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INTER- AND INTRASPECIFIC VARIATION IN INTRODUCED AND NATIVE PARASITES (HYMENOPTERA: APHIDIIDAE) OF THE PEA APHID IN NORTH AMERICA: LIFE HISTORY TRAITS, THERMAL COEFFICIENTS AND MORPHOLOGY

by

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THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

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in the Department

of

Biological Sciences

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SIMON FRASER UNIVERSITY

October 1987

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ABSTRACT

This study was a first attempt to investigate, *a posteriori*, the possible reasons for the continent-wide decline of *Aphidius smithi* Sharma & Subba Rao, an introduced parasite of the pea aphid in North America. Two hypotheses, among many possible, were tested. First, because *A. smithi* was established with small founder populations, it was hypothesized that the resulting genetic impoverishment may have precluded its long-term establishment. To test this, divergence levels in quantitative characters among three populations each of two introduced species, *A. smithi* and *Aphidius ervi* Haliday, were compared with each other and with those among three populations of a native species, *Praon pequodorum* Viereck, to detect any evidence of random genetic drift. Second, because *A. ervi* rapidly became the dominant species of the pea aphid subsequent to the decline of *A. smithi*, the possibility of displacement due to differences in life history traits was tested.

Intraspecific studies indicated that the divergence level between populations of the two introduced species did not consistently differ from each other. But the distance between any two populations of the introduced species was consistently greater than that between corresponding populations of the native species in both life history and morphological traits, suggesting drift of alleles affecting these two characters. The results suggest the possibility of drift of other alleles which may have also contributed to the decline of *A. smithi*. The drift does not appear to have affected the establishment of *A. ervi*, probably because of larger and more diverse founder populations. In addition, *A. ervi* appears to possess a "general purpose" genotype as evidenced by its predominance of the parasite guild of aphids infesting alfalfa in a wide range of climates. Both these factors may have enabled it to overcome any deleterious effects on adaptation of random genetic drift.

Interspecific comparison of life history traits indicated that *A. smithi* is superior, or at least at no obvious disadvantage, relative to *A. ervi*, *Aphidius pisivorus* Smith or *P. pequodorum*. It had a higher fecundity, a shorter developmental time and generally performed better than any of the above species under the experimental conditions. This suggests that differential reproductive capacity and thermal coefficients did not contribute significantly to the decline of *A. smithi*. The protocol for the introduction, and the dynamics of pea aphid parasites in North America, suggest a strong need for pre- and post-release studies on introduced biological control agents.

QUOTATION

"There as successive generations bloom,
New powers acquire and larger limbs assume,
Whence countless groups of vegetation spring,
And breathing realms of fur and feet and wing."

Erasmus Darwin

DEDICATION

To my parents, for bringing me into this world.

ACKNOWLEDGEMENTS

I wish to express my gratitude to my senior supervisor, Dr. M. Mackauer, for his patience, guidance and encouragement. I appreciate the opportunity to learn from him. Without his insightful advice, this thesis would not have been possible. I also thank Drs. B.D. Roitberg and M.L. Winston for their critical views on the project, which kept me on my toes.

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I thank faculty and colleagues in the Department for moral support and sharing numerous beers in the process. I especially thank Dr. F.J. Chow, Mr. M.B. Cohen, Mr. R.G. Foottit, Dr. M.R. Gross, Dr. K.K. Nair, Mr. J.P. Panno, Ms. S.T. Sharp and Dr. R.D. Ydenberg for valuable discussions and help. The help and generosity of staff of the Department and the Computing Services is appreciated.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

GENERAL INTRODUCTION

Sustained or long-term establishment of introduced natural enemies is one of the goals of classical biological control of insect pests (Coppel and Mertins 1977, DeBach 1964). Once implemented, biological control is expected to provide pest population regulation for a number of years, with little or no further human input. However, as in many natural colonizations (Mayr 1965), some introduced natural enemies may decline after an initial flush phase (DeBach 1965, Turnbull and Chant 1961). By contrast, other species may increase in relative abundance from initially low densities after a few years. Although many explanations have been given for such changes (e.g., DeBach 1965), very few cases have in fact been studied in detail (e.g., DeBach and Sundby 1963, Kfir and Luck 1984, Luck *et al.* 1982). In order to understand the dynamics of introduced species and therefore make success of introductions more predictable, there is a need to examine the factors underlying such changes. In this study, I shall attempt to identify, *a posteriori*, the possible reasons for changes in the relative abundance of parasites of the pea aphid in North America that occurred after the introduction of several species from Europe and India.

1.1 History of the pea aphid and its parasites in North America

The pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), was inadvertently introduced into North America from Europe early in the 19th century (Halfhill *et al.* 1972). The first damaging populations were noticed in the late 1800s. By 1900, the aphid had spread from the eastern seaboard to Wisconsin and, by 1926, to the Pacific coast and to parts of Canada and Mexico (Hagen *et al.* 1976). The pea aphid, on occasion, is considered a pest of alfalfa (*Medicago sativa* L.), peas (*Pisum sativum* L.), and some other Leguminosae in North America (Campbell 1974).

A number of native parasites, including *Aphidius pisivorus* Smith, *Ephedrus californicus* Baker, *Monoctonus paulensis* Ashmead, *Praon occidentale* Baker, *Praon pequodorum* Viereck (Hymenoptera: Aphidiidae), and *Aphelinus semiflavus* Walker (Hymenoptera: Aphelinidae) were reported to parasitize the pea aphid in North America early in this century, although some identifications may be questionable (Halfhill *et al.* 1972, Mackauer and Finlayson 1967). Some of these parasites were possibly accidentally introduced from Europe together with their host, whereas others are native to North America. The general consensus among early workers was that these parasites had little or no impact on pea aphid populations (Halfhill *et al.* 1972).

To supplement the native parasite species, a number of aphidiids were introduced into North America: *Aphidius avenae* Haliday, *Aphidius ervi* Haliday, *Aphidius medicaginis* Marshall, *Aphidius smithi* Sharma & Subba Rao, and *Aphidius urticae* Haliday (Clausen 1978). Of these, only *A. smithi* and *A. ervi* are known to have become established. *A. medicaginis* was later identified as *A. ervi* (Unruh *et al.* 1986).

A. smithi was imported from India in 1958. The original samples consisted of two shipments, collected at one location in northwestern India and shipped to the U.S.A. at about the same time. One sample was sent to California and subsequently used for releases in western North America; it consisted of 5 males and 4 females (Dr. K.S. Hagen, pers. comm.). The second shipment was received in New Jersey and included 17 females and an unknown number of males (Angalet and Coles 1966); it served as a source for releases in eastern North America. In order to produce a large number of parasites for field release, these samples were expanded by insectary propagation between 1958 and 1960. *A. smithi* became readily established at all release sites in California (van den Bosch *et al.* 1966, 1967, Hagen and Schlinger 1960). Releases were also made during the same period from Maine to Florida

in the eastern U.S.A., in Colorado, and in the Pacific Northwest (Clausen 1978). The first evidence of *A. smithi's* establishment in eastern North America was obtained by Mackauer and Bisdee (1965a), who found the parasite in southern Ontario. They suggested that *A. smithi* may have immigrated from the U.S.A. through either the Niagara Peninsula or the Upper St. Lawrence River area. Surveys carried out in the early 1960s in eastern North America revealed that *A. smithi* was the most common pea aphid parasite west of longitude 80° W, but *A. pisivorus* was generally dominant east of that line (Mackauer 1971).

After an apparently successful establishment, *A. smithi* started to decline in relative abundance in eastern North America and was virtually extinct by the early 1970s. Campbell and Mackauer (1973) suggested that neither a presumed inability to survive the low winter temperatures as proposed by Hagen and Schlinger (1960), nor direct competition with native or other introduced parasites, shown to be unlikely by Mackauer (1971), could satisfactorily account for the parasite's gradual decline and apparent extinction.

A. smithi colonized western Canada probably from Washington and Idaho and was found in British Columbia and Alberta in 1965 (Mackauer and Campbell 1973, Mackauer and Finlayson 1967). In British Columbia, it constituted 22% of the total parasite population in 1969, and 80% in 1971 in the Kamloops area. Over the same period, the relative abundance of *A. pisivorus* declined from 51.6% to 11.5% and that of *P. pequodorum* from 26.4% to 8.2% (Campbell 1974). Recent surveys of alfalfa fields in the southern Interior, however, indicated that *A. smithi* represents less than 1% of the pea aphid parasite population (Mackauer and Kambhampati 1986). A similar decline of *A. smithi* to less than 10% of the total parasite population was reported from California (Gonzalez *et al.* 1978).

The second exotic parasite, *A. ervi*, was imported from various locations including France, West Germany, Spain and Sweden, and was released in North America between 1959 and 1981 (Dr. R.W. Fuester pers. comm.). The importation consisted of a total of 36 shipments which yielded 9148 males and females. Most of the releases, however, took place in the eastern U.S.A. between 1959 and 1968 and in the western U.S.A. between 1961 and 1964 (Halfhill *et al.* 1972, Stary 1974). Although *A. ervi* became well established, it stayed at relatively low densities at most release sites (Hagen *et al.* 1976, Halfhill *et al.* 1972). Subsequent to the decline of *A. smithi* in eastern North America, *A. ervi* became the most common parasite of the pea aphid.

A. ervi was found in British Columbia for the first time near Kamloops in 1970, presumably as a result of immigration from release sites in the U.S.A. It remained at relatively low levels in the Interior, constituting less than 1% of pea aphid parasites between 1970 and 1972 (Campbell 1974). However, *A. ervi* constituted between 70% and 80% of the parasite population in the coastal regions of British Columbia and Washington state (Campbell 1974). Surveys conducted between 1983 and 1985 in the Interior and the coastal region of British Columbia revealed that *A. ervi* is the most common pea aphid parasite constituting between 80–85% and between 98–100% of the parasite populations, respectively (Mackauer and Kambhampati 1986). At present, *A. ervi* is the most common pea aphid parasite in virtually all of North America (Gonzalez *et al.* 1978, Mackauer and Kambhampati 1986, Mertins 1985, Dr. R.W. Fuester, pers. comm.). Changes in relative abundance of several pea aphid parasite species in British Columbia are summarized in Appendix I.

Although many cases are known in which established exotic parasites subsequently declined in numbers, these changes were usually confined to localized areas (e.g., DeBach

1965, DeBach and Sundby 1963, Turnbull and Chant 1961). A unique feature of the pea aphid parasite complex is the fact that the changes in relative abundance have taken place on a continent-wide basis, apparently with a lag time between changes in eastern and western North America. A number of factors such as genetic impoverishment, differential reproductive potential and host utilization, extrinsic and intrinsic competitive ability, climatic adaptedness etc., may have contributed either singly or in combination to the decline of *A. smithi*. The first and second of the above factors are examined in this thesis.

1.2 Founder effects

In nature, new populations are often established by a small group of emigrants (Mayr 1965, Hartl 1980). The genetic consequences of such founding events are known collectively as founder effects. The genetic variation in the new population is initially limited to those alleles that are present in the founders and, thus, the variation may not necessarily be representative of that in the parent population. Erratic changes in gene frequency due to random genetic drift and linkage disequilibrium may also ensue (Wright 1949). Loss or fixation of alleles is disadvantageous to the population when a rapid adaptation to the new environment is required, as is the case with species introduced for biological control, and may lead to eventual extinction (Nei *et al.* 1975). Experimental and theoretical evidence for founder effects is available in the literature for both plants and animals (e.g., Avise and Selander 1972, Barton and Charlesworth 1984, Bonnell and Selander 1974, Bryant *et al.* 1986a, 1986b, Carson and Templeton 1984, Chakraborty and Nei 1978, Haigh and Maynard Smith 1962, Lewontin 1974, Prakash 1972, 1973, 1977, Prakash *et al.* 1969, Rich *et al.* 1984, Schwaegerle and Schaal 1979, Selander and Kaufman 1973, Taylor and Gorman 1975).

As in natural colonizations, deliberate introductions for the purpose of biological control often involve small founder populations, as in the case of *A. smithi*, and to a lesser extent, *A. ervi*. Before release, the initial sample is propagated in insectaries for a few generations where further loss of alleles and inadvertent selection may take place (Mackauer 1981). All these factors may contribute to the decline of introduced biological control agents. Founder effects, however, may not be apparent depending on the size of the founding population, the rate of population growth and the mutation rate subsequent to the founding event (Chakraborty and Nei 1978, Nei *et al.* 1975).

Considering the evidence for genetic consequences of founding events, and the protocol for the introduction of pea aphid parasites, it is possible that populations of *A. smithi* were subjected to founder effects, which in turn, may have led to their decline. Random genetic drift, one of the more common phenomenon in founder populations, is generally studied by comparing after many generations, the divergence levels between a number of populations derived from a small number of founders with those between populations derived from a large number of founders. Greater divergence between the populations derived from a small number of founders relative to those derived from a large number of founders is taken as indirect evidence of drift (see, e.g., Bonnell and Selander 1974, Bryant *et al.* 1986a, 1986b, Dobzhansky and Pavlovsky 1957, Rich *et al.* 1979, 1984, Schwaegerle and Schaal 1979, Templeton 1980). This is because random genetic drift may cause large fluctuations in allele frequency between different generations ultimately leading to loss or fixation of alleles (Hedrick 1983). In a large, well-established population, the allelic frequencies are relatively stable over time. At a given sampling time, then, replicate populations established with a small number of founders may display a greater variation in character means between populations, relative to those established with a large number of founders. For this part of the study, I carried out

a comparison of divergence levels between populations of the introduced parasites of the pea aphid, established recently with a small number of founders, and native parasites, which had been in North America for a long period of time, to detect evidence, if any, of random genetic drift in the former.

The first objective of this thesis, then, was to measure geographic variation in quantitative characters and to compare divergence levels between populations of the introduced and the native parasites of the pea aphid in North America. As a result of small founder populations, it is conceivable that populations of the introduced species may exhibit a different degree of genetic variation relative to populations of the native species. In addition, populations of introduced species established with a smaller number of founders (i.e., *A. smithi*) may exhibit a different degree of genetic variation relative to that among populations of introduced species established with a larger number of founders (i.e., *A. ervi*). In either case, measurable and consistent differences in divergence levels may be taken as indirect evidence of random genetic drift.

I.3 Reproductive attributes

Although it is known that *A. ervi* became the most common parasite of the pea aphid fairly rapidly after the decline of *A. smithi*, it is less certain if the former species competitively displaced the latter, or simply moved into an empty niche. If *A. smithi* was competitively displaced, differential reproductive potential and/or thermal coefficients could have been one of the contributing factors. Some of the characters that define the reproductive attributes of a parasite include average fecundity, searching efficiency, host utilization efficiency, etc.; characteristics that can be measured and compared among members of a parasite guild

attacking the same host or host complex (Coppel and Mertins 1977, Mackauer 1983).

The second part of this thesis is concerned with examining in detail the possibility that the decline of *A. smithi* (or the increase of *A. ervi*) was a consequence of measurable differences in reproductive attributes and thermal coefficients that could be considered important in the field dynamics of pea aphid parasites, e.g., host utilization, searching efficiency, oviposition rates, developmental times and threshold temperatures. In spring, when pea aphids on alfalfa are relatively scarce (Campbell 1974), searching efficiency and threshold temperatures are probably more important than total clutch size. In summer, however, when hosts are usually abundant, average fecundity and relative developmental times may determine the relative abundance of a species.

Ideally, to compare parasite performance and host utilization, the functional response of parasite females to various host densities must be known. Because a large number of populations were involved in my studies, I decided instead to assess the performance characteristics of each population at one, reasonably high host density. Attributes that directly or indirectly indicate reproductive potential and host utilization efficiency can be measured with ease in the laboratory under controlled conditions. For example, Force and Messenger (1964) assessed the intrinsic rate of increase of *Trioxys complanatus* Quilis Perez, *Praon exsoletum* (Nees) and *Aphelinus asychis* Walker, all parasites of the spotted alfalfa aphid, *Therioaphis trifolii*, (Monell) at different temperatures. Force and Messenger (1965) also carried out laboratory studies on competition in these three species of parasites. Kambhampati *et al.* (1987) and Mackauer (1983) quantified the performance, host utilization and other life history traits of *A. smithi* as affected by host density. The results of all these studies indicate that many performance criteria measured in the laboratory can be used as indices of parasite

performance. Other laboratory studies that quantify parasite performance and host utilization of aphidiids include those of Chua (1979), Cloutier (1984), Cloutier *et al.* (1984), Collins *et al.* (1981), Dransfield (1979), Force and Messenger (1968), Hart *et al.* (1978), Messenger (1968), and Shirota *et al.* (1983). Although laboratory evaluation can be a useful tool in comparing reproductive characteristics of various parasite species, caution should nevertheless be exercised in extrapolating such data to field performance (Mackauer and van den Bosch 1973).

The second objective of this thesis therefore, was to compare, under laboratory conditions, the various life history traits, including reproductive potential, parasite performance, host utilization and thermal coefficients, between species within the pea aphid parasite complex from different regions, to determine if *A. smithi*'s decline in numbers could be attributed to differential reproductive potential and/or thermal coefficients.

CHAPTER II

GENERAL MATERIALS AND METHODS

2.1 Collection and rearing of insect material

Aphids: Pea aphids used in the experiments were collected on alfalfa at the Agriculture Canada Research Station in North Kamloops in 1972. Large stock colonies of the aphid were maintained in the laboratory on potted broad beans, (*Vicia faba* L., cv. "Broad Windsor"). The bean plants were grown in "Garden Mix" soil with 6–7 seeds per 12.6 cm pot. The cultures were kept at 19–20 °C, 55–60% R.H., and a 16h L: 8h D photoperiod to maintain the aphids in a parthenogenetic, viviparous condition. The aphids were transferred to fresh bean plants once every week.

To obtain a cohort of even-aged aphids for experiments and for rearing of parasite material, about 200 reproductive aphids were caged on a pot of broad bean plants for 8h. After that period, adults were removed from the plants. Thus, all the nymphs that were produced were within ±4h of one another in age. The nymphs were then reared at 20±1 °C until needed.

Parasites: Laboratory colonies of pea aphid parasites used in this study were established from field collected material. Populations from a given area were collected from a single, cultivated alfalfa field. The Chilliwack alfalfa field is located near the Fraser River. It was about 2.5 ha in size and was usually under an alfalfa monoculture. Populations from Kamloops were collected in an alfalfa field on the property of the Agriculture Canada Research Station in North Kamloops. Sussex populations were obtained from laboratory colonies at Fordham University in New York, U.S.A. These parasites were originally collected in an alfalfa field near Sussex, Sussex County, New Jersey, U.S.A.

Pupal stage of the parasite inside a mummy was collected in the field and brought back to the laboratory. The mummies were individually placed in gelatin capsules (Parke Davis, #00) and adults were allowed to emerge in a growth chamber at 20±1 °C. Because the color of the parasites is influenced by the temperature regime under which they complete development, identification of field collected parasites to the species level is often difficult and sometimes unreliable. To overcome this problem, a male and a female, presumed to be conspecifics, were allowed to mate and the progeny of each such pair was raised under known, controlled conditions. For each species, 20 such pairs were set up. A small proportion of the progeny was killed and prepared for scanning electron microscope identification according to the key provided by Marsh (1977). After identification to the species level, conspecifics obtained by the above prodcedure were merged to establish a laboratory culture.

Stock colonies of parasites were maintained in plexiglass rearing cages (33 x 34 x 44 cm) fitted with fine mesh. To avoid contamination among various species and populations during rearing, cultures were kept temporally and spatially segregated. All colonies were maintained at 20–22 °C, 55–60% R.H., and 24h light. About 200 third-instar (3–4 day-old) nymphs of the pea aphid were exposed to 20–25 female parasites overnight in wax paper cups (9.5 x 11 cm). The parasites were then removed and the aphids were placed on bean seedlings. Two such cups were set up once approximately every two weeks for each species and population. The mummies, which formed after about 9 days under the rearing conditions, were collected by gently scraping them off the leaves. They were placed in wax paper cups with a 9 cm plastic Petri dish lid, and the adults were allowed to emerge. The adults were fed a 50% honey solution ("Heavenly Honey", S.F.U.) streaked on the inside of the lid. They were allowed to mate for two days, after which the whole process was repeated. All colonies were maintained at an average size of about 300–500 insects.

2.2 Experiments

All experiments were undertaken soon after the cultures of the parasites were well established in the laboratory, usually after about 5 generations. Small plastic cages, such as those described by Mackauer and Bisdee (1965b), were used for rearing field collected material and for replicating experiments. Depending on the experiment, two sizes of cages were used: 8.5 cm diameter x 3.5 cm high, or 15.5 cm diameter x 4 cm high. The cages were fitted with fine mesh covers and had a 1.5 cm hole in the side wall. A broad bean or an alfalfa shoot was inserted in the hole and held in place with non-toxic plasticine, which also sealed the hole. The cage was then placed on top of a milk bottle containing fresh tap water, so that the cut end of the plant shoot was immersed in water.

Experiments and rearings requiring controlled temperature, humidity, and photoperiod were conducted in a "Conviron" Model E15 growth chamber (Controlled Environments, Winnipeg, Manitoba). Temperature inside the plastic cages was monitored with a "Keithly" Model 871 digital thermometer, with a probe (Keithly Instruments Inc., Cleveland, Ohio, U.S.A.).

2.3. Study areas

As stated earlier, populations of pea aphid parasites were obtained from three geographic areas. Each area has a unique history of pea aphid parasite introduction/colonization and relative abundance.

Chilliwack, British Columbia (49.10° N, 121.57° W): This area is characterized by a mild, wet coastal climate. Some alfalfa is grown here and the pea aphid occurs on alfalfa, peas and wild clover. *A. ervi* has been the most common pea aphid parasite since the late 1960s

(Campbell 1974, Mackauer and Kambhampati 1986). *A. pisivorus*, *A. smithi* and *P. pequodorum* are rare. Species collected: *A. ervi*, *A. smithi*, *P. pequodorum*.

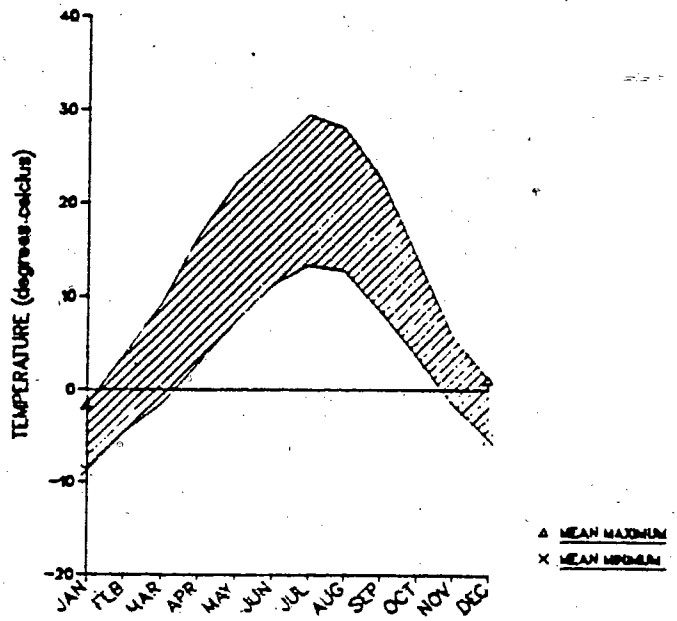
Kamloops, British Columbia (50.40° N, 120.20° W): Kamloops and vicinity is the major alfalfa-growing area in British Columbia. Hot summers and cold winters characterize the Kamloops area. Precipitation, both rain and snow, is low. Four species of pea aphid parasites are found here, namely *A. ervi*, *A. pisivorus* and *A. smithi* and *P. pequodorum* (Campbell 1974, Mackauer and Kambhampati 1986). *A. smithi* was the most common parasite from the early 1970s to probably the late 1970s. Since then *A. ervi* has been the most common species. Species collected: *A. ervi*, *A. pisivorus*, *A. smithi*, *P. pequodorum*.

Sussex, New Jersey (41.13° N, 74.37° W): Sussex and vicinity is predominantly an agricultural area. The summers are moderately hot and the winters very cold. Precipitation is moderate. New Jersey was one of the many eastern states in the U.S.A. where large scale releases of *A. smithi* and *A. ervi* were made. *A. smithi* was presumably the most common pea aphid parasite in this region until about 1970-71. Later, *A. ervi* became the most common parasite with rare occurrences of *P. pequodorum*. *A. pisivorus* and *A. smithi* are probably extinct. Species collected: *A. ervi*, *P. pequodorum*.

Climatographs for each of the three study areas are shown in Figure 1.

FIGURE 1: Long term averages of temperature (1950–1981) and precipitation for the three study sites. (a): Mean annual maximum and minimum temperature in Kamloops, (b): Mean annual maximum and minimum temperature in Chilliwack, (c): Mean annual minimum and maximum temperature in Sussex, (d): Mean monthly precipitation in Kamloops, Chilliwack, and Sussex.

(a)


TEMPERATURE (degrees celcius)
40
30
20
10
0
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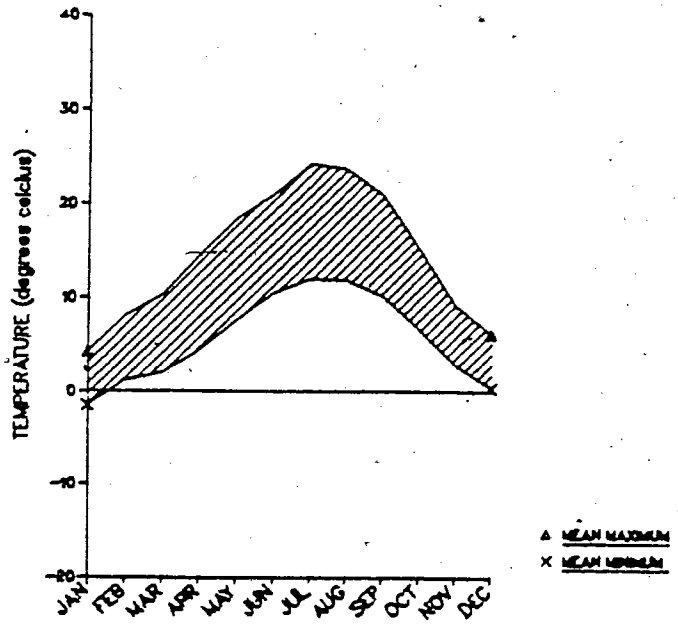
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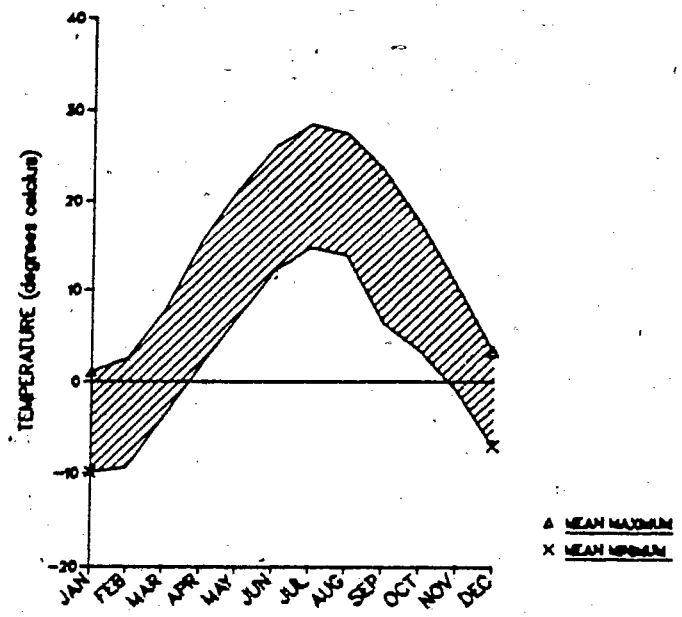
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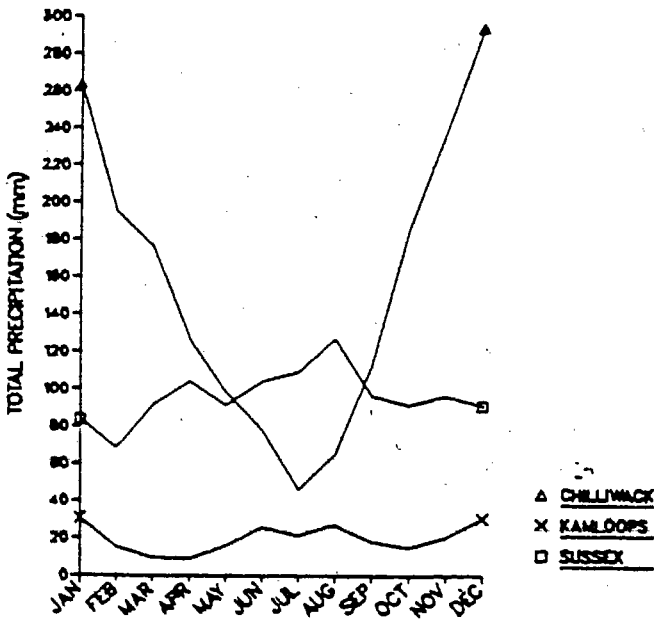
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CHILLIWACK
KAMLOOPS
SUSSEX

2.4 Characters studied

Three broad categories of characters were quantified to study inter- and intraspecific variation among pea aphid parasites. The importance of each of these character groups to biological control is discussed in respective chapters.

1. **Life history traits:** These included lifetime fecundity and longevity, parasite performance and host utilization patterns, life table statistics, and analysis of frequency distribution of eggs, all measured at a host density of 40 aphids per day per female.

2. **Temperature requirements:** This category included developmental time from egg to adult emergence at four constant temperatures, lower threshold temperature for development, and degree days required to complete development from egg to adult.

3. **Morphology:** Variation in morphology was quantified using morphometric techniques. For each parasite female, 34 morphological characters were measured.

CHAPTER III

VARIATION IN LIFE HISTORY TRAITS

3.1 Introduction

Life history traits of an organism are defined by three primary characters, namely, survival probability, fecundity, and development time and they can jointly be thought of as being synonymous with fitness (Istock 1981). Any other behavioral and physiological adaptations that directly or indirectly influence the primary life history traits are implicit in the above definition. Secondary characters that may influence one or more of the above primary characters in protelean parasites include host utilization, intrinsic and extrinsic competitive ability, and host discrimination ability.

In general, there is considerable variation in life history traits among populations of a species (Mayr 1970). Spatially segregated populations are presumed to be adapted to, or shaped by, their local abiotic and biotic environment. Life history traits and polygenic variation in fitness characters provide selection regimes and essential raw material for microevolution (Istock 1981). Physical extremes of a locality set the ultimate constraints on seasonal rate of reproduction and population growth. Within these limits, interspecific interactions (e.g., occurrence of hosts, natural enemies and competitors) and intraspecific interactions (e.g., occurrence of mates) may also shape a species' life history pattern (Tauber and Tauber 1982). Variation, of course, is also limited by an organism's genotypic plasticity. The interaction between the environment and the genetic plasticity of an organism determines the life history pattern. In some cases, such variation between populations may lead to reproductive isolation and to speciation.

Life history traits and parasite performance characteristics can be useful tools for evaluating biological control agents. It has been suggested (see, e.g., Coppel and Mertins 1977, DeBach 1964, Huffaker 1971, Huffaker and Messenger 1976) that a high reproductive potential

is one of the desirable attributes of a candidate biological control agent. Once an introduced parasite becomes established, reproductive potential may play a role in its effectiveness as a biological control agent.

This chapter has two objectives. (1) To quantify geographic variation in life history traits of pea aphid parasites and compare the degree and pattern of variation among populations of the introduced species with that among populations of the native species. I will use discriminant function analysis and generalized distance analysis to compare on a multivariate basis, the divergence levels between populations of the introduced and the native species. (2) To interspecifically compare parasite performance criteria and host utilization patterns to determine if the decline of *A. smithi* and the relative abundance of pea aphid parasites in the field could be attributed to reproductive characteristics. To this end, several performace criteria derived from the egg distribution data will be used to draw conclusions regarding interspecific differences in reproductive potential, host utilization, searching efficiency and oviposition rates. I will compare these criteria on a univariate and a multivariate basis.

3.2 Materials and methods

3.21 Experiments

A colony of parasites ,was established using third-instar pea aphids as described in Chapter II to obtain a cohort of parasite females for use in the fecundity experiments. Upon emergence, an unbiased sample of 0-24h old adult parasites was collected from the cohort. It was ensured that all females intended for use in the experiments were mated. After mating, the females were placed in a wax paper cup with 50% honey solution streaked across a Petri dish lid until needed.

Reproductive attributes of pea aphid parasites were determined at a host density of 40 aphids per day per female. This host density was chosen because at ≥40 aphids/day/female, the fecundity and oviposition rate of *A. smithi* are not measurably influenced by host density (Mackauer 1983). Experiments were performed in small plastic cages (15.5 cm diameter x 4.0 cm high) which enclose the apical portion of a young broad bean shoot as described in Chapter II. All experiments were conducted at 23.5±1 °C inside the cage (20.5 °C ambient), 55-60% R.H., and a 16h L: 8h D photoperiod in a "Conviron" controlled environment chamber. A cohort of forty 2-3 day old aphids, obtained from a synchronous colony (Chapter II), was introduced into each cage with the help of a moist camel hair brush on the day preceding the introduction of parasites. This enabled the aphids to settle freely on bean shoots. Mated female parasites were introduced into replicate cages and were not provided with any supplementary food but had free access to aphid honeydew and plant secretions. The aphids were exposed to parasites for a period of 24h, after which the parasites were transferred to new, identical cages. This was continued until all parasite females in the experimental cohort died. The exposed aphids were allowed to develop for a further 72h. This

enabled the parasite progeny to develop to late embryonic stage or first larval instar and ensured easy recognition within the aphids, which were preserved in 70% alcohol and subsequently dissected. For each individual parasite female, number of eggs laid per aphid and per day was estimated by dissecting an unbiased sample of 20 aphids from the original 40 aphids under a dissecting microscope. Parasites that did not survive a minimum of 4 days (age of peak reproduction; Mackauer 1983), or those that escaped or were injured during the experiment, were not included in the analysis (see Appendix II for details).

3.22 Data analysis

Because of the optimal conditions under which the fecundity experiments were performed, it is likely that parasites had a longevity (and therefore reproductive potential) that is greater than what is generally realized in the field (Gilbert and Gutierrez 1973, Mackauer 1983). Some adjustment should thus be made to obtain a more realistic estimate of a parasite's reproductive potential. For this purpose, in addition to lifetime fecundity and longevity, another criterion was used to compare the reproductive potential of various parasite species and populations i.e., period of intensive egg laying (PIEL). PIEL was defined by Mackauer (1983) as the time from day one of adult life (which is the age of first reproduction in aphidiids) to that day in each parasite's life when oviposition showed a marked decline and one half or more of the available aphids escaped parasitism. A number of PIEL performance criteria that indicate general parasite performance and host utilization patterns were also derived from the fecundity data for each individual parasite (after Mackauer 1983). This enabled a multivariate comparison of the performance of the various species and populations. The variables are shown in Table I.

Table I: Code names and description of performance criteria derived from the fecundity data pertaining to period of intensive egg laying (PIEL). See text for details.

