 3.1. Feeding rates and relative voracity equivalents of insect predators feeding on pea aphids from the present study (Appendix 2) and other studies found in the literature.

Predator	Mean Equivalent No. of Aphids Eaten per Day (M)	Experimental Temperature (° C) (T)	Mean Equivalent No. of Aphids Eaten per Quip* (F)	Equivalent Predator Voracity (V)	Source of Data
<i>COCCINELLIDAE</i>					
<i>C. transversoguttata</i>					
larvae	22.1	19.7	9.6	1.00	Laboratory
adults	28.6	19.7	12.4	1.29	Laboratory
<i>H. convergens</i>					
adult	51.9 (89.4)**	23.9	15.7	1.63	Simpson & Burkhardt (1960)
adult	44.5 (17.3)***	22.8	14.7	1.53	Hagen & Sluss (1966)
<i>CHRYSOPIDAE</i>					
<i>Chrysopa carnea</i>					
larvae	11.9	25.8	3.2	0.33	Laboratory
larvae	19.5 (33.6)**	25.0	5.5	0.57	Simpson & Burkhardt (1960)
larvae	17.7 (17.7)****	26.7	4.5	0.47	Burke & Martin (1956)
<i>NABIDAE</i>					
<i>Nabis alternatus</i>					
nymphs and adults	15.0	25.8	4.0	0.42	Laboratory
<i>Nabis ferus</i>					
nymphs and adults	9.0 (15.5)**	21.7	3.3	0.34	Simpson & Burkhardt (1960)
<i>SYRPHIDAE</i>					
<i>Allogropta obliqua</i>					
larvae	19.3 (33.2)**	23.3	6.1	0.64	Simpson & Burkhardt (1960)

\* 1 quip = 4.22 day-degrees above 10°C (Appendix 1).

\*\* Values in brackets were actually *Therioaphis maculata* adults eaten/day and were converted to pea aphid biomass (1.0 *T. maculata* adult = 0.58 third and fourth instar pea aphids).

\*\*\* Values in brackets were actually *A. pisum* adults eaten/day and were converted to pea aphid biomass (1.0 *A. pisum* adult = 2.57 third and fourth instar pea aphids).

\*\*\*\* Values in brackets were actually *Aphis gossypii* adults eaten/day. No biomass conversion used. (See text in Appendix 3 for explanation of symbols.)

APPENDIX 4  
TABLE 4-1. ALFALFA TIP SAMPLE DATA FOR TOTAL APHIDS, PARASITES AND PREDATORS PER 100 TIPS; SUMMER, 1971.

SAMPLE NO.-DAY	APHID POPULATION NUMBERS						PARASITE NUMBERS						PREDATOR NUMBERS				
	N1	N2	N3	AP4	ALT	OTHER TOTAL	N3	AP4	AL4	APT	ALT	OTHER	TOTAL	SYR-	COCCIN NA-	CARY TO-	
CROP 1																	
1	36	9.5	6.5	1.0	0.5	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.1	1.0	0.0	0.0
2	41	15.5	8.0	3.5	5.0	1.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	1.0	0.5	0.0
3	49	46.5	10.0	5.5	2.5	0.5	7.5	0.0	0.0	0.0	0.0	0.0	0.0	0.5	1.0	0.0	0.0
4	55	65.0	21.0	10.5	8.0	6.0	3.5	0.0	0.0	0.0	0.0	0.0	0.0	1.0	2.5	0.0	0.0
5	64	282.0	54.0	21.0	23.0	13.0	33.0	6.0	0.0	3.0	0.0	4.0	0.0	7.0	5.0	1.0	0.0
6	68	264.0	100.0	17.0	13.0	40.0	9.0	0.0	0.0	6.0	0.0	2.0	0.0	8.0	10.0	0.0	0.0
CROP 2																	
7	79	21.5	4.5	12.0	11.0	6.0	9.5	5.0	0.0	1.0	0.0	5.0	0.0	6.0	1.0	0.5	0.0
8	84	56.0	8.0	10.0	9.0	0.0	14.0	20.0	0.0	1.0	0.0	5.0	0.0	6.0	4.0	0.0	0.0
9	91	107.0	64.0	42.0	27.0	0.0	23.0	14.0	0.0	277.0	6.0	5.0	2.0	18.0	5.0	1.0	0.0
10	58	238.0	65.0	80.0	68.0	2.0	93.0	17.0	0.0	563.0	21.0	30.0	3.0	80.0	16.0	7.0	0.0
11	105	275.0	76.0	75.0	72.0	9.0	96.0	0.0	0.0	553.0	32.0	42.0	4.0	114.0	49.0	3.0	0.0
12	112	66.0	23.0	41.0	31.0	2.0	16.0	5.0	0.0	184.0	21.0	20.0	0.0	43.0	24.0	3.0	0.0
13	119	52.0	18.0	23.0	16.0	0.0	5.0	1.0	0.0	115.0	7.0	6.0	0.0	14.0	14.0	1.5	0.0
CROP 3																	
14	128	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15	133	6.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	7.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
16	140	7.0	2.0	1.0	0.0	0.0	0.0	2.5	0.0	12.5	1.0	0.0	0.0	2.0	0.0	0.0	0.0
17	147	14.0	3.0	5.0	6.0	0.0	9.0	3.0	0.0	40.0	0.0	1.0	0.0	4.0	1.0	0.0	0.0
18	153	91.0	15.0	9.0	10.0	0.0	15.0	6.0	0.0	146.0	3.0	2.0	0.0	8.0	2.0	0.0	0.0
19	161	165.0	62.0	53.0	40.0	3.0	38.0	4.0	0.0	365.0	19.0	14.0	0.0	41.0	16.0	2.5	0.0
20	169	214.0	55.0	45.0	56.0	29.0	73.0	0.0	2.0	474.0	15.0	30.0	8.0	71.0	17.0	2.0	0.0
21	175	284.0	71.0	55.0	47.0	15.0	71.0	0.0	6.0	549.0	21.0	22.0	6.0	63.0	25.0	3.0	0.0
22	182	155.0	35.0	31.0	26.0	12.0	53.0	0.0	6.0	318.0	14.0	15.0	2.0	41.0	31.0	4.0	0.0
23	189	223.0	37.0	10.0	23.0	3.0	40.0	0.0	3.0	339.0	2.0	11.0	1.0	25.0	17.0	2.0	0.0

OTHER= FUNDATRICES IN SPRING OR SEXUALS IN AUTUMN; DAY = DAYS AFTER APRIL 1ST; N = NYMPHAL INSTARS 1-2-3;  
AP OR APT = APTERAE; AD = ADULT; NA = NYMPHS & ADULTS; L =LARVAE

APPENDIX 4  
TABLE 4.2. ALFALFA TIP SAMPLE DATA FOR TOTAL APHIDS, PARASITES AND PREDATORS PER 100 TIPS; SUMMER, 1972.