Code name	Description
1. PIELL	Length of period of intensive egg laying
2. PIELFEC	Total fecundity during PIEL
3. FOUR	Number of eggs laid in the 1st four days
4. PFOUR	Proportion of eggs laid in the 1st four days
5. NAPHIDS	Number of aphids parasitized
6. PAPHIDS	Proportion of aphids parasitized
7. EGGS	Number of aphids parasitized per egg laid
8. NESCAPE	Number of aphids escaping parasitism
9. PESCAPE	Proportion of aphids escaping parasitism
10. SUPER	Proportion of aphids superparasitized
11. NWASTE	Number of eggs lost due to superparasitism
12. PWASTE	Proportion of eggs lost due to superparasitism
13. MEANEGGS	Mean number of eggs laid per aphid
14. MEANDAY	Mean number of eggs laid per day

Each of these variables was initially analysed by one-way analysis of variance (ANOVA) and Student-Newman-Keul's (SNK) test to ascertain if any discernible inter- and intraspecific trends were evident in the data. I used the multivariate procedure, multiple discriminant analysis (MDA), which includes discriminant function analysis and generalized distance analysis, to determine the the divergence levels between populations as well as to compare the various species. Detailed accounts of, and mathematical basis for, discriminant analysis can be found in Blackith and Reyment (1971), Cacoullos (1973), Cooley and Lohnes (1962), Klecka (1981), Lachenbruch (1975) Reyment *et al.* (1984) and Sneath and Sokal (1973).

ANOVA and MDA were performed using SPSS (and SPSSx) subprograms ONEWAY and DISCRIMINANT (Nie *et al.* 1975, SPSS Inc. 1983) and BMDP subprogram 3D (Dixon 1981). Most other analyses were done using either SPSS, SPSSx, BMDP or computer programs written in FORTRAN. All analyses were run on Simon Fraser University's IBM 3033 computer system. Unless otherwise stated, statistical significance was assessed at a probability level of 5%.

3.3 Results

3.31 Fecundity and longevity

Intraspecific comparisons: The fecundity of pea aphid parasites varied considerably among populations of a species (Table II, Appendix II). Average fecundity of *A. ervi* females at Chilliwack, Kamloops and Sussex was estimated as 361.8, 283.7 and 582.8 eggs/female respectively. The lifetime fecundity of the Chilliwack and Kamloops populations did not differ significantly from each other. Fecundities of these two populations were, however, significantly different from that of the Sussex population. Females of *A. smithi* at Chilliwack had an average fecundity of 666.9 eggs/female, whereas fecundity for the Kamloops population was estimated as 734.8 eggs/female. Difference in fecundity between the two *A. smithi* populations was not significant. Among *P. pequodorum* populations, the Chilliwack females had the highest average fecundity (635.0 eggs/female) followed by Kamloops (520.0) and Sussex (440.0). Mean fecundity of the Kamloops population was not significantly different from that of either Chilliwack or Sussex population. Chilliwack and Sussex populations of this species, however, differed significantly from each other.

In summary, the fecundity of populations of a given species at Chilliwack and Kamloops did not differ from each other. Populations at both these areas, however, differed from the Sussex population. No discernible regional trends were apparent in mean total fecundity of the populations. That is, populations of all species originating in a region did not consistently display a higher or a lower fecundity relative to populations in other regions.

Mean longevity of females also varied between populations (Table III), although the differences were significant only among the *P. pequodorum* populations. Mean longevity of *A.*

TABLE II: Intraspecific comparison of mean lifetime fecundity (eggs/female) among pea aphid parasite populations.

Species (Locality)	n	Mean	SEM	F-Ratio (DF)	P
A. ervi(Kam)	12	283.7 [a]	27.8	15.560	<0.0001
A. ervi(Chk)	9	361.8 [a]	30.3	(2,30)	
A. ervi(Sus)	12	582.8 [b]	53.8		
A. smithi(Kam)	10	734.8 [a]	80.3	0.571	0.4602
A. smithi(Chk)	9	666.9 [a]	31.1	(1,17)	
P. pequodorum(Kam)	9	520.0 [a,b]	24.6	6.718	<0.0001
P. pequodorum(Chk)	12	635.0 [b]	49.2	(2,29)	
P. Pequodorum(Sus)	11	440.0 [a]	32.3		

Significance of differences between populations within a species tested by one-way ANOVA and Student-Newman-Keuls test. Means followed by the same letter are not significantly different from each other at a probability level of 5%.
n = sample size: number of females tested.

TABLE III: Intraspecific comparison of mean longevity (in days) of females among pea aphid parasite populations.

Species (Locality)	Mean	SEM	F-Ratio (DF)	P
A. ervi(Kam)	9.4[a]	1.2	1.668	0.2100
A. ervi(Chk)	7.4[a]	0.6	(2,30)	
A. ervi(Sus)	10.3[a]	1.0		
A. smithi(Kam)	12.7[a]	0.8	0.005	0.9500
A. smithi(Chk)	12.8[a]	0.8	(1,17)	
P. pequodorum(Kam)	14.6[a]	1.2	9.260	<0.0001
P. pequodorum(Chk)	16.5[a]	0.8	(2,29)	
P. Pequodorum(Sus)	11.4[b]	0.8		

Significance of differences between populations tested by one-way ANOVA and Student-Newman-Keuls test. Means followed by the same letter are not significantly different from each other at a probability level of 5%. Sample sizes as in Table II.

ervi females was 7.4 days at Chilliwack, 9.4 days at Kamloops and 10.3 days at Sussex. Females of *A. smithi* at Chilliwack had a mean longevity of 12.8 days, whereas those at Kamloops lived for 12.7 days. Among *P. pequodorum*, the Chilliwack population had a longevity of 16.5 days, the Kamloops population 14.6 days, and the Sussex population 11.4 days. The Kamloops and Chilliwack populations did not differ significantly from each other, while they differed from the Sussex population.

Interspecific comparisons: Comparisons among species at each study site showed significant differences in mean total fecundity (Table IV). At Kamloops, the mean lifetime fecundity ranged from a high of 734.8 eggs/female for *A. smithi*, to a low of 283.7 eggs/female for *A. ervi*. The mean fecundities of *A. pisivorus* and *P. pequodorum* were 457.8 and 520.0 eggs/female, respectively. At Chilliwack, the mean fecundity of *A. ervi*, *A. smithi*, and *P. pequodorum* was 361.8, 666.9, and 635.0 eggs/female, respectively. At Sussex, the mean fecundity of *A. ervi* females was 582.8 eggs, and it differed significantly from that of *P. pequodorum* females with 440.0 eggs.

In summary, *A. smithi* had the highest mean total fecundity among all parasites tested, at both Chilliwack and Kamloops. *A. ervi* had the lowest fecundity at Chilliwack and Kamloops, but its fecundity at Sussex was higher than that of *P. pequodorum*.

Interspecific variation in longevity among the pea aphid parasites was also significant in all three localities (Table V). At Kamloops, *P. pequodorum* females had the longest lifespan of 14.6 days. They were followed by *A. smithi* (12.7 days), *A. pisivorus* (11.3 days) and *A. ervi* (9.4 days). *P. pequodorum* females also had the longest lifespan (16.5 days) at Chilliwack. They were followed by *A. smithi* (12.8 days) and *A. ervi* (7.4 days). Although the Sussex population of *P. pequodorum* had a longer lifespan (11.4 days), it did not differ significantly

TABLE IV: Comparison of mean lifetime fecundity (eggs/female) among pea aphid parasites from three regions in North America.

LOCALITY Species	Mean	SEM	F-Ratio (DF)	P
KAMLOOPS				
A. ervi	283.7 [a]	27.8	16.073	<0.0001
A. smithi	734.8 [b]	80.3	(3,40)	
A. pisivorus	457.7 [c]	53.8		
P. pequodorum	520.0 [c]	24.6		
CHILLIWACK				
A. ervi	361.8 [a]	30.3	15.530	<0.0001
A. smithi	666.9 [b]	31.1	(2,27)	
P. pequodorum	635.0 [b]	49.2		
SUSSEX				
A. ervi	582.8 [a]	53.8	4.954	0.0370
P. pequodorum	440.0 [b]	32.3	(1,21)	

Significance of differences between species within a region tested by one-way ANOVA and Student-Newman-Keuls test. Means followed by the same letter are not significantly different from each other at a probability level of 5%. Sample sizes as in Table II.

TABLE V: Comparison of mean longevity (in days) of females among pea aphid parasites from three regions in North America.

LOCALITY Species	Mean	SEM	F-Ratio (DF)	P
KAMLOOPS				
A. ervi	9.4[a]	1.3	3.908	0.0154
A. smithi	12.7[a,b]	0.8	(3,40)	
A. pisivorus	11.3[a,b]	0.9		
P. pequodorum	14.6[b]	1.2		
CHILLIWACK				
A. ervi	7.4[a]	0.6	39.340	<0.0001
A. smithi	12.8[b]	0.8	(2,27)	
P. pequodorum	16.5[c]	0.8		
SUSSEX				
A. ervi	10.3[a]	1.0	0.744	0.3980
P. pequodorum	11.4[a]	0.8	(1,21)	

Significance of differences between species within a region tested by one way ANOVA and Student-Newman-Keuls test. Means followed by the same letter are not significantly different from each other at a probability level of 5%. Sample sizes as in Table II.

from that of *A. ervi* females (10.3 days).

Correlation between fecundity and longevity was significant for six of the nine species and populations tested. The exceptions were *A. smithi* at Chilliwack, and *P. pequodorum* at Chilliwack and at Kamloops.

3.32 Period of intensive egg laying

In general, the PIEL attributes (Table I) had small standard errors. Although most attributes for the various species and populations had non-significant values of skewness and kurtosis, all proportions were transformed to arcsine $\sqrt{x}$, where x is the proportion.

Intraspecific comparisons: Intraspecific comparisons were made by one-way ANOVA and SNK test for several PIEL performance criteria derived from the fecundity data. In general, the trends for PIEL attributes were similar to those observed for lifetime fecundity. The two *A. smithi* populations did not differ from each other in 9 of the 14 (64.3%) variables tested (Table VI). Values of the variables number of aphids parasitized per egg laid, proportion of aphids superparasitized, proportion of eggs lost due to superparasitism, mean number of eggs laid per day and per aphid were significantly different between these two populations. The three *A. ervi* populations differed from one another in all but two performance criteria, namely proportion of eggs laid in the first four days and number of aphids escaping parasitism (Table VII). The Chilliwack and Kamloops populations did not differ from each other in 7 of the 12 (58.3%) significantly different variables. These variables were length of PIEL, PIEL fecundity, number of hosts parasitized per egg laid, proportion of aphids superparasitized, number and proportion of eggs lost due to superparasitism, and mean number

TABLE VI: Parasite performance and host utilization patterns pertaining to PIEL: Intraspecific comparisons between populations of *A. smithi*. See Table I for details of variable names.

Variable	A. smithi (Kam)	A. smithi (Chk)	F Ratio (DF=1,17)	P
1.PIELL ($\bar{X}$)	9.10	10.78	2.090	0.1664
(SEM)	0.98	0.55		
2.PIELFEC	708.80	661.33	0.255	0.6198
	84.84	31.09		
3.NFOUR	351.60	317.78	1.979	0.1775
	20.00	12.10		
4.PFOUR	0.55	0.49	1.062	0.3173
	0.06	0.03		
5.NAPHIDS	355.80	395.33	0.861	0.3665
	36.78	18.44		
6.PAPHIDS	0.94	0.92	1.183	0.2920
	0.02	0.02		
7.EGGS	0.52	0.60	5.794	0.0277
	0.03	0.01		
8.NESACPE	20.20	35.78	3.530	0.0775
	4.07	7.49		
9.PESCAPE	0.06	0.08	1.113	0.3062
	0.02	0.02		
10.SUPER	0.55	0.40	10.166	0.0054
	0.04	0.02		
11.NWASTE	353.00	266.00	2.350	0.1437
	51.79	15.79		
12.PWASTE	0.48	0.40	5.794	0.0277
	0.03	0.01		
13.MEANEGGS	1.85	1.22	7.364	0.0147
	0.11	0.06		
14.MEANDAY	78.20	61.53	5.606	0.0300
	6.60	1.63		

Table VII: Parasite performance and host utilization patterns pertaining to PIEL: Intraspecific comparisons among populations of *A. ervi*. See Table I for details of variable names.

Variable*	A. ervi (Kam)	A. ervi (Chk)	A. ervi (Sus)	F ratio (DF=2,30)	P
1.PIELL ($\bar{X}$)	5.08[a]	6.33[a]	7.83[b]	5.565	0.0090
(SEM)	0.38	0.65	0.75		
2.PIELFEC	246.17[a]	346.22[a]	557.83[b]	19.610	<0.0001
	22.14	32.14	49.41		
3.FOUR	199.50[a]	250.67[b]	363.00[c]	39.458	<0.0001
	15.58	8.46	14.06		
4.PFOUR	0.83	0.75	0.70	1.091	0.3461
	0.03	0.05	0.05		
5.NAPHIDS	161.00[a]	221.11[a,b]	284.00[b]	9.122	0.0008
	12.67	21.27	26.90		
6.PAPHIDS	0.79[a]	0.87[b]	0.91[b]	10.671	0.0003
	0.02	0.02	0.01		
7.EGGS	0.67[a]	0.64[a]	0.51[b]	29.121	<0.0001
	0.02	0.02	0.01		
8.NESCAPE	39.83	32.22	29.33	1.167	0.3500
	4.56	5.99	5.25		
9.PESCAPE	0.22[a]	0.13[b]	0.09[c]	11.051	0.0004
	0.02	0.02	0.01		
10.SUPER	0.38[a]	0.38[a]	0.54[b]	17.411	<0.0001
	0.02	0.02	0.02		
11.NWASTE	80.58[a]	125.11[a]	273.83[b]	33.389	<0.0001
	12.02	13.12	24.18		
12.PWASTE	0.33[a]	0.36[a]	0.49[b]	29.122	<0.0001
	0.02	0.02	0.01		
13.MEANEGS	1.22[a]	1.38[a]	1.80[b]	28.860	<0.0001
	0.06	0.05	0.06		
14.MEANDAY	48.06[a]	55.29[b]	72.07[c]	37.914	<0.0001
	1.87	2.01	2.27		

* Means followed by the same letter within a row are not significantly different from each other at 5% level.

of eggs laid per aphid. Differences in 7 of the 14 (50.0%) PIEL performance criteria tested for the three *P. pequodorum* populations were significant (Table VIII). The populations did not differ in number of eggs laid in the first four days, proportion of aphids parasitized, number and proportion of aphids escaping parasitism, number of eggs lost due to superparasitism, and mean number of eggs laid per day and per aphid. The Chilliwack and Kamloops populations did not differ from each other in 2 of the 7 significantly different variables (28.6%), namely, length of PIEL and number of aphids parasitized.

Interspecific comparisons: Differences in most PIEL performance criteria were significant among the species in all three study areas. At Chilliwack, *A. ervi*, *A. smithi* and *P. pequodorum* did not differ from one another in only one variable, namely, proportion of aphids superparasitized (Table IX). *A. ervi* females were marginally superior in two performance criteria, relative to other species. These were number of aphids escaping parasitism, and mean number of eggs laid per aphid. They did not, however, differ significantly from *A. smithi* females in both these variables. *P. pequodorum* females were superior in number of aphids parasitized (did not differ from *A. smithi*), number of aphids parasitized per egg laid, length of PIEL, number of eggs lost due to superparasitism (did not differ from *A. ervi*), and proportion of eggs lost due to superparasitism. In the remaining performance characteristics, *A. smithi* females were generally superior.

The trend at Kamloops was similar to that at Chilliwack (Table X). *A. ervi* females were superior in proportion of eggs laid in the first four days of reproduction, and number of eggs lost due to superparasitism (did not differ from *P. pequodorum* or *A. pisivorus*). *P. pequodorum* females were better as judged by the number of aphids parasitized (did not differ from *A. smithi*), number of aphids parasitized per egg laid (did not differ from *A. ervi* or

Table VIII: Parasite performance and host utilization patterns pertaining to PIEL. Intraspecific comparisons among populations of *P. pequodorum*. See Table I for details of variable names.

Variable*	P. pequo (Kam)	P. pequo (Chk)	P. pequo (Sus)	F Ratio (DF=2,29)	P
1.PIELL ($\bar{x}$)	11.22 [a]	12.83 [a]	9.00 [b]	10.126	0.0005
(SEM)	0.43	0.77	0.52		
2.PIELFEC	492.22 [a]	594.33 [a,b]	425.27 [a]	4.327	0.0227
	23.77	55.22	32.53		
3.FOUR	169.78	155.67	203.27	2.489	0.1006
	11.95	20.44	10.95		
4.PFOUR	0.34 [a]	0.26 [b]	0.50 [c]	16.804	<0.0001
	0.02	0.03	0.04		
5.NAPHIDS	369.33 [a]	418.67 [a]	282.00 [b]	6.956	0.0034
	18.32	34.10	21.17		
6.PAPHIDS	0.82	0.81	0.78	0.709	0.5003
	0.03	0.04	0.02		
7.EGGS	0.75 [a]	0.72 [a,b]	0.67 [b]	5.147	0.0102
	0.02	0.20	0.02		
8.NESCAPE	79.56	94.67	78.00	0.457	0.6366
	11.73	18.69	6.63		
9.PESCAPE	0.18	0.19	0.22	0.711	0.4996
	0.03	0.04	0.02		
10.SUPER	0.27 [a]	0.36 [a]	0.37 [b]	4.224	0.0246
	0.06	0.09	0.08		
11.NWASTE	122.89	175.67	143.27	1.960	0.1590
	10.78	24.30	15.00		
12.PWASTE	0.25 [a]	0.28 [a,b]	0.33 [b]	5.155	0.0120
	0.02	0.02	0.02		
13.MEANEGGS	1.10	1.15	1.18	0.361	0.7003
	0.05	0.08	0.05		
14.MEANDAY	44.04	45.92	47.11	0.361	0.7003
	2.07	3.03	1.82		

* Means followed by the same letter within a row are not significantly different from each other at 5% level.

Table IX: Parasite performance and host utilization patterns pertaining to PIEL: Interspecific comparisons among pea aphid parasite species in Chilliwack, B.C. See Table I for details of variable names.

Variable*	A.smithi	A.ervi	P.pequod.	F Ratio (DF=2,27)	P
1.PIELL ($\bar{x}$)	10.78 [a]	6.33 [b]	12.83 [a]	23.051	<0.0001
(SEM)	0.55	0.65	0.77		
2.PIELFEC	661.33 [a]	346.22 [b]	594.33 [a]	12.500	<0.0001
	31.09	32.14	55.22		
3.FOUR	317.78 [a]	250.67 [b]	155.68 [c]	26.540	<0.0001
	12.10	8.46	20.44		
4.PFOUR	0.49 [a]	0.75 [b]	0.26 [c]	47.047	<0.0001
	0.03	0.05	0.03		
5.NAPHIDS	395.33 [a]	221.11 [b]	418.67 [a]	14.393	<0.0001
	18.44	21.27	34.10		
6.PAPHIDS	0.92 [a]	0.87 [a,b]	0.81 [b]	3.952	0.0312
	0.02	0.02	0.04		
7.EGGS	0.60 [a]	0.64 [a]	0.72 [b]	13.044	<0.0001
	0.01	0.02	0.02		
8.NESCAPE	35.78 [a]	32.22 [a]	94.67 [b]	6.801	0.0041
	7.49	5.99	18.69		
9.PESCAPE	0.08 [a]	0.13 [a,b]	0.19 [b]	3.972	0.0307
	0.02	0.02	0.04		
10.SUPER	0.40	0.38	0.35	1.730	0.1967
	0.02	0.02	0.03		
11.NWASTE	266.00 [a]	125.11 [b]	75.67 [b]	11.491	<0.0001
	15.79	13.12	24.30		
12.PWASTE	0.40 [a]	0.36 [a]	0.28 [b]	13.043	<0.0001
	0.01	0.02	0.02		
13.MEANEGGS	1.38 [a]	1.22 [a]	1.15 [b]	11.130	0.0003
	0.05	0.06	0.08		
14.MEANDAY	55.29 [a]	61.53 [a]	45.92 [b]	11.130	0.0003
	2.01	1.63	3.03		

* Means followed by the same letter within a row are not significantly different from each other at the 5% level.

Table X: Parasite performance and host utilization patterns pertaining to PIEL: Interspecific comparisons among pea aphid parasite species in Kamloops, B.C. See Table I for details of variable names.

Variable*	A.smithi	A.ervi	P.pequod.	A.pisivor.	F Ratio (DF=3,40)	P
1.PIELL (X)	9.10 a	5.08 b	11.22 c	8.39 a	15.320	<0.0001
(SEM)	0.98	0.38	0.43	0.63		
2.PIELFEC	708.00 a	246.17 b	492.22 c	438.00 c	16.330	<0.0001
	84.84 a	22.14 b,c	23.77 b	37.53 c		
3.FOUR	351.60	199.50	169.78	230.46	21.750	<0.0001
	20.00 a	15.58 b	11.95 c	15.56 a		
4.PFOUR	0.55	0.83	0.34	0.56	22.720	<0.0001
	0.06	0.03	0.02	0.05		
5.NAPHIDS	355.80 a	161.00 b	369.33 a	284.69 c	16.540	<0.0001
	36.78	12.67	18.32	21.73		
6.PAPHIDS	0.94 a	0.79 b	0.82 b,c	0.88 c	9.620	<0.0001
	0.02 a	0.02 b	0.03 b	0.03 b		
7.EGGS	0.52	0.67	0.75	0.72	13.650	<0.0001
	0.03 a	0.02 a	0.02 b	0.03 a		
8.NESCAPE	20.20	39.83	79.56	37.23	11.660	<0.0001
	4.07	4.56	11.73	6.29		
9.PESCAPE	0.06 a	0.22 b	0.18 b,c	0.12 c	9.630	<0.0001
	0.02 a	0.02 b	0.03 c	0.03 c		
10.SUPER	0.55	0.38	0.27	0.32	13.662	<0.0001
	0.04 a	0.02 b	0.02 b	0.30 b		
11.NWASTE	353.00	80.58	122.90	138.15	20.020	<0.0001
	51.79 a	12.02 b	10.78 b	16.05 b		
12.PWASTE	0.48	0.33	0.25	0.28	7.192	0.0006
	0.03 a	0.02 a	0.02 b	0.03 a		
13.MEANEGGS	1.22	1.36	1.85	1.10	12.474	<0.0001
	0.06	0.11	0.11	0.05		
14.MEANDAY	78.20 a	48.06 a	44.04 b	51.79 a	16.159	<0.0001
	6.60	1.87	2.81	2.07		

* Means followed by the same letter within a row are not significantly different from each other at the 5% level.

A. pisivorus), length of PIEL, and proportion of aphids superparasitized (did not differ from *A. pisivorus*). Females of *A. smithi* performed better as measured by the remaining criteria. In pairwise comparisons between *A. smithi* and *A. ervi*, the former species appears to perform better under the experimental conditions. Females of *A. ervi* were, however, more efficient at utilizing the available hosts as indicated by the variable number of aphids parasitized per egg laid at both Chilliwack and Kamloops. *A. ervi* and *P. pequodorum* at Sussex did not differ from each other in the length of PIEL and in the number of aphids parasitized (Table XI). In most of the host utilization criteria, *P. pequodorum* females were superior, while *A. ervi* females were generally superior in variables that indicate reproductive potential and oviposition rate.

It is worth noting, however, that some PIEL performance criteria were correlated with PIEL fecundity and with the length of PIEL. Moreover, PIEL fecundity and length of PIEL were also positively correlated with each other in all species and populations, except in the case of *P. pequodorum* at Kamloops. Number of eggs laid in the first four days of reproduction and number of aphids parasitized were both positively correlated with PIEL fecundity. Proportion of eggs laid in the first four days was negatively correlated with PIEL fecundity except in the case of *P. pequodorum* populations at Kamloops and Chilliwack. The number, but not the proportion, of eggs lost due to superparasitism was correlated with PIEL fecundity in all species and populations. Correlations for the remaining variables were inconsistent across species and populations.

Number of aphids parasitized and number of eggs lost due to superparasitism were positively correlated with the length of PIEL. Proportion of eggs laid in the first four days of reproduction was negatively correlated. Again, correlations for other variables were not con-

Table XI: Parasite performance and host utilization patterns pertaining to PIEL: Interspecific comprisons between pea aphid parasite species in Sussex, N.J. See Table I for details of variable names.

Variable	A. ervi	P.pequodorum	F Ratio (DF=1,21)	P
1.PIELL ($\bar{x}$)	7.83	9.00	1.582	0.2222
(SEM)	0.75	0.52		
2.PIELFEC	557.88	425.27	4.830	0.0394
	49.41	32.53		
3.FOUR	363.00	203.27	78.284	<0.0001
	14.06	10.95		
4.PFOUR	0.70	0.50	7.748	0.0111
	0.05	0.04		
5.NAPHIDS	284.00	282.00	0.003	0.9450
	26.90	21.17		
6.PAPHIDS	0.91	0.78	29.491	<0.0001
	0.01	0.02		
7.EGGS	0.51	0.67	52.125	<0.0001
	0.01	0.02		
8.NESCAPE	29.33	78.00	33.715	<0.0001
	5.25	6.63		
9.PESCAPE	0.09	0.22	29.447	<0.0001
	0.01	0.02		
10.SUPER	0.54	0.37	26.201	<0.0001
	0.02	0.02		
11.NWASTE	273.83	143.27	20.153	0.0002
	24.18	15.00		
12.PWASTE	0.49	0.33	52.125	<0.0001
	0.01	0.02		
13.MEANEGGS	1.80	1.18	71.901	<0.0001
	0.06	0.06		
14.MEANDAY	72.07	47.11	71.901	<0.0001
	2.27	1.82		

sistent across species and populations to suggest any meaningful patterns. The lack of a correlation between PIEL fecundity or length of PIEL and most performance criteria suggests that each species has a unique oviposition pattern, oviposition rate and host utilization efficiency that is independent of fecundity and longevity.

3.33 Multiple discriminant analysis of PIEL attributes

Some trends were apparent in the univariate analysis of PIEL attributes. For example, mean values of many variables for Chilliwack and Kamloops populations were not significantly different from each other. In order to understand how the various species and populations are related to one another when all the variables are considered simultaneously and visually represent the spatial relationship among them, eight non-redundant variables from the original 14 PIEL attributes were included in a stepwise discriminant analysis: PIELL, PIELFEC, PFOUR, PAPHIDS, EGGS, SUPER, MEANEGGS, and MEANDAY. The minimum tolerance level for the exclusion of a variable from the analysis was set at 0.001%, assessed on the maximum Mahalanobis distance between the groups.

The analysis was done in two parts. The first part included all species and populations of pea aphid parasites with the exception of *A. pisivorus* for which only one population was available. The second part of the analysis was carried out separately on populations of *A. smithi*, *A. ervi* and *P. pequdorum* to quantify geographic variation.

3.331 Discriminant analysis of all groups excluding A. pisivorus

Seven of the eight variables included in the analysis made a significant contribution to discrimination. The variable mean number of eggs laid per day was not included in the analysis as it did not meet the minimum tolerance requirements. It is clear from the scatterplot of individuals projected onto the first and second discriminant functions (Figure 2) that all populations of any given species were plotted close to one another, albeit with some overlap. This indicates that the variables used in the analysis were species-specific and contained sufficient information to enable discrimination both among species and among populations of a species. The percent of correctly classified cases for each group is shown in the classification table (Table XII). On average, 72.6% of the individuals in each group were correctly classified. An examination of the misclassified individuals indicated that, in general, the values of some of their variables were closer to the mean of the group into which they were classified than to the mean of their true group.

Five discriminant functions that had a significant chi-square associated with Wilk's lambda were used in the analysis. The first function accounted for 63.7% of the total among-group variation. The second through fifth functions explained 19.4, 8.6, 4.0, and 3.1% of among-group variation, respectively, with 98.8% of the total variation accounted for.

The standardized discriminant function coefficients, which indicate the relative contribution of each variable to discriminantion, are shown in Table XIII. Considered over the five functions, the variables MEANEGGS, PIELFEC, SUPER, PIELL and EGGS contributed the most to discrimination in that order. While the other two variables i.e., PAPHIDS and PFOUR, also contributed to overall discrimination, they were relatively less important. The standardized discriminant function coefficients indicated that the various groups differed mainly

Table XII: Classification table showing the actual and predicted group membership of cases from discriminant analysis of PIEL attributes. The average percent of correctly classified cases is 72.62%. See text for details.

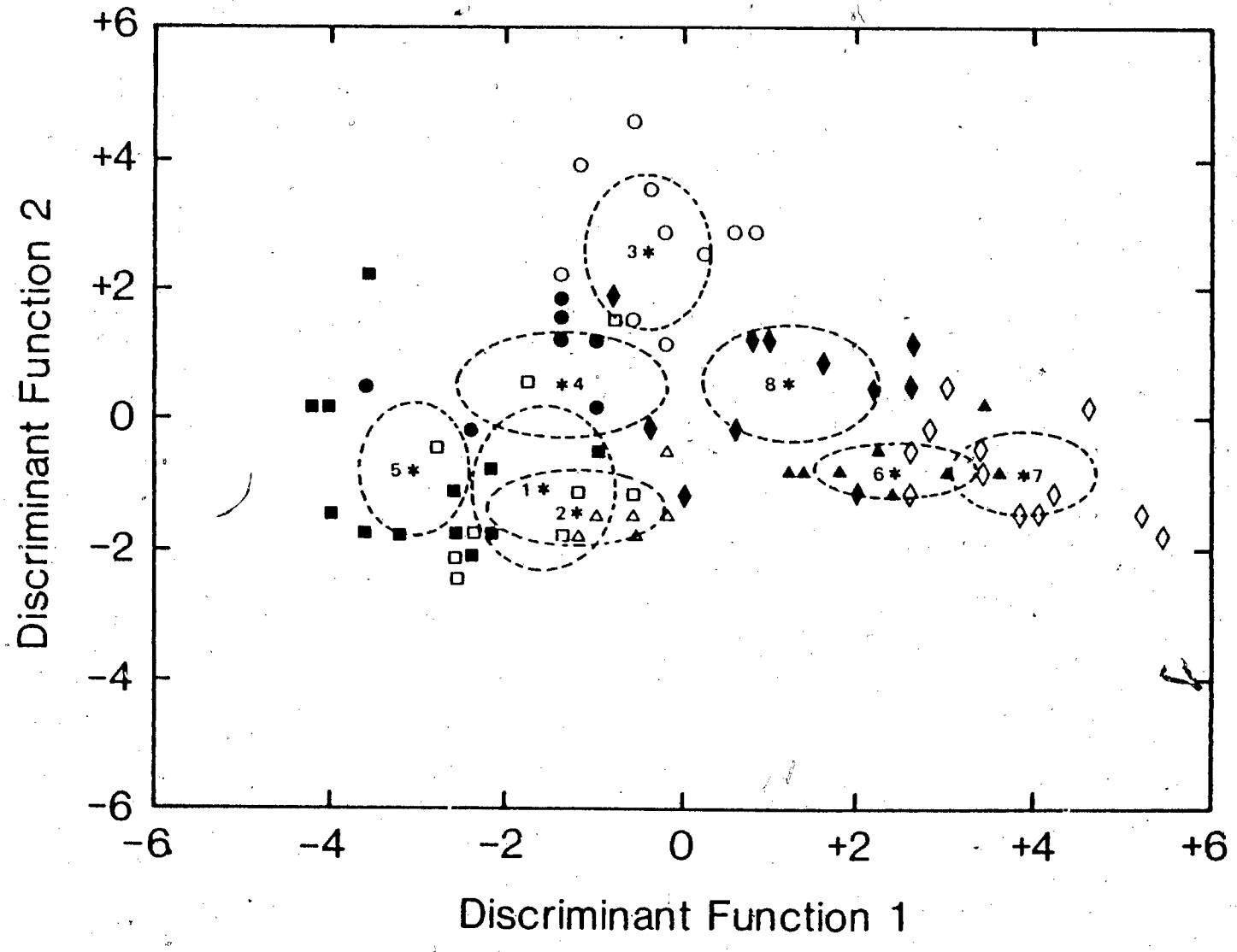
		PREDICTED GROUP(in %)							
ACTUAL GROUP	n	A.s(K)	A.s(C)	A.e(K)	A.e(C)	A.e(S)	P.p(K)	P.p(C)	P.p(S)
A. smithi(K)	10	70.00	10.00	-	20.00	-	-	-	-
A. smithi(C)	9	-	100.00	-	-	-	-	-	-
A. ervi(K)	12	-	-	66.67	16.67	8.33	-	-	8.33
A. ervi(C)	9	-	11.11	-	66.67	11.11	-	-	11.11
A. ervi(S)	12	-	16.67	-	-	83.33	-	-	-
P. pequodorum(K)	9	-	-	-	-	-	66.67	22.22	11.11
P. pequodorum(C)	12	-	-	-	-	-	16.67	83.33	-
P. pequodorum(S)	11	-	9.11	9.11	9.11	-	27.33	-	45.55

n = number of females tested

Table XIII: Standardized discriminant function coefficients for PIEL attributes included in discriminant analysis of populations of *A. ervi*, *A. smithi* and *P. pequodorum*. See Table I for details of variable names.

Variable	DISCRIMINANT FUNCTION				
	1	2	3	4	5
PIELFEC	-0.95083	1.30241	1.06276	-2.89975	-0.59399
PIELL	0.86904	-1.19822	-0.52980	2.37346	0.35799
PFOUR	-0.58190	0.61055	0.13999	0.09785	0.14806
PAPHIDS	0.56765	0.02735	-0.85133	-1.01170	-0.82976
EGGS	1.69430	0.63630	2.27687	-0.07519	1.89346
SUPER	2.23733	1.07085	2.19933	-0.10468	-0.47912
MEANEGGS	-0.95622	-1.53763	0.70321	2.09998	2.93342

FIGURE 2: Scatterplot of populations of *A. ervi*, *A. smithi* and *P. pequodorum* projected onto discriminant axes 1 and 2 from discriminant analysis of PIEL attributes. The ellipses enclose the 95% confidence limits around the group centroids, which are represented by asterisks. The numbers beside the asterisks refer to the species and populations listed below in that order. □ : *A. smithi* (Kamloops), △ : *A. smithi* (Chilliwack), ○ : *A. ervi* (Kamloops), ● : *A. ervi* (Chilliwack), ■ : *A. ervi* (Sussex), ▲ : *P. pequodorum* (Kamloops), ◇ : *P. pequodorum* (Chilliwack), ◆ : *P. pequodorum* (Sussex).


+6
+4
+2
0
-2
-4
-6
-6
-4
-2
0
+2
+4
+6
Discriminant Function 2
Discriminant Function 1
1*
2*
3*
4*
5*
6*
7*
8*

in variables related to reproductive potential and host utilization and to a lesser degree in aspects of oviposition rate.

3.332 Discriminant analysis of populations of each species

In this part of the analysis, *A. smithi*, *A. ervi* and *P. pequodorum* populations were compared among themselves. Differences between populations from the various localities were accentuated without cross-species noise. The average percentage of correctly classified cases was 100% for the two *A. smithi* populations, 90.9% for the three *A. ervi* populations, and 90.6% for the three *P. pequodorum* populations. In the case of *A. ervi* populations, three individuals were misclassified into the Chilliwack population. A total of three *P. pequodorum* individuals were misclassified. Two individuals from Chilliwack and one from Sussex were classified into the Kamloops population.

Scatterplots of various populations of each of the three species are shown in Figures 3, 4 and 5. The first and second discriminant functions explained 79.7% and 20.3% of the total variation, respectively, for *A. ervi*, and 81.3% and 18.7%, respectively, for *P. pequodorum* populations. Standardized discriminant function coefficients for this part of the analysis are given in Tables XIV, XV and XVI. The number of variables included in the analysis was 6 for *A. smithi*, 7 for *A. ervi* and 4 for *P. pequodorum* populations.

A matrix of D values (square root of Mahalanobis D^2 statistic) (Mahalanobis 1936), obtained from comparisons between all possible pairs is shown in Table XVII. The phenotypic distance between a pair is directly proportional to the magnitude of the Mahalanobis distance. All D values shown in the matrix were significant ($P < 0.01$ or 0.05). The matrix indicated that the phenotypic distances between populations of *A. smithi* and *A. ervi* were greater than those between corresponding populations of *P. pequodorum*. The matrix also indicated that the

Table XIV: Standardized discriminant function coefficients for PIEL attributes included in discriminant analysis of populations of *A. smithi*. See Table I for details of variable names.

Variable	DISCRIMINANT FUNCTION 1
PIELFEC	3.78670
PFOUR	3.34526
PAPHIDS	-1.02055
EGGS	3.95976
SUPER	3.32445
MEANDAY	0.93669

Table XV: Standardized discriminant function coefficients for PIEL attributes included in discriminant analysis of populations of *A. ervi*. See Table I for details of variable names.

Variable	DISCRIMINANT FUNCTION	
	1	2
PIELFEC	1.45964	1.94639
PAPHIDS	-0.22496	-1.19465
PFOUR	1.20534	1.27567
EGGS	-0.48231	2.96816
SUPER	-0.77309	3.12816
MEANEGGS	-1.26909	2.62394
MEANDAY	1.95595	-2.32334

Table XVI: Standardized discriminant function coefficients for PIEL attributes included in discriminant analysis of populations of *P. pequodorum*. See Table I for details of variable names.

Variable	DISCRIMINANT FUNCTION	
	1	2
PFOUR	-0.82654	0.02673
EGGS	2.07573	1.04763
SUPER	1.63843	2.45493
MEANDAY	0.57538	-0.89954

Table XVII : Matrix of Mahalanobis generalized distance (D) between populations of pea aphid parasites for PIEL attributes. Unmarked values are significant at the 1% level, an asterik indicates significance at the 5% level.

Species (Locality)	A.s(K)	A.s(C)	A.e(K)	A.e(C)	A.e(S)	A.p(K)	P.p(K)	P.p(C)	P.p(S)
A. smithi(K)	0.000								
A. smithi(C)	3.471	0.000							
A. ervi(K)	3.058	7.990*	0.000						
A. ervi(C)	2.478	5.174*	3.604*	0.000					
A. ervi(S)	2.287	2.804	5.371*	4.239*	0.000				
A. pisiv(K)	2.448*	3.446*	4.388*	2.065	5.629*	0.000			
P. pequo(K)	3.800*	5.862*	6.372*	4.639*	7.059*	2.733	0.000		
P. pequo(C)	2.912*	6.418*	6.627*	5.786*	8.804*	3.031*	2.613	0.000	
P. pequo(S)	3.343*	3.925*	3.714*	2.978	4.831*	3.426*	3.048	2.896	0.000

FIGURE 3. Scatterplot of populations of *A. smithi* projected onto discriminant axis 1 from discriminant analysis of PIEL attributes. The arrows indicate group centroids. Each individual parasite is represented by four symbols for both populations. ⊡: *A. smithi* (Kamloops), △ : *A. smithi* (Chilliwack).

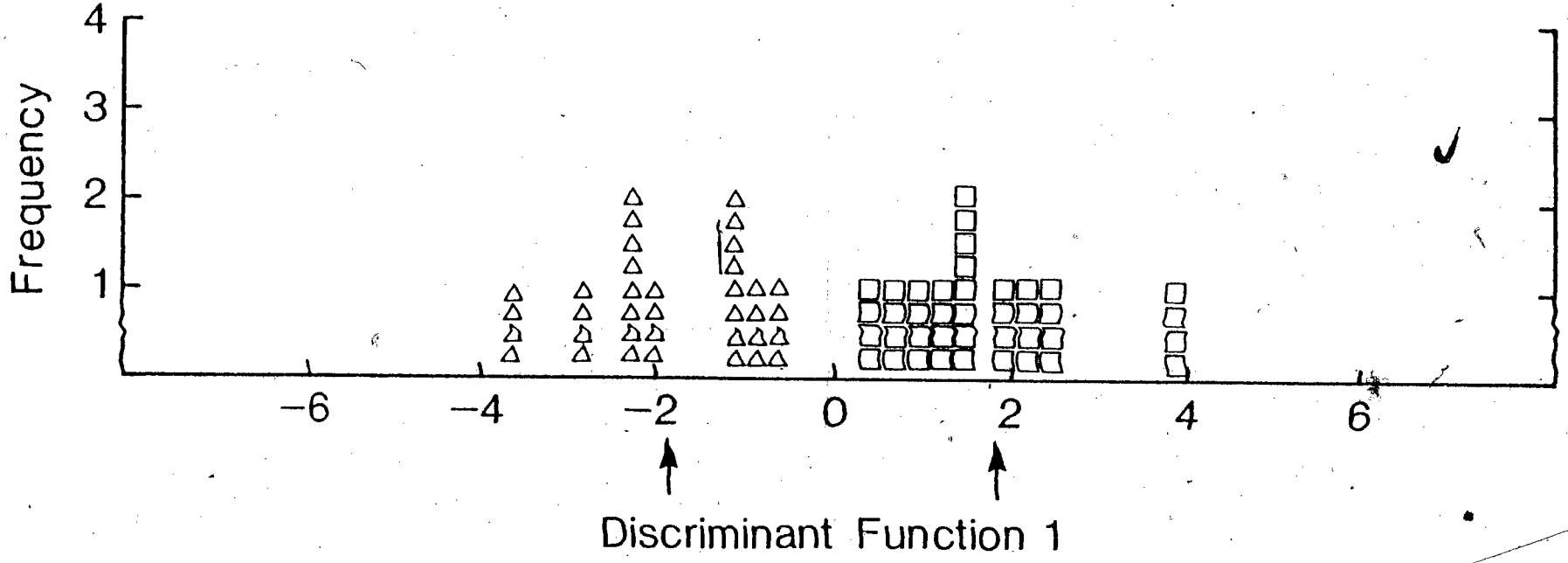

Frequency
4
3
2
1
−6
−4
−2
0
2
4
6
Discriminant Function 1

FIGURE 4. Scatterplot of populations of *A. ervi* projected onto discriminant axes 1 and 2 from discriminant analysis of PIEL attributes. The ellipses enclose the 95% confidence limits around the group centroids, which are represented by asterisks. The numbers beside the asterisks refer to the populations listed below in that order. □ : *A. ervi* (Kamloops), ○ : *A. ervi* (Chilliwack), △ : *A. ervi* (Sussex).

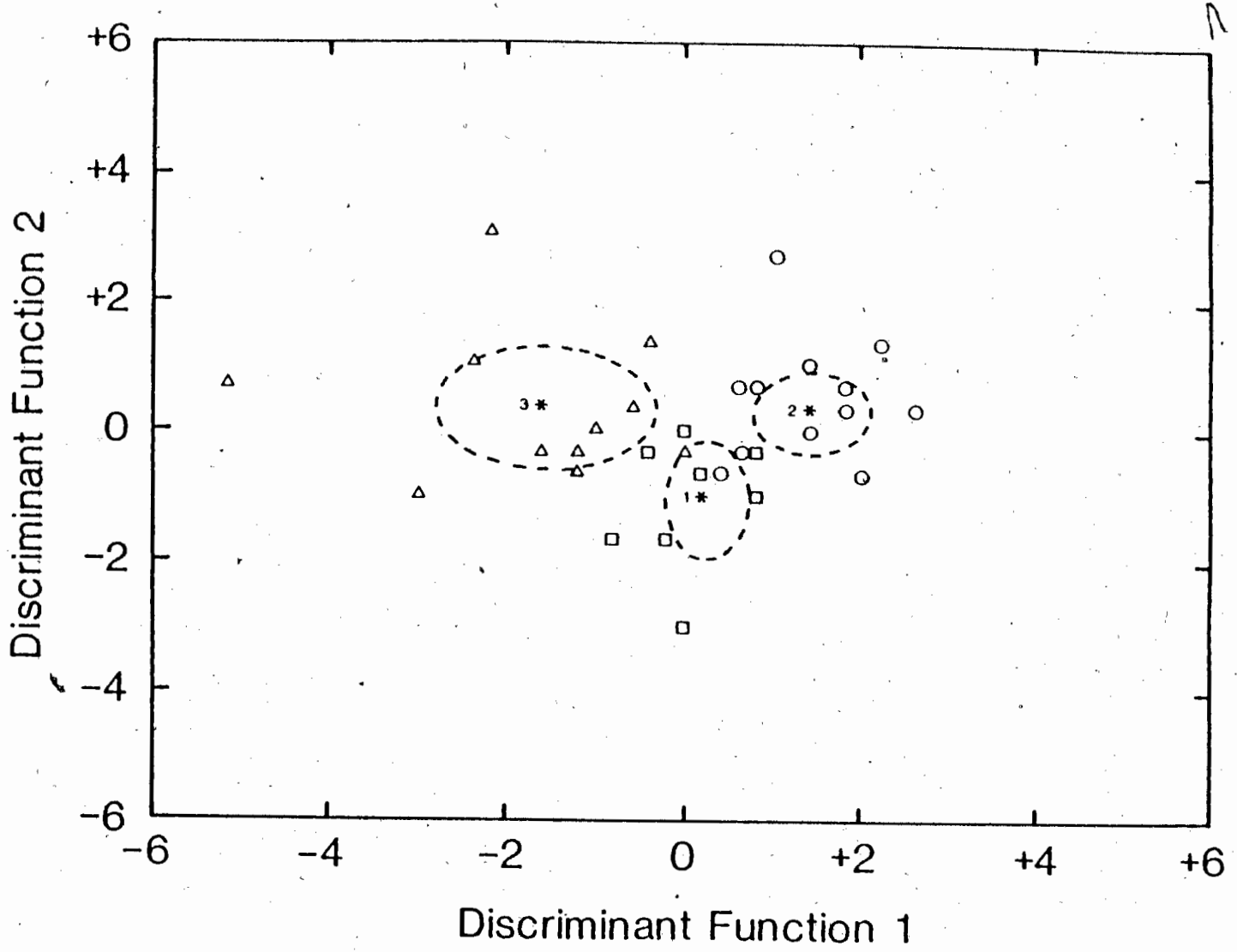
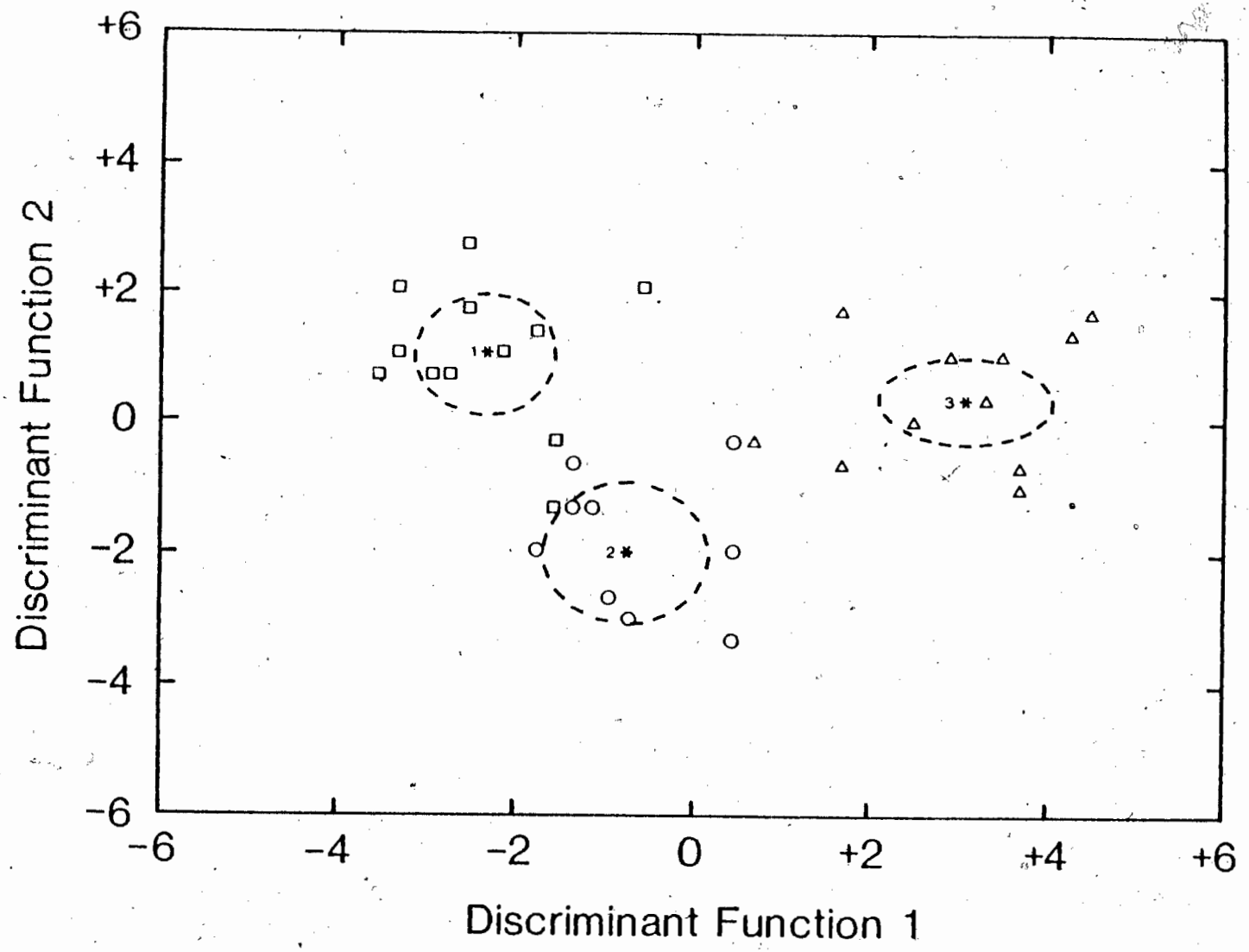

+6
+4
+2
0
-2
-4
-6
-6
-4
-2
0
+2
+4
+6
Discriminant Function 2
Discriminant Function 1
3*
2*
1*

FIGURE 5. Scatterplot of populations of *P. pequodorum* projected onto discriminant axes 1 and 2 from discriminant analysis of PIEL attributes. The ellipses enclose the 95% confidence limits around the group centroids, which are represented by asterisks. The numbers beside the asterisks refer to the populations listed below in that order. □ :*P. pequodorum* (Kamloops), ○ :*P. pequodorum* (Chilliwack), △ :*P. pequodorum* (Sussex).


+6
+4
+2
0
-2
-4
-6
-6
-4
-2
0
+2
+4
+6
Discriminant Function 2
Discriminant Function 1
1*
2*
3*

generalized distance between populations of *A. ervi* and *P. pequodorum* originating in Chilliwack and Kamloops is smaller than that obtained by comparing either of the above two populations with Sussex populations, as indicated by univariate analysis.

3.34 Life table analysis

Based on the daily fecundity and survival schedules measured in the laboratory, *mx* (age-specific fecundity) and *lx* (age-specific survival probability) values were calculated for each parasite species and population. The intrinsic rate of increase (*rm*, in females/female/day) was calculated by iteratively solving the Lotka-Euler equation (Andrewartha and Birch 1954):

$$\sum e^{-r_m x}\, lx\, mx = 1 \qquad (1)$$

Gross reproductive rate (GRR = $\sum mx$, in females/female/generation), net reproductive rate (R_0 = $\sum lxmx$, in females/female/generation), finite rate of natural increase ($\lambda = e^r$, in females/female/day), the generation time ($T = ln\ R_0/r$, in days) and doubling time ($DT = ln\ 2/r$, in days), were also calculated. A sex ratio of 1:1 males:females was assumed for all calculations, although the field sex ratio of aphidiids is slightly female biased (Cohen 1985, Kambhampati unpubl., Mackauer 1976). Parasite larval and pupal mortality was assumed to be zero. The age to first reproduction was based on the developmental time estimated at 23.6 °C (Chapter IV), which closely approximated the temperature inside the cage in fecundity experiments.

Life table statistics do not have an error term associated with them because they are population parameters rather than measurements of individual parasites. Therefore differences in life table statistics of various species of populations cannot be statistically examined by

ordinary techniques. To overcome this problem, jack-knife, a randomization technique which allows a reduction in bias of an estimate of the population value of a statistic, was utilized (Lenski and Service 1982, Meyer *et al.* 1986, Sokal and Rohlf 1981, p. 795).

The intrinsic rate of increase varied considerably both within and between species. Life table statistics and *lx* and *mx* curves for species and populations of pea aphid parasites are shown in Table XVIII and Figures 6 through 9, respectively. Intrinsic rate of increase for the Kamloops, Chilliwack and Sussex populations of *A. ervi* was estimated as 0.371, 0.384, and 0.416 females/female/day, respectively. Populations of *A. smithi* at Kamloops and at Chilliwack had an *rm* value of 0.454 and 0.486, respectively. The Chilliwack population of *P. pequodorum* had the largest value at 0.336, followed by Kamloops (0.321), and Sussex (0.306). The value of *rm* for *A. pisivorus* from Kamloops was estimated as 0.383. Similar differences were also apparent in the finite rate of increase and in doubling time.

Significant differences in life table statistics were also apparent among species attacking the pea aphid in each of the three study sites. However, the values did not reflect the relative abundance of each species in the field. At both Kamloops and Chilliwack, *A. smithi* had the largest value for intrinsic rate of increase and was generally superior in other life table statistics. At Kamloops, *A. smithi* was followed by *A. pisivorus*, *A. ervi* and *P. pequodorum*. At Chilliwack, it was followed by *A. ervi* and *P. pequodorum*. At Sussex, *P. pequodorum* had a lower rate of population growth than *A. ervi*. Despite the relatively high fecundity of *P. pequodorum*, especially at Chilliwack, *rm* value for this species was low because of a longer developmental time compared with other species.

Jack-knifed estimates of *rm* values along with their standard errors and 95% confidence limits are shown in Table XIX. The jack-knifed values differed from the original values and

TABLE XVIII: Life table statistics for pea aphid parasites at 23.5±1 °C, 55-60% R.H. and 16h L:8h D photoperiod. A zero larval mortality and 1:1 male:female sex ratio was assumed.

Species	Reproductive Rate[1]		Generation	Doubling	Rate of Increase[3]	
(Locality)	Gross	Net	Time[2]	Time[2]	Intrinsic	Finite
A. ervi(K)	141.83	124.02	12.993	1.868	0.371	1.449
A. ervi(C)	179.56	159.03	13.201	1.805	0.384	1.468
A. ervi(S)	290.83	259.21	12.360	1.666	0.416	1.516
A. smithi(K)	367.40	350.78	12.908	1.527	0.454	1.575
A. smithi(C)	333.44	320.83	11.874	1.426	0.486	1.626
A. pisivorus(K)	228.85	206.05	13.912	1.810	0.383	1.467
P. pequodorum(K)	259.99	247.32	17.167	2.159	0.321	1.379
P. pequodorum(C)	317.33	302.31	16.998	2.063	0.336	1.399
P. pequodorum(S)	219.99	207.63	17.437	2.265	0.306	1.358

1: in females/female/generation

2: in days

3: in females/female/day

TABLE XIX: Jack-knifed estimates of intrinsic rate of increase (in females/female/day) of pea aphid parasites. See text for details.

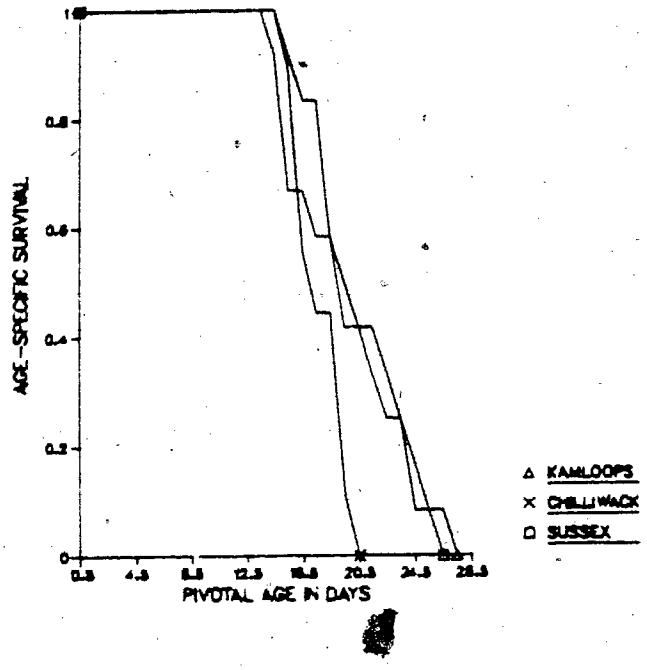
Species/ (Locality)	Original estimate*	Jack-knifed estimates			
		Mean[1]	SEM	95% C. I. L1	L2
A. ervi(K)	0.371	0.364	0.000348	0.3632	0.3648
A. ervi(C)	0.384	0.385	0.000118	0.3846	0.3852
A. ervi(S)	0.416	0.410	0.000435	0.4090	0.4110
A. smithi(K)	0.454	0.451	0.000316	0.4504	0.4522
A. smithi(C)	0.486	0.487	0.001179	0.4843	0.4897
A. pisivorus(K)	0.383	0.377	0.000480	0.3759	0.3781
P. pequodorum(K)	0.321	0.322	0.000118	0.3217	0.3223
P. pequodorum(C)	0.336	0.334	0.000174	0.3336	0.3344
P. pequodorum(S)	0.306	0.301	0.000447	0.2999	0.3021

* Estimates from equation (1) with all females included

1: in females/female/day

FIGURE 6: Age-specific survival (a) and age-specific fecundity (b) of populations of *A. ervi* estimated at 23.5 ± 1 °C, 55-60% R.H., 16h L: 8h D photoperiod and a host density of 40 aphids per day per female. A zero larval and pupal mortality and 1:1 male:female sex ratio was assumed.

(a)


AGE-SPECIFIC SURVIVAL
PIVOTAL AGE IN DAYS
KAMLOOPS
CHILLIWACK
SUSSEX

(b)

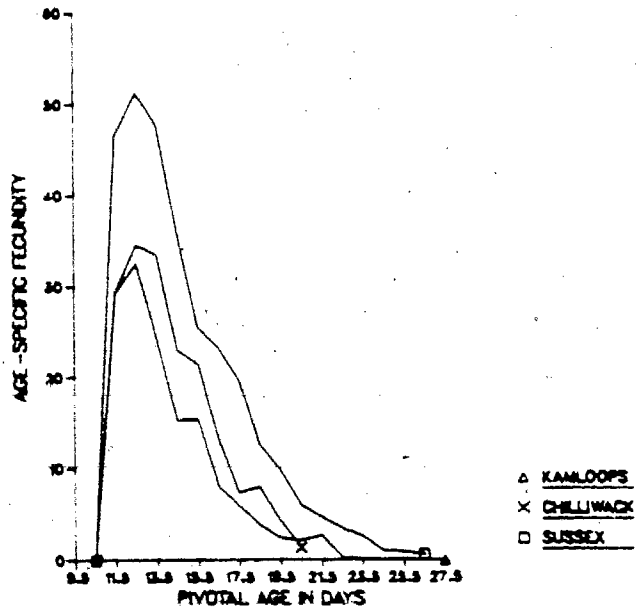
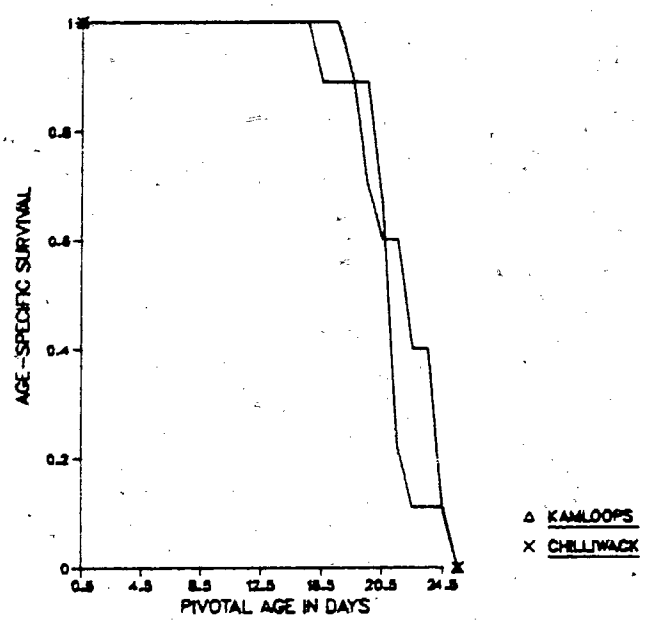

AGE-SPECIFIC FECUNDITY
PIVOTAL AGE IN DAYS
KAMLOOPS
CHILLIWACK
SUSSEX

FIGURE 7: Age–specific survival (a) and age–specific fecundity (b) of populations of *A. smithi* estimated at 23.5 ± 1 ° C, 55–60% R.H., 16h L: 8h D photoperiod and a host density of 40 aphids per day per female. A zero larval and pupal mortality and 1:1 male:female sex ratio was assumed.

(a)


AGE-SPECIFIC SURVIVAL
1
0.8
0.6
0.4
0.2
0
0.5
4.5
8.5
12.5
16.5
20.5
24.5
PIVOTAL AGE IN DAYS
Δ KAMLOOPS
× CHILLIWACK

(b)

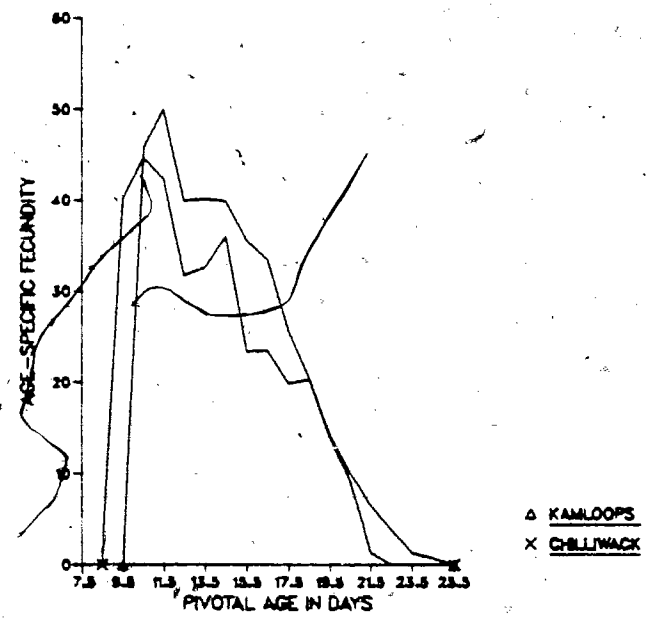
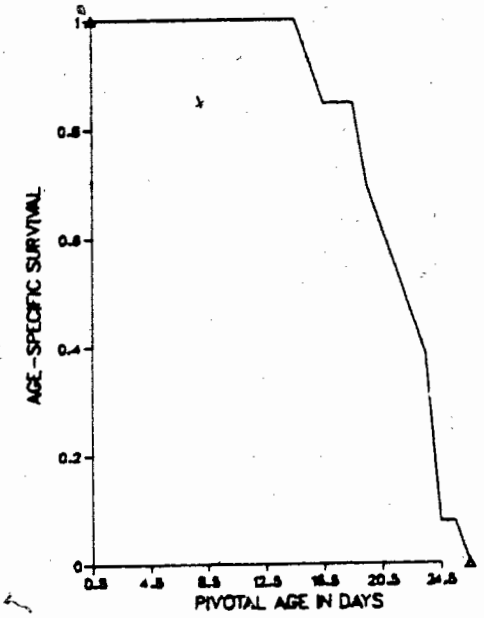

AGE-SPECIFIC FECUNDITY
60
50
40
30
20
10
0
7.5
9.5
11.5
13.5
15.5
17.5
19.5
21.5
23.5
25.5
PIVOTAL AGE IN DAYS
Δ KAMLOOPS
× CHILLIWACK

FIGURE 8: Age–specific survival (a) and age–specific fecundity (b) of *A. pisivorus* estimated at 23.5 ± 1 ° C, 55–60% R.H., 16h L: 8h D photoperiod and a host density of 40 aphids per day per female. A zero larval and pupal mortality and 1:1 male:female sex ratio was assumed.

(a)


AGE-SPECIFIC SURVIVAL
1.0
0.8
0.6
0.4
0.2
0
0.5
4.5
8.5
12.5
16.5
20.5
24.5
PIVOTAL AGE IN DAYS

(b)

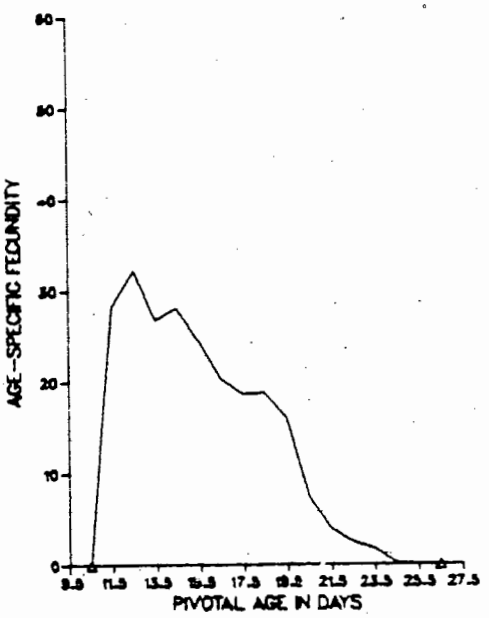
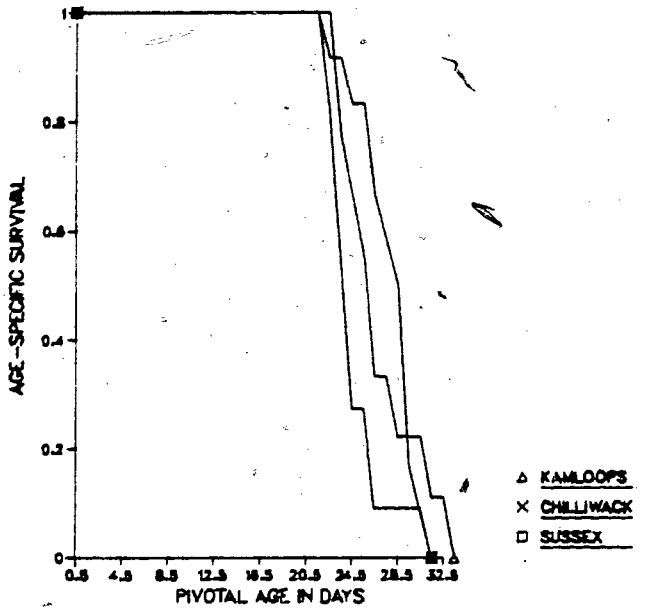
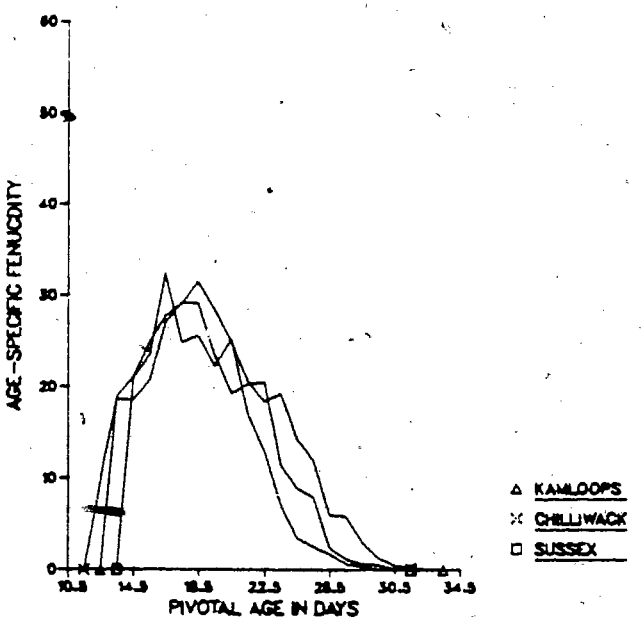

AGE-SPECIFIC FECUNDITY
60
50
40
30
20
10
0
9.5
11.5
13.5
15.5
17.5
19.5
21.5
23.5
25.5
27.5
PIVOTAL AGE IN DAYS

FIGURE 9: Age–specific survival (a) and age–specific fecundity (b) of populations of *P. pequodorum* estimated at 23.5 ± 1 ° C, 55–60% R.H., 16h L: 8h D photoperiod and a host density of 40 aphids per day per female. A zero larval and pupal mortality and 1:1 male:female sex ratio was assumed.

(a)


AGE-SPECIFIC SURVIVAL
PIVOTAL AGE IN DAYS
KAMLOOPS
CHILLIWACK
SUSSEX

(b)


AGE-SPECIFIC FECUNDITY
PIVOTAL AGE IN DAYS
KAMLOOPS
CHILLIWACK
SUSSEX

were often smaller. The general trend among the various species and populations, however, remained unchanged. The fact that none of the values overlapped in their 95% confidence limits indicated that the differences in *rm* values were statistically significant.

Lewontin (1965) proposed a model whereby changes in the values of the intrinsic rate of increase can be quantified as a function of changes in life history traits such as developmental time (age to first reproduction), fecundity, etc. Using his conceptual framework, one could pose the question: how much of an adjustment in developmental time or fecundity of other species of parasites is required to match the greater *rm* value of *A. smithi*? It can be shown, for example, that a reduction of about 1.5 days in developmental time of pea aphid parasites has the same effect on *rm* values as doubling their fecundity. For the Chilliwack population of *A. ervi*, a reduction in developmental time of two days yielded an *rm* value of 0.456, whereas doubling the fecundity yielded 0.439. A reduction of almost three days in developmental time of *A. ervi* is required to match the *rm* value of *A. smithi* (0.486). Similarly, for the Kamloops population of *A. ervi*, a reduction of two days in developmental time resulted in an *rm* value of 0.442, while doubling the fecundity yielded 0.427. To match the *rm* value of *A. smithi* (0.454), a reduction in developmental time of about 2.5 days of *A. ervi* at Kamloops is required. A two day reduction in developmental time for *A. pisivorus* on the other hand, resulted in an *rm* value of 0.453, which is comparable to that of *A. smithi*. A doubling of fecundity of *A. pisivorus* yielded an *rm* value of 0.437. In the case of *P. pequodorum* populations, either a reduction in developmental time of three days or a doubling of fecundity did not raise their *rm* to a value greater than that of *A. smithi*. A reduction of four days or more in the developmental time is required to yield a *rm* value of 0.45 or greater for *P. pequodorum* populations.

A factor perhaps more important in the field than magnitude of the *rm* value itself, is the rate at which this value is realized, i.e., how does the value change as a function of female age. Due to an uncertain environment in the field, the lifespan of the parasites is limited and therefore, the rate rather than the magnitude becomes important. Each age class of a life table cohort which has a positive age-specific fecundity makes a contribution to that cohort's growth rate. The ultimate value of intrinsic rate of increase is, then, the sum of all age-specific contributions to *rm* (King 1982). It can be examined by progressively summing the proportionate age-specific contribution from day one of reproductive life to death and plotting the *rm* value as it is realized each day after the initiation of parturition by parasites. This relationship is shown for the various species and populations of pea aphid parasites in Figures 10 through 13. Differences in the rate at which various species realize their lifetime *rm* values were not as striking as those in the total *rm* values. *A. smithi* at Chilliwack and Kamloops realized 96.1% and 95.6% of their total *rm*, respectively, in the first four days of adult life. During the same period, *A. ervi* populations at Chilliwack, Kamloops and Sussex relaized 95.8%, 92.7%, and 96.7% of their lifetime *rm*, respectively. Populations of *P. pequodorum* from the three regions realized 94.5%, 95.6% and 94.8% of lifetime *rm* value, respectively.