SAMPLE NO. DAY	APHID POPULATION NUMBERS				PARASITE NUMBERS				PREDATOR NUMBERS															
	N1	N2	N3	AL4	AP4	AL4	APT	ALT	OTHER TOTAL	M3	AP4	AL4	APT	ALT	OTHER	TOTAL	LARVAE	MUMMYPHID	NELLID	BID	SOPA	TAL		
CROP 1																								
1	14	1-6	1-2	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	
2	27	8-0	1-6	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	
3	34	13-2	6-4	1-2	2-0	0-0	0-0	0-0	2-4	25-2	0-5	1-0	0-0	0-0	0-0	2-8	3-2	0-0	0-0	0-0	0-0	0-0	0-0	
4	41	7-2	4-8	5-6	0-8	1-6	0-0	0-0	0-8	25-6	1-0	2-0	1-0	0-0	0-0	0-0	4-0	0-0	0-0	0-0	0-5	0-0	0-0	
5	46	58-7	11-7	4-0	0-0	0-7	10-3	0-0	0-0	89-0	1-0	2-0	0-0	1-0	0-0	0-0	4-0	0-3	0-0	0-0	1-0	1-0	0-0	
6	53	60-0	36-5	14-0	6-5	16-0	1-5	0-0	170-5	15-0	15-5	3-0	6-0	1-0	0-0	40-5	15-0	1-0	0-0	1-0	0-0	0-0	2-0	
7	60	17-0	26-0	44-0	45-5	30-0	8-5	0-5	0-0	171-5	30-0	34-0	18-0	4-0	0-0	86-0	14-5	0-0	1-0	1-0	2-0	0-0	4-0	
8	67	109-5	25-5	22-0	11-0	24-5	7-0	0-0	226-0	7-5	8-0	1-5	6-0	1-5	0-0	24-5	16-5	1-0	2-0	1-0	0-0	0-0	4-0	
CROP 2																								
9	80	12-0	3-0	2-0	0-0	1-0	0-0	0-0	0-0	22-0	1-3	0-7	0-0	0-0	0-0	2-7	0-3	0-5	3-0	0-0	0-0	0-0	0-5	4-0
10	85	22-0	5-0	3-5	2-5	0-5	2-0	2-5	0-0	38-0	1-0	1-0	0-0	0-5	0-5	3-0	2-5	0-0	1-0	0-0	0-0	1-0	2-0	2-0
11	88	16-3	5-0	8-0	4-3	0-7	3-7	1-3	0-0	39-3	3-7	2-0	0-3	1-7	0-0	7-7	5-0	1-0	0-0	0-5	0-0	0-5	2-0	2-0
12	95	33-5	12-5	9-5	4-0	0-0	9-5	1-0	0-0	70-0	3-0	2-0	3-5	0-5	0-0	9-0	6-5	1-0	0-0	0-0	0-0	0-0	1-0	1-0
13	98	33-0	13-0	14-0	11-0	0-0	11-0	7-0	0-0	89-0	6-0	7-0	0-0	7-0	2-0	22-0	7-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
14	102	31-5	12-0	13-5	12-5	0-0	6-5	6-0	0-0	82-0	6-5	11-0	0-0	4-0	1-5	23-0	6-5	0-0	0-0	2-0	1-0	0-0	3-0	3-0
15	109	10-5	7-0	8-5	3-0	0-0	4-0	0-0	0-0	33-0	3-5	2-0	0-0	2-5	0-0	8-0	9-0	0-0	0-0	0-0	1-0	0-0	1-0	1-0
16	112	25-0	8-0	6-0	0-0	2-0	1-0	1-0	0-0	50-0	4-0	7-0	0-0	1-0	0-0	12-0	9-0	0-0	0-0	1-0	2-0	1-0	4-0	4-0
17	116	23-5	5-5	3-5	5-5	0-0	3-5	7-0	0-0	48-5	1-0	3-0	0-0	0-0	1-0	5-0	4-5	2-0	0-0	0-0	0-0	2-0	4-0	4-0
18	123	26-0	12-2	11-5	6-0	0-0	5-5	3-0	0-0	64-2	5-5	2-0	0-0	1-5	2-0	11-0	2-0	0-0	0-0	0-0	0-0	3-0	3-0	3-0
CROP 3																								
19	130	5-0	0-0	0-5	1-0	0-0	1-0	1-0	0-0	8-5	0-0	0-5	0-0	0-0	0-0	0-5	0-5	0-0	0-0	0-0	2-0	0-0	2-0	2-0
20	134	1-5	0-0	0-0	0-0	0-0	1-5	1-0	0-0	4-0	0-0	0-0	0-0	0-5	0-0	0-5	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
21	137	1-0	1-0	0-0	0-0	0-0	0-0	0-0	0-0	2-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
22	144	1-0	1-0	2-0	1-0	0-0	1-0	0-0	0-0	6-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
23	150	3-0	1-0	0-0	0-0	0-0	1-0	2-0	0-0	7-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0
24	156	6-0	0-0	1-0	4-0	0-0	0-0	2-0	0-0	7-0	1-0	2-0	0-0	0-0	1-0	4-0	1-0	0-0	0-0	0-0	2-0	0-0	2-0	2-0

OTHER= FUNDATRICES IN SPRING OR SEXUALS IN AUTUMN; DAY = DAYS AFTER APRIL 1ST; N = NYMPHAL INSTARS 1,2,3;  
AP OR APT = APTERAE; AD = ADULT; NA = NYMPHS & ADULTS; L = LARVAE

APPENDIX 5. NUMBER OF APHIDICPHAGOUS INSECTS COLLECTED PER 100 SWEEPS IN THE STUDY FIELD NEAR KAMLOOPS, DURING 1972.

SAMPLE NO. DAY	COCCINELLIDS				CHRYSOPIIDS			SYRPHIDS			NABIDS			A.S.W.		A.S.O.		A.P.		A.E.		PRAON TOTAL		
	L1	L2	L3	L4	L1	L2	L3	L4	L1	L2	L3	ADLT	N1	N2	N3	M	F	M	F	M	F	M	F	
CROP 1																								
1	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	
3	27	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	
5	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
6	34	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	
8	40	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	
10	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
15	51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
14	53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
18	60	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
20	67	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
22	68	6	1	0	1	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
CROP 2																								
31	80	3	7	3	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
35	88	0	3	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
40	95	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
46	102	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
49	109	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
54	116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
56	123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
CROP 3																								
63	137	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
67	144	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
69	150	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
70	154	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
TOTAL	13	11	5	4	172	2	1	6	0	14	0	2	3	20	0	12	290	345	91	184	0	0	0	0

L = LARVAL INSTARS 1-2,3,4 ; N = NYMPHAL INSTARS 1-2,3 ; ADLT = ADULT ; M = MALE ; F = FEMALE ;  
A.S.W. = APHIDIUS SMITHI (WILD) ; A.S.O. = A.S.MITHI (ORANGE) ; A.P. = APHIDIUS E. PULCHER ; A.E. = A.E-ERVI ;  
PRAON = PRAON PEQUODORUM

TABLE 6.1. Percent species composition of pea aphid parasites that emerged from mummy samples collected in southern British Columbia during summer, 1971. (Only one sample per location taken unless shown otherwise.) (Location numbers correspond to those in Fig. 25.)

No.	Location Area	Date	Total Parasites Emerged (No.)	<i>Praon</i> <i>pequodorum</i> (%)	<i>Aphidius</i> <i>pulcher</i> (%)	<i>Aphidius</i> <i>ervi</i> (%)	<i>Aphidius</i> <i>smithi</i> (%)
1	Spences Bridge Hwy. 1	1 June	31	—	9.7	—	90.3
2	Cache Creek 5 m W. Hwy. 1	1 June	39	7.7	10.3	—	82.0
3	Cache Creek 24 m E. Hwy. 1	7 June	57	1.7	8.8	—	89.5
4	Kamloops C.D.A. Station Field #1	23 June- 6 Oct.	1,924 <sup>a</sup>	5.2	12.7	0.1	81.9 <sup>b</sup>
5	Round Lake 5 m S. Hwy. 5	8 August	77	3.9	1.3	1.3	93.5
6	Winfield Hwy. 97	30 July	75	10.7	12.0	1.3	76.0
7	Summerland Hwy. 97	30 July	102	5.9	2.0	—	92.1
8	Bridesville 16 m W. Hwy. 3	30 July	311	4.5	1.0	—	94.5 <sup>c</sup>
9	Eholt 2 m W. Hwy. 3	31 July	142	2.1	0.7	—	97.2
10	Trail 9 m N. Hwy. 3	31 July	83	3.6	6.0	—	90.4
11	Creston 3 m W. Hwy. 3	31 July	249	3.2	4.0	—	92.8
12	Balfour 2 m W. Hwy. 3A	1 August	146	4.8	1.4	—	93.8
13	Kokanee 7 m S. Hwy. 6	1 August	53	11.3	—	—	88.7
14	Nakusp 16 m S. Hwy. 6	1 August	69	4.4	—	—	95.6
15	Cherryville 3 m W. Hwy. 6	1 August	247	3.4	4.8	—	91.8
16	Forte Steele Park Hwy. 93	31 July	38	18.5	36.8	—	44.7
17	Westsyde 10 m N. Kamloops C.D.A. Station	1 June- 27 August	820 <sup>d</sup>	12.9	26.9	—	60.0
18	McLure Hwy. 5	4 July	38	23.7	13.2	—	63.2
19	Chilliwack Prost Rd. & Hwy. 1	6 August- 15 Sept.	304 <sup>e</sup>	9.5	0.7	88.2	1.6

<sup>a</sup> = 13 samples included.

<sup>b</sup> = 0.3% *A. smithi*, 'orange' included.

<sup>c</sup> = 0.6% *A. smithi*, 'orange' included.

<sup>d</sup> = Add 0.2% for *Monoctonus paulensis*; also includes 12 samples.

<sup>e</sup> = includes 2 samples.

<sup>m</sup> = miles; W = west; E = east; N = north; S = south; Hwy. = highway.

TABLE 6.2. Percent species composition of pea aphid parasites that emerged from mummy samples collected in southern British Columbia during summer, 1972. (Only one sample per location taken unless shown otherwise.) (Location numbers correspond to those in Fig. 25.)

No.	Location Area	Date	Total Parasites Emerged No.	%				
				<i>Fraon pequodorum</i>	<i>Aphidius pulcher</i>	<i>Aphidius erwi</i>	<i>Aphidius smithi</i>	%
18	McLure Hwy. 5	7 August	135	14.8	17.8	—	67.4	
17	Westsyde	7 August	54	24.1	20.4	—	55.5	
4	Kamloops C.D.A. Station Field 2	1 July- 10 August	806a	10.3	19.4	0.1	70.2	
6	Winfield Hwy. 97	4 August	62	4.8	25.8	—	69.4	
7	Summerland Hwy. 97	5 August	35	5.7	2.9	—	91.4	
8	Bridesville 16 m W. Hwy. 3	5 August	101	1.0	11.9	—	87.1	
19	Chilliwack Prost Rd. & Hwy. 1	29 August	109	13.8	0.9	82.6	2.7	

a = includes 9 samples.

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C*****
C
C APPENDIX 7.
C
C A SAMPLE LISTING OF THE BASIC FORTRAN COMPUTER PROGRAMME FOR THE
C KAMLOOPS ALFALFA - PEA APHID - PARASITE MODEL
C MAY,1973
C
C THE FOLLOWING PROGRAMME SIMULATES THE INTERACTIONS BETWEEN POPULATIONS OF THE
C PEA APHID (ACYRTHOSIPHON PISUM) AND ITS THREE MAIN PARASITES (APHIDIUS SMITHI
C . APHIDIUS E. PULCHER, PRADON PEGUDDORUM) FOUND IN AN ALFALFA FIELD IN
C KAMLOOPS, B.C., DURING THE SUMMERS, 1971, 1972.
C THE BASIC UNIVERSE IN THIS MODEL IS AN AVERAGE ALFALFA TIP
C
C THE FOLLOWING IS A GLOSSARY OF THE TERMS USED IN THE MODEL INCLUDING
C SOME OF THE MODEL'S ASSUMPTIONS :
C
C TERMS OR DESCRIPTION
C SYMBOLS
C A TOTAL APTEROUS PROGENY PRODUCED BY ALATAE (WORKING SUM)
C A1 NO. OF FIRST INSTAR APHIDS AGE 1-4 QUIPS (APTERAE+ALATAE)
C A2 NO. OF SECOND INSTAR APHIDS AGES 5-8 QUIPS (APTERAE+ALATAE)
C A3 NO. OF THIRD INSTAR APHIDS AGES 9-12 QUIPS (APTERAE+ALATAE)
C ADD A FRACTION TO ADJUST INITIAL PARASITE NUMBERS
C AL4 NO. OF FOURTH INSTAR ALATE APHIDS AGES 13-19 QUIPS
C ALATE(I) CURRENT NO. OF ALATE A.PISUM OF KNOWN AGE (I) QUIPS
C ALIMM(NS) NO. OF IMMIGRANT UNPARASITIZED ALATAE AGE (24) QUIPS ENTERING FIELD
C DATA OBTAINED FROM ALFALFA TIP SAMPLES IS READ IN AS NO. OF ALATAE
C PER TIP AT EACH OBSERVED SAMPLING PERIOD KSAM(KA).
C ALT NO. OF ADULT ALATE APHIDS AGES 20-93 QUIPS
C AP4 NO. OF FOURTH INSTAR APTEROUS APHIDS AGES 13-18 QUIPS
C APHIDT TOTAL PARASITIZED & UNPARASITIZED APHIDS OF 9 QUIPS OR OLDER
C APT NO. OF ADULT APTEROUS APHIDS AGES 19-93 QUIPS
C APTRA(I) CURRENT NO. OF APTEROUS A.PISUM OF KNOWN AGE (I) QUIPS.
C ASTART(I) INITIAL NO. OF ALATAE OF AGES (I) QUIPS.
C AX TOTAL APTEROUS AND ALATE PROGENY PRODUCED BY APTERAE (WORKING SUM)
C EMIG(KA) SURVIVAL RATE OF EMIGRANT ALATAE; USUALLY SET TO ZERO.
C HYPER HYPERPARASITE ACTIVITY EXPRESSED AS A SURVIVAL RATE ON EMERGING
C PRIMARY PARASITES. HYPER CALCULATED FROM FIELD SAMPLE DATA.
C I AGE OF PARASITE OR APHID IN QUIPS
C J AGE OF PARASITE OR APHID IN QUIPS
C KA TIME STEP OF PROGRAMME AND ALFALFA SEASON = 1 QUIP
C TIME DURING SEASON IN QUIPS; USUALLY INCREMENTED BY 1 QUIP (1-350)
C FROM THE 15TH OF APRIL TO 10TH OCTOBER, INCLUSIVE
C KSAM GIVES THE TIMES IN QUIPS (KA) DURING SEASON WHEN SAMPLES WERE MADE
C AND ALSO WHEN PRINT OUT OF CURRENT PREDICTED APHID & PARASITE
C NUMBERS ARE WANTED.
C LXX MEAN REPRODUCTIVE RATE OF AN APHID OR PARASITE AT AGE (I) PRODUCT OF
C LX=SURVIVAL RATE AND MX=FECDUNDITY RATE
C MAXO END OF CROP OR MAX INCREMENT VALUE FOR THE MAIN DO STATEMENT 500
C MINO BEGINNING OF CROP OR LOWER VALUE OR QUIP FOR DO STATEMENT 500 WHICH
C IS INCREMENTED BY ONE QUIP KA