3.35 Analysis of frequency distribution of eggs

Statistical analysis of frequency distributions of eggs is generally used as an indicator of host discrimination ability of a parasite female. A parasite female that distributes her eggs among available hosts in a non-random fashion can considered to be exercising some degree of host discrimination ability. This is applicable in particular to solitary parasites, in which only one egg develops to maturity and all supernumerary eggs are, in effect, inviable. In other words,

FIGURE 10: Relationship between pivotal age and percent of total intrinsic rate of increase realized by the three populations of *A. ervi*. See text for details.

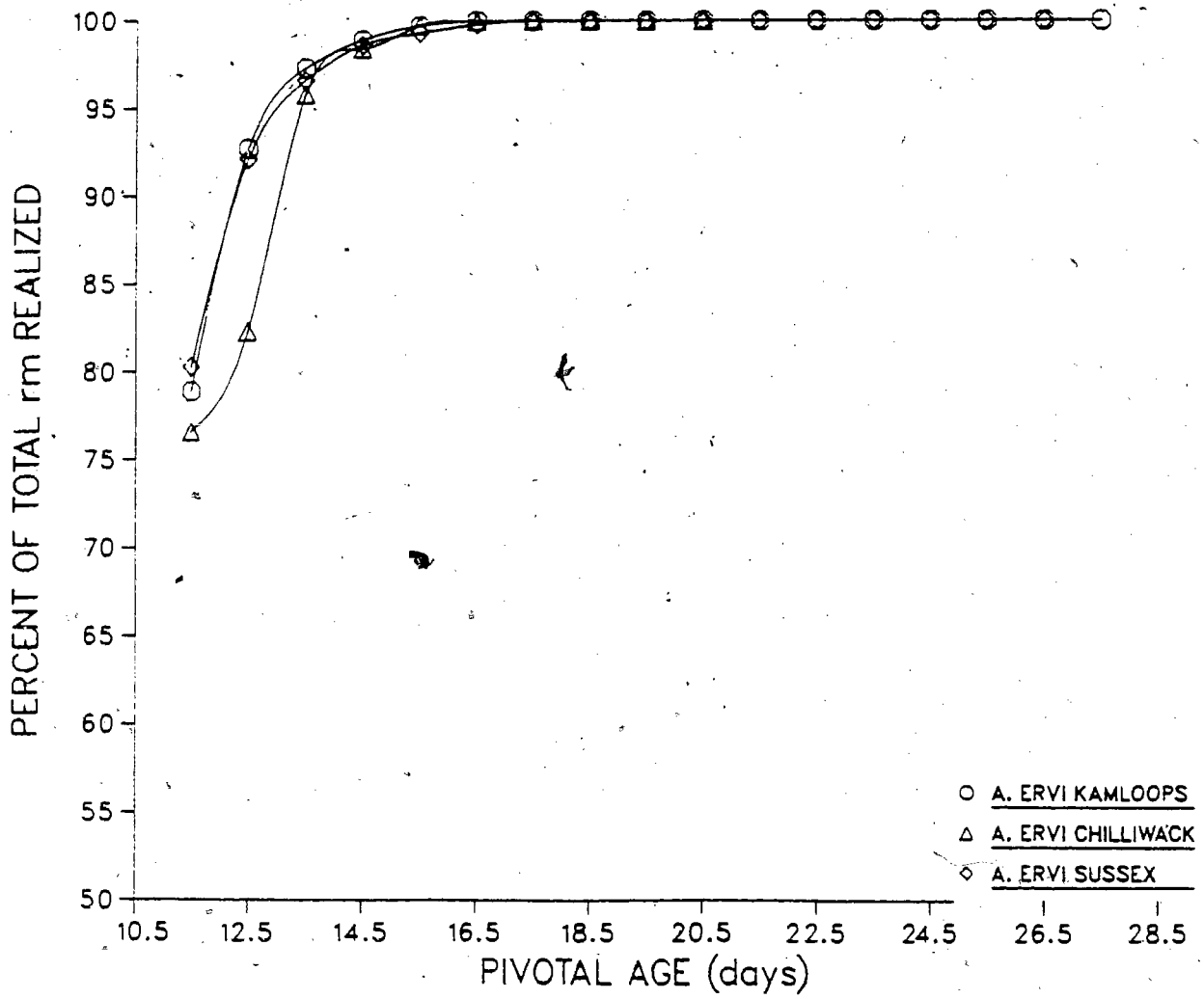

PERCENT OF TOTAL rm REALIZED
100
95
90
85
80
75
70
65
60
55
50
10.5
12.5
14.5
16.5
18.5
20.5
22.5
24.5
26.5
28.5
PIVOTAL AGE (days)
A. ERVI KAMLOOPS
A. ERVI CHILLIWACK
A. ERVI SUSSEX

FIGURE 11: Relationship between pivotal age and percent of total intrinsic rate of increase realized by the two populations of *A. smithi*. See text for details.

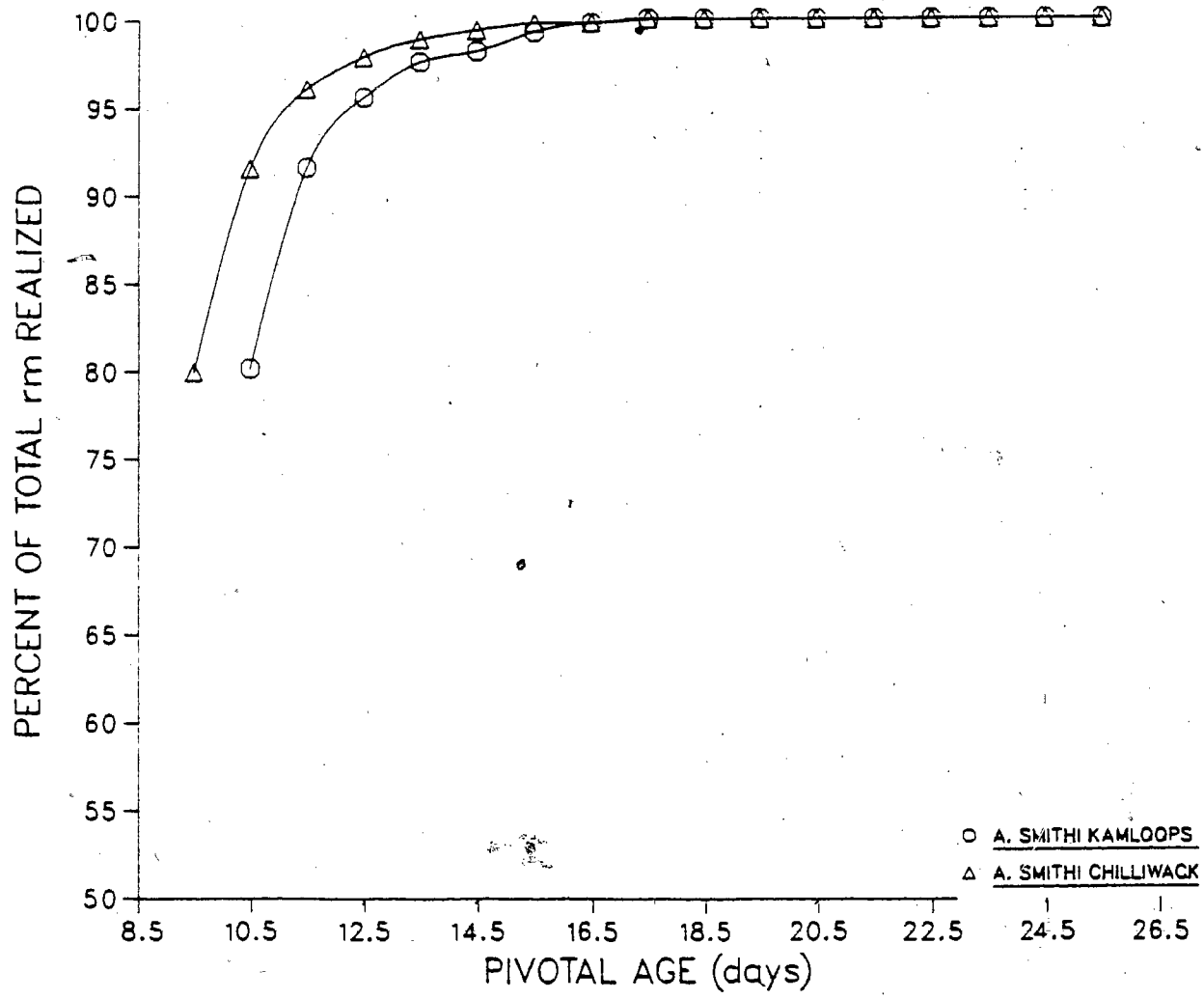

PERCENT OF TOTAL rm REALIZED
100
95
90
85
80
75
70
65
60
55
50
8.5
10.5
12.5
14.5
16.5
18.5
20.5
22.5
24.5
26.5
PIVOTAL AGE (days)
A. SMITHI KAMLOOPS
A. SMITHI CHILLIWACK

FIGURE 12: Relationship between pivotal age and percent of total intrinsic rate of increase realized by females of *A. pisivorus*. See text for details.

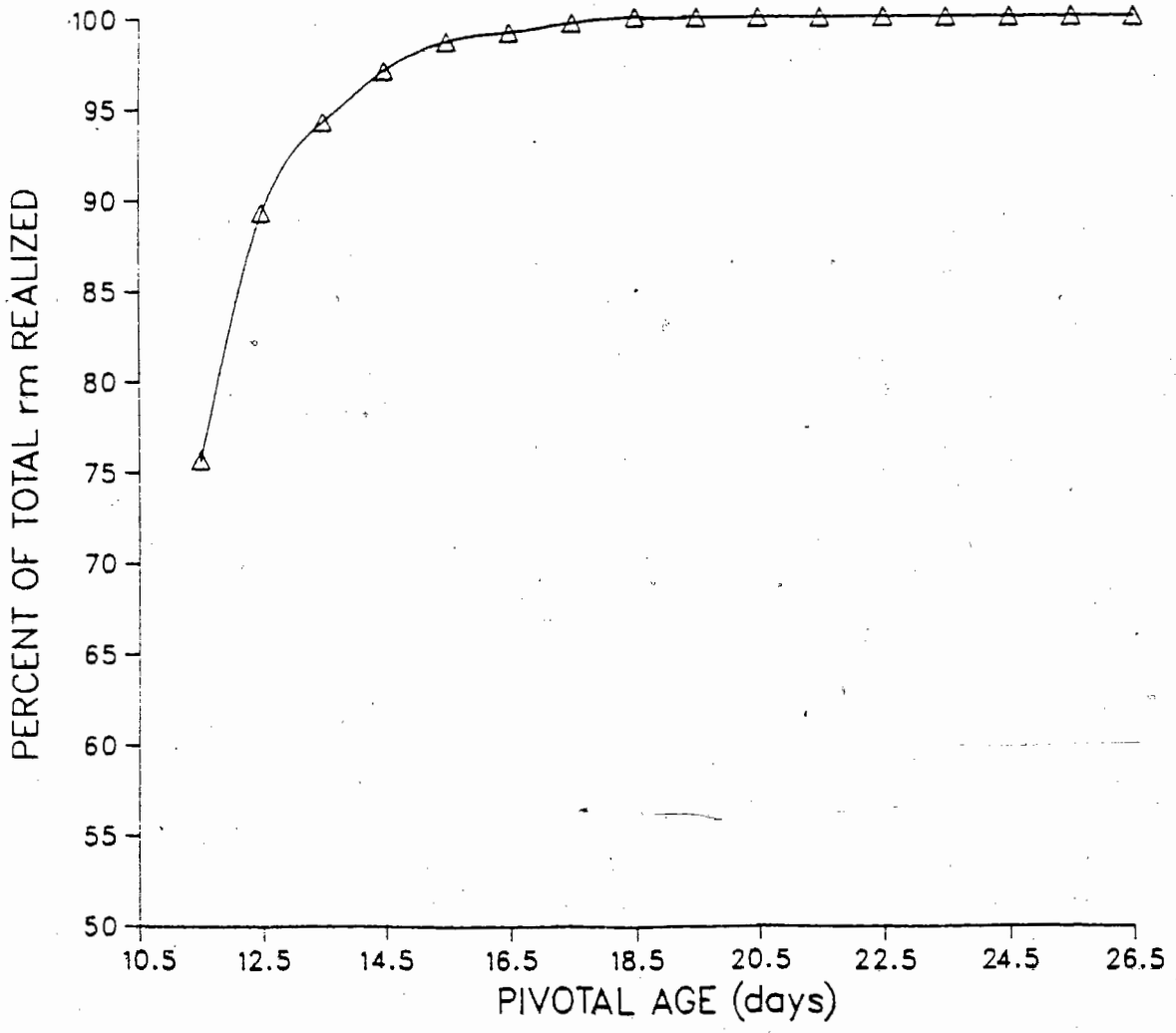
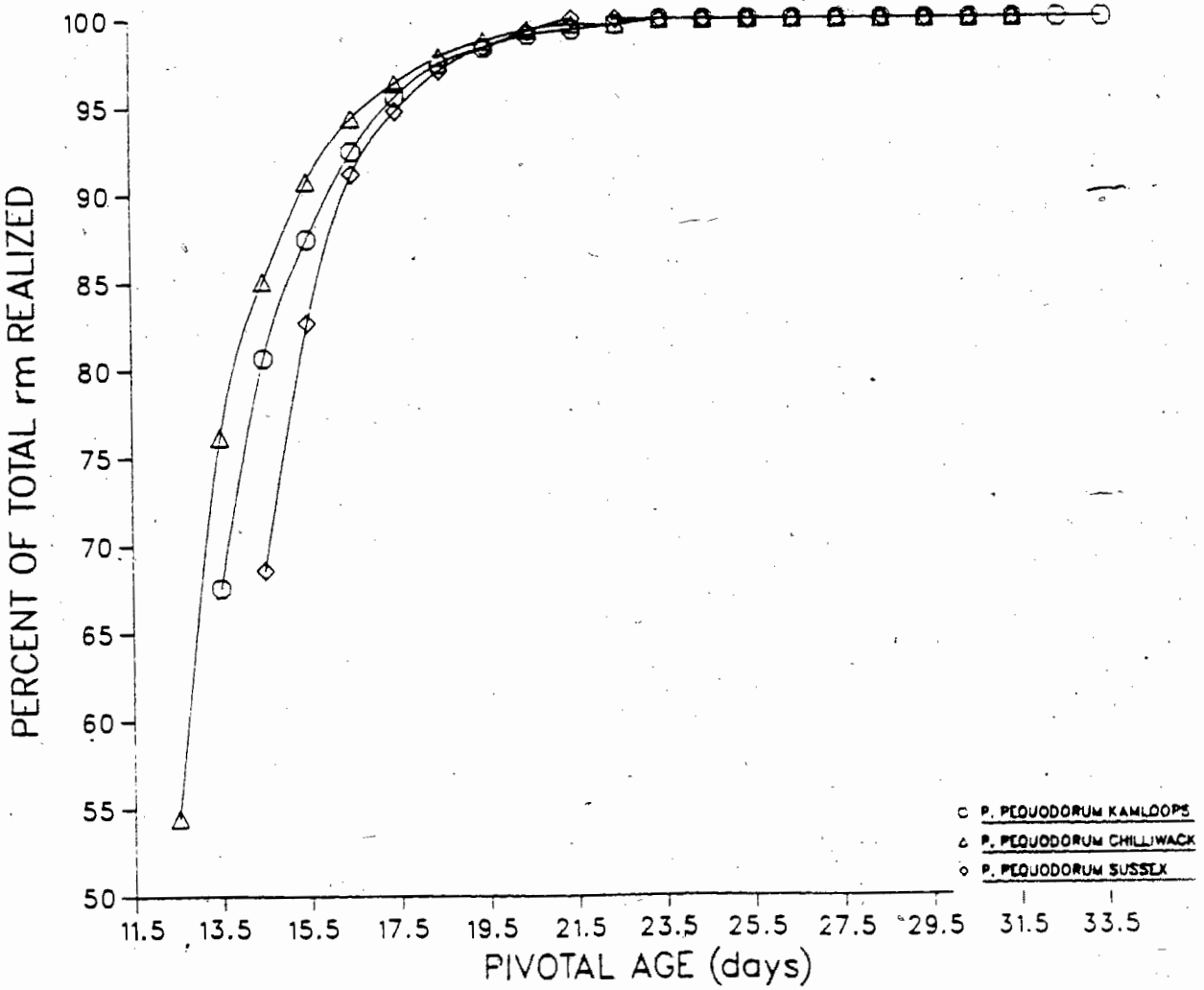

PERCENT OF TOTAL rm REALIZED
100
95
90
85
80
75
70
65
60
55
50
10.5
12.5
14.5
16.5
18.5
20.5
22.5
24.5
26.5
PIVOTAL AGE (days)

FIGURE 13: Relationship between pivotal age and percent of total intrinsic rate of increase realized by the three populations of *P. pequodorum*. See text for details.


PERCENT OF TOTAL rm REALIZED
100
95
90
85
80
75
70
65
60
55
50
11.5
13.5
15.5
17.5
19.5
21.5
23.5
25.5
27.5
29.5
31.5
33.5
PIVOTAL AGE (days)
P. PEQUODORUM KAMLOOPS
P. PEQUODORUM CHILLIWACK
P. PEQUODORUM SUSSEX

the female must be able to discriminate between parasitized and unparasitized hosts, in order to minimize the loss of eggs resulting from oviposition in hosts already parasitized. The presence of a number of conspecific competitors inside the aphid may also have deleterious effects on the fitness attributes of the one parasite that eventually emerges. While some parasites show virtually complete host discrimination e.g., *Aphelinus semiflavus* (Mackauer 1982), this process tends to fail in many others over a range of parasite:host ratios leading to superparasitism or multiple parasitism (van Alphen and Nell 1982, Bakker *et al.* 1967, Cloutier 1984, Mackauer 1983).

Quantification of host discrimination using some form of goodness of fit test (e.g., Bakker *et al.* 1967, 1972, Cloutier *et al.* 1984, Liu and Morton 1986, Rogers 1972, 1975) is inadequate for two reasons. Laboratory studies are not always suitable for predicting parasite behavior under natural conditions except in a general way (Mackauer and van den Bosch 1973). The second problem arises from an attempt to fit an observed frequency distribution to a theoretical distribution that is dependent on the validity of a set of statistical assumptions (Iwao and Kuno 1971, Patil and Stiteler 1974, Taylor 1984). These problems were discussed in more detail by Kambhampati *et al.* (1987).

To overcome or avoid these problems in comparing frequency distributions of eggs among species and populations, a computer-aided method that is not dependent on statistical assumptions was developed to quantify age-specific patterns of egg laying by parasite females. The basic methodology is derived from, and is similar to, pattern analysis as applied to digitized images of cell nuclei (Bartels *et al.* 1972, Nair *et al.* 1980, Panar and Nair 1975, Panno and Nair 1984, Sprenger *et al.* 1973, Vidal *et al.* 1973).

Kambhampati *et al.* (1987) used this method to analyse changes in frequency distribution of eggs by *A. smithi* females as a function of host density. It was shown that pattern analysis confirmed and expanded on the results obtained by conventional analysis of the same data set by Mackauer (1983). In addition, the analysis also provided more information on parasite behavior than could be obtained by methods based on goodness of fit tests.

3.351 Methodology of pattern recognition

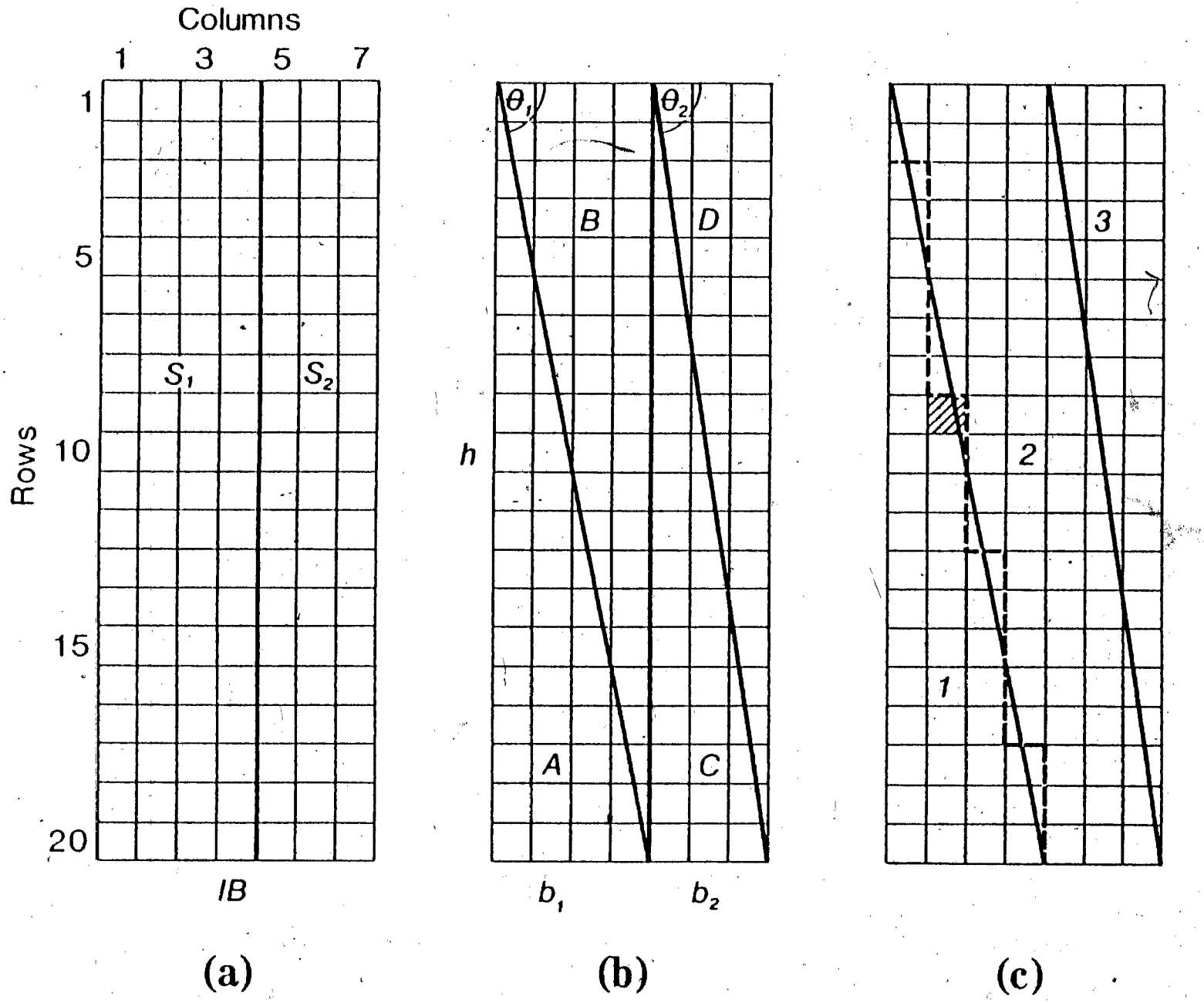
For each parasite female, the number of eggs and/or larvae found in dissected hosts were compiled into a rectangular integer array, Yrc, with dimension r_i rows and c_j columns (Figure 14). The number of rows in each array was 20, corresponding to the number of aphids dissected for each female. The number of columns corresponded to the number of days that the parasite survived. Each element, Y_{ij}, in the array represented the number of parasite eggs/larvae found in a particular aphid from the subsample dissected for a given day. The elements in each column were arranged in an ascending order beginning with the lowest number. The arrays are in effect visual representations of oviposition rates for each parasite female, with the columns representing parasite age and the column totals representing age-specific fecundity.

The procedure for analysing the arrays is as follows. First, each array was divided into three distinct domains 1, 2, and 3, by a computer program, based on the inherent pattern of changes in the age specific fecundity of the parasite. That is, domain 1 corresponded to the early days of adult life when fecundity was high (and increased), while domain 3 corresponded to the final days when fecundity was low (and declined). This pattern is clearly visible in Figure 14. The computer program then calculated an initial boundary (IB) that divided the array into two, not necessarily equal sections, S_1 and S_2 (Figure 15a). The value

FIGURE 14: An example of a two-dimensional fecundity array which was constructed for each individual female of the nine species and populations of pea aphid parasites for pattern analysis. Each digit in the array represents the number of parasite eggs/larvae found in each of the 20 aphids dissected. Each column represents the fecundity for any given day and the number of columns represents the longevity of the female. Note the inherent age-specific pattern in the array. See text for further details.

1 1 1 1 1 1 1 1 1 0 0 0 0
1 1 1 1 1 1 1 1 1 0 0 0 0
1 2 2 1 1 1 1 1 0 0 0 0
2 2 2 2 1 1 1 1 0 0 0 0
2 2 2 2 1 1 1 1 0 0 0 0
2 3 2 2 1 1 1 1 1 0 0 0
2 3 2 2 1 1 1 1 1 0 0 0
2 3 2 2 2 1 1 1 1 0 0 0
2 3 2 2 2 1 1 1 1 0 0 0
2 3 3 2 2 1 1 1 1 1 0 0
2 3 3 2 2 2 1 1 1 1 0 0
2 3 3 2 3 2 2 2 1 1 0 0
2 3 3 2 3 2 2 2 1 1 0 0
3 4 4 2 4 2 2 2 1 1 0 0
3 4 4 3 4 2 2 2 1 1 0 0
4 4 5 3 4 3 2 2 2 1 0 0
4 5 6 4 4 3 3 2 2 2 1 0
5 8 9 4 4 5 3 2 2 2 1 0

FIGURE 15: Diagrammatic representation of the computer algorithm used for assigning each of the array elements to one of the three domains 1, 2 and 3. See text for deatails.


Columns
1
3
5
7
1
5
10
15
20
Rows
S_1
S_2
IB
(a)
θ_1
θ_2
B
D
h
A
C
b_1
b_2
(b)
3
2
1
(c)

of IB was obtained by multiplying the number of columns in the array with a user-selected variable called domain factor (DF). The value of the domain factor depends on the objective of the analysis. In the present analysis, the criterion used was an equitable size distribution among the three domains, and by trial and error, a domain factor of 0.3 was chosen. The sections S_1 and S_2 were each divided into two triangles of equal area, S_1 into triangles A and B with base b_1, and S_2 into triangles C and D with base b_2. The height h of all four triangles is the same, equalling the number of array rows (Figure 15b). Domain 1 now includes triangle A, domain 2 triangles B and C, and domain 3 triangle D. The tangents of the angles θ_1 and θ_2 for triangles B and D, respectively, were calculated as

$$\tan_n = r_t / b_n \qquad (2)$$

where r_t is the total number of rows in the array and b_n is the base of the triangle measured in the number of columns, with $n = 1$ for triangle B and $n = 2$ for triangle D.

The second step in the analysis was to assign all elements Y_{ij} in each array to one of the three domains in accordance with a decision boundary. The boundary was obtained by solving the following equation for a specific row r in each column c

$$r = c \tan_n \qquad (3)$$

where $n = 1$ for all elements in section S_1 and $n = 2$ for all elements in section S_2.

However, because the array consisted of integers rather than real coordinates, Equation (3) was modified to

$$r' = r - \{(r-r_1)/2\} \qquad (4)$$

where r' is the new boundary, r is the expected row according to Equation (2) and $r_1 = tan$

(c-1). The calculated value of r^4 was converted to an integer by adding 0.5 and rounding off to the nearest whole number (Figure 15c).

The algorithm then calculated symmetries for all three domains on a scale from 0 to 10. For the purposes of this analysis, domain 1 was assigned a maximum symmetry score of 10 when all the elements within the domain belonged to frequency class 2 or greater. Similarly, domains 2 and 3 were assigned a score of 10 when all array elements in these domains belonged to frequency class 1 and 0, respectively. Once the sums of the three frequency classes had been accumulated for each domain, the program calculated three symmetry features (SF) according to the generalized expression

$$SF_N = 10(S_M / A_N) \qquad (5)$$

where N is the domain number from 1 to 3, M is the particular frequency class for domain N, S_M the total number of elements of class M in domain N, and A_N the area or the total number of array elements in domain N. The symmetry of the entire array was estimated by means of a global symmetry feature

$$GSF = (SF_1)^2+(SF_2)^2+(SF_3)^2 \qquad (6)$$

In practice, frequency classes of greater than 2 can be analysed if the definition of maximum symmetry for a particular domain is changed. Six frequency classes, ranging from 0 eggs per aphid to ≥5 eggs per aphid, were defined for each array, in order to increase the resolution of the analysis. That is, two frequency classes per domain were defined. Domain 1 was defined in terms of frequency classes 2 and ≥5, domain 2 in terms of 1 and 4 and domain 3 in terms of 0 and 3. The frequency classes follow a descending order from left to

right in accordance with the age-specific fecundity pattern of the parasites (see Figure 14). In summary, based on the six frequency classes, eight symmetry features were extracted from each array, namely, $SF_{1,2}$, $SF_{1,5}$, $SF_{2,1}$, $SF_{2,4}$, $SF_{3,0}$, $SF_{3,3}$, GSF_1 and GSF_2, where the first subscript refers to the domain number and the second subscript to the frequency class evaluated. The first global symmetry feature, GSF_1, refers to the squared total symmetry score of frequency classes 0, 1, and 2 and the second global symmetry feature, GSF_2, to the squared symmetry score of frequency classes 3, 4, and ≥5 as defined in Equation {6}.

In addition, six quantitative features were also extracted, corresponding to the six frequency classes defined above. These were obtained by totalling the number of aphids in the array with a given number of parasite eggs, i.e., summing all the aphids belonging to a particular frequency class. To reduce the bias due to differences in longevity among species and populations, the frequencies were converted to percentages and transformed to their arcsines according to the equation (Anscombe 1948):

$$FEC = n + 0.500 \arcsin (f + 0.375)/(n + 0.750) \qquad (7)$$

where x is one of the various frequency classes from 0 to ≥5, n is the number of aphids dissected per day (20), and f, the number of aphids in a given frequency class. For the quantitative features, FEC_0, FEC_1, FEC_2, FEC_3, FEC_4 and FEC_5, the subscripts refer to the six frequency classes of parasite eggs/larvae.

The 14 variables thus extracted from each array were compared among the species and populations by one-way ANOVA and a stepwise discriminant analysis using SPSS (Nie *et al.* 1975). The minimum tolerance level for the exclusion of a variable was set at 0.001% assessed on the maximum Mahalanobis distance between the groups. The matrix of

Mahalanobis generalized distance was obtained by an all-possible-pairwise-comparison using the BMDP subprogram 3D (Dixon 1981).

As a final step in the analysis, a representative array was selected for each of the species and populations. This was achieved by another program that compared all the arrays in each group with mean values of the features that were provided, and indicated the one array that corresponded closest to the mean values. Because none of the individual arrays are likely to agree with the means of all fourteen variables, the selection procedure gave the greatest weight to those variables that contributed most to among-group discrimination.

3.352 Results

The mean and standard deviation for each of the 14 variables extracted from the fecundity arrays of pea aphid parasites by pattern analysis are given in Appendix III. Means of all the variables had small standard errors associated with them. The values of the distribution statistics, skewness and kurtosis were non-significant for a majority of cases. Some variables, such as FEC_4, FEC_5, and $SF_{1,5}$, had significant kurtosis values. Despite this, because of the robustness of both ANOVA and MDA, all variables were included in the analysis.

3.353 Univariate analysis of image features

There was considerable variability in the mean value of the various species and populations for any given character. One way ANOVA was carried out to determine if the variables enabled differentiation between populations when examined one at a time.

The two populations of *A. smithi* at Chilliwack and Kamloops did not differ from each other in 10 of the 13 characters (76.3%) (the variable $SF_{3,3}$ had a symmetry score of zero for both populations). The three variables the populations differed in were FEC_1, FEC_4 and

$SF_{2,1}$. Trends in the frequency distributions of eggs for these populations were similar to those observed for lifetime fecundity and PIEL attributes.

The three populations of *A. ervi* differed in all but two variables, namely FEC_1 and $SF_{3,3}$. The number of variables from SNK test that had homogeneous subsets composed of *A. ervi* (Chilliwack) and *A. ervi* (Kamloops), and *A. ervi* (Kamloops) and *A. ervi* (Sussex) was five each. Two variables had three subsets each.

Mean values of the 14 features were most consistent for the three *P. pequodorum* populations. Consequently, they differed in only 5 of the 14 (35.7%) features. They differed in FEC_1, FEC_2, FEC_4, $SF_{2,4}$, and GSF_2. In 4 of the 5 significantly different variables, the Chilliwack and the Kamloops populations did not differ from each other but differed from the Sussex population.

3.354 Multiple discriminant analysis of image features

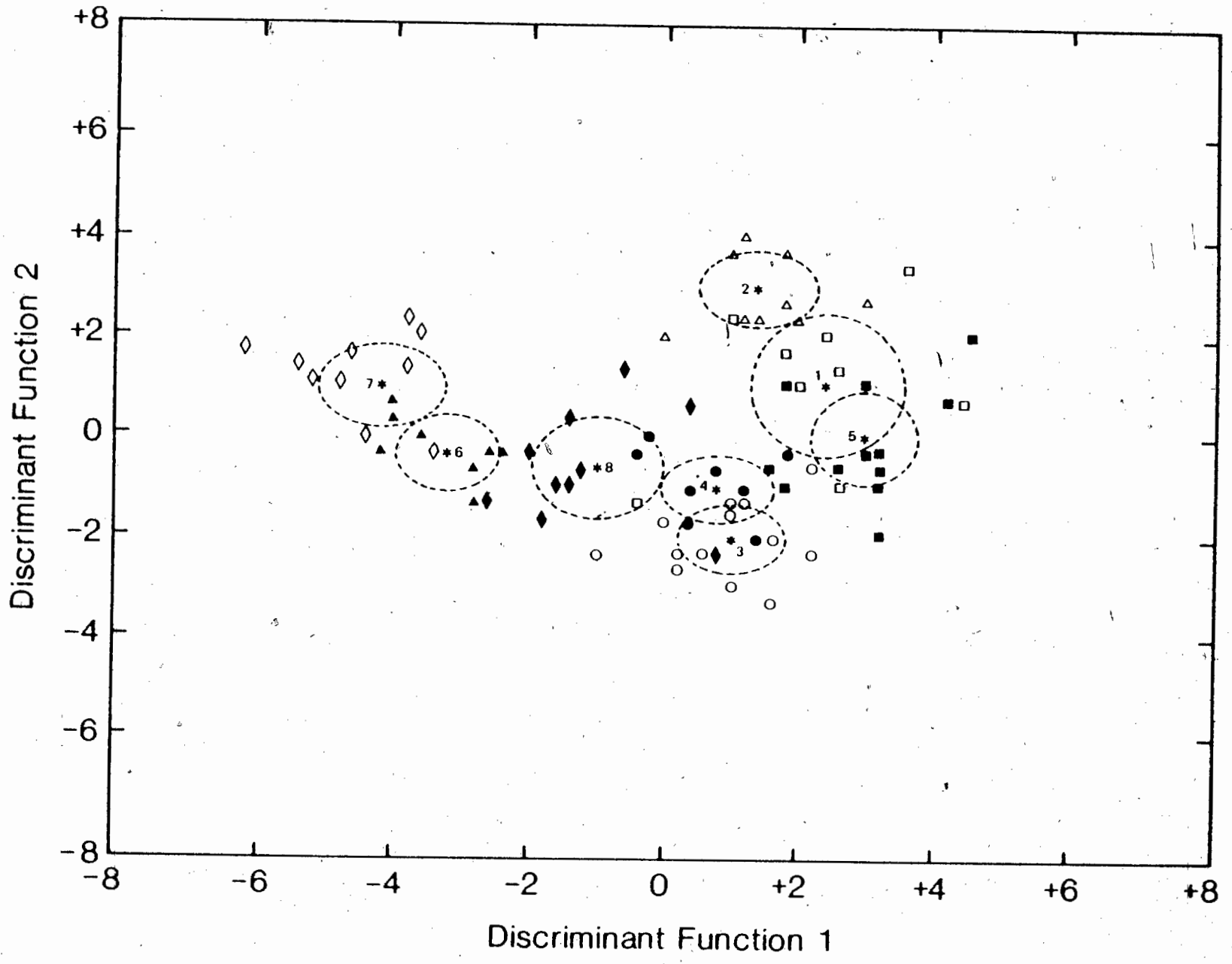
As in the case of discriminant analysis of PIEL attributes, *A. pisivorus* (Kamloops) was not included in the analysis to enable an easier interpretation of differences among populations. A scatterplot of group centroids projected onto first and second discriminant axes is shown in Figure 16. It is clear from the scatterplot that populations of any given species resemble each other in variables extracted from the fecundity arrays. However, there was also a certain degree of separation between populations of a species. Table XX shows how individuals of each population and species were classified by discriminant analysis. On average, 84.5% of the cases were correctly classified. Of the 14 original variables included in the analysis, 12 made a significant contribution to group discrimination, while $SF_{2,4}$ and $SF_{1,5}$ were excluded. Of the 5 discriminant functions used in the analysis, (the other two functions had a non-significant chi-square value associated with Wilk's lambda), the first function accounted for 58.2% of the

Table XX: Classification table showing actual and predicted group membership of cases used in discriminant analysis of image features. The average percent of correctly classified cases is 84.52%. See text for details.