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C N1 FIRST INSTAR APHIDS = A1  
 C N2 SECOND INSTAR APHIDS = A2  
 C N3 THIRD INSTAR APHIDS = A3  
 C NS A SUBSCRIPT USED IN ALIMM OR PLIMM  
 C PARA(I,J) A TABLE OR MATRIX (41,20) WHICH KEEPS ACCOUNT OF THE NUMBERS OF  
 C PARASITIZED APTERAE. APHID AGES (I=1-41) QUIPS AND PARASITE  
 C JUVENILES AGES (J=1-20) QUIPS.  
 C PARAL(I,J) A TABLE OR MATRIX (41,20) WHICH KEEPS ACCOUNT OF THE NUMBERS OF  
 C PARASITIZED ALATAE. APHID AGES (I=1-41) QUIPS AND PARASITE  
 C JUVENILES AGES (J=1-20) QUIPS.  
 C PAREP1(I) NEWLY PARASITIZED APTERAE  
 C PAREP2(I) NEWLY PARASITIZED ALATAE  
 C PASU SURVIVAL RATE OF PRIMARY PARASITES APPLIED TO NORMAL PARASITE  
 C REPRODUCTIVE RATES AT ALL AGES. PASU REPRESENTS ADULT PARASITE  
 C SURVIVAL IN THE FIELD INCLUDING MORTALITY DUE TO OLD AGE, WEATHER  
 C CONDITIONS AND EMIGRATION. THE VALUE OF PASU IS CHOSEN AS AN  
 C ARBITRARY CONSTANT SURVIVAL RATE.  
 C P1 PROPORTION (%) PARASITE JUVENILES/ TOTAL APHID POPULATION  
 C (TOTAL APHIDS 9 QUIPS OR OLDER)  
 C P2 PROPORTION (%) (PARASITE JUVENILES+MUMMIES)/(TOTAL APHIDS+  
 C MUMMIES)  
 C P3 PROPORTION (%) A. SMITHI IN TOTAL MUMMIES  
 C P4 PROPORTION (%) A. E. PULCHER IN TOTAL MUMMIES  
 C P5 PROPORTION (%) P. PECUODORUM IN TOTAL MUMMIES  
 C P6 PROPORTION (%) APHID MORTALITY DUE TO PREDATION  
 C PLIMM(NS) NO. OF IMMIGRANT PARASITIZED ALATAE AGE (24) QUIPS ENTERING FIELD  
 C ALATAE READ IN AT AGE (24) QUIPS AND PARASITE JUVENILES AT AGES  
 C (4-13) QUIPS AT EACH OBSERVED SAMPLING PERIOD KSAM(KA).  
 C PRAON(I) CURRENT NO. OF P. PECUODORUM OF KNOWN AGE (I) QUIPS  
 C PRED(KA) NO. OF PREDATORS PER TIP FOR EACH TIME STEP KA. NOS. EXPRESSED AS  
 C EQUIVALENT NO. OF CCCCINELLID LARVAE WITH A VORACITY OF 9.6 APHIDS  
 C PER QUIP.  
 C PRED1 PROPORTION OF APHIDS KILLED BY PREDATORS  
 C PRED(KA) TOTAL EQUIVALENT PREDATORS FROM ALFALFA TIP SAMPLES  
 C PREDN PREDATION FACTOR CALCULATED IN TERMS OF APHID SURVIVAL FROM  
 C PREDATORS  
 C PRJ TOTAL JUVENILE P. PECUODORUM OF 4-25 QUIPS IN APHIDS OF 9Q OR OLDER  
 C PARASITE EGGS OF AGES 1-3 QUIPS USUALLY TOO SMALL TO BE SEEN  
 C PRM TOTAL NO. OF MUMMIES OF P. PECUODORUM AGES 26-35 QUIPS  
 C PRST(I) INITIAL NO. OF P. PECUODORUM OF AGES (I) QUIPS  
 C PSTART(I) INITIAL NO. OF APTERAE OF AGES (I) QUIPS  
 C PROP PROPORTION OF ALATE PROGENY CALCULATED FROM APHID DENSITY  
 C PSURV TOTAL APHID SURVIVAL FROM PARASITE ATTACK (ALL 3 SPECIES)  
 C PUJ TOTAL JUVENILE A. PULCHER OF 4-22 QUIPS IN APHIDS 9 QUIPS OR OLDER  
 C PULCH(I) CURRENT NO. OF A. PULCHER OF KNOWN AGE (I) QUIPS  
 C PUM TOTAL NO. OF MUMMIES OF A. PULCHER AGES 23-31 QUIPS  
 C PUST(I) INITIAL NO. OF A. PULCHER OF AGES (I) QUIPS  
 C QUIP A QUARTER INSTAR PERIOD OF THE PEA APHID MEASURED IN PHYSIOLOGICAL  
 C TIME (DEGREE-DAYS). A QUIP IS THE BASIC TIME UNIT USED IN THIS MODEL  
 C WHICH IS 6.2 DAY-DEGREES ABOVE 5.56 DEGREES CENTIGRADE  
 C REPAL(I) AGE SPECIFIC FECUNDITY (LXMX) OF ALATAE, SURVIVING TO AGE (I)  
 C REPAP(I) AGE SPECIFIC FECUNDITY (LXMX) OF APTERAE, SURVIVING TO AGE (I)



C REPR(I) AGE SPECIFIC FECUNDITY (LXMX) OF P.PEQUODORUM, SURVIVING TO AGE (I)  
 C REPU(I) AGE SPECIFIC FECUNDITY (LXMX) OF A.PULCHER, SURVIVING TO AGE (I)  
 C RESM(I) AGE SPECIFIC FECUNDITY (LXMX) OF A.SMITHI, SURVIVING TO AGE (I)  
 C RPPR(I) REPRODUCTIVE RATE (LXMX) OF P.PEQUODORUM= (PASU\*REPR)  
 C RPPU(I) REPRODUCTIVE RATE (LXMX) OF A.PULCHER=(PASU\*RESM)  
 C RPSM(I) REPRODUCTIVE RATE (LXMX) OF A.SMITHI= (PASU\*RESM)  
 C S PRED(KA)\*SK  
 C SK NORMAL SURVIVAL OF PARASITIZED APHIDS AGES 1-41 QUIPS.  
 THIS CONSTANT IS ARBITRARILY CHOSEN.  
 C SMITH(I) CURRENT NO. OF A.SMITHI OF KNOWN AGE (I) QUIPS  
 C SMJ TOTAL JUVENILE A.SMITHI OF 4-20 QUIPS IN APHIDS OF 9 QUIPS OR OLDER  
 C SMM TOTAL NO. OF MUMMIES OF A.SMITHI AGES 21-29 QUIPS  
 C SMST(I) INITIAL NO. OF A.SMITHI OF AGES(I) QUIPS  
 C SP TOTAL PROPORTION OF NEW PARASITES (ALL 3 SPECIES)  
 C SPAL CURRENT TOTAL OF PARASITIZED ALATAE AGES 21-33 QUIPS (WORKING SUM)  
 C SPP CURRENT TOTAL OF PARASITIZED APTERAE AGES 21-33 QUIPS (WORKING SUM)  
 C SPR APHID SURVIVAL FROM P.PEQUODORUM ATTACK  
 C SPU APHID SURVIVAL FROM A.PULCHER ATTACK  
 C SRPR PROPORTION OF P.PEQUODORUM FEMALES EMERGING FROM PRAON MUMMIES  
 ALL SEX RATIOS ARE CONSTANTS CALCULATED FROM PARASITE EMERGENCES  
 IN MUMMY SAMPLES.  
 C SRPU PROPORTION OF A.PULCHER FEMALES EMERGING FROM A.PULCHER MUMMIES  
 C SRSM PROPORTION OF A.SMITHI FEMALES EMERGING FROM A.SMITHI MUMMIES  
 C SSM APHID SURVIVAL FROM A.SMITHI ATTACK  
 C TJ TOTAL PARASITE JUVENILES OF 3 SPECIES  
 C TM TOTAL MUMMIES OF 3 SPECIES  
 C TN CURRENT TOTAL APHID POPULATION OF UNPARASITIZED APTERAE AND ALATAE  
 ALATAE AGES 3-22 QUIPS AVAILABLE TO BE PARASITIZED (WORKING SUM)  
 C TNP CURRENT TOTAL APHID POPULATION (TN) PLUS PARASITIZED APTERAE  
 OF AGES 3-22 QUIPS WITH PARASITE EGGS OF AGE 1 QUIP (WORKING SUM).  
 C APHIDS OF AGES 3 TO 22 QUIPS ARE SUSCEPTIBLE TO PARASITE ATTACK,  
 SO ARE APHIDS WITH PARASITE EGGS OF AGE 1 QUIP.  
 C TOT TOTAL NO. OF LIVING APHIDS (PARASITIZED & UNPARASITIZED)  
 C TOTAL CURRENT TOTAL ALATAE (WORKING SUM)  
 C TPR TOTAL NO. OF EGGS P.PEQUODORUM FEMALES TRY TO LAY DURING KA  
 C TPU TOTAL NO. OF EGGS A.PULCHER FEMALES TRY TO LAY DURING KA  
 C TSM TOTAL NO. OF EGGS A.SMITHI FEMALES TRY TO LAY DURING KA  
 C XPR PROPORTION OF NEW P.PEQUODORUM PARASITES  
 C XPU PROPORTION OF NEW A.PULCHER PARASITES  
 C XSM PROPORTION OF NEW A.SMITHI PARASITES  
 C XX CURRENT TOTAL PARASITE JUVENILES AGES(1-10) QUIPS (WORKING SUM)

C\*\*\*\*\*

C DIMENSION ALL VECTORS AND MATRICES  
 0001 DIMENSION ALATE(100),APTRA(100),REPAL(100),REPAP(93),  
 1PSTART(93),ASTART(100),KSAM(100)  
 0002 DIMENSION FREQ(20),EMIG(350),PRED(350),ALIPM(100),PLIMM(100)  
 0003 DIMENSION SMITHI(71),PULCH(71),PRAON(72),PARA(41,20)  
 0004 DIMENSION RESM(71),REPU(71),REPR(71),PARAL(41,20)  
 0005 DIMENSION RPSM(71),RPPU(71),RPPR(71)  
 0006 DIMENSION SMST(71),PUST(71),PRST(71)  
 0007 DIMENSION PAREP1(22),PAREP2(22)

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C*****
C   READ IN ALL REPRODUCTIVE AND INITIAL NOS WITH DATA STATEMENTS
0008  DATA REPAP/20*0.0,.24,1.08,1.58,2.13,2.41, 2.42, 2.66, 2.55, 2.67,REPAPLMX
      1 2.61, 2.56, 2.68, 2.51, 2.40, 2.35, 2.60, 2.66, 2.66, 2.54, 2.46,REPAPLMX
      2 2.45, 2.25, 2.09, 2.28, 2.26, 2.13, 1.90, 1.79, 1.80, 1.80, 1.86,REPAPLMX
      3 1.57, 1.26, 1.11, 1.09, 0.99, 1.09, 0.94, 0.83, 0.86, 0.73, 0.58,REPAPLMX
      4 0.51, 0.44, 0.36, 0.28, 0.22, 0.22, 0.18, 0.17, 0.16, 0.15, 0.12,REPAPLMX
      5 0.12, 0.08, 0.08, 0.06, 0.06, 0.03, 0.02, 0.03, 0.03, 0.02, 0.02,REPAPLMX
      6 0.01, 8*0.0/
0009  DATA REPAL/22*0.0, 0.29, 0.85, 0.89, 1.31, 1.55, 2.00, 2.27, 2.23,REPALLMX
      1 2.18, 2.36, 2.57, 2.36, 2.25, 2.46, 2.54, 2.17, 2.09, 2.29, 2.49,REPALLMX
      2 2.48, 2.56, 2.46, 2.37, 2.27, 2.11, 2.04, 1.92, 1.81, 1.68, 1.63,REPALLMX
      3 1.57, 1.44, 1.41, 1.15, 1.20, 1.24, 1.12, 1.19, 1.33, 1.36, 1.78,REPALLMX
      4 1.03, 1.07, 0.97, 0.71, 0.75, 0.73, 0.85, 0.54, 0.56, 0.48, 0.45,REPALLMX
      5 0.46, 0.41, 0.29, 0.30, 0.22, 0.31, 0.21, 0.19, 0.05, 0.06, 0.05,REPALLMX
      6 0.05, 0.04, 0.06, 0.06, 0.02, 0.01, 0.01, 0.00, 0.00, 0.02, 0.02,REPALLMX
      7 0.02, 0.02, 0.02, 0.00/
0010  DATA RESM/30*0.0,37.56,37.56,43.78,43.78,43.78,51.69,51.69,48.78,RESM
      148.77,45.24,36.39,36.39,30.26,28.63,24.20,24.20,23.17,15.00,15.00,RESM LMX
      213.89,13.89,11.56, 9.82, 9.82, 5.57, 5.33, 3.87, 3.04, 2.28, 2.28,RESM LMX
      3 2.28, 1.87, 1.87, 1.00,7*C.0/ RESM LMX
0011  DATA REPU/32*0.0,27.50,27.50,29.61,29.61,29.61,24.24,24.24,19.50,REPU LMX
      119.50,15.53,15.09,15.09, 8.57, 7.33, 5.81, 5.51, 4.71, 2.56, 2.56,REPU LMX
      2 .94, .46, .20, .13, .13,15*0.0/
0012  DATA REPR/36*0.0, 9.97, 9.97,13.85,13.85,13.84,15.61,15.61,14.17,REPR LMX
      114.17,11.55,10.22,10.21, 7.03, 6.65, 5.12, 3.87, 3.87, 2.65, 2.59,REPR LMX
      2 1.76, 1.64, 1.13, .92, 0.92, 0.96, 0.93, 0.54, 0.94, 0.41, 0.41,REPR LMX
      3 0.41, 0.11, 0.03, 0.02, 0.00/ REPR LMX
C
0013  201 FORMAT(' *.1X, *CROP 1')
0014  MINO=4
0015  MAXQ=73
0016  DATA KSAM/4.11,17.25,33.42,57.73,92*0/ IF1 72
0017  DATA PSTART/4*.004,4*.00299,4*.001,6*.0,6*.00076,69*0/ IF
0018  DATA ASTART/100*0.0/ IF1 72
0019  DATA SMST/7*0.0,5*.00121,18*0.0,10*.0004,21*0.0/ IF1 72
0020  DATA PLST/7*0.0,3*.0008,3*.00321,8*.0000,12*0.0,10*.0004,28*0.0/
0021  DATA PRST/3*.00191,31*0.0,1*.0040,36*0.0/ IF1 72
0022  DATA EMIG/350*0.0/ IF1 72
0023  DATA ALIMM/.0,.0,.0,.0,.0,.005,.055,92*0.0/ IF1 72
0024  DATA PLIMM/5*.0,.01,.0,.015,92*0.0/ IF1 72
0025  DATA PRED/24*0.0,6*.01,3*.018,9*.022,7*.025,8*.03,8*.035,8*.042,
      123*.05,1*.069,1*.05,1*.04,1*.03,1*.02,8*.015,24*.01,3*.02,4*.033,
      216*.005,7*.02,30*.015,157*0.0/ 1972
C
C*****
C   INITIALIZE ALL APHID AND PARASITE INFORMATION
0026  DO 500 IP= 5,100,5
0027  Z=1.
C
C   INITIALIZE APHID NOS OF ALL AGE GROUPS
0028  TOT=0.0