		PREDICTED GROUP (in %)							
ACTUAL GROUP	n	A.s(K)	A.s(C)	A.e(K)	A.e(C)	A.e(S)	P.p(K)	P.p(C)	P.p(S)
A. smithi(K)	10	80.00	-	20.00	-	-	-	-	-
A. smithi(C)	9	-	100.00	-	-	-	-	-	-
A. ervi(K)	12	-	-	83.33	8.33	-	-	-	8.33
A. ervi(C)	9	-	-	-	88.89	-	-	-	11.11
A. ervi(S)	12	8.33	-	-	-	91.67	-	-	-
P. pequodorum(K)	9	-	-	-	-	-	66.67	22.22	11.11
P. pequodorum(C)	12	-	-	-	-	-	16.67	83.33	
P. pequodorum(S)	11	-	-	-	9.11	-	9.11	-	81.78

n= number of females tested

FIGURE 16: Scatterplot of populations of *A. ervi*, *A. smithi* and *P. pequodorum* projected onto discriminant axes 1 and 2 from discriminant analysis of image features extracted from fecundity arrays. The ellipses enclose the 95% confidence limits around the group centroids, which are represented by asterisks. The numbers beside the asterisks refer to the species and populations listed below in that order. □ : *A. smithi* (Kamloops), △ : *A. smithi* (Chilliwack), ○ : *A. ervi* (Kamloops), ● : *A. ervi* (Chilliwack), ■ : *A. ervi* (Sussex), ▲ : *P. pequodorum* (Kamloops), ◇ : *P. pequodorum* (Chilliwack), ◆ : *P. pequodorum* (Sussex).


+8
+6
+4
+2
0
-2
-4
-6
-8
Discriminant Function 2
-8
-6
-4
-2
0
+2
+4
+6
+8
Discriminant Function 1
1
2
3
4
5
6
7
8

total among-group variation. The remaining four functions explained 18.4, 10.2, 8.1 and 3.0% of among-group variation, respectively, for a total of 97.9%.

Standardized discriminant function coefficients for each of 12 variables and five functions are given in Table XXI. Considered over the five functions, GSF_1 contributed most to group discrimination followed by FEC_2, $SF_{2,1}$, $SF_{3,0}$ and FEC_1.

Populations of each species were also analysed among themselves. Average percent of correctly classified cases was 94.7% for the two *A. smithi* populations, 100% for the three *A. ervi* populations and 96.9% for the three *P. pequodorum* populations. One individual of *A. smithi* from Kamloops was misclassified. In the case of *P. pequodorum*, one individual from Kamloops was grouped with the Chilliwack population. Number of variables included in the analysis was 5 for *A. smithi*, 9 for *A. ervi*, and 11 for *P. pequodorum* populations. Scatterplots for populations of each of the species are shown in Figures 17, 18 and 19, and the standardized discriminant function coefficients in Tables XXII, XXIII, and XXIV.

A matrix of Mahalanobis generalized distance derived from pairwise comparisons of groups based on the variables from pattern analysis is shown in Table XXV. All but 9 of the pairwise comparisons were significant at a probability level of 5% or smaller. The general intraspecific trend in image features was identical to the one observed for the PIEL attributes. The values for pairwise comparisons between populations of *A. smithi* and *A. ervi* were greater than between the corresponding populations of *P. pequodorum*. In addition, the Chilliwack and Kamloops populations resembled each other more than either resembled the Sussex population.

Table XXI: Standardized discriminant function coefficients for image features extracted from fecundity arrays and included in MDA involving all pea aphid parasites except *A. pisivorus*. See text for details of variable names.

Variable	DISCRIMINANT FUNCTION				
	1	2	3	4	5
FEC_0	-0.45767	0.66281	-0.14642	0.10735	1.66413
FEC_1	-0.01155	-0.78755	0.71184	-0.12254	-1.46738
FEC_2	-0.91204	1.44415	-0.63020	0.78477	0.94891
FEC_3	0.10252	-0.57546	0.54183	-0.16243	-0.54233
FEC_4	1.04320	0.24278	0.14871	0.45446	0.25099
FEC_5	0.49015	1.00395	-0.45315	-0.41911	-0.06319
$SF_{1,2}$	0.62900	0.72117	-0.11814	-0.18088	0.41708
$SF_{2,1}$	-0.42777	0.70297	0.25696	-0.61277	1.77162
$SF_{2,4}$	-0.56448	0.36385	0.70772	0.15194	0.27072
$SF_{3,0}$	-0.06491	-1.88176	0.96178	0.12315	-1.02383
GSF_1	0.56089	1.13475	-1.10883	0.92485	-1.01963
GSF_2	0.20733	0.58516	0.84613	0.22868	0.52067

Table XXII: Standardized discriminant function coefficients for image features extracted from fecundity arrays and included in discriminant analysis of populations of *A. smithi*. See text for details of variable names.

Variable	DISCRIMINANT FUNCTION
	1
FEC_0	0.98508
FEC_3	0.71072
FEC_5	-1.11465
$SF_{2,1}$	-0.77157
GSF_2	-0.77157

Table XXIII: Standardized discriminant function coefficients for image features extracted from fecundity arrays and included in discriminant analysis of populations of *A. envi*. See text for details of variable names.

Variable	DISCRIMINANT FUNCTION	
	1	2
FEC_0	-0.54166	0.59684
FEC_3	0.50794	1.04348
FEC_4	0.78776	-2.59238
$SF_{1,5}$	-0.52937	1.93259
$SF_{2,1}$	0.15169	2.29325
$SF_{2,4}$	0.24389	2.10000
GSF_1	0.24454	-4.51268
GSF_2	1.21298	-1.81468

Table XXIV: Standardized discriminant function coefficients for image features extracted from fecundity arrays and included in discriminant analysis of populations of *P. pegubdorum*. See text for details of variable names.

Variable	DISCRIMINANT FUNCTION	
	1	2
FEC_1	-1.93659	-0.80009
FEC_3	-0.17897	1.00137
FEC_4	1.11637	-0.21611
FEC_5	-1.11210	0.30121
$SF_{1,2}$	1.69476	-1.26531
$SF_{2,1}$	2.80884	0.85668
$SF_{2,4}$	-1.15751	0.46771
$SF_{3,0}$	2.49244	-3.87600
$SF_{3,3}$	0.40762	0.70026
GSF_1	-4.11323	4.03278
GSF_2	1.97641	-0.69330

Table XXV: Matrix of Mahalanobis generalized distance (D) between populations of pea aphid parasites based on image features extracted from fecundity arrays. Values marked by asteriks are non-significant, unmarked values are significant at the 5% level and those marked by ' at the 1% level.

Species (Locality)	A.s(K)	A.s(C)	A.e(K)	A.e(C)	A.e(S)	A.p(K)	P.p(K)	P.p(C)	P.p(S)
A. smithi(K)	0.000								
A. smithi(C)	6.403*	0.000							
A. ervi(K)	5.281	10.824'	0.000						
A. ervi(C)	5.246*	9.089	5.553	0.000					
A. ervi(S)	6.275	6.631	7.137'	6.442	0.000				
A. pisiv(K)	4.020*	10.135'	3.887	5.498	6.307'	0.000			
P. pequo(K)	10.433'	15.892	17.999'	11.539*	23.586'	4.410*	0.000		
P. pequo(C)	11.401'	28.403'	6.327'	7.528'	14.531'	4.943	3.336*	0.000	
P. pequo(S)	4.553*	9.868'	7.982'	5.221*	5.722	2.285*	6.993	5.076	0.000

FIGURE 17: Scatterplot of populations of *A. smithi* projected onto discriminant axis 1 from discriminant analysis of image features extracted from fecundity arrays. The arrows indicate group centroids. Each individual parasite is represented by four symbols for both populations. □ : *A. smithi* (Kamloops), △ : *A. smithi* (Chilliwack).

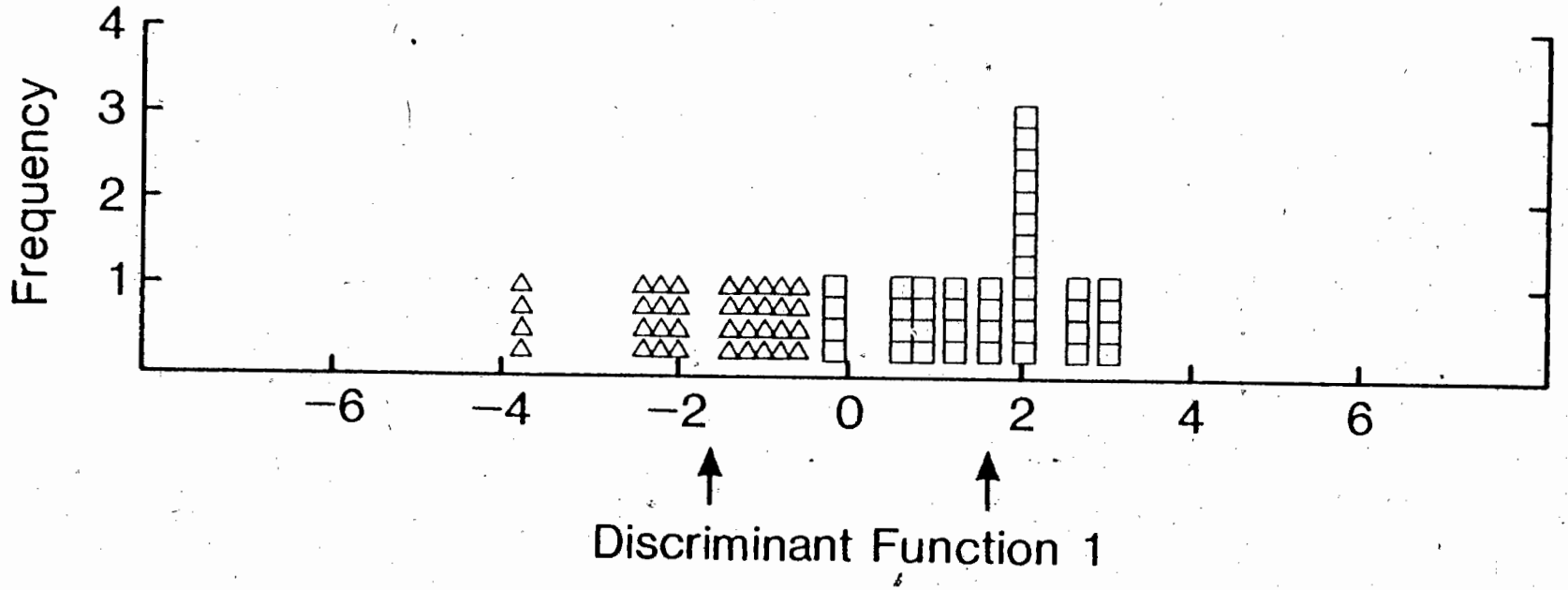

Frequency
4
3
2
1
−6
−4
−2
0
2
4
6
Discriminant Function 1

FIGURE 18: Scatterplot of populations of *A. ervi* projected onto discriminant function 1 and 2 from discriminant analysis of image features extracted from fecundity arrays. The ellipses enclose the 95% confidence limits around the group centroids, which are represented by asterisks. The numbers beside the asterisks refer to the populations listed below in that order. □: *A. ervi* (Kamloops), △ : *A. ervi* (Chilliwack), ○ : *A. ervi* (Sussex).

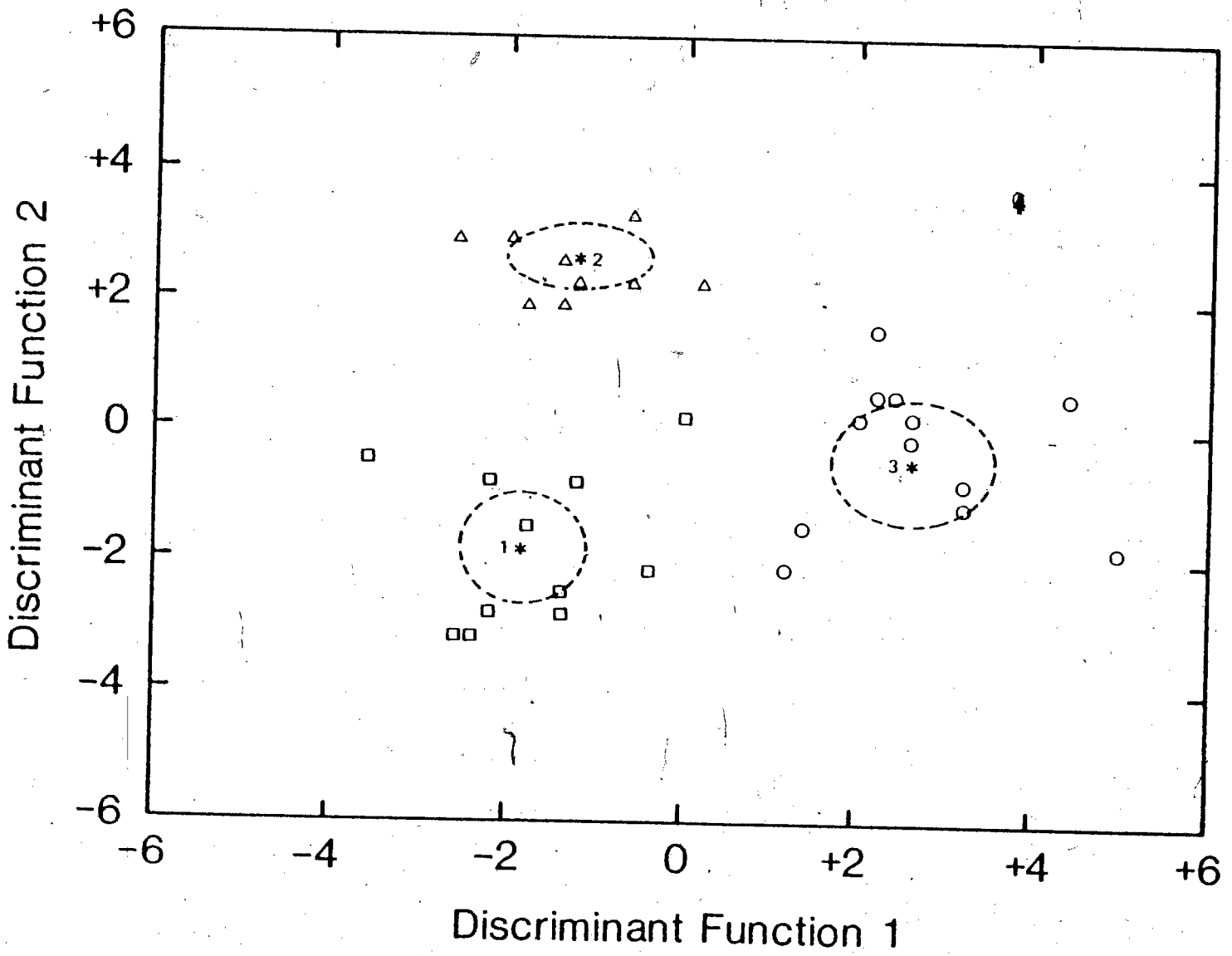
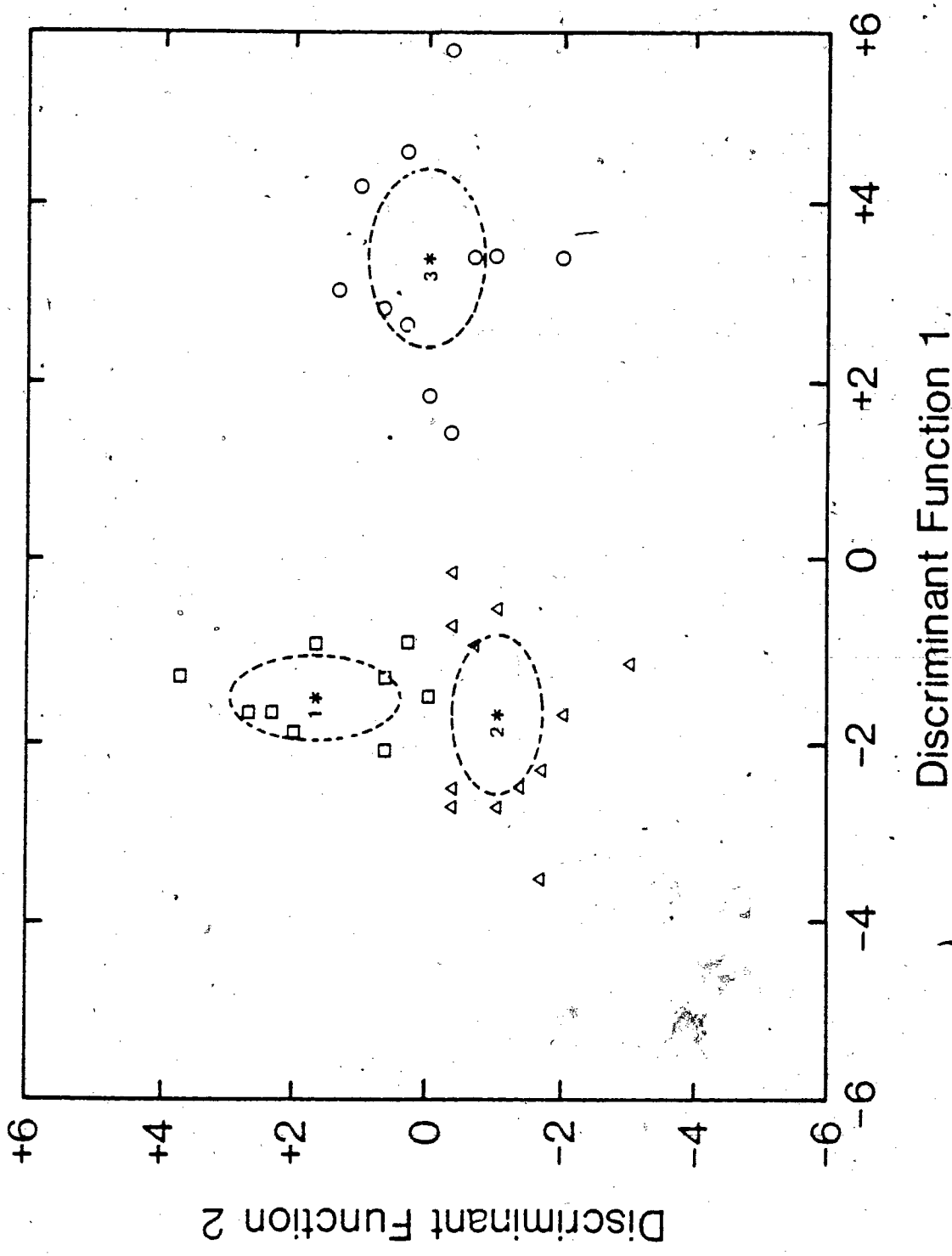

+6
+4
+2
0
-2
-4
-6
-6
-4
-2
0
+2
+4
+6
Discriminant Function 2
Discriminant Function 1
1*
2*
3*

FIGURE 19: Scatterplot of populations of *P. pequodorum* projected onto discriminant function 1 and 2 from discriminant analysis of image features extracted from fecundity arrays. The ellipses enclose the 95% confidence limits around the group centroids, which are represented by asterisks. The numbers beside the asterisks refer to the populations listed below in that order. □ : *P. pequodorum* (Kamloops), △ : *P. pequodorum* (Chilliwack), ○ : *P. pequodorum* (Sussex).


Discriminant Function 2
+6
+4
+2
0
-2
-4
-6
Discriminant Function 1
+6
+4
+2
0
-2
-4
-6
1*
2*
3*

As the final step in the analysis, a representative array depicting the typical pattern of egg distribution for each species and population is shown in Figure 20. Each array was extracted based on mean values of 10 most important variables of the twelve included in the first part of the analysis.

The univariate and the multivariate analyses suggested that the image features extracted from fecundity arrays are, to a certain extent, species-specific. This is substantiated by the fact that only two of the six quantitative features are consistently correlated with lifetime fecundity, namely FEC_2 and FEC_3. That is, the intensity of superparasitism was correlated with fecundity, but only to a certain degree. FEC_2 was the second most important variable for group discrimination in discriminant analysis of eight groups, a fact suggesting that the hosts were a limiting factor leading to a "breakdown" of host discrimination process at higher fecundities.

There was no particular pattern of correlation between the symmetry features and fecundity. However, the major contribution of symmetry features to discrimination suggested differences in age-specific egg laying pattern independent of fecundity. Indeed, GSF_1, which represents the overall oviposition pattern, contributed most to among-group variation. The next three variables that contributed substantially to discrimination i.e., $SF_{2,1}$, $SF_{3,0}$, and FEC_1, are also related to age-specific oviposition pattern and searching efficiency. In summary, it appears that the differences in host discrimination and oviposition rates among the various groups were inherent, rather than being an artifact of fecundity. The results of pattern analysis suggested that the egg laying pattern of pea aphid parasites is underlain by a number of different factors such as oviposition rate, host-searching efficiency, etc, in addition to age-specific fecundity.

FIGURE 20: Computer selected average fecundity arrays for species and populations of pea aphid parasites. (a): *A. ervi* (Kamloops), (b): *A. ervi* (Chilliwack), (c): *A. ervi* (Sussex), (d): *A. smithi* (Chilliwack), (e): *A. smithi* (Kamloops), (f): *A. pisivorus* (Kamloops), (g): *P. pequodorum* (Kamloops), (h): *P. pequodorum* (Chilliwack), (i): *P.pequodorum* (Sussex). See text for details.

(a)

0 0 1 0 0 0 0 0 0 0
0 1 1 0 0 0 0 0 0 0
0 1 1 0 0 0 0 0 0 0
0 1 1 0 0 0 0 0 0 0
0 1 1 0 0 0 0 0 0 0
0 1 1 0 0 0 0 0 0 0
1 1 1 0 0 0 0 0 0 0
1 1 1 1 1 0 0 0 0 0
1 2 1 1 1 0 0 0 0 0
1 2 2 1 1 0 0 0 0 0
1 2 2 1 1 0 0 0 0 0
1 2 2 1 1 0 0 0 0 0
1 2 2 1 1 0 0 0 0 0
1 2 2 1 1 1 0 0 0 0
2 2 2 1 1 1 0 0 0 0
2 2 2 1 1 1 1 0 0 0
2 3 2 1 1 1 1 0 0 0
2 3 2 1 1 1 1 0 0 0
3 3 3 1 2 1 1 0 0 0
3 3 4 2 2 2 1 0 0 0

(b)

0 0 0 0 0 0 0
0 0 0 1 0 0 0
1 0 1 1 0 0 0
1 1 1 1 0 0 0
1 1 1 1 0 0 0
1 1 1 1 0 0 0
1 1 1 1 0 0 0
1 1 1 1 1 0 0
1 1 1 1 1 0 0
1 1 1 1 1 1 0
1 1 1 1 1 1 0
1 1 1 1 1 1 1
1 1 1 1 1 1 1
1 1 1 1 1 1 1
1 1 1 2 1 1 1
1 1 1 2 1 1 1
2 2 2 2 1 1 1
2 2 2 2 1 1 1
2 2 2 3 1 1 1
2 2 2 3 2 1 1
3 2 2 4 2 1 1
3 3 4 5 5 2 2

(c)

1 0 1 1 0 0 0 0 0 0
1 1 1 1 0 1 0 0 0 0
1 1 1 1 1 1 1 0 0 0
1 2 1 1 1 1 1 0 0 0
1 2 2 1 1 1 1 0 0 0
2 2 2 1 1 1 1 0 0 0
2 2 2 1 1 1 1 0 0 0
2 2 2 1 1 1 1 0 0 0
2 2 2 1 1 1 1 1 0 0
2 2 2 1 1 1 1 1 1 0
2 2 2 1 1 1 1 1 1 0
2 2 3 2 1 1 1 1 1 0
2 3 3 2 1 1 1 1 1 1
2 3 3 2 1 1 1 1 1 1
3 3 3 2 1 1 2 1 1 1
3 3 3 2 1 1 2 1 1 1
4 4 3 3 1 2 2 1 1 1
4 4 3 3 2 2 2 1 1 1
4 4 4 3 2 2 2 1 1 1
5 5 5 4 2 2 3 1 1 1
5 5 6 6 4 3 3 2 2 2

(d)

1 1 1 1 1 1 1 1 0 0 0
1 1 1 1 1 1 1 1 0 0 0
1 2 1 1 1 1 1 1 0 0 0
1 2 1 1 1 1 1 1 0 0 0
1 2 1 1 2 1 1 1 0 0 0
1 2 1 1 2 1 2 1 1 0 0
1 2 2 1 2 1 2 1 1 0 0
1 2 2 2 2 1 2 1 1 0 0
1 2 2 2 2 1 2 1 1 0 0
2 2 2 2 2 1 2 2 1 0 0
2 2 2 2 2 1 2 2 1 0 0
2 2 2 2 2 2 2 2 1 0 0
2 3 2 3 3 2 3 2 1 0 0
2 3 2 3 3 3 3 2 1 0 0
3 3 2 3 3 3 3 2 1 1 1
3 3 2 3 3 4 4 2 1 1 1
3 3 3 4 3 4 4 3 2 1 1
3 3 4 4 4 4 4 3 2 1 1
4 4 4 4 4 5 4 3 2 1 1
6 4 4 6 6 5 5 3 3 2 1

(e)

1 0 0 1 1 0 0 0 0 0 0 0 0
1 1 0 1 1 0 0 0 0 0 0 0 0
1 1 1 1 1 0 0 0 1 0 1 0
1 1 1 1 1 1 0 1 1 0 1 0
2 1 1 1 1 1 1 1 1 0 1 0
2 2 1 1 1 1 1 1 1 1 1 0
2 2 1 1 1 1 1 1 1 1 1 0
2 2 1 1 1 1 1 1 1 1 1 0
2 2 1 1 1 1 1 1 1 1 1 0
2 2 1 1 1 1 1 1 1 1 1 0
3 2 1 1 2 1 1 1 1 1 1 0
3 2 1 2 2 1 1 1 1 1 2 0
3 3 1 2 2 1 1 1 1 1 2 0
3 3 2 2 2 1 1 1 1 1 2 0
3 3 2 2 4 1 1 1 2 2 2 0
3 4 2 2 4 2 1 1 2 2 2 0
3 5 2 2 4 2 1 1 2 2 2 0
3 5 2 3 4 2 2 1 2 2 3 0
4 6 2 3 5 2 2 1 2 3 3 1
6 6 6 5 5 3 2 2 5 3 3 1

(f)

1 1 1 0 1 1 0 0 0 0 0 0
1 1 1 1 1 1 1 0 0 0 0 0
1 1 1 1 1 1 1 0 1 0 0 0
1 1 1 1 1 1 1 0 1 0 0 0
1 1 1 1 1 1 1 1 1 0 0 0
1 1 1 1 1 1 1 1 1 0 0 0
1 1 1 1 1 1 1 1 1 0 0 0
1 1 1 1 1 1 1 1 1 0 0 0
1 2 1 1 1 1 1 1 1 0 0 0
1 2 1 2 1 1 1 1 1 0 0 0
1 2 1 2 1 1 1 1 1 0 0 0
2 2 1 2 1 1 1 2 1 0 0 0
2 2 1 2 1 1 1 2 1 0 0 0
2 2 1 2 1 1 1 2 2 0 0 0
2 2 2 2 2 1 1 2 2 1 1 0
2 2 2 2 2 2 2 2 2 1 1 0
2 2 2 3 2 2 2 2 2 1 1 0
2 3 2 3 2 2 2 3 2 1 1 0
2 3 3 3 3 2 2 4 2 1 1 0
3 5 4 3 3 3 3 4 3 1 2 0

(g)

```
0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0
0 0 0 1 0 1 1 0 1 1 0 0 0 0 0 0 0
1 0 1 1 0 1 1 0 1 1 0 0 0 0 0 0 0
1 0 1 1 0 1 1 0 1 1 0 0 0 0 0 0 0
1 0 1 1 0 1 1 1 1 1 0 0 0 0 0 0 0
1 0 1 1 1 1 1 1 1 1 0 0 0 0 0 0 0
1 0 1 1 1 1 1 1 1 1 0 0 0 0 0 0 0
1 0 1 1 1 1 2 1 1 1 1 1 0 0 0 0 0
1 0 1 1 1 1 2 1 1 1 1 1 0 0 0 0 0
1 0 1 1 1 1 2 1 1 1 1 1 0 0 0 0 0
1 0 1 1 1 1 2 1 1 1 1 1 0 0 0 0 0
1 0 1 1 1 1 2 1 1 1 1 1 0 0 0 0 0
1 1 1 1 1 1 2 1 1 1 1 1 0 0 0 0 0
1 1 1 2 1 1 2 1 1 1 1 1 0 0 0 0 0
1 1 1 2 2 1 2 1 1 1 1 1 0 0 0 0 0
1 1 1 2 2 2 2 1 1 1 1 1 0 0 0 0 0
1 1 1 2 2 2 2 2 1 2 1 1 1 0 0 0 0
1 1 2 2 2 2 2 2 1 2 2 1 1 0 0 0 0
2 1 2 2 2 2 2 2 2 2 2 2 1 0 0 0 0
2 1 3 3 2 2 3 2 2 2 2 2 1 1 0 0 0
3 2 3 3 3 3 3 3 2 2 3 2 1 1 1 1
```

(h)

```
0 1 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0
0 1 1 1 1 1 1 1 1 0 0 0 0 0 0 0 0 0
0 1 1 1 1 1 1 1 1 1 0 1 1 0 0 0 0 0
0 1 1 1 1 1 1 1 1 1 1 1 1 1 0 0 0 0
0 1 1 1 1 1 1 1 1 1 1 1 1 1 0 0 0 0
0 1 1 1 1 1 2 1 1 1 1 1 1 1 0 0 0 0
0 1 1 1 1 1 2 1 1 1 1 1 1 1 0 0 0 0
0 1 1 1 1 1 2 2 1 1 1 1 1 1 0 0 0 0
0 1 1 1 1 1 2 2 1 1 1 1 1 1 0 0 0 0
0 1 1 1 1 1 2 2 1 1 1 1 1 1 1 0 0 0
0 1 1 1 1 1 2 2 1 1 1 1 1 1 1 0 0 0
0 1 1 1 1 1 2 2 1 1 1 1 1 1 1 1 0 0
0 1 1 2 1 1 2 2 1 2 1 1 2 1 1 1 0 0
0 1 1 2 2 1 2 2 2 2 1 1 2 1 1 1 0 0
1 1 1 2 2 2 2 2 2 2 1 2 2 1 1 1 1 0
1 1 2 2 2 2 2 2 2 2 1 2 2 2 1 1 1 0
1 1 2 2 3 2 2 2 2 2 1 2 2 2 1 1 1 0
1 1 2 2 3 2 3 3 2 2 2 2 2 2 1 1 1 0
1 1 2 3 3 2 3 3 2 2 2 2 2 2 2 1 2 0
1 1 2 3 3 2 3 3 2 2 2 2 3 2 2 2 2 1
```

(i)

```
0 0 1 0 0 0 0 0 0
0 0 1 0 1 0 1 0 0
0 0 1 0 1 0 1 0 0
0 0 1 0 1 0 1 0 0
0 0 1 0 1 0 1 0 0
0 1 1 0 1 0 1 0 0
0 1 1 1 1 1 1 0 0
0 1 1 1 1 1 1 0 0
1 1 1 1 2 1 1 1 0
1 1 1 1 2 1 1 1 0
1 1 1 1 2 1 1 1 0
1 1 1 1 2 1 2 1 0
1 1 2 1 2 1 2 1 0
1 1 2 1 2 1 2 1 0
1 2 2 1 2 1 2 1 0
1 2 2 1 2 2 2 1 0
1 2 2 1 2 2 2 1 0
1 2 2 1 2 2 2 1 0
2 2 3 2 3 2 2 2 0
2 2 3 2 4 2 3 2 1
```

3.4 Discussion

The observed variation in life history traits among populations of pea aphid parasites is comparable in degree to that reported for other species of Aphidiidae. The average fecundity of a European strain of *Diaeretiella rapae* (M' Intosh), a common parasite of the cabbage aphid, *Brevicoryne brassicae* (L.), was estimated as 190 eggs/female by Hafez (1961). But fecundity of an Australian strain of the same species, originally imported from Europe, was estimated as 320 eggs/female (Gilbert and Hughes 1963, Hughes 1963). Flint (1979), in a study of geographic variation in three populations of *Trioxys complanatus*, a parasite of the spotted alfalfa aphid, *Therioaphis maculata*, also reported significant variation in fecundity and developmental time. The lifetime fecundity of an Iranian, an Italian, and a Californian population was 349, 437 and 588 eggs/female, respectively. The populations, however, did not differ in longevity.

A number of studies on a variety of insects have also reported significant variation between populations in life history traits (see, e.g., Baldwin and Dingle 1986, Birch *et al.* 1963, Denno and Dingle 1981, Diehl and Bush 1984, Dingle 1978, Futuyama and Peterson 1985, Fried and Pimentel 1986, Gilbert 1984, 1986, Labeyrie 1978).

The results of intraspecific comparisons indicated that the introduced and native pea aphid parasites differed from one another in the divergence levels between their populations. Mahalanobis generalized distances for PIEL attributes and egg frequency distributions between the populations of *A. smithi* and *A. ervi* were greater than those between the populations of *P. pequodorum*. The two introduced species, despite being initiated with founder populations different both in size and diversity, did not differ measurably from each other in this respect. Populations established from small numbers of founders that show a greater degree of

variability in their character means, relative to populations derived from larger numbers, are mentioned in the literature (e.g., Bryant *et al.* 1986a, 1986b, Dobzhansky and Pavlovsky 1957, Rich *et al.* 1984). This phenomenon can be observed in some populations with a known history of a genetic bottleneck or a founding event and is generally attributed to random genetic drift. I will discuss this aspect of variation further in Chapter VI.