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```

0029         TOTAL=0.0
0030         DO 1212 I=93,100
0031 1212 ALATE(I)=ASTART(I)
0032         DO 10 I=1,93
0033         APTRA(I)=PSTART(I)
0034         ALATE(I)=ASTART(I)
C           SUM UP TOTAL INITIAL NOS CF APTERAE AND ALATAE
0035         TOTAL=TOTAL+ALATE(I)
0036 10 TOT=TOT+APTRA(I)
C           INITIALIZE PARASITE NOS OF ALL AGE GROUPS
0037         ADD=.1
0038         DO14 I=1,71
0039         SMITH(I)=SMST(I)*ADD
0040         PULCH(I)=PUST(I)*ADD
0041 14 PRAON(I)=PRST(I)*ADD
C
C           INITIALIZE RP FOR PARASITE REPRODUCTION FROM ORIGINAL LXX VALUES
C           SET IMMATURE PARASITE REPRDUCTION EQUAL TO ZERO
0042         DO 16 I=1,30
0043         RPSM(I)=RESM(I)
0044         RPPU(I)=REPU(I)
0045 16 RPPR(I)=REPR(I)
C           APPLY PASU OR ADULT SURVIVAL EXPRESSED THROUGH
C           PARASITE REPRODUCTION OF ADULTS AGE 30 QUIPS OR OLDER
0044         PASU=.01*IP
C           CALCULATE POPULATION CHANGES WITH DIFFERENT VALUES OF PASU
0047         X=1.0
0048         X=PASU*X
0049         DO 15 I=30,71
0050         RPSM(I)=RESM(I)*X
0051         RPPU(I)=REPU(I)*X
0052 15 RPPR(I)=REPR(I)*X
C
C           CHECK SUM OF CHANGES IN PARASITE TOTAL FECUNDITY AFTER PASU IS APPLIED
0053         SS1=0.0
0054         SS2=0.0
0055         SS3=0.0
0056         DO 18 I=30,71
0057         SS1=SS1+RPSM(I)
0058         SS2=SS2+RPPU(I)
0059 18 SS3=SS3+RPPR(I)
0060         WRITE(6,929)
0061 929 FORMAT('-.1X,*N= NYMPHAL INSTARS; AP + APT = APTERAE; AL + ALT =
1ALATAE; PER1 = PROPORTION PARASITE LARVAE/ TOTAL APHIDS (9 QUIPS O
2R OLDER); *./,2X,*PER2= PROPORTION OF PARASITE LARVAE + MUMMIES/TOTAL
3 APHIDS + MUMMIES; PER = PROPCRTIGN OF EACH PARASITE SPECIES/TOTAL
4 NUMBER OF *./,2X,*MUMMIES ; SMITH = A.SMITHI; PULCH = A.E.PULCHER;
5PRAON = P.PEQUODORUM; PROP = PROPORTION OF ALATE PROGENY')
C
C           INITIALIZE MATRICES PARA & PARAL; THE NO. OF PARASITIZED APHIDS
0062         DO20I=1,41
0063         DO20J=1,20

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0064      PARAL(I,J)=0.0
0065      20 PARA (I,J)=0.0
C          INITIALIZE NO. OF PARASITIZED APHIDS OF AGE I (1-31) AND PARASITES
C          OF AGE J (1-22) AND PUT INTO PARA MATRIX
0066      DO21J=1,20
0067      X=SMITH(J)+PULCH(J)+PRACN(J)
C          INITIAL PARASITIZED APHIDS ADDED TO TOTAL APHID COUNT
C          THAT IS TCT=TOTAL NOS CF APHIDS PARASITIZED OR UNPARASITIZED
0068      TOT=TOT+X
0069      X=X/20.
0070      NST=J+2
0071      NFIN=J+21
0072      DO21I=NST,NFIN
0073      21 PARA(I,J)=X
C
C          TOTAL APTERAE AND ALATAE TOGETHER
0074      TOT=TOT+TOTAL
C
C          WRITE (6,323)
0075      323 FORMAT('C',1X,'PREDICTED DATA FROM MODEL',
0076      1/, 20X,'APHIDS/TIP',37X,'PARASITES/TIP',29X,'PREDATION',
      2/, 2X,'QUIP',2X,'N1      N2      N3      AP4      AL4      APT      ALT',4X,
      3'TOTAL PRCP TOTAL TOTAL',
      411X,'SMITHI PULCH PRACN',1X,'MORTALITY ',/,66X,'LARVAE MUMMIES',
      51X,'PER1 PER2 PER      PER      PFR',2X,'PROPORTION')
0077      WRITE (6,201)
0078      PREDN=EXP(-9.6*PRED(MINQ)/TOT)
0079      P6=1.0-PREDN
C          INITIAL COUNTER FOR PRINT CUT
0080      NS=1
C
C*****
C          START APHID-PARASITE-PREDATOR INTERACTIONS MAKING CALCULATIONS EVERY QUIP
C
0081      DO 500 KA=MINQ,MAXQ
0082      PROP=0.0
0083      IF(KA.EQ.MINQ) GO TO 140
C
C          PROPORTION OF ALATAE CALCULATED USING AGE OF PLANT & APHID DENSITY
0084      TLOG=ALOG10(TOT*100)
0085      IF(KA=85) 1512,1512,1612
0086      1512 PROP=(.3059*TLOG)-.2179
0087      GO TO 1622
0088      1612 PROP=(.2408*TLOG)-.2844
0089      1622 IF (PROP.GT.1) PROP=1
0090      IF (PROP.LT.0) PROP=0.0
C
C          NORMAL REPRODUCTION OF ALATAE AND APTERAE (UNPARASITIZED)
C          A= APTEROUS PROGENY FROM ALATAE SUM SET TO ZERO
0091      A=0.0
C          AX= APTERCUS OR ALATE PROGENY FROM APTERAE SUM SET TO ZERO
0092      AX=0.

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CROP 1

CROP 2+3

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0093      DO 111 I=20,93
0094      AX=AX+APTRA(I)*REPAP(I)
0095      111 A=A+ALATE(I)*REPAL(I)
C
C      REPRODUCTION OF PARASITIZED APTERAE & ALATAE
0096      DO 115 I=21,33
C      SET WORKING SUMMS EQUAL TO ZERO
0097      SPP=0.0
C098      SPAL=0.0
C      TOTAL REPRODUCTIVE PARASITIZED APTERAE AND ALATAE
0099      DO 114 J=1,12
0100      SPAL=SPAL+PARAL(I,J)
0101      114 SPP=SPP+PARA(I,J)
C      PARASITIZED APTERAE & ALATAE AGES 21-33 REPRODUCE FOR A MAXIMUM OF 12QUIPS
C      PROGENY FROM TOTAL PARASITIZED APHIDS OF AGE(I) ADDED TO TOTAL
C      APTERAE AND ALATE PRCGENY AX & A
0102      A=A+SPAL*REPAL(I)
0103      115 AX=AX+SPP*REPAP(I)
C
C      PREDATION FACTOR CALCULATED
0104      PREDN=EXP(-9.6*PREC(KA)/TOT)
0105      P6=1.0-PREDN
C      N.B. IN SCME CASES (ESPECIALLY IN CROPI, 1972) PREDATORS WERE TOO
C      SEVERE CAUSING APHIDS TO GO EXTINCT. THIS WAS PROBABLY DUE TO INCORRECT
C      ESTINATION OF PREDATOR VORACITY WHICH COULD BE ADJUSTED BY MAKING THE
C      FEEDING RATE 2.0 INSTEAD OF 9.6.
C
C      SK= SURVIVAL OF PARASITIZED APHID FACTOR
0106      SK=.97
0107      S=SK*PREDN
C
C      UPDATE PARASITE INDIVIDUALS AND APPLY PARASITE REPRODUCTION
0108      TSM=0.0
0109      TPU=0.0
0110      TPR=0.0
0111      I=70
0112      1100 J=I+1
0113      IF (I.LE.25) GO TO 1102
0114      SMITH(J)=SMITH(I)
0115      PULCH(J)=PULCH(I)
0116      PRAON(J)=PRAON(I)
C      PARASITE REPRODUCTION      ADJUSTED TO PARASITE SURVIVAL
0117      IF (I.LT.31) GO TO 1105
0118      TSM=TSM+SMITH(J)*RPSM(J)
0119      TPU=TPU+PULCH(J)*RPPU(J)
0120      TPR=TPR+PRAON(J)*RPPR(J)
0121      GO TO 1105
C      PREDATION AND NATURAL SURVIVAL RATES APPLIED TO PARASITES YOUNGER THAN
C      25 QUIPS WHILE PARASITE JUVENILES ARE UPDATED.
0122      1102 SMITH(J)=SMITH(I)*S
0123      PULCH(J)=PULCH(I)*S
0124      PRAON(J)=PRAON(I)*S