The introduced and the native species did not, however, differ in their pattern of variation. The Chilliwack and Kamloops populations of all three species resembled each other in many of the variables. And in the case of *A. ervi* and *P. pequodorum*, populations from the above two areas were significantly different from the Sussex population. Matrices of generalized distances between populations for PIEL criteria and egg distributions, when examined specieswise, clearly show this trend.

It is possible that Chilliwack and Kamloops share common abiotic and biotic natural selection agents because of their geographic proximity. Organisms living in these areas may therefore be subjected to similar selection pressures, leading to convergent evolution (see, e.g., Benton and Uetz 1986, Endler 1977, 1982, 1986, Gould and Johnston 1972, Johnson 1976, Mooney 1977, Packard 1972). In addition, migration from a common climatic regime or gene pool may have contributed to this pattern. No sustained releases of pea aphid parasites have been made in British Columbia except for about 13,000 specimens of the "orange" phenotype of *A. smithi*, which were released near Kamloops in 1972 (Campbell and Mackauer 1973). No specimens have been recovered since. As mentioned earlier, there had been numerous large scale releases of *A. smithi* and *A. ervi* in the Pacific Northwest, including the states of Washington and Idaho (Halfhill *et al.* 1972). The first report of *A. smithi* occurring in British Columbia was in 1965, at Christina Lake in the Columbia River Basin close to the

Canada-United States border (Mackauer and Finlayson 1967). The most plausible routes of migration are: the Okanagan and Columbia River system into the Interior, and along the coast from northwestern Washington state into the Vancouver area and from there east into the lower Fraser River Basin (Campbell and Mackauer 1973). There is some evidence that *A. ervi* also spread through these two routes, but perhaps mainly through the cool and wet coastal area. Migration within British Columbia is aided by two factors: human transport, in particular transportation of parasitized aphids and mummies on baled alfalfa hay, and wind (Campbell and Mackauer 1973, Taylor and Palmer 1972). It is likely that such migration through all avenues is an ongoing process. The indigenous parasites are also probably subject to the same movement patterns. The migration that Campbell and Mackauer (1973) proposed is possibly annual and of a low density or rate. It may, however, be sufficient to result in an increased similarity between Chilliwack and Kamloops populations, depending on the intensity of selection.

Regardless of the factors responsible for the variation in life history traits, the variation itself has important implications for biological control. As mentioned earlier, reproductive potential is considered to be an important attribute. In biological control practice, one seeks to import and establish the most fecund phenotype into a new area, although fecundity may vary depending on the local abiotic and biotic factors.

But apparently, a higher reproductive potential does not assure a parasite's greater relative abundance or its long-term establishment. At both Chilliwack and Kamloops, *A. smithi* had the highest fecundity, followed by *P. pequodorum*. *A. pisivorus* had the third highest fecundity at Kamloops. The fecundity of *A. ervi*, the most common species in all three study sites, was the lowest, and about one half of that of *A. smithi*. At Sussex, however, *A. ervi*

females had a greater fecundity than that of *P. pequodorum* females.

In terms of longevity, *A. smithi* females had the second longest lifespan, after *P. pequodorum* at both Chilliwack and Kamloops. At Kamloops, *A. pisivorus* had the third longest lifespan. In all three study areas, *A. ervi* females had the lowest mean life expectancy of all pea aphid parasite species.

From these data, it is clear that *A. ervi* did not simply outnumber *A. smithi* because of a greater fecundity or longevity. Moreover, the relative abundance of pea aphid parasites is correlated neither with lifetime fecundity nor with longevity. Assuming the hierarchy of fecundity of the various species remained the same between 1971-72 and now (see e.g., Mackauer 1971), it appears that the relative abundance then *was* correlated with lifetime fecundity. If this was indeed the case, and since *A. smithi* still retains the high fecundity, the data indicate that interspecific differences in lifetime fecundity or longevity did not play a role in the decline of *A. smithi.*

It also appears that *A. ervi* is highly unlikely to have displaced *A. smithi* because of a more efficient host utilization and/or searching efficiency. As I have mentioned earlier, although lifetime fecundity may determine relative abundance in the mid-growing season, searching efficiency is probably more important during spring and late summer, when host density is relatively low. The detailed analyses that I have carried out to explore this possibility indicated that *A. smithi* females were superior or at least at no clear disadvantage relative to those of other species in the complex. *A. smithi* females generally performed better in 6 of the 14 PIEL performance criteria that were considered. These included variables pertaining to reproductive potential (PIEL fecundity, number of eggs laid in the first four days) and searching efficiency (number and proportion of aphids parasitized or escaping

parasitism). *P. pequodorum* performed the best in variables pertaining to host utilization efficiency (number of hosts parasitized per egg laid, proportion of eggs lost due to superparasitism, proportion of aphids superparasitized). Although *A. ervi* had a higher oviposition rate (proportion of eggs laid in the first four days, mean number of eggs laid per day), judged by most other criteria, it did not perform as well.

Pairwise comparisons between *A. ervi* and *A. smithi* revealed that the former performed better, albeit marginally, in variables pertaining to host utilization and oviposition rate. The latter performed significantly better in variables pertaining to reproductive potential and searching efficiency. The analysis of egg frequency distributions confirmed some of these findings. The image features extracted from the fecundity arrays indicated that *A. smithi* had a greater tendency to superparasitize under the experimental conditions, relative to the other species. The results of the analysis also indicated that there were differences in the age-specific egg laying pattern (i.e., oviposition rate), between the various species. However, because some of the indices of host utilization obtained from both PIEL attributes and pattern analysis were correlated with fecundity, the results should be interpreted with caution. This low host utilization efficiency of *A. smithi*, reflected in variables such as number of hosts parasitized per eggs laid, proportion of aphids superparasitized, number and proportion of eggs lost due to superparasitism, FEC_2, and FEC_3, is likely to have resulted because of two aspects of the experimental set-up. First, the parasite females were not at liberty to leave the experimental cage once all or most of the hosts had been exploited. Alternately, the number of hosts available in a 24h period period is finite, leading to repeated encounters with some host individuals. If these constraints are non-existent, as in the field, it is likely that *A. smithi*'s host utilization efficiency would improve significantly. In fact, Mackauer (1983) using a different strain of *A. smithi*, showed that the host utilization efficiency of the females

improves as a function of host density and predicted that at a host density of 150 aphids/day/female, there would be little or no superparasitism. In other words, if the number of available hosts was a limiting factor in my studies, and at higher host densities *A. smithi* can be expected to perform better than or as well as *A. ervi*, then it can be concluded that differential host utilization, searching efficiency and oviposition rate can not explain the changes in relative abundance of pea aphid parasites.

Multivariate analysis of PIEL performance criteria and egg frequency distributions indicated that many of the variables were species-specific. This suggests that both the variables and the methodology that were employed can be useful for discriminating between species, as well as between populations of a species. In discriminant analysis of PIEL attributes, the various species differed mainly in variables related to reproductive potential and oviposition rate, in that order. All the groups were well-separated when projected onto discriminant functions 1 and 2, especially along species lines, with some overlap between populations of a species. Discriminant analysis of image features confirmed the results of analysis of PIEL attributes. It indicated that the various species differed mainly in the degree of superparasitism and oviposition rate.

The life table analysis indicated that *A. smithi* had the highest potential rate of population growth of all species at both Chilliwack and Kamloops. *A. ervi*'s intrinsic rate of increase, gross and net reproductive rates were significantly lower than those of *A. smithi*'s. However, the difference between these two species becomes less striking if one were to consider only the effective number of eggs and disregard all superparasitism. Moreover, in the first four days of adult life, females of *A. smithi* had realized a greater proportion of their lifetime *rm* value than the females of *A. ervi*. *A. smithi* also had a considerably shorter

generation and doubling times than other species in the complex. It appears from a preliminary analysis that a reduction of approximately 2.5 days in the developmental time, or a reduction of approximately 1 day and a doubling of fecundity of *A. ervi*, is required to match the intrinsic rate of increase of *A. smithi*. As in the case of lifetime fecundity and PIEL attributes, *A. smithi* females were at no disadvantage with regard to life table statistics relative to *A. ervi* or other species in the complex.

In summary, there is no evidence to indicate that the changes in the relative abundance of pea aphid parasites were due to interspecific differences in reproductive potential, PIEL performance criteria (host utilization, searching efficiency, oviposition rate) or rate of population growth. On the contrary, the univariate and the multivariate analyses showed that *A. smithi* outperformed not only *A. ervi*, but also *A. pisivorus* and *P. pequodorum* in virtually all aspects of reproduction. The results of the inter- and intraspecfic studies in combination indicate that *A. ervi* did not displace *A. smithi*, but moved into an empty niche subsequent to the decline of *A. smithi* due to genetic impoverishment.

CHAPTER IV

VARIATION IN THERMAL COEFFICIENTS

4.1 Introduction

Temperature is perhaps the most important climatic variable affecting poikilothermic animals, including insects. It affects both their physiological as well as behavioral activities. In order to survive and reproduce, an insect must be adapted to the temperature cycles of its environment.

The thermal coefficients of both pest and beneficial insects are of importance to applied studies. The coefficients include, among others, developmental time and rate for any given stage, lower temperature threshold for development and degree days required to complete development. For classical biological control, thermal coefficients are important for three reasons. First, quantifying how the coefficients vary among species and populations may eventually aid in predicting the likely threshold value of a population from a region with a given climatic profile. Second, the imported parasite population should be compatible with the intended region of introduction. In other words, introduction of a parasite with a threshold temperature too high or too low relative to the target host should be avoided. In the first case, it is likely the parasite will not be an effective biological control agent. In the latter situation, the parasite may fail to become established, unless it is polyphagous and can find other host species. The third, related reason is that one would want to introduce a population with the lowest possible threshold temperature, but above that of the host.

The relationship between rate of development and temperature is usually a shallow sigmoid curve (Figure 1 in Campbell *et al.* 1974). Over a range of temperatures, the relationship is linear, and when the straight line is extrapolated, threshold temperature (t) is the point at which the line cuts the x-axis. Below this temperature no measureable development takes place. The rate of development is not linear close to t and it curves to

the left, into the lower temperature range. The rate of development also deviates from a linear relationship in the high temperature range. The straight line is best characterized in terms of t, and number of degree days required to complete development, K (Campbell *et al.* 1974). K is calculated as the reciprocal of slope b in the linear regression equation employed to estimate developmental thresholds. To obtain an accurate estimate of thermal coefficients a large sample of insects (≥50 individuals) are reared and time-to-adult or to the desired stage is noted. A number of models can then be used to estimate constants.

A large body of literature on geographic variation in temperature requirements of a variety of insects has appeared in the past few decades (see, e.g., Andrewartha and Birch 1954, Baldwin and Dingle 1986, Bonnemaison 1951, Bursell 1964, Campbell *et al.* 1974, Denno and Dingle 1980, Dingle 1978, Dingle and Hegmann 1981, Liu and Hughes 1984). As noted earlier, because insects must adapt to their local temperature regime to survive, populations of a species almost invariably differ in their temperature requirements, within the constraints set by their genotype. Variation in thermal coefficients among populations of a species from climatically different regions can therefore be taken as evidence of a degree of adapataion to the local climate through directional selection (Campbell *et al.* 1974). Based on the observed variation, conclusions can be drawn as to the degree and pattern of variation among populations of introduced and native species.

This chapter has the following objectives: (1) to quantify geographic variation in thermal cefficients and compare its degree and pattern among introduced and native species of pea aphid parasites from different regions, and (2) to ascertain if interspecific differences in thermal coefficients could explain the observed changes in relative abundance of the pea aphid parasites in North America.

4.2 Materials and methods

Developmental time from egg to adult eclosion for the pea aphid parasites was estimated at four constant temperatures. Temperatures inside the experimental cages were 14.0, 16.5, 20.3, and 23.6 °C (±1 °C) (ambient = 12.0, 15.0, 17.8, and 20.5 °C respectively). All experiments were conducted at 55–60% R.H. and 24h light. For each experiment involving a species or a population, a cohort of 200 two to three day-old aphids were obtained as described in Chapter II. This cohort of aphids was divided into five groups of 40 aphids each. Aphids were parasitized individually by placing one aphid and one mated parasite female in a gelatin capsule (Parke-Davis, #00). The parasite was allowed only one ovipositional strike per aphid to prevent superparasitism. About 25 parasite females were used to parasitize the 200 aphids. The time it took to parasitize 40 aphids was noted and typically it took between 10–20 minutes to parasitize one group. The parasitized aphids were transferred into small plastic cages (8.5 cm diameter x 3.5 cm high) containing a young bean shoot. Each cage had a density of 20 aphids. Cages containing the parasitized aphids were transferred to a "Conviron" controlled environment chamber immediately after parasitization. The resulting mummies were gently scraped from the leaves and placed in wax paper cups fitted with plastic Petri dish lids and returned to the growth chamber. At this time all the mummies in one group (i.e., 40 or thereof) were placed in one cup. Temperature inside the cup was monitored and was found to be within ±0.5 °C of that in the original experimental cages.

Median emergence time (ET_{50}) was estimated by a quantal response method (Finney 1962, Hewlett and Plackett 1979). This method is akin to the methodology used to estimate LD_{50} from dose-response curves, also known as probit analysis (Gaddum 1933, Bliss 1934, 1935). Dose in this case is time in hours, and response, percent emergence of adult parasites

at any given time. A dry run was performed at each temperature to obtain a rough estimate of median emergence time. Each of the five subgroups was then observed once at a predetermined time, approximately evenly spaced around the estimated median emergence time. Percent emergence and sex of the emerged parasites in each subgroup were then recorded. The resulting five data points were transformed to probits (Finney 1962), and regressed against $\log_{10}$(time). The predicted probits were incorporated into a probit analysis as described by Finney (1962). This enabled the determination of median emergence time, its standard error and 95% confidence limits, and the slope and intercept of the regression equation.

Median emergence times for each of the various populations and species were plotted and a linear regression equation obtained. The lower threshold temperature for development was then estimated by extrapolation of the regression equation. Because a number of authors have shown that there was no significant difference between the median emergence time of male and female aphidiids (e.g., Cohen 1985, Campbell 1974, Liu and Hughes 1984), data for both the sexes were pooled for the analysis. In some cases, the point for the highest temperature was in the non-linear range of the temperature curve (Figure 1 in Campbell *et al.* 1974). In such cases, the calculation of threshold was based on developmental time at three temperatures excluding the highest temperature.

4.3 Results

4.31 Developmental time from egg to adult emergence

Median developmental time from egg to adult of pea aphid parasites was influenced by temperature and increased linearly with an increase in temperature. It varied considerably both between species and between populations of each species. at all four temperatures (Table XXVI).

Among species, *A. smithi* at both Chilliwack and Kamloops had the shortest developmental time at all temperatures, except at 16.5 °C, at which *A. ervi* at Kamloops had the shortest developmental time. At Kamloops, *A. smithi* was followed by *A. pisivorus* and *P. pequodorum*, while at Chilliwack it was followed by *A. ervi* and *P. pequodorum*. At Sussex, *A. ervi* had a shorter developmental time than *P. pequodorum* at all four temperatures.

4.32 Developmental thresholds

Threshold temperatures varied considerably between species, as well as between populations of a species, and are shown along with the regression equations in Table XXVII. Populations of all species had highly significant ($P<0.01$) regression coefficients of rate of development against temperature.

Among species, the threshold values ranged from a low of 5.6 °C (*A. pisivorus* at Kamloops) to a high of 7.8 °C (*P. pequodorum* at Kamloops). At Kamloops, *A. pisivorus* was followed by *A. ervi* (6.0 °C), *A. smithi* (6.3 °C), and *P. pequodorum* (7.8 °C). At Chilliwack,

Table XXVI: Median developmental time from egg to adult eclosion for pea aphid parasites (in days). The SEM is given in parentheses.

Species (Locality)	TEMPERATURE (in °C)			
	14.0	16.5	20.3	23.6
A. ervi(K)	26.30(0.04)	17.08(0.05)	13.98(0.05)	11.98(0.08)
A. ervi(C)	27.30(0.07)	18.66(0.05)	13.29(0.04)	11.63(0.04)
A. ervi(S)	26.09(0.06)	17.94(0.04)	13.67(0.06)	12.16(0.09)
A. smithi(K)	24.22(0.03)	17.99(0.03)	13.32(0.05)	11.27(0.06)
A. smithi(C)	23.13(0.04)	15.99(0.04)	12.68(0.06)	10.24(0.04)
A. pisivorus(K)	25.52(0.17)	16.77(0.06)	13.89(0.06)	11.94(0.06)
P. pequodorum(K)	30.65(0.03)	22.90(0.04)	15.46(0.06)	13.70(0.09)
P. pequodorum(C)	32.09(0.04)	23.07(0.04)	17.09(0.05)	12.91(0.05)
P. pequodorum(S)	31.87(0.04)	22.83(0.05)	17.46(0.06)	14.73(0.09)

Table XXVII: Regression equations and thermal constants for species and populations of pea aphid parasites estimated from developmental times shown in Table XXVI.

Species	Regression Equation*	r^2	t(°C)	K(day °C)
A. ervi(K)	Y=0.0052X-0.0314	0.94	6.0	192.31
A. ervi(C)	Y=0.0052X-0.0334	0.98	6.4	192.31
A. ervi(S)	Y=0.0055X-0.0366	0.99	6.7	181.82
A. smithi(K)	Y=0.0053X-0.0331	0.99	6.3	188.68
A. smithi(C)	Y=0.0055X-0.0324	0.97	5.9	181.82
A. pisivorus(K)	Y=0.0051X-0.0286	0.93	5.6	196.08
P. pequodorum(K)	Y=0.0051X-0.0398	0.99	7.8	196.08
P. pequodorum(C)	Y=0.0046X-0.0333	0.99	7.2	217.39
P. pequodorum(S)	Y=0.0041X-0.0247	0.99	6.0	243.90

*Estimates of threshold values based on developmental times at the three lowest temperatures for all populations except *A. ervi* (Chwk). See text for details.

however, *A. smithi* had the lowest threshold temperature of 5.9 °C, followed by *A. ervi* (6.4 °C) and *P. pequodorum* (7.2 °C). At Sussex, *P. pequodorum* (6.0 °C) had a lower threshold than *A. ervi* (6.7 °C). The number of day degrees above the threshold temperature required by an insect to complete development from egg to adult generally reflected the trend observed in developmental time from egg to adult. *A. smithi* populations at Chilliwack and Kamloops had the smallest value of *K* followed by *A. ervi*, *A. pisivorus* and *P. pequodorum*. At Sussex, *A. ervi* had a lower value of *K* compared with *P. pequodorum*.

There was considerable variation in temperature thresholds between populations of all species. However, populations of introduced species differed from those of native species in their degree of variability in threshold temperatures. *A. smithi* and *A. ervi* at Kamloops and Chilliwack differed from each other by 0.4 °C, while *P. pequodorum* populations differed by 0.6 °C. Populations of *A. ervi* at Kamloops and Chilliwack differed from the Sussex population by 0.3 and 0.7 °C, respectively, while the same comparison for *P. pequodorum* yielded 1.2 and 1.8 °C. The *K* values also showed a similar trend. Populations of *A. smithi* at Kamloops and Chilliwack differed from each other by 6.86 day °C, while *A. ervi* populations did not differ from each other in this respect. The same comparison for *P. pequodorum* populations yielded 21.31 day °C. Populations of *A. ervi* at Kamloops and Chilliwack diffred from their Sussex counterparts by 10.49 day °C, while *P. pequodorum* populations differed by 26.51 and 47.82 day °C, respectively.

4.4 Discussion

Inter- and intraspecific variation in thermal coefficients of several pea aphid parasites was examined in this chapter. The data indicated that considerable inter- and intraspecific variation exists in thermal coefficients In general, the data are comparable to those reported for pea aphid parasites (Campbell and Mackauer 1975), and other aphidiids (Campbell *et al.* 1974, Cohen 1985, Flint 1979, Liu and Hughes 1984). The pattern in developmental times reported by Campbell and Mackauer (1975) and by Campbell *et al.* (1974), i.e., *A. smithi* with the shortest developmental time and *P. pequodorum* the longest, was confirmed in this study. Liu and Hughes (1984) reported small differences in both developmental times and thresholds of a French and a Japanese stock of *Aphidius sonchi* Marshall, a parasite of the sowthistle aphid, *Hyperomyzus lactucae* (L.). Flint (1979) estimated developmental times of three populations of *Trioxys complanatus* at six constant temperatures and found significant differences among them. She reported differences of up to 0.65 °C in threshold temperatures among the three populations, which ranged from 8.48 to 9.09 °C.

A number of models have been proposed to estimate the developmental thresholds of insects (e.g., Bieri *et al.* 1983, Schaffer 1983, Wagner *et al.* 1984). One drawback of the linear model, i.e., dependent on estimates of developmental times in the linear range, used in this study is that the threshold temperatures tend to be slightly overestimated. This is because, at lower temperatures the developmental rate is non-linear. This may preclude the use of such estimates in field situations and in phenology models that are dependent on field data. However, a number of authors have found the linear model to be adequate both for relating the threshold to the host and for inter- and intraspecific comparisons (e.g., Cohen 1985, Campbell *et al.* 1974, Butts and McEwen 1981, Johnson *et al.* 1979, Obrycki and Tauber

1982, Tauber and Tauber 1982). Linear models have two advantages over the more complex models. Many of the latter models require estimation of developmental times in the non-linear range of the development curve on both ends. This could be laborious and time consuming, particularly at temperatures close to threshold value and at high temperatures, wherein developmental time is prolonged. The range of temperatures for which developmental times need to be estimated for linear models can be easily carried out in a laboratory. These models also enable a relatively easy calculation and interpretation of thermal constants. Thresholds estimated from linear models will suffice for comparative purposes, as long as the extent of overestimation can be assumed to be the same for all species and populations. Moreover, estimates of t and K are negatively correlated (Campbell *et al.* 1974). A small positive error in t then, is automatically corrected by a corresponding error in K, so that predicted rates of development are affected minimally.

The variation in developmental time among populations of the introduced pea aphid parasites, *A. smithi* and *A. ervi*, is comparable in degree to that among populations of the native species, *P. pequodorum*, although populations of the latter species were slightly more variable. The divergence in threshold temperatures between populations of the introduced species was, however, less than that between corresponding populations of the native species. A similar trend was apparent for the K values. I can only speculate that this lower variability in threshold temperature is of significance in the field, and that it is a result of the small founder populations. It is possible, however, that the introduced species have not been in North America long enough to permit a "fine tuning" of their threshold temperatures. They may thus show the same degree of divergence as the native species in evolutionary time. I will discuss this further in Chapter VI. It is also of interest to note that, as in the case of life history traits, populations of both introduced and native parasite species from Kamloops

and Chilliwack are more similar to each other in threshold values than either is to the Sussex population (see Section 3.4).

The idea that variation in developmental times and threshold temperatures is an indicator of adaptation to the local environment is widely accepted (e.g., Baldwin and Dingle 1986, Campbell *et al.* 1974, Diehl and Bush 1984, Tauber and Tauber 1982, see, however, Lamb *et al.* 1987). It has been reported that there is an inverse relationship between latitude and threshold values within a hemisphere. That is, populations inhabiting warmer climates have a higher threshold than those from cooler climates so that the threshold temperature closely corresponds to the onset of the growing season. Lower t values then, generally occur in populations that experience cool vernal conditions, while higher t values typify populations experiencing warmer springs.

The predicted trends in thresholds were observed for the pea aphid parasites. Based on long-term averages considered over April and early May (Environment Canada 1982), Kamloops has the warmest spring temperatures followed by Chilliwack and Sussex. As was expected, the Kamloops population of *A. smithi* and of *P. pequodorum* had a higher threshold than the Chilliwack population. *P. pequodorum* at Kamloops also had a higher threshold than that of the Sussex population. *A. ervi* populations however, did not follow this trend, for which the Sussex population had the highest threshold followed by those at Chilliwack and Kamloops. Campbell *et al.* (1974), in a study of geographic variation in the thermal constants of a number of aphids and parasites, also found a few exceptions to this rule. Three out of five populations of various species of aphids and parasites they studied did not show the expected trend. It is of interest that in the study by Campbell *et al.* (1974), *A. smithi* populations did not conform to the expected trend, while *A. ervi* populations did.

It is often difficult to attribute such anomalies to any particular factor. They could result from errors in estimation of the thermal constants. On the other hand, thresholds may be affected by a variety of factors. For example, they may depend on how representative the laboratory population is in relation to the population in the field. Migratory events may also preclude detection of clear adaptive patterns because such events result in gene flow. Finally, such anomalies may also result from small numbers of founders colonizing a new area, because they are not representative of their parent population.

Interspecific comparisons among the pea aphid parasites in the three study sites revealed that the developmental times and threshold temperatures of all species were within a fairly narrow range. *A. smithi* had the shortest developmental time of all species at virtually all the temperatures at both Chilliwack and Kamloops. A consistently shorter developmental time over a number of generations throughout the season gives *A. smithi* a cumulative advantage analogous to compound interest (Stearns and Koells 1986). In addition to the high fecundity reported in the previous chapter, a shorter developmental time has contributed to its high rate of population growth. *A. ervi*, on the other hand, had the third longest developmental time among the species, preceded by *A. pisivorus* and followed by *P. pequodorum* at all temperatures. As with high fecundity, a shorter developmental time does not appear to confer any advantage as far as the relative abundance of pea aphid parasites is concerned. The trend in developmental times expressed in degree days, not surprisingly, was similar to that observed for developmental times expressed in days. *A. smithi* required the smallest number of degree days, followed by *A. ervi*, *A. pisivorus* and *P. pequodorum*.

With regard to threshold temperatures, again, *A. smithi* was superior or comparable to other species in the complex. In Chilliwack, *A. smithi* had the lowest threshold temperature

of the three species studied. Although at Kamloops *A. smithi* had only the third lowest threshoid temperature of the four species studied, the differences between *Aphidius* spp. were small (range: 0.4° C). It is unlikely that such a small difference would place a parasite at a disadvantage in the beginning of the season. In other words, if *A. ervi* and *A. pisivorus* were to emerge from diapause, say, a day earlier than *A. smithi* due to their lower threshold temperatures, they possibly could not deprive *A. smithi* of hosts. Moreover, because of a shorter developmental time, *A. smithi* is likely to quickly make-up this apparent early season disadvantage.

In conclusion, the results of interspecific studies indicated that the changes in relative abundance of pea aphid parasites in North America were not a consequence of large differences in thermal coefficients. Specifically, *A. smithi* does not appear to be at a competitive disadvantage either early in the season due to higher threshold temparatures, or all through the season due to a longer developmental time from egg to adult. As in the fecundity studies, the relative abundance of pea aphid parasites is correlated neither with developmental times nor with threshold temperatures. However, the results of intraspecific comparisons were not as conclusive. The populations of the introduced species did not vary in their threshold temperatures as much as those of the native species. It would be speculation to suggest that this is a result of their introduction to North America. In order to confirm that the lower variability observed in this study is in fact real, many more populations need to be studied. The next step would be to explore by simulation modelling, the consequences of such lower variability on the population dynamics of the introduced species.

CHAPTER V

VARIATION IN MORPHOLOGICAL CHARACTERS

5.1 Introduction

A large number of studies concerning geographic variation in morphology of insects have appeared in the past few years (examples in Atchley and Bryant 1975, Blackith and Reyment 1971, Bryant and Atchley 1975, Daly 1985, Gould and Johnston 1972, Pimentel 1979, Reyment *et al.* 1984, Sneath and Sokal 1973, Thorpe 1976). The study of geographic variation in morphological attributes is of importance to systematics as well as evolutionary theory. Many taxonomic studies rely on the study of form as a basis for taxonomic judgments. On the other hand, the study of geographic variation can be used as a tool to understand selection agents and mechanisms involved in morphological evolution (Thorpe 1976). Morphological variation is important to biological control because it may ultimately lead to reproductive isolation and speciation following releases of biological control agents. Moreover, morphological variation rarely occurs in isolation, and is often accompanied by variation in other characters.

The study of geographic variation in morphology is more informative when it involves populations of closely related species and is done in conjunction with a study of variation in ecological characters. Because rates of life history and morphological evolution may differ within the same organism (Arthur 1984), studying both types of variation facilitates an examination of their patterns of variation and the degree of congruency between them. Despite the potential differences in their evolutionary rates, congruency between these types of variation can sometimes be observed because they have some factors in common, such as polygenic control.

A number of statistical techniques can be used to quantify geographic variation in morphology. However, the multivariate methods provide a number of advantages, because they involve consideration of a number of characters simultaneously. They also provide a great deal

of information such as identifying the relative importance of variables and how they covary within and between populations. With the widespread use of digital computers, these methods have been developed and are now powerful tools for the study of comparative morphology (Blackith and Reyment 1971, Pimentel 1979, Reyment *et al.* 1984, Sneath and Sokal 1973).

The objective of this chapter is to quantify geographic variation in the morphology of pea aphid parasites from three regions in North America and to compare the divergence levels between populations of the two introduced species and between the introduced and the native species. Although it is unlikely that functional or "non-functional" morphology had a direct role in the decline of *A. smithi*, I used morphological variation as an additional measure to compare the degree and pattern of geographic variation in introduced and native species of pea aphid parasites. I will compare the results from this chapter with those from Chapter III to assess the degree of congruency between them. A high degree of congruency suggests that the observed differences in divergence levels between introduced and native species discussed earlier are reliable.

5.2 Materials and methods

Ideally, for a morphometric study, field collected material should be used. However, the only species that could be obtained in sufficiently large numbers from all three regions was *A. ervi*. The other three species of pea aphid parasites were either locally extinct or encountered too infrequently to form a large enough sample base for this study. To overcome this problem, specimens of all species for this study were reared in the laboratory under optimum conditions using even-aged host aphids. One advantage of this procedure is that simple size variation due to a number of extraneous environmental factors can be eliminated. Any observed residual variation can then presumed to be genetically based (Arthur 1984, Claridge *et al*. 1984, Thorpe 1976).

Parasite colonies were set up as described in Chapter II in order to obtain specimens for the morphometric study. Even-aged third-instar aphid nymphs were exposed to parasite females overnight in a wax paper cup. Aphids exposed to the parasites were then reared at 20.5±1 °C, 55-60% R.H., and a 16h L: 8h D photoperiod. The resulting mummies were gently scraped from the leaves, and the adults were allowed to emerge under the same conditions. The parasites were preserved in 70% ethanol within 24h of emergence. This prevented any age-related changes in body size and shape. Only female parasites were used in this study because sexual dimorphism in characters may render the cumulative distribution of characters of the two sexes platykurtic or bimodal.

Microscope slides were prepared according to Hille Ris Lambers' (1950) procedure for soft-bodied insects. Parasites were first boiled in 95% ethanol in a water bath for 3-4 minutes to remove some of the pigments. Next, they were cleared by boiling in 10% potassium hydroxide (KOH) for 3 minutes. In the final stage, parasites were boiled in

chloralphenol for 2 minutes to soften body parts and to further clear the specimens. After clearing, the head, the body, and the wings were mounted dorsally under separate cover glasses on the same microscope slide in Hoyer's medium (Hille Ris Lambers 1950), a water based mounting medium. Measurements were made after air drying of the slides. Only those specimens whose body parts were all intact and were mounted to enable accurate measurement were used. A uniform sample size of 20 female specimens was used for each species and population. To accurately represent size and shape variation, both length and width of body parts were measured whenever appropriate.

5.21 Selection and measurement of characters

Three criteria were used to select characters for measurement (after Foottit 1979):

(1) Characters should be amenable to measurement with a reasonable degree of precision, i.e., a low coefficient of variation.

(2) Body parts to be measured should be resistant to distortion by the mounting process.

(3) Characters measured should represent a large proportion of the body.

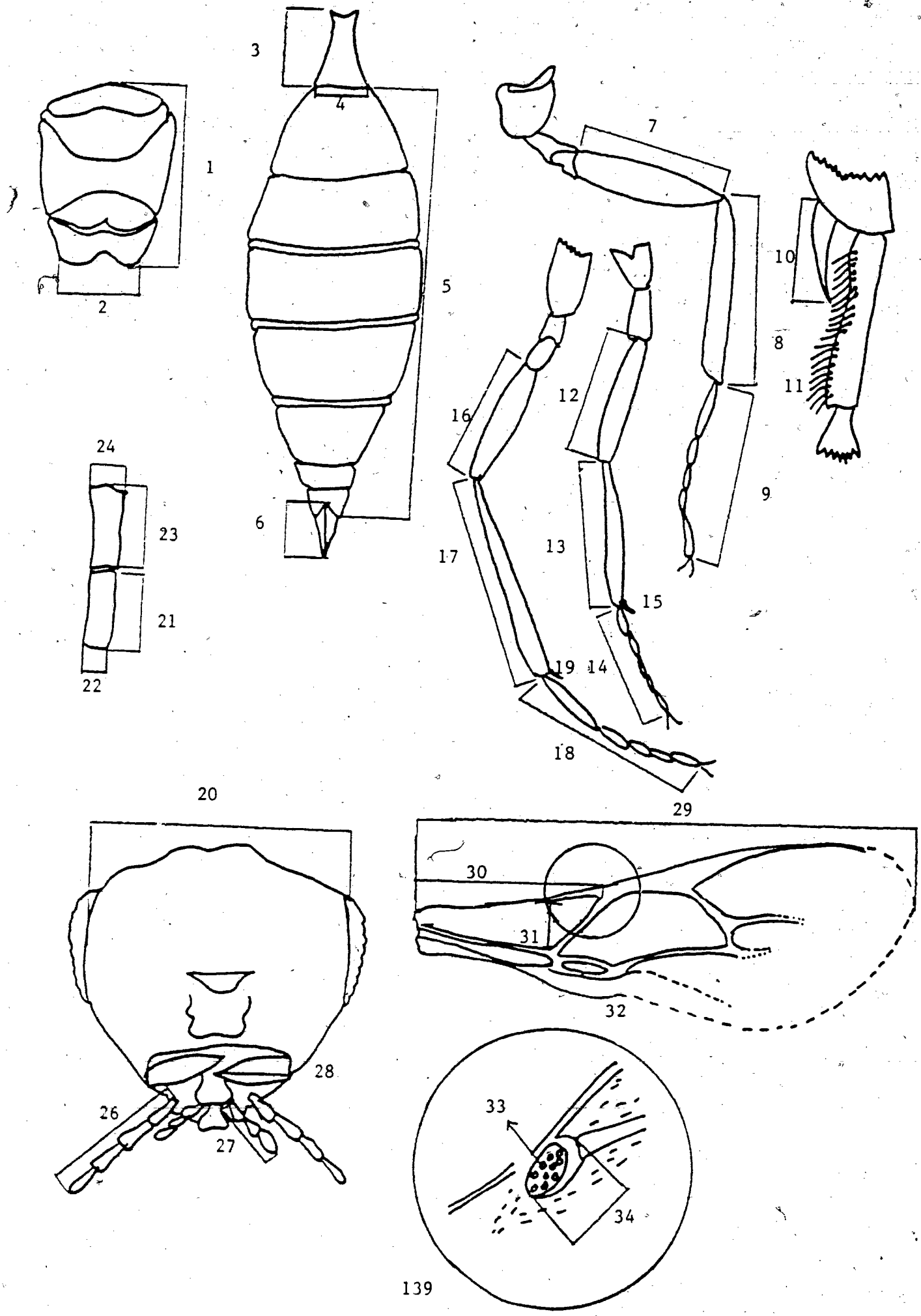
Based on the above criteria, 31 continuous and 3 discrete (meristic) variables were chosen. These are shown in Table XXVIII. For paired structures, only one of the two parts was measured and the measurements were restricted to the same side for all slides whenever possible. The character locations on the insect body are shown in Figure 23.

Measurements were taken using a compound microscope fitted with an ocular micrometer etched with 100 divisions. All characters were measured at a magnification of 80X, except abdomen length and wing length, which were measured at 20x. The measurements were then transformed to millimeters by multiplying them with a conversion factor obtained by calibrating the ocular micrometer with a stage micrometer.

Table XXVIII: Code names and description of morphological characters of pea aphid parasites measured to study geographic variation in morphology. See Figure 23 and text for details.

	Code name	Description
1.	TL	Thorax length
2.	TW	Thorax width
3.	PL	Petiole length
4.	PW	Petiole width
5.	AL	Abdomen length
6.	OSL	Ovipositor sheath length
7.	FFL	Front leg femur length
8.	FTIL	Front leg tibia length
9.	FTAL	Front leg tarsus length
10.	FSL	Front leg spur length
11.	FSPINE	Number of spines on front tibia
12.	MFL	Mid leg femur length
13.	MTIL	Mid leg tibia length
14.	MTAL	Mid leg tarsus length
15.	MSL	Mid leg spur length
16.	HFL	Hind leg femur length
17.	HTIL	Hind leg tibia length
18.	HTAL	Hind leg tarsus length
19.	HSL	Hind leg spur length
20.	HW	Head width
21.	AL1	First flagellar antennal segment length
22.	AW1	First flagellar antennal segment width
23.	AL2	Second flagellar antennal segment length
24.	AW2	Second flagellar antennal segment width
25.	SEG	Number of flagellar antennal segments
26.	MAX	Maxillary palp length
27.	LAB	Labial palp length
28.	MAND	Mandible length
29.	WINGL	Wing length
30.	CSCL	Costal + sub-costal vein length
31.	BCW	Basal cell width
32.	CCW	Cubital cell width
33.	PIT	Tracheal pit length (on the wing)
34.	TRACH	Number of tracheal openings (on the wing)

FIGURE 21: Schematic diagram of a generalized *Aphidius* showing the operational dimensions of morphological characters measured for studying geographic variation among pea aphid parasites. See text for details of characters. The numbers refer to the variables listed in Table XXVIII.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5.22 Data analysis

The characters were initially examined with regard to measures of central tendency and dispersion and distribution statistics and were then analysed by one way ANOVA and SNK test, to ascertain if any discernible trends were evident in the data.

Data were also analysed by multivariate methods, i.e., stepwise multiple discriminant analysis, discriminant function analysis and UPGMA (unweighted pair group method using arithmetic averages) cluster analysis (Rohlf 1963, Sokal and Michener 1958), to quantify geographic variation. The minimum tolerance level for the exclusion of a variable from discriminant analysis was set at 0.001% of the maximum Mahalanobis distance among groups. Cluster analysis was performed using the SPSSx subprogram CLUSTER (SPSSx Inc. 1986) incorporating the Mahalanobis distance matrix.

5.3 Results

5.31 Variability and normality of data

The mean and the standard deviation for each of the 34 morphological characters for various species and populations of pea aphid parasites are given in Appendix IV. Standard deviations of all variables were small, a fact indicating a high precision of measurement. Coefficient of variation (CV), which is a measure of sample variability relative to the mean of the variable, was fairly consistent for all variables across species. Most characters had CV values ranging from about 2% to about 8%. This range is considered optimal because for most taxonomic characters, comparisons made with variables that exhibit some, but not unreasonably large, variability are more reliable (Simpson *et al.* 1960). The only character that had a relatively large CV was abdomen length, ranging from about 5% to about 14%.

Both the univariate and the multivariate analysis used in this study assume a normal distribution of variables. In addition, discriminant analysis assumes an equality of group covariance matrices. For most characters, values of skewness and kurtosis were non-significant ($P>0.05$). Meristic variables, i.e., FSPINE, SEG, and TRACH, deviated from the normal distribution. Because of the robustness of both ANOVA and MDA, however, no attempt was made to transform or exclude these variables. To avoid any bias due to heteroscedasticity of group covariance matrices, the chi-square associated with Wilk's lambda was used to determine the number of discriminant functions to be included in the analysis (Klecka 1981).

5.32 Univariate trends in morphological characters

There was considerable heterogeneity among various species and populations of pea aphid parasites for any given character. For a majority of characters, the Chilliwack population of *A. smithi* and *P. pequodorum*, and Kamloops population of *A. ervi* had the largest means.

One-way ANOVA was performed to detect any trends in sample means of each character. The analysis was carried out in different combinations of species and populations, as follows.

5.321 Species of Aphidius *including* A. pisivorus

Differences between means of all characters of various species and populations in the genus *Aphidius* were significant. Because of the relatively larger size of Kamloops population of *A. ervi*, in many subsets of SNK, it was grouped with *A. pisivorus* from Kamloops. *A. ervi* from Chilliwack had the smallest mean for many characters and was usually different from all the other groups. The two *A. smithi* populations and *A. ervi* from Sussex were often grouped together in one subset.

5.322 Populations of A. smithi

The Chilliwack population of *A. smithi* had a larger mean for 28 of the 34 characters (82.4%) compared with Kamloops population, which indicates that in general, the former had a larger body size. However, differences in means of the two populations were significant for only 19 of the 34 characters (55.9%).

5.324 Populations of A. ervi

Differences between means of all characters of the three *A. ervi* populations were significant. As mentioned earlier, the Kamloops population had the largest mean for a majority of characters. Consequently, for 11 characters two subsets were derived, one comprised of Chilliwack and Sussex populations and the other comprised of Kamloops population. However, for 17 characters three subsets were derived comprised of one *A. ervi* population each. For the remaining six characters, two subsets were derived, of which one was comprised of *A. ervi* from Chilliwack and Kamloops, and the other of *A. ervi* from Sussex.

5.325 Populations of P. pequodorum

Differences between means of 30 of the 34 characeters (88.2%) among the three populations of *P. pequodorum* were significant. Means of the variables TL, AL, AL1 and AW1 were not significantly different among the three populations. For 15 of the 30 significantly different variables (50.0%), homogeneous subsets from the SNK test were comprised of Kamloops and Sussex populations. For the remaining characters, either three subsets or two subsets with various combinations of the populations were derived.

In summary, the univariate analysis indicated that statistically significant differences exist among various species and populations in the 34 morphological characters that were considered. Although there was some grouping along species lines in the SNK test, for a number of variables differences exist in sample means, and consequently no clear geographic trends could be observed.

5.33 Multivariate analysis of morphological data

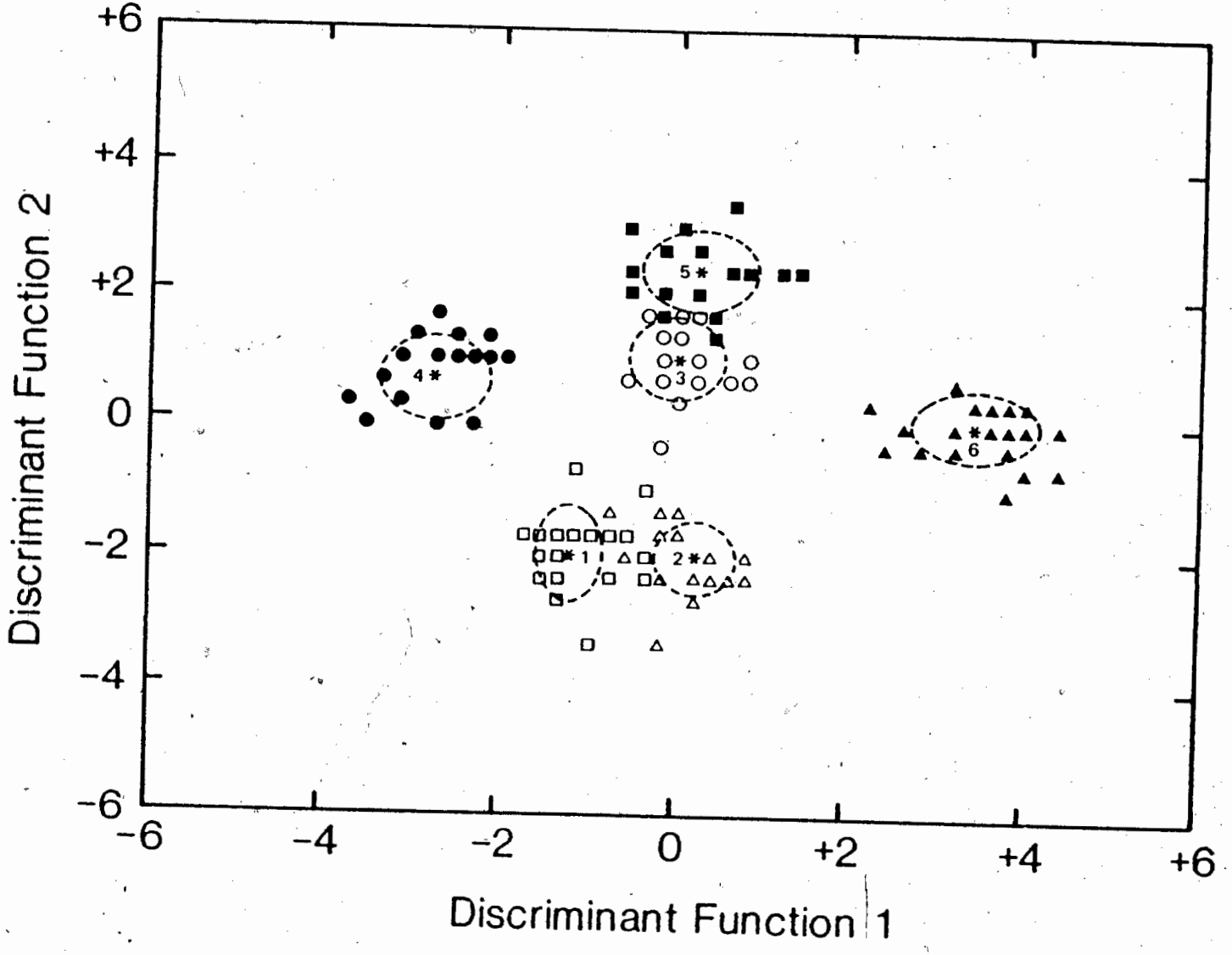
The 34 variables were analysed by multiple discriminant analysis, discriminant function analysis, and cluster analysis. The data were analysed in two parts. First, various species and populations in the genus *Aphidius* were included in the analysis to determine how well the characters could discriminate between species and populations in this genus. Second, the populations of each of the three species (excluding *A. pisivorus*) were analysed among themselves to quantify geographic variation.

5.331 Species and populations of the genus Aphidius

Multiple discriminant analysis of the genus *Aphidius* indicated that the characters measured had sufficient information to enable discrimination among the various species. Separation among the six groups was complete, i.e., 100% of the cases were correctly classified. A scatterplot of the groups projected along first and second discriminant functions is shown in Figure 22. Populations of each species, despite some overlap, were differentiated when projected onto the two discriminant functions. All but 5 of the 34 original variables, i.e., FTIL, FTAL, MTAL, AW2, and MAND, were included in the analysis based on the minimum tolerance level.

Five discriminant functions, the maximum number that can be derived for six groups, were included in the analysis. The first discriminant function accounted for 38.1% of among-group variation, while the second through fifth functions explained 26.4, 16.1, 14.1, and 5.4%, respectively. Variation explained by the first function in morphometric studies is generally considered to represent, to a large extent, simple size variation (Gould and Johnston 1972, Kambhampati *et al.* 1984, Sneath and Sokal 1973). Because the first function in this case explained only about 38% of total variation, it is clear that separation among the groups was

FIGURE 22: Scatterplot of populations of *A. ervi*, *A. pisivorus*, and *A. smithi* projected onto discriminant axes 1 and 2 from discriminant analysis of morphological characters. The ellipses enclose the 95% confidence limits around the group centroids, which are represented by asterisks. The numbers beside the asterisks refer to species and populations listed below in that order. □ : *A. smithi* (Kamloops), △ : *A. smithi* (Chilliwack), ○ : *A. ervi* (Kamloops), ● : *A. ervi* (Chilliwack), ■ : *A. ervi* (Sussex), ▲ : *A. pisivorus* (Kamloops).


+6
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-2
-4
-6
-6
-4
-2
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+2
+4
+6
Discriminant Function 2
Discriminant Function 1
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based on attributes other than simple size variation. In other words, about 62% of among-group variation was based on variation in both body shape and size, rather than size alone. Of course, changes in shape could result from changes in size itself due to allometric interactions between these two components. Relative contribution of the variables to discrimination, expressed as standardized discriminant function coefficients, is given in Table XXIX.

A matrix of Mahalanobis generalized distance values derived from discriminant function analysis based on pairwise comparisons is shown in Table XXX. All values in the matrix were significant ($P < 0.01$ or 0.05). There was a wide range of D values among the various species and populations in the genus *Aphidius*, ranging from a low of 12.85 to a high of 43.13. In general, distance between groups was correlated with their taxonomic proximity, as was expected. One exception was the distance between the Kamloops population of *A. ervi* and the Chilliwack population of *A. smithi*, perhaps due to the larger body size of *A. ervi* (Kamloops) relative to the other two *A. ervi* populations. A phenogram derived from UPGMA cluster analysis for the *Aphidius* species is shown in Figure 23.

5.332 Analysis of populations of each species

The second part of discriminant and cluster analysis, included populations of each of the three species. The results indicated that morphological variation among spatially segregated populations is pronounced. Discrimination among populations of all three species was complete, i.e., 100% of the cases were correctly classified. Separation between the populations of *A. smithi* was achieved with 16 of the original 34 variables, and among *A. ervi* and *P. pequodorum* populations with 21 of the 34 variables. Scatterplots with the relative positions of various populations of each species are shown in Figures 24, 25 and 26. It is clear from the stand

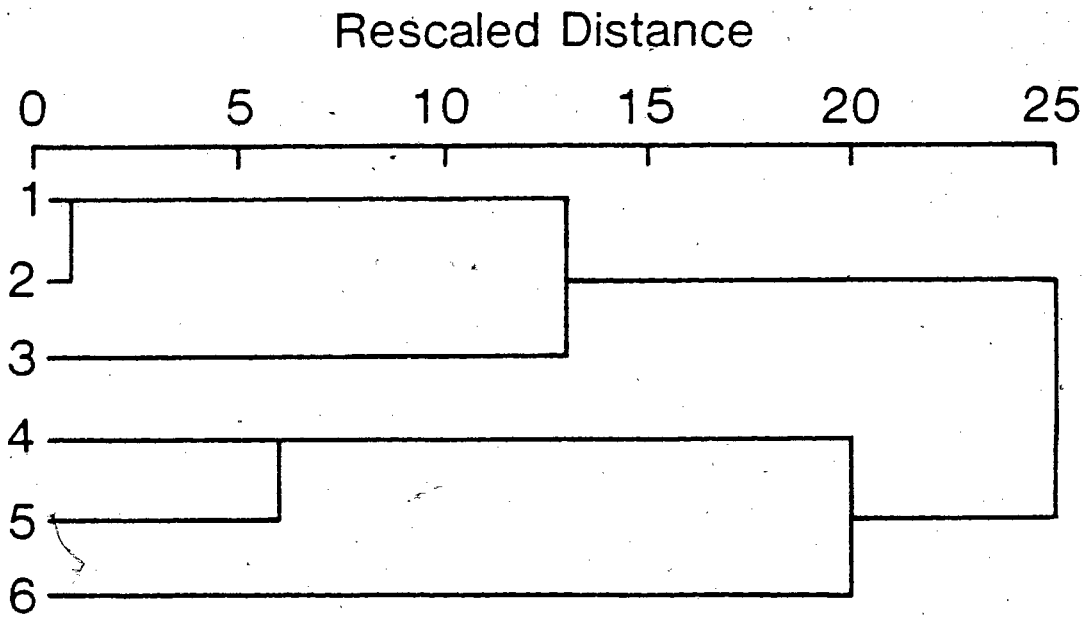
Table XXIX: Standardized discriminant function coefficients for morphological characters included in discriminant analysis of populations of *A. ervi*, *A. smithi*, and *P. pequodorum*. See Table XXVIII for details of variable names.

Variable	DISCRIMINANT FUNCTION				
	1	2	3	4	5
TL	-0.40557	0.14124	0.10298	-0.36021	-0.35255
TW	0.08339	0.36014	-0.11288	-0.10879	-0.12835
PL	-0.36354	-0.31404	-0.19993	0.80137	-0.22498
PW	-0.17981	0.00740	0.48233	-0.09220	0.26788
AL	-0.22204	0.01687	0.14933	-0.12076	-0.30877
OSL	0.38844	-0.12511	0.32347	0.30125	0.14401
FFL	0.38690	-0.20855	0.35021	-0.51982	0.28505
FSL	-0.00944	-0.15527	0.18709	-0.18949	-0.44229
FSPINE	-0.05175	0.57809	-0.00478	0.18455	-0.21753
MFL	0.72324	0.21015	-0.10303	-0.14126	0.05522
MTIL	0.07135	0.40656	-0.18505	0.14754	0.63620
MSL	0.24221	0.45862	0.58501	-0.20322	-0.47873
HSL	-0.10248	-0.17571	-0.20335	-0.05349	-0.36198
HTIL	0.16662	0.26373	-0.10469	-0.43589	-0.00707
HTAL	-0.54395	0.27436	-0.00936	-0.06815	0.10255
HSL	0.05649	0.00204	0.18606	0.46247	0.19597
HW	-0.29696	-0.02301	-0.37828	-0.00353	0.12832
AL1	0.67113	0.09619	0.30621	0.07185	0.43268
AW1	-0.09594	0.09981	0.34977	-0.08741	0.29952
AL2	-0.35615	-0.39363	-0.04430	0.02119	0.09970
SEG	-0.05690	-0.15765	0.08968	-0.32394	0.02521
MAX	0.47561	0.28430	-0.16132	-0.36025	-0.03087
LAB	0.50500	0.15921	0.32199	0.29775	-0.26712
WINGL	-0.26737	0.97159	-0.25367	0.27269	-0.35669
CSCL	0.29575	-0.78693	-0.64381	0.56077	-0.33532
BCW	0.01157	0.53022	1.10795	0.21854	0.02014
CCW	-0.18493	0.19962	-0.31191	0.18960	0.57942
TRACH	-0.19181	-0.48156	0.30157	-0.20700	0.45736
PIT	-0.15553	0.16588	-0.13258	-0.06418	0.53382

Table XXX: Matrix of Mahalanobis generalized distance (D) between populations of pea aphid parasites based on morphological characters. An asterik indicates significant difference at the 5% level, unmarked values are significant at the 1% level.

Species/ (Locality)	A.s(K)	A.s(C)	A.e(K)	A.e(C)	A.e(S)	A.p(K)	P.p(K)	P.p(C)	P.p(S)
A. smithi(K)	0.000								
A. smithi(C)	15.769	0.000							
A. ervi(K)	23.137	12.852	0.000						
A. ervi(C)	20.893	43.129	25.485	0.000					
A. ervi(S)	29.726	20.052	16.241	19.143	0.000				
A. pisiv(K)	19.033	17.637	40.181	20.606	15.889	0.000			
P. pequo(K)	101.451	49.559	163.372	108.532	107.161	66.548	0.000		
P. pequo(C)	60.939	73.576	69.577	68.644	106.009	53.557	11.728*	0.000	
P. pequo(S)	102.0555	73.071	75.755	103.641	71.293	61.399	13.811*	22.117	0.000

FIGURE 23: Phenogram derived from UPGMA cluster analysis for popualtions of *A. ervi*, *A. pisivorus* and *A. smithi* incorporating the matrix of Mahalanobis generalized distance for the morphological characters. (1): *A. smithi* (Chilliwack), (2): *A. ervi* (Kamloops), (3): *A. smithi* (Kamloops), (4): *A. ervi* (Sussex), (5): *A. pisivorus* (Kamloops), (6): *A. ervi* (Chilliwack).


Rescaled Distance
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5
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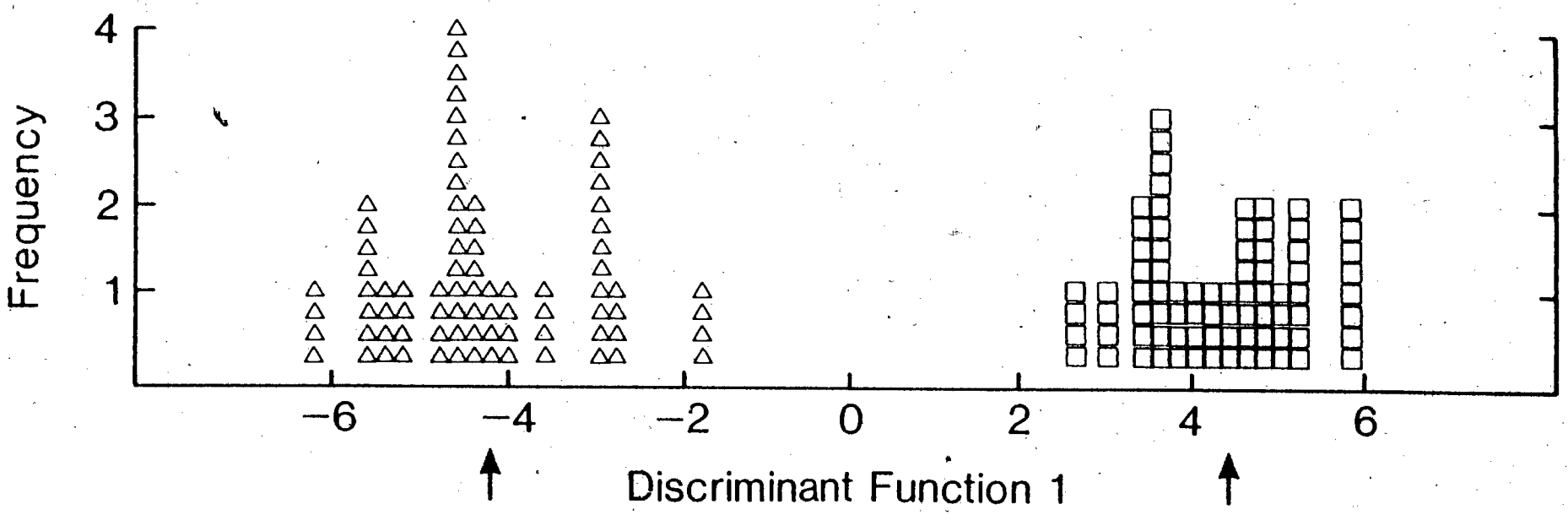
FIGURE 24: Scatterplot of populations of *A. smithi* projected onto discriminant axis 1 from discriminant analysis of morphological characters. The arrows indicate group centroids. Each individual parasite is represented by four symbols for both populations. △ : *A. smithi* (Kamloops), ◫ : *A. smithi* (Chilliwack).


Frequency
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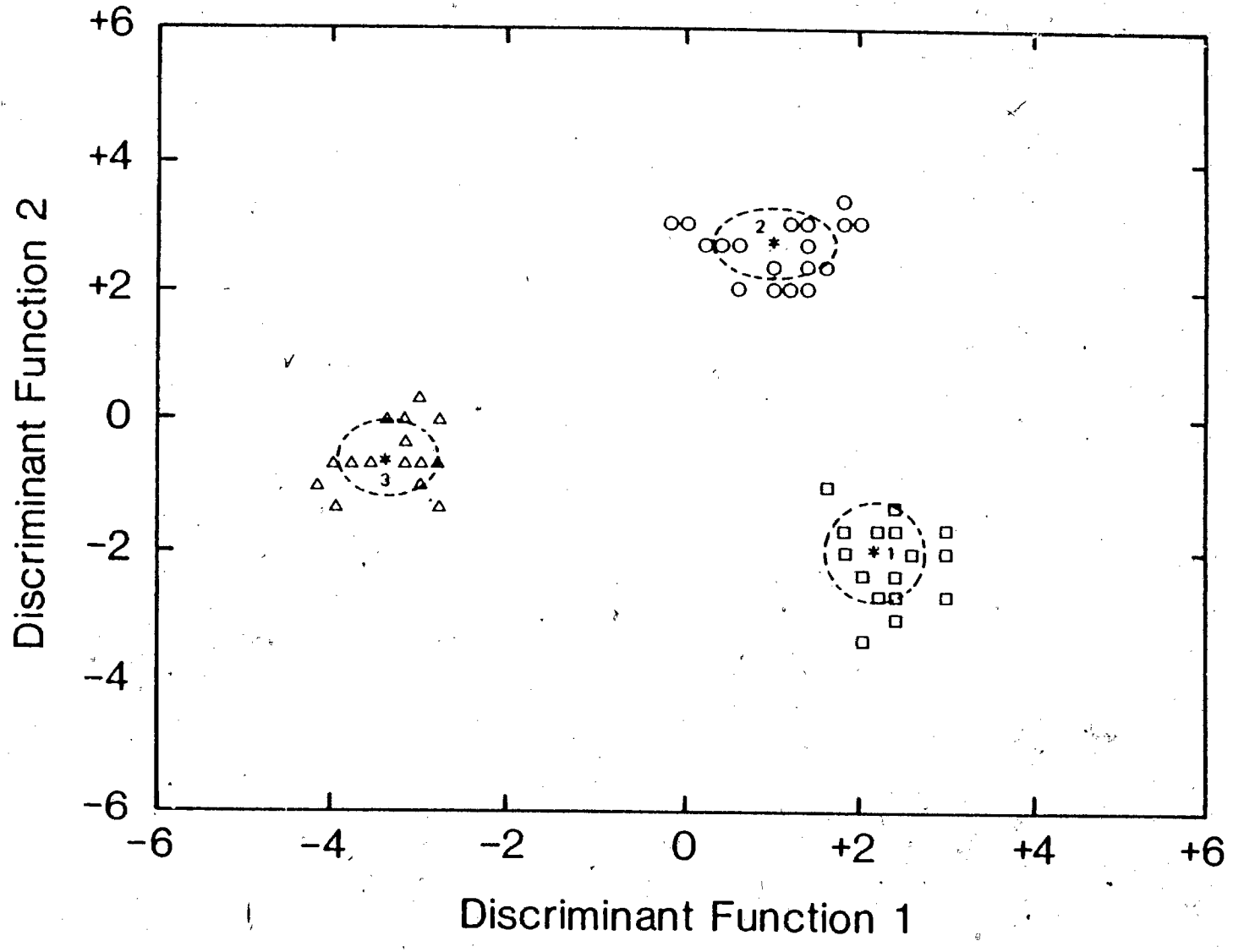
Discriminant Function 1

FIGURE 25. Scatterplot of populations of *A. ervi* projected onto discriminant axes 1 and 2 from discriminant analysis of morphological characters. The ellipses enclose the 95% confidence limits around the group centroids, which are represented by asterisks. The numbers beside the asterisks refer to the populations listed below in that order. □ : *A. ervi* (Kamloops), ○ : *A. ervi* (Chilliwack), △ : *A. ervi* (Sussex).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+2
+4
+6
Discriminant Function 2
Discriminant Function 1
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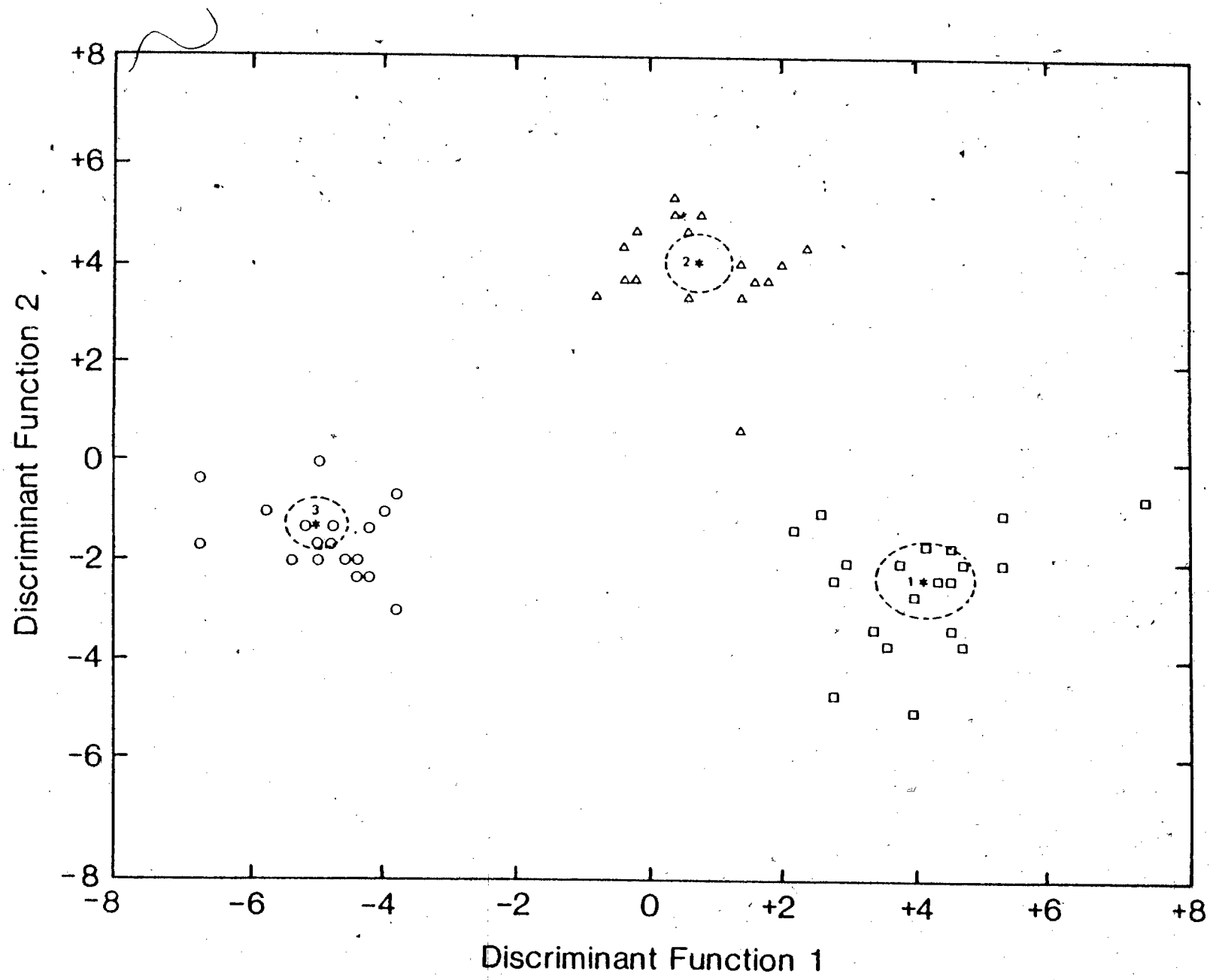
2
3

FIGURE 26: Scatterplot of populations of *P. pequodorum* projected onto discriminant axes 1 and 2 from discriminant analysis of morphological characters. The ellipses enclose 95% confidence limits around the group centroids, which are represented by asterisks. The numbers beside the asterisks refer to the populations listed below in that order. □ :*P. pequodorum* (Kamloops), △ :*P. pequodorum* (Chilliwack), ○ :*P. pequodorum* (Sussex).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-2
-4
-6
-8
Discriminant Function 2
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-6
-4
-2
0
+2
+4
+6
+8
Discriminant Function 1
1
2
3

ardized discriminant function coefficients (Tables XXXI, XXXII, and XXXIII), that the variables that contributed the most to discrimination were not necessarily the same for populations of all three species. The first discriminant functions for *A. ervi* and *P. pequodorum* populations accounted for about 60% and 64% of the total variation, respectively. Their respective second functions explained the remaining variation, indicating that while size variation was a component, shape variation also played an important role in discriminating among the various populations of both species.

When considering the matrix of Mahalanobis generalized distance (Table XXX), in the context of this part of the analysis, it is most meaningful to consider the generalized distance between populations of any given species. The pairwise distance between populations of the introduced species was greater than that between populations of the native species. The matrix also indicated that the populations of *P. pequodorum* at Chilliwack and Kamloops were more similar to each other than either was to the Sussex population. The univariate analysis has already indicated that the two populations of *A. smithi* did not differ from each other in 44% of the characters. For populations of both these species then, the trend in morphological characters was similar to that observed for life history traits. The populations of *A. ervi*, however, deviated from this trend. The Sussex and Kamloops populations were more similar to each other than either was to the Chilliwack population. Phenograms from the UPGMA cluster analysis based on a dissimilarity matrix of generalized distances confirm these observations (Figures 29 and 30).

Table XXXI: Standardized discriminant function coefficients for morphological characters included in discriminant analysis of populations of *A. smithi*. See Table XXVII for details of variable names.

Variable	DISCRIMINANT FUNCTION 1
TL	-1.76755
TW	2.24307
FFL	1.55591
FTIL	1.44136
FSL2	1.20056
FSPINE	-1.40977
MTAL	-0.90174
HTAL	-0.99466
AL1	2.20043
AL2	-1.75482
AW2	0.33810
MAX	1.35036
LAB	0.60357
WINGL	-3.49204
BCW	1.02078
CCW	-1.45305

Table XXXII: Standardized discriminant function coefficients for morphological characters included in discriminant analysis of populations of *A. ervi*. See Table XXVII for details of variable names.

Variable	DISCRIMINANT FUNCTION	
	1	2
TW	-0.20583	0.40916
PL	-0.48716	-1.47930
OSL	0.47223	-0.46593
FTIL	-0.39767	0.91418
FTAL	-0.53382	0.03080
FSL	0.24737	0.35768
MFL	0.91951	0.36307
MSL	-0.11941	0.45412
HTIL	0.12978	0.52506
HTAL	-0.76934	-0.26720
HSL	0.02471	-0.64766
HW	-0.39889	-0.23190
AL1	0.37589	-0.25935
AL2	-0.43371	-0.43594
SEG	0.29425	0.26593
MAX	0.64846	0.53624
LAB	0.77645	0.13862
MAND	-0.38961	0.27639
CSCL	0.10249	-0.61994
BCW	1.18915	-0.17985
CCW	-0.34830	0.39785

Table XXXIII: Standardized discriminant function coefficients for morphological characters included in discriminant analysis of populations of *P. pequodorum*. See Table XXVII for details of variable names.

Variable	DISCRIMINANT FUNCTION	
	1	2
TW	0.79086	-0.69291
PL	-0.71600	-1.47930
PW	0.27659	0.55891
AL	-0.00965	-0.70890
FTIL	-0.43997	-0.34442
FSL	0.48004	0.59513
FSPINE	0.34556	-0.47542
MFL	-1.06365	-0.48535
MTIL	-0.03420	0.53760
MSL	0.11550	0.50566
HFL	1.13075	0.37892
HTAL	-0.39969	0.47971
HW	-1.29172	-0.49213
AL1	0.24191	-0.49213
AL2	1.19357	-0.10200
SEG	0.32411	0.59804
MAX	0.33377	1.09180
WINGL	-3.23796	-0.06221
CSCL	1.12355	-0.06311
BCW	1.59150	-0.02776
CCW	0.35446	-0.02226

FIGURE 27: Phenogram derived from UPGMA cluster analysis for populations of *A. ervi* based on the matrix of Mahalanobis generalized distance for morphological characters. (1): *A. ervi* (Kamloops), (2): *A. ervi* (Sussex), (3): *A. ervi* (Chilliwack).