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0125      1105 I=1-1
0126      IF (I) 1110,1110,1100
C        PARASITES DIE OF OLD AGE
0127      1110 SMITH(64)=0.0
0128      PULCH(56)=0.0
0129      PRAON(70)=0.0

C
C        SEX RATIOS OF PARASITES
0130      SRSM=.554
0131      SRPR=.555
0132      SRPU=.571

C        HYPERPARASITE ACTIVITY OVER SEASON ADJUSTMENT
0133      IF(KA- 23) 1161,1161,1162      1F1 72
0134      1161 HYPER=.945-.01111*KA      1F1 72
0135      GO TO 1160
0136      1162 IF(KA- 33) 1163,1163,1164      1F1 72
0137      1163 HYPER=.694      1F1 72
0138      GO TO 1160
0139      1164 IF(KA- 42) 1165,1165,1166      1F1 72
0140      1165 HYPER=1.652-.02888*KA      1F1 72
0141      GO TO 1160
0142      1166 IF(KA- 57) 1167,1167,1168      1F1 72
0143      1167 HYPER=.02615*KA-.6595      1F1 72
0144      GO TO 1160
0145      1168 IF(KA- 73) 1169,1169,1170      1F1 72
0146      1169 HYPER=1.5849-.01329*KA      1F1 72
0147      GO TO 1160
0148      1170 IF(KA-109) 1171,1171,1172      2F1 72
0149      1171 HYPER=.02085*KA-1.357      2F1 72
0150      GO TO 1160
0151      1172 IF(KA-124) 1173,1173,1174      2F1 72
0152      1173 HYPER=.9145      2F1 72
0153      GO TO 1160
0154      1174 IF(KA-156) 1175,1175,1176      2F1 72
0155      1175 HYPER=2.149-.01005*KA      2F1 72
0156      GO TO 1160
0157      1176 HYPER=.593      2F1 72
0158      GO TO 1160

C        PROPORTION OF PRIMARY PARASITES SURVIVING FROM HYPERPARASITE ACTIVITY
C        SEX RATIO APPLIED TO EMERGING PARASITES OF EACH SPECIES
0159      1160 IF(HYPER.GT.1.) HYPER=1.0
0160      IF(HYPER.LT.0.2) HYPER=0.12
0161      SMITH(30)=SMITH(30)*SRSM*HYPER
0162      PULCH(32)=PULCH(32)*SRPU*HYPER
0163      PRACN(36)=PRACN(36)*SRPR*HYPER

C
C        APHID - PARASITE INTERACTIONS
C        MORTALITY OF APHIDS DUE TO PRIMARY PARASITES
0164      TN=0.0
0165      TNP=0.0
0166      DO 1200 I=3,22
0167      TN=TN+APTRA(I)+ALATE(I)

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0168      1200 TNP=TNP+PARA(I,1)+PARAL(I,1)
0169          TNP=TNP+TN
0170          SSM=EXP(-TSM/TNP)
0171          SPU=EXP(-TPU/TNP)
0172          SPR=EXP(-TPR/TNP)
0173          PSURV=SSM*SPU*SPR
0174          SP=3.0-SSM-SPU-SPR
0175          IF(SP.EQ.0.)GOTO1250
C
0176          C PROPORTION OF EACH NEW PARASITE SPECIES DETERMINED
0177          XSM=(1.0-PSURV)*(1.0-SSM)/SP
0178          XPU=(1.0-PSURV)*(1.0-SPU)/SP
0179          XPR=(1.0-PSURV)*(1.0-SPR)/SP
0180          GOTO1280
0181      1250 XSM=0.0
0182          XPU=0.0
0183          XPR=0.0
0184      1280 DO1300I=3,22
C          C NO. OF NEWLY PARASITIZED APHIDS OF AGE 3,22 OF BOTH APTERAEE AND ALATAE
C          C DETERMINED
0184          PAREP1(I)=APTRA(I)*(1.0-PSURV)
0185          PAREP2(I)=ALATE(I)*(1.0-PSURV)
C          C THE NO. OF APHIDS ESCAPING PARASITISM
0186          APTRA(I)=APTRA(I)*PSURV
0187      1300 ALATE(I)=ALATE(I)*PSURV
C          C THE NO. OF NEW PARASITES OF EACH SPECIES AGE 1 QUIP DETERMINED
0188          SMITH(I)=TN*XSM
0189          PULCH(I)=TN*XPU
0190          PRAON(I)=TN*XPR
C
C          C UNPARASITIZED APHIDS UPDATED & PREDATION & EMIGRATION APPLIED
0191          TOT=0.
0192          I=92
0193      120 J=I+1
0194          APTRA(J)=APTRA(I)*PREDN
0195          ALATE(J)=ALATE(I)*PREDN
0196          TOT=TOT+APTRA(J)+ALATE(J)
0197          I=I-1
0198          IF(I)130,130,120
0199      130 ALATE(21)=ALATE(21)*EMIG(KA)
C
C          C PARASITIZED APHIDS UPDATED & PREDATION & NATURAL SURVIVAL OF PARASITIZED
C          C APHIDS (S = PREDN*SK) APPLIED
0200          I=40
0201      1120 J=19
0202          IF(I.LT.22)J=I-2
0203          NFIN=I-22
0204          IF(I.LT.22)NFIN=0
0205      1130 PARA(I+1,J+1)=PARA(I,J)*S
0206          PARAL(I+1,J+1)=PARAL(I,J)*S
0207          TOT=TOT+PARA(I+1,J+1)+PARAL(I+1,J+1)
0208          J=J-1
0209          IF(J-NFIN)1140,1140,1130

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0210      1140 I=I-1
0211      IF(I-2)1150,1150,1120
C      EMMIGRATION OF PARASITIZED ALATAE
C      EMIGRATION OF PARASITE JUVENILES AGED 1-10 QUIPS IN PARASITIZED ALATAE AGED
C      21 QUIPS.
0212      1150 DO 32 J=1,10
0213          XX=SMITH(J)+PULCH(J)+PRACN(J)
0214          IF(SMITH(J).EQ.0.0) GO TO 30
0215          SMITH(J)=SMITH(J)-(PARAL(21,J)*(SMITH(J)/XX))
0216          30 IF(PULCH(J).EQ.0.0) GO TO 21
0217          PULCH(J)=PULCH(J)-(PARAL(21,J)*(PULCH(J)/XX))
0218          31 IF(PRACN(J).EQ.0.0) GC TC 32
0219          PRAON(J)=PRAON(J)-(PARAL(21,J)*(PRAON(J)/XX))
0220          32 PARAL(21,J)=0.0
C
C      ADDITION OF NEW INDIVIDUALS (ALATES AND/OR APTERAEE) TO POPULATION
0221      XAL=AX*PROP
0222      ALATE(1)=XAL
0223      APTRA(1)=AX-XAL+A
0224      TOT=TOT+AX+A
C
C      ADD NEWLY PARASITIZED APHIDS WITH EGGS TO PARA MATRIX
0225      DO 1360 I=3,22
0226      PARA(I,1)=PAREP1(I)
0227      PARA(I,1)=PAREP2(I)
0228      1360 TOT=TOT+PAREP1(I)+PAREP2(I)
0229      IF (KA.EQ.KSAM(NS)) GO TO 140
0230      GO TO 500
C
C*****
C      PRINT OUT CURRENT PREDICTED POPULATION LEVELS AT SAMPLE TIMES IN QUIPS FOR
C      DESIGNATED SAMPLE PERIOD (KSAM).
C
C      REMOVE ALL ADULT ALATAE TO MAKE ROOM FOR NEW SAMPLE VALUES
0231      140 DO 42 I=24,93
0232          42 ALATE(I)=0.0
0233          DO 43 I=24,41
0234              DO 43 J=1,20
0235          43 PARAL(I,J)=0.0
C      ADD IMMIGRANT ALATES (PARASITIZED) AS OBSERVED FROM FIELD SAMPLES
0236      IF (PLIMM(NS).EQ.0.0) GO TO 41
0237      DO 40 J=4,13
0238          PARAL(24,J)=PLIMM(NS)/10
0239          SMITH(J)=SMITH(J)+PLIMM(NS)/30
0240          PULCH(J)=PULCH(J)+PLIMM(NS)/30
0241          40 PRAON(J)=PRAON(J)+PLIMM(NS)/30
0242          41 ALATE(24)=ALATE(24)+ALIMM(NS)
0243          NS=NS+1
C      SET WORKING SUMS EQUAL TO ZERO
0244      AL=0.0
0245      A1=0.0
0246      A2=0.0

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0247          A3=0.0
0248          AP=0.
C          UNPARASITIZED APHID STAGES COUNTED
0249          AL4=ALATE(17)+ALATE(18)+ALATE(19)
0250          AP4=APTRA(17)+APTRA(18)
0251          DO145J=1,17
0252          AL4=AL4+PARAL(17,J)+PARAL(18,J)+PARAL(19,J)
0253          145 AP4=AP4+PARA(17,J)+PARA(18,J)
0254          DO 150 I=1,4
0255          A1=A1+APTRA(I)+ALATE(I)
0256          A2=A2+APTRA(I+4)+ALATE(I+4)
0257          A3=A3+APTRA(I+8)+ALATE(I+8)
0258          AL4=AL4+ALATE(I+12)
0259          AP4=AP4+APTRA(I+12)
C          PARASITIZED APHID STAGES CCUNTED & ADDED TO UNPARASITIZED APHID STAGES
0260          DO 150 J=1,14
0261          A1=A1+PARA(I,J)+PARAL(I,J)
0262          A2=A2+PARA(I+4,J)+PARAL(I+4,J)
0263          A3=A3+PARA(I+8,J)+PARAL(I+8,J)
0264          AL4=AL4+PARAL(I+12,J)
0265          150 AP4=AP4+PARA(I+12,J)
0266          DO 160 I=19,93
0267          160 AP=AP+APTRA(I)
0268          DO 161 I=20,93
0269          161 AL=AL+ALATE(I)
0270          NST=I
0271          DO 165 I=20,41
0272          IF(I.GT.22)NST=I-21
0273          DO165J=NST,20
0274          AL=AL+PARAL(I,J)
0275          165 AP=AP+PARA(I,J)
0276          DO 171 J=1,17
0277          171 AP=AP+PARA(19,J)
C          PARASITE IMMATURE STAGES OF EACH SPECIES COUNTED
0278          SMJ=0.
C          PUJ= PULCHER JUVENILES OR IMMATURES, ETC.
0279          PUJ=PULCH(21)+PULCH(22)
0280          PRJ=PRAON(23)+PRAON(24)+PRACN(25)+PRAON(21)+PRACN(22)
0281          APHIDT=PUJ+PRJ
0282          TJ=0.0
0283          DO 172 I=9,41
0284          DO 172 J=3,20
0285          172 TJ=TJ+PARA(I,J)+PARAL(I,J)
0286          TJ=TJ+PUJ+PRJ
C          SMH= SMITHI MUMMIES, ETC.
0287          SMH=SMITH(21)+SMITH(22)+SMITH(23)+SMITH(24)+SMITH(25)
0288          PUM=PULCH(30)+PULCH(31)+PULCH(23)+PULCH(24)+PULCH(25)
0289          PRM=PRACN(32)+PRACN(33)+PRACN(34)+PRAON(30)+PRAON(31)
0290          DO 180 I=26,29
0291          SMH=SMH+SMITH(I)
0292          PUM=PUM+PULCH(I)
0293          180 PRM=PRM+PRAON(I)

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0294          TM=SMM+PUM+PRM
0295          APHIDT=APHIDT+A3+AL4+AP4+AP+AL
C          RATIOS OF PARASITES VS APHIDS
0296          IF (TJ.EQ.0.0) GO TO 223
0297          P1=TJ/APHIDT
0298          GO TO 226
0299          223 P1=0.0
0300          226 IF (TM+TJ.EQ.0.0) GO TO 224
0301          P2=(TM+TJ)/(APHIDT+TM)
0302          GO TO 227
0303          224 P2=0.0
0304          227 IF (TM.EQ.0.0) GO TO 225
0305          P3=SMM/TM
0306          P4=PUM/TM
0307          P5=PRM/TM
0308          GO TO 222
0309          225 P3=0.0
0310          P4=0.0
0311          P5=0.0
0312          222 WRITE(6,200)KA,A1,A2,A3,AP4,AL4,AP,AL,TCT,FRCP,TJ,TM,
          1P1,P2,P3,P4,P5,P6
0313          200 FORMAT(' ',I3, 8F7.3,F5.2,2F7.3,6F6.3)
0314          500 CONTINUE
0315          STOP
0316          END

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## CURRICULUM VITAE

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## EDUCATION

1950 - 1958. Elementary schools in Hong Kong; Hawkhurst Court Preparatory School, Petworth, England.

1958 - 1962. Clayesmore Public School, Iwerne Minster, Blandford Forum, Dorset, England.

1963 - 1967. Macdonald College of McGill University, Montreal Undergraduate programme in Biology with emphasis on entomology and ecology. Graduated with B.Sc. (Agriculture) Honours.

1967 - 1969. The Entomology Department, University of Manitoba, Winnipeg, Manitoba. M.Sc. programme in entomology with emphasis on insect behaviour and ecology.

M.Sc. Thesis title: The predatory behaviour of the larvae of *Colymbetes sculptilis* (Harris) and *Graphoderus occidentalis* Horn. (Coleoptera: Dytiscidae).

1969 - 1973. Doctoral programme in the Pestology Centre of the Department of Biological Sciences, Simon Fraser University.

## AWARDS

1967 - 1969. University of Manitoba Fellowship.

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## RESEARCH EMPLOYMENT

Summer 1964. Collecting insects for the Lyman Museum, Macdonald College of McGill University, Ste. Anne de Bellevue, Quebec. (Dr. V. R. Vickery, Curator, Lyman Museum, Macdonald College.)

Summer 1966. Ecological study of wood and grassland area by identifying animal tracks on sand lanes. (Dr. J. R. Bider, Macdonald College.)

## TEACHING EXPERIENCE

Teaching Assistant in the following courses at Simon Fraser University:

Fall 1969, 1971, 1972. BiSc 003-3, "Human Ecology and the Population Explosion".

Fall 1970. BiSc 304-3, "Animal Ecology".

Spring 1971, 1972. BiSc 407-3, "Population Dynamics".

## SOCIETIES

1. Canadian Society of Zoologists
2. Entomological Society of America
3. Entomological Society of Canada
4. Entomological Society of British Columbia

## PUBLICATIONS

Mackauer, M. and A. Campbell. 1972. The establishment of three exotic aphid parasites (Hymenoptera: Aphidiidae) in British Columbia. *J. ent. Soc. Brit. Columbia* 69: 54-58.

Campbell, A. and M. Mackauer. 1973. Some climatic effects on the spread and abundance of two exotic pea aphid parasites in British Columbia (Hymenoptera: Aphidiidae - Homoptera: Aphididae). *Z. angew. Ent.* 73 (in press).

## PAPERS PRESENTED AT MEETINGS

"The predatory behaviour of *Colymbetes sculptilis* (Harris) and *Graphoderus occidentalis* Horn. (Coleoptera: Dytiscidae)". Annual Meeting of the Entomological Society of Canada, 24-26 August, 1970, Winnipeg.

"The parasite complex of the pea aphid in southern British Columbia". Joint Meeting of the Entomological Society of British Columbia and the Pacific Branch of the Entomological Society of America, 20-22 June, 1972, Victoria, B.C.