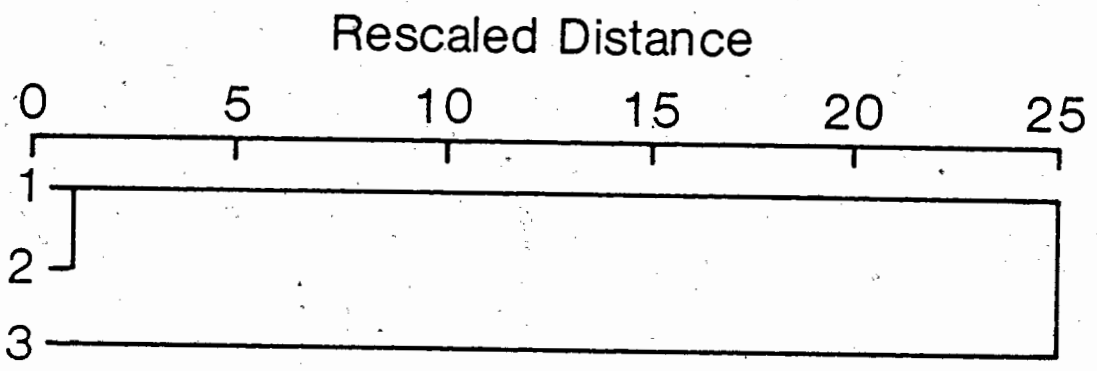
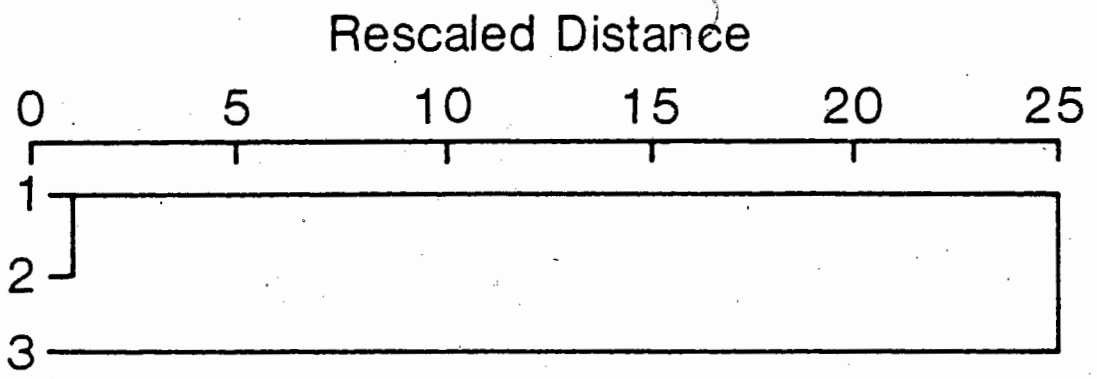

Rescaled Distance
0
5
10
15
20
25
1
2
3

FIGURE 28: Phenogram derived from UPGMA cluster analysis for populations of *P. pequodorum* based on the matrix of Mahalanobis generalized distance for morphological characters. (1): *P. pequodorum* (Kamloops), (2): *P. pequodorum* (Chilliwack), (3): *P. pequodorum* (Sussex).


Rescaled Distance
0
5
10
15
20
25
1
2
3

5.4 Discussion

The results of this study revealed the existence of well-defined geographical variation in morphological traits among populations of pea aphid parasites in North America. In general, the degree of variation is comparable to that reported for other insect species (e.g., Atchley 1971, Atchley and Cheney 1974, Blackith and Reyment 1971, Foottit 1979, Sneath and Sokal 1973, Reyment *et al.* 1984, Zimmermann and Ludwig 1974). The observed morphological trends are a likely result of the interaction between the size of the founder populations, the effects of selection, the mutation rate and the amount of gene flow between the various populations.

Analysis of variance and the range test on each of the 34 morphological characters indicated that the populations of all species differed significantly from one another in many of the variables. The multivariate analysis confirmed and expanded on the results of the univariate analysis. In all the discriminant analyses that were done, each with a different combination of species and populations, the discrimination between groups was complete, i.e., 100% of the cases were correctly classified. From the results of the univariate analysis, it appears that a high degree of separation could have been realized in the discriminant analysis with a fewer number of characters. Variables from all parts of the body contributed substantially to among-group variation: the general body (thorax length, petiole length), the head (length of first antennal segment, maxillary palp length, labial palp length), the legs (front leg femur length, mid leg spur length) and the wings (costal + sub-costal vein length).

The values of the generalized distance between populations of all species of the pea aphid parasites calculated based on morphological characters were considerably larger than those based on PIEL attributes and egg frequency distributions. This could be a likely result of the fact that the rates of life history and morphological evolution may vary even within the same

organism (Arthur 1984). The phenotypic distance analysis indicated that the introduced species differed from the native species in their divergence levels. Although the populations of all species were completely separated by the discriminant analysis, the distances between populations of the introduced species was consistently greater than those between corresponding populations of the native species. In other words, the results of intraspecific variation in morphological characters were consistent with the effects of random genetic drift (e.g., Bryant *et al.* 1986a, 1986b, Dobzhansky and Pavlovsky 1957, Rich *et al.* 1979, 1984). They confirmed the results from the study of intraspecific variation in PIEL attributes and egg frequency distributions, which also showed that the populations of the introduced species diverged to a greater degree relative to the native species. There was, however, no measurable difference in the divergence levels between the populations of the two introduced species, *A. ervi* and *A. smithi*. While it is unlikely that the drift of morphological alleles had contributed directly to the decline of *A. smithi* in North America, this part of the study served two important purposes. First, the results confirmed the observed differences in divergence levels between the introduced and the native species in life history traits, suggesting that the differences are indeed reliable. Second, although they may not have had a direct role, the drift of these alleles points to the possibility of drift in other alleles that may have had an effect on the long-term establishment of *A smithi*. I will discuss this aspect of variation further in Chapter VI.

The pattern of variation in morphological traits was also identical to that observed in life history traits in two out of three parasite species. Populations of *A. smithi* from Chilliwack and Kamloops did not differ from each other in 15 of 34 (44%) characters on a univariate basis, although they were completely separated by discriminant analysis. The phenotypic distance between *P. pequodorum* populations indicated that the Chilliwack and

Kamloops populations were more similar to each other than either was to the Sussex population. As suggested for life history traits, in addition to common selection agents (e.g., Endler 1977, Gould and Johnston 1972, Johnson 1976, Mooney 1977, Power and Ainley 1986, Thorpe 1976), migration between Washington state and British Columbia, and within British Columbia, may have contributed to the similarity between populations originating in Chilliwack and Kamloops.

The pattern of variation for *A. ervi* populations was ambiguous. The univariate analysis indicated that in 50% of the characters, all three populations differed from one another and in 33% of the characters, the Chilliwack and Sussex populations were not significantly different from each other. Overall, however, as indicated by the phenotypic distance measurements, the Kamloops and Sussex populations resembled each other. A number of factors could potentially explain the deviation of pattern in populations of *A. ervi*, relative to the other species. It may be a function of sampling of populations. While every effort was made to obtain a representative sample of the population, there is no assurance that this in fact was realized. As I have mentioned earlier, Arthur (1984) also pointed out that in general, morphological evolution has a relatively more variable rate than life history evolution, resulting in partial or complete non-congruence between pattern of variation in ecological and morphological traits.

The congruency of patterns in life history and morphological traits may have resulted from each of these traits evolving independently of each other. On the other hand, an identical pattern could result from pleiotropic effects of genes favored by selection or "hitchhiking" of genes. In other words, because most ecologically important characters are controlled by polygenes, and polygenes almost certainly have pleiotropic effects (Clutton-Brock and Harvey 1979, Johnson 1976, Lande 1981), morphological variation is sometimes incidental

in the sense that it results from a selection for ecological or other characters. For example, Palmer and Dingle (1986) recently showed that in *Oncopeltus fasciatus*, some traits responded rapidly to directional selection, and that a number of other characters, both morphological and ecological, showed correlated responses to selection due to genetic correlation and pleiotropic effects. It is therefore more useful to consider an organism as an integrated whole, in which behavioral, physiological and morphological evolution interact, each complementing and constraining the other, to produce the observed design of an organism (Gould and Lewontin 1979, Levins and Lewontin 1985).

CHAPTER VI

GENERAL DISCUSSION AND CONCLUSIONS

In the preceding chapters, I have examined inter- and intraspecific variation in several pea aphid parasite species from North America. This was done to identify the possible reasons for the continent-wide decline of *A. smithi*, which had been introduced with apparent success, as a biological control agent of the pea aphid. Two hypotheses concerning the decline of *A. smithi* in North America were considered; other explanations are possible but are outside the scope of this thesis. In the ensuing discussion I will overview the results to ascertain if they provide evidence for or against, one or both, hypotheses.

6.1 Intraspecific comparisons

A comparison of geographic variation among populations of pea aphid parasites (Chapters III, IV and V) indicated that the introduced species differed from the native species in the degree, but not in the pattern, of variation. The divergence in mean character values between populations of the introduced species was consistently greater than that between corresponding populations of the native species, as indicated by the Mahalanobis generalized distances for PIEL performance criteria, egg frequency distributions and morphological traits.

As I have mentioned in Section 1.2, a large body of evidence in the literature indicates that increased divergence levels occur in natural and experimental populations after a founding event or a genetic bottleneck. Dobzhansky and Pavlovsky (1957) referred to this phenomenon as degree of indeterminacy and attributed it to random genetic drift. They tracked changes in the frequency of PP chromosomes in two sets of 10 experimental populations each of *Drosophila pseudoobscura*; one set of which was initiated from 20 flies and the other from 4000 flies. Four and 19 generations after the bottleneck, both the range and the variance of the mean frequency were significantly greater in populations initiated with a small number of

founders than in populations derived from a large number of founders.

More recently, Bryant *et al.* (1986a, 1986b) studied the effect of experimental bottlenecks of varying severity on quantitative genetic variation of morphometric traits and morphological differentiation in the housefly, *Musca domestica* L. Divergence between replicate populations derived from groups that had been subjected to bottlenecks was significantly greater than that in the control population. Rich *et al.* (1979, 1984) reached a similar conclusion in studies of genetic drift in *Tribolium castaneum* L. Changes in pupal weight, reproductive fitness and body color were tracked for a number of generations in control and bottleneck populations of varying severity. Again, divergence between replicate populations in means of all three traits was inversely proportional to the size of the bottleneck.

Other examples relating bottlenecks or founding events to genetic variation were given by Buri (1956), Carson (1968), Dodeswell and Ford (1952, 1953), Ford (1953), Frankham (1980), James (1971), Lowe (1955), Powell (1978), Powell and Richmond (1974), Prakash *et al.* (1969), Schwaegerle and Schaal (1979), Templeton (1980), Watterson (1984) (see also Section 1.2). The subject was recently reviewed by Barton and Charlesworth (1984) and Carson and Templeton (1984).

In light of the above theoretical and experimental evidence, the results of this study are consistent with the effects of random genetic drift. As the above studies suggest, divergence levels in reproductive and morphological traits between any two populations of the introduced pea aphid parasite species were greater than those between corresponding populations of the native species. It appears, then, that the decline of *A. smithi* was due to small founder populations and the accompanying genetic impoverishment. It is difficult to say if the decline resulted as a direct consequence of drift of the traits in question. The significance of the

results lies in the fact that they suggest drift of many other alleles, which may have had a direct influence on the long-term establishment of *A. smithi*.

The long-term establishment of a population is influenced either by the fixation or loss of alleles under drift. The loss or fixation of alleles is detrimental to the survival of the population because it may prevent the formation of a genome that permits a rapid adaptation to the new environment (Nei *et al.* 1975). In other words, such phenomena deprive the population of the genotypic flexibility that is needed to adapt to the new environment. In addition to the obvious effects of loss or fixation, a small founder population may result in a number of other unpredictable effects and lead to the eventual extinction of a newly established population. The founder population differs from the parent population not only in the amount of genetic variation present, but also in the new biotic and genetic environment it faces. The new environment often presents selective pressures which are harder to cope with due to the absence of a full complement of alleles in the population, which results in density independent mortality (Haldane 1956). Moreover, the new population is rapidly transformed from an open to a small, closed population. While the genome of the parent population is dynamic due to emigration and immigration producing viable heterozygotes, such gene flow is abruptly cut-off in the new population. In other words, unless the extant genome of the population is preadapted to the new environment at least to a certain degree, the probability of its establishment and further expansion in range is greatly reduced. While it is theoretically possible that, in spite of reduced genetic varitaion, a small founder population may indeed find an "adaptive peak" and rapidly expand in the new environment (see, e.g., Baker and Stebbins 1965, p. 123-125), more often than not, the population ends up in an "adaptive valley".

Because of the small founder population, inbreeding depression may also ensue, leading to increased homozygosity and in turn, to reduction in fertility and viability. Also, as a consequence of their increased frequency in the founder population, homozygotes will be more exposed to selection and genes that are specially viable in a homozygous condition are favored, regardless of their selective value in the parental population (Mayr 1963, p. 533). Whereas a newly established population requires an accelerated evolutionary rate to enable a rapid adaptation to the new environment, Haldane (1957) postulated extremely low evolutionary rates in populations established with a small number of founders.

In addition to random genetic drift, the above and related factors could have precluded *A. smithi* from rapidly adapting to the North American climate. Since *A. ervi* too showed effects of drift, an important question to ask is why did it not also decline? There are a number of possible explanations. Because of its European origin, *A. ervi* was likely preadpated, at least to a degree, to the North American climate. In addition, large and diverse founder populations would have the effect of minimizing any deleterious effects of drift (cf. Rich *et al.* 1979, 1984). Finally, *A. ervi* appears to possess what can loosely be termed a "general purpose genotype", i.e., it is adapted to a broad range of climates and habitats. It has been reported as the most common parasite of aphids infesting alfalfa in such diverse regions as high plateaus, deserts, temperate and sub-temperate zones (Gonzalez *et al.* 1978). All the above factors could have enabled *A. ervi* to rapidly adapt to the North American climate.

Since the results of this study are an indirect evidence of drift in populations of *A. smithi*, factors other than drift should also be considered as possible explanations for the observed differences in divergence levels between the introduced and the native species. For example, the observed differences in divergence levels could be a result of interspecific

differences in evolutionary rates (Arthur 1984). Two important factors, however, suggest that this is unlikely. First, the various species within the pea aphid parasite complex are phylogenetically very closely related and sometimes even hybridize (Mackauer 1969, Stary 1970) and likely share a number of common genes. Second, they are ecological homologues, inhabiting the same habitat and exploiting the same host. They are therefore likely subjected to similar selection pressures, both direct ones and those mediated through the host. Nevertheless, before random genetic drift can be considered the sole factor for the observed divergence levels, the following must be known (Falconer 1960): (1) that the effective population size was small enough (2) that the populations were completely isolated with no gene flow between them and (3) that the genes concerned are subject to little or no selection.

Variation in temperature thresholds among populations of the introduced species was measurably less than that among populations of the native species. This may be a result of alleles lost subsequent to their introduction to North America. It is also possible that the introduced pea aphid parasites may not have had sufficient time in North America to "fine-tune" the thresholds throughout their range. Lack of variation in threshold temperatures may have potentially serious consequences as far as parasite survival and effectiveness are concerned. As mentioned earlier, threshold temperatures almost always vary among populations of poikilortherms as a function of climate, a condition reflecting adaptedness to the local temperature cycles. If there is no variability in threshold temperatures, reaching towards an optimum for each locality, the insects would emerge at different times of the growing season in different places. Although the calendar dates may vary, a well-adapted insect should emerge at approximately the same stage of the growing season throughout its range. Specifically, a parasite is expected to emerge either at the same time or shortly after the host emergence. If

the observed variability in the introduced species is in fact real, their thresholds are fine tuned to only a part of their range. In other areas, they may emerge too early in the season and not find any hosts, or emerge too late and find that most of the hosts are already parasitized by "better-adapted" competitors. The apparent lower variability did not effect the establishment of *A. ervi* in North America, a fact suggesting that perhaps an early season advantage is not critical in determining the relative abundance of pea aphid parasites in North America. In addition, an oligophagous species such as *A. ervi* can reproduce and multiply on other host species and switch to the pea aphid later in the season.

In summary, the intraspecific studies suggested that the decline of *A. smithi* has occurred as a conseqeunce of small founder populations and the accompanying effects on the genetic structure of its populations. Although *A. ervi* also displayed the effects of drift, it had a number of factors in its favor, including the size and the diversity of its founder populations, a degree of preadpaptedness, and a broad adaptedness; factors that are likely to enhance the probabaility of establishment.

6.2 Interspecific comparisons

An interspecific comparison of repoductive attributes (Chapter III), and thermal constants (Chapter IV) among pea aphid parasites indicated that, in general, *A. smithi* was at no obvious disadvantage relative to other species in the complex. *A. smithi* had the highest fecundity at both Chilliwack and Kamloops. In addition, its females performed better under the experimental conditions in most aspects of performance such as the number and proportion of aphids parasitized, PIEI, fecundity, number of eggs laid in the first four days and the number and proportion of aphids escaping parasitism. That is, *A. smithi* females performed

better in variables pertaining to reproductive potential and searching efficiency. *A. ervi* females were marginally superior in some aspects of performance as indicated by the variables number of hosts parasitized per egg laid and the proportion of eggs laid in the first four days, i.e., host utilization efficiency and oviposition rate, respectively. The life table analysis revealed that *A. smithi* had a significantly higher rate of population growth than any of the other species and generally was superior in other life table statistics including gross and net reproductive rates, finite rate of natural increase, doubling time and generation time.

A. smithi also had the shortest developmental time from egg to adult emergence of all species at both Chilliwack and Kamloops. Threshold temperature for the development of *A. smithi* was comparable to that of *A. ervi* at Kamloops, and lower than that of *A. ervi* at Chilliwack. The differences in variables in which *A. ervi* had performed better than *A. smithi* are probably too small to put either species at a disadvantage in the field. Indeed, the relative abundance of the pea aphid parasites is correlated neither with reproductive attributes nor thermal constants. Previously published comparisons of fecundity (Mackauer 1971), and thermal constants (Campbell 1974, Campbell and Mackauer 1975, Campbell *et al.* 1974) reported an identical pattern of interspecific variation.

The fact that the decline of *A. smithi* was not a direct result of differences in reproductive potential between the various species is clear from the results of the interspecific studies. It is highly unlikely that minor differences in life history traits of *A. smithi* and *A. ervi* may have contributed to changes in relative abundance, although this needs to be verified. For this purpose, more detailed studies, incorporating functional response and simulation models to explore the long-term consequences of such minor differences in performance criteria, may be needed.

In conclusion, there is no evidence to suggest that *A. ervi* displaced *A. smithi* because of superior life history traits. On the contrary, the results from intra- and interspecific studies in combination suggest that *A. ervi* simply occupied the niche as the most common parasite of the pea aphid subsequent to the decline of *A. smithi* due to genetic impoverishment.

6.3 Conclusions for biological control

Changes in the relative abundance of pea aphid parasites in North America suggest a strong need for long-term, post-introductory studies of introduced species. Such studies may help in identifying the critical characteristics of founder populations that result in establishment. Ultimately, the phenotype and/or genotype of candidate biological control agents that is most likely to result in establishment can be defined.

The results from this study and the dynamics of pea aphid parasite relative abundance suggest that the various "desirable attributes" (e.g., Coppel and Mertins 1977, Debach 1964, Huffaker and Messenger 1976) and Clausen's (1951) "3-year or generation" rule are of little or no consequence when the basic principles of population genetics and evolutionary theory are ignored in practice. *A. smithi* has many of the attributes of a desirable biological control agent, such as high fecundity, short developmental time, high searching efficiency and high host specificity. Three years after its introduction, it was the most common pea aphid parasite in many parts of North America. Yet, its predominance was short-lived, apparently as a consequence of small founder populations. I do not suggest that small founder populations invariably result in the extinction of natural colonizations and deliberate introductions. However, a great majority of natural colonizations, which are generally typified by a small number of founders, result in extinction after an initial flush phase, presumably due to genetic

impoverishment (Mayr 1965). Because the aim of biological control is a sustained establishment, the probability of such establishment is enhanced if introductions are based on sound genetic and ecological principles.

Three aspects in particular should be considered in this regard. Firstly, the founder population should be large, so that it is representative of the parent population as a whole (see, e.g., Beirne 1975, Mackauer 1981). Secondly, an array of locations should be sampled to make the founder population diverse, so that many alleles are included in the sample. Thirdly, pre- and post-release studies should be made an integral part of the biological control protocol. Biological control should be an ongoing process, rather than the typical 2-3 year, post-introductory study to report establishment or non-establishment. Long-term monitoring of changes in relative abundance and in genetic variation may suggest ways of enhancing the establishment rate.

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APPENDIX I

Percent composition of pea aphid parasites in British Columbia alfalfa fields. The percentage values for each species were calculated from the number of male and female parasites at each sampling location. Mummies that yielded hyperparasites are not included. Data for 1971 and 1972 are from Campbell (1974) and for 1983 and 1984 from Mackauer and Kambhampati (1986).

	YEAR			
Species	1971	1972	1983	1984
INTERIOR OF BRITISH COLUMBIA:				
No. localities	18	6	10	13
No. parasites emerged	4501	1193	3700	1809
Aphidius ervi	0.09	0.08	80.81	84.52
Aphidius pisivorus	12.04	18.44	16.87	12.49
Aphidius smithi	81.27	71.25	0.89	0.61
Monoctonous paulensis	0.04	0.00	0.00	0.00
Praon pequodorum	6.56	10.23	1.43	2.38
COASTAL REGION OF BRITISH COLUMBIA:				
No localities	1	1	1	1
No parasites emerged	304	109	170	98
Aphidius ervi	88.16	82.57	100.00	98.98
Aphidius pisivorus	0.66	0.92	0.00	1.02
Aphidius smithi	1.64	2.75	0.00	0.00
Praon pequodorum	9.54	13.76	0.00	0.00

APPENDIX II

Age-specific fecundity data of pea aphid parasites. The total number of eggs produced by each female was estimated by doubling the number of eggs/larvae found in 20 aphids that were dissected from the original 40 exposed to the parasite females. See Chapter III for details.

Aphidius ervi (Chilliwack)

Day	PARASITE NUMBER *								
	1	2	3	4	5	7	8	9	13
1	52	56	82	74	56	68	46	38	56
2	48	72	44	72	98	60	58	92	78
3	52	76	62	58	66	108	60	68	52
4	68	54	52	60	58	60	70	44	38
5	38	54	34	36	60	50	62	34	18
6	24	34	30	16	2	42	46	44	
7			2	18		42	56	14	
8				36		42	42	24	
9				0		42	24	10	
10						24			
Totals:	282	346	306	370	340	538	464	368	242

* Parasite # 11 died on day 2, #6 and #2 died on day 3, and #10 was injured during transfer. All excluded from analysis.

Aphidius ervi (Kamloops)

Day	PARASITE NUMBER*											
	1	2	3	4	5	6	8	9	10	11	12	13
1	44	34	78	28	56	80	74	60	70	66	46	64
2	70	52	64	60	44	88	80	64	64	82	52	60
3	68	32	54	44	28	74	50	52	28	70	38	44
4	28	14	8	46	12	52	50	18	8	52	30	48
5	30	4	62	46	4	50	26	28		46	42	30
6	16		34	6		32	34	30		22	20	
7	10		32	24		0	36	6		16	18	
8	0		14	8			18	12		22	18	
9	0		12	12			12	6		4	10	
10			6	6				10		14	14	
11			8	8				10		24	14	
12			2	2						2	0	
13			2							0	0	
14			0							0	0	
15			0							2		
16										0		
17										0		
Total	266	136	376	290	144	376	380	296	170	422	302	246

* Parasite # 7 escaped during the experiment.

Aphidius ervi (Sussex)

Day	PARASITE NUMBER*											
	1	2	3	5	6	7	8	9	10	11	12	13
1	88	74	52	82	54	70	86	98	82	136	112	182
2	118	82	100	134	108	98	126	104	74	80	108	98
3	120	74	72	132	90	96	114	104	86	68	126	64
4	66	82	112	76	78	90	70	78	18	62	66	66
5	70	70	78	88	0	20	64	48	0	54	62	56
6	60	64	100	62	0		68	50	0	48	66	40
7	58	24	108	42	0		54	54		40	52	40
8	66	34	40	54	0		22	26		4	32	26
9	44	28	46	40				20			20	36
10	46	20	30	0							6	42
11	36	12	8								30	26
12	46	6	0								8	22
13	16		0								20	26
14	0										6	18
15												22
16												14
Total	1834	570	746	710	330	374	604	582	260	492	714	778

* Parasite # 4 died on day 3, excluded from analysis.

Aphidius smithi (Chilliwack)

Day	PARASITE NUMBER*								
	1	2	3	4	5	8	9	10	12
1	84	70	88	68	76	0	120	100	118
2	58	94	94	106	122	100	64	76	90
3	86	70	84	72	92	106	66	82	104
4	54	68	74	64	82	58	48	70	52
5	50	68	56	72	68	68	66	62	76
6	54	70	56	70	64	88	50	56	50
7	50	42	40	44	52	46	46	62	38
8	0	60	48	50	48	38	70	64	44
9		52	38	50	38	36	40	56	46
10		40	36	42	44	54	52	62	34
11		34	4	52	8	46	40	44	22
12		34	6	32	4	60	0	22	4
13		8	12		0	4		0	0
14			0			0			
15						0			
16						0			
17						0			
Totals	436	710	636	722	698	704	662	756	678

* Parasite #s 6,7 and 11 escaped during the experiment.

Aphidius smithi (Kamloops)

Day	PARASITE NUMBER*									
	1	2	3	4	5	6	7	8	9	10
1	72	98	60	82	106	126	72	92	88	120
2	112	84	142	96	108	84	98	124	64	88
3	106	56	62	82	58	88	100	124	26	96
4	88	38	110	94	100	100	96	86	30	60
5	92	40	110	98	72	106	92	92	28	68
6	94	16	80	86	58	120	92	68	36	62
7	78	4	130	98	52	128	76	60	18	26
8	72	2	76	70	56	88	62	56	24	6
9	52	0	38	40	66	110	42	48	12	0
10	44	2	28	14	48	64	40	32	14	
11	36		22	12	40	64		20	6	
12	38		4		50	32		4	2	
13	34		0		30	12		0	0	
14	10		0		16				0	
15	10		0		4				0	
16			0							
Totals:	938	340	862	772	864	1122	770	806	348	526

* #11 removed from analysis because it produced only 32 eggs in 13 days in an irregular pattern.

Aphidius pisivorus (Kamloops)

Day	PARASITE NUMBER												
	1	2	3	4	5	6	7	8	9	10	11	12	13
1	22	68	62	28	58	66	72	72	32	56	60	82	56
2	46	76	68	18	72	90	70	46	40	72	74	78	88
3	44	90	58	30	48	60	64	54	44	40	60	44	58
4	54	74	64	32	44	62	54	54	52	36	68	62	74
5	72	66	64	16	36	62	40	52	34	36	56	48	52
6	60	58	48		38	42	42	52	52	36	52	50	0
7	46	52	30		38	48	32	56	52	40	50	40	
8	58	62	8		20	58	44	60	44	42	60	32	
9	62	48	6		30	4	50	58	54	52	52	0	
10	62	34	0			0	22	30	12	18	12		
11	34	0				0	22	6	8	16	14		
12	26	0					8	2	0	28	0		
13	4	0					24	2	0	14			
14	2						2	0	0	0			
15							0						
16							0						
Tot	592	628	408	124	384	492	546	544	424	486	558	436	328

Praon pequodorum (Chilliwack)

Day	PARASITE NUMBER											
	1	2	3	4	5	6	7	8	9	10	11	12
1	2	36	44	12	0	56	0	52	0	2	0	34
2	12	40	62	40	40	32	46	50	84	6	0	42
3	30	44	60	48	54	40	54	72	32	18	0	54
4	64	46	60	60	24	64	36	72	68	36	24	44
5	30	50	50	60	52	70	76	70	70	72	50	34
6	40	64	86	50	58	60	72	72	64	56	62	14
7	44	76	66	74	82	62	50	76	80	52	36	58
8	54	66	56	72	70	50	68	84	84	36	16	42
9	40	38	48	52	50	70	68	48	82	52	16	34
10	46	4	74	52	46	44	34	36	60	48	26	22
11	20	8	46	40	60	46	42	42	58	54	8	16
12	48		66	48	54	34	20	44	38	48	36	24
13	26		54	54	48	26	6	32	36	22	20	18
14	22		44	44	38	10		28	22	50	10	18
15	30		28	26	20	14		10	2	10	4	0
16	36		42	20	12	12		4		8	6	
17	20		24	16	6	0				0	8	
18	22		2	2	2	2					2	
19	12										0	
20	4											
Tot.	602	472	912	770	716	692	572	776	782	548	308	470

Praon pequodorum (Kamloops)

Day	PARASITE NUMBER*								
	1	3	5	6	7	9	10	11	12
1	46	44	44	20	46	28	22	44	42
2	34	20	38	66	40	42	6	42	46
3	28	48	48	44	44	38	22	44	56
4	60	60	58	40	60	52	32	66	58
5	62	46	64	60	58	62	34	54	86
6	60	54	58	62	42	44	70	56	78
7	50	68	52	50	58	22	40	54	28
8	36	44	52	54	42	38	2	36	42
9	48	44	28	36	18	32	54	44	60
10	56	48	44	28	30	40	42	40	40
11	20	36	26	40	26	28	26	4	0
12	18	32		34	34	36	0	6	
13	24	10		26	34	10		38	
14	14	4		16	10	0			
15	6	2		14					
16	8	2		2					
17	6			4					
18	2			0					
19	4			0					
20	0								
21	0								
Totals:	582	562	512	596	542	472	350	528	536

*Parasite #2 injured during transfer, #4 died on day 3 and #8 escaped during transfer. All excluded from analysis.

Praon pequodorum (Sussex)

Day	PARASITE NUMBER*										
	1	2	3	4	5	6	7	8	9	11	12
1	24	46	62	46	44	48	14	28	46	46	56
2	32	34	26	58	50	50	56	42	56	68	44
3	56	98	54	74	82	82	56	60	68	42	42
4	26	48	36	62	46	42	50	32	82	74	48
5	62	54	32	36	34	70	38	68	40	82	46
6	48	40	58	8	46	58	34	38	52	68	38
7	32	38	22	26	64	78	78	58	48	64	44
8	46	32	26	6	50	38	20	28	40	50	36
9	24	30	50	0	44	44	16	2	0	58	16
10	28	16	36	0	6	34			0	34	0
11	16	16	0	0	0	44				0	
12	18	4				34					
13	2	2				34					
14						34					
15						8					
16						0					
17						0					
18						0					
Totals	414	458	402	316	466	678	362	356	432	586	370

* Parasite #10 escaped during transfer. Excluded from analysis.

APPENDIX III

Mean and standard deviations of image features extracted from the fecundity arrays by pattern analysis for species and populations of pea aphid parasites. The quantitative features are untransformed values and expressed as average percentage of aphids belonging to a given frequency class. See Chapter III for further details.

Variable	A. smithi (Kam)	A. smithi (Chwk)	A. pisi. (Kam)
FEC_0	24.850 ± 17.392	12.661 ± 8.372	28.714 ± 8.240
FEC_1	34.365 ± 7.983	52.550 ± 7.132	47.162 ± 6.105
FEC_2	22.515 ± 7.634	22.293 ± 4.433	18.745 ± 6.473
FEC_3	10.769 ± 5.690	6.427 ± 1.762	3.870 ± 2.286
FEC_4	4.714 ± 2.557	2.102 ± 1.086	1.104 ± 0.973
FEC_5	2.784 ± 1.450	3.967 ± 1.694	0.403 ± 0.483
$SF_{1,2}$	3.460 ± 1.175	3.944 ± 1.310	4.301 ± 2.093
$SF_{1,5}$	1.115 ± 0.476	1.194 ± 0.497	0.212 ± 0.311
$SF_{2,1}$	3.781 ± 1.609	5.550 ± 0.592	5.810 ± 1.217
$SF_{2,4}$	0.426 ± 0.409	0.161 ± 0.118	0.099 ± 0.111
$SF_{3,0}$	5.898 ± 3.160	3.389 ± 2.280	6.691 ± 1.484
$SF_{3,3}$	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
GSF_1	73.617 ± 50.665	64.300 ± 15.145	104.466 ± 37.65
GSF_2	1.779 ± 0.993	1.684 ± 1.263	0.155 ± 0.311

Variable	*A. ervi* (Kam)	*A. ervi* (Chwk)	*A. ervi* (Suss)
FEC_0	41.840 ± 17.158	20.458 ± 9.277	16.160 ± 8.129
FEC_1	38.557 ± 9.368	51.040 ± 7.576	40.711 ± 4.624
FEC_2	14.412 ± 5.066	18.775 ± 3.618	22.550 ± 6.198
FEC_3	3.891 ± 2.511	6.674 ± 2.057	10.762 ± 4.027
FEC_4	1.099 ± 1.727	1.825 ± 0.823	5.767 ± 2.765
FEC_5	0.201 ± 0.484	1.228 ± 0.790	4.051 ± 2.256
$SF_{1,2}$	4.806 ± 0.921	3.315 ± 0.903	3.461 ± 1.311
$SF_{1,5}$	0.086 ± 0.168	0.611 ± 0.571	1.556 ± 1.188
$SF_{2,1}$	5.621 ± 0.922	5.308 ± 1.301	4.168 ± 1.676
$SF_{2,4}$	0.065 ± 0.150	0.150 ± 0.145	0.639 ± 0.575
$SF_{3,0}$	8.424 ± 2.479	5.047 ± 2.316	4.248 ± 2.185
$SF_{3,3}$	0.000 ± 0.000	0.000 ± 0.000	0.111 ± 0.385
GSF_1	132.837 ± 34.187	71.629 ± 31.881	55.935 ± 34.410
GSF_2	0.058 ± 0.143	0.705 ± 0.853	4.573 ± 3.646

Variable	P. pequodorum(Kam)	P. pequodorum (Chwk)	P.pequodorum (Sus)
FEC_0	26.939 ± 11.314	30.102 ± 14.000	28.412 ± 8.079
FEC_1	53.962 ± 8.744	46.134 ± 7.867	45.658 ± 7.090
FEC_2	14.991 ± 3.806	20.054 ± 7.436	18.467 ± 4.187
FEC_3	3.793 ± 2.645	3.367 ± 2.578	5.617 ± 3.529
FEC_4	0.165 ± 0.202	0.283 ± 0.396	1.423 ± 1.173
FEC_5	0.149 ± 0.225	0.059 ± 0.140	0.424 ± 0.635
$SF_{1,2}$	2.011 ± 1.055	2.564 ± 1.406	2.902 ± 0.965
$SF_{1,5}$	0.027 ± 0.083	0.000 ± 0.000	0.212 ± 0.373
$SF_{2,1}$	5.832 ± 1.070	5.092 ± 1.005	5.085 ± 0.929
$SF_{2,4}$	0.019 ± 0.037	0.042 ± 0.063	0.221 ± 0.245
$SF_{3,0}$	5.719 ± 2.257	6.041 ± 1.780	6.079 ± 1.928
$SF_{3,3}$	0.014 ± 0.042	0.000 ± 0.000	0.000 ± 0.000
GSF_1	77.298 ± 35.225	74.646 ± 26.601	76.241 ± 28.139
GSF_2	0.010 ± 0.020	0.005 ± 0.115	0.276 ± 0.404

APPENDIX IV

Mean and standard deviation (in mm) of morphological features measured for species and populations of pea aphid parasites. See Chapter V for details of characters measured.

Variable	*A. smithi* (Kam)	*A. smithi* (Chwk)	*A. pisivorus* (Kam)
TL	0.904 ± 0.036	0.919 ± 0.031	0.961 ± 0.058
TW	0.461 0.034	0.465 0.027	0.509 0.030
PL	0.445 0.023	0.441 0.017	0.462 0.026
PW	0.245 0.017	0.256 0.018	0.248 0.025
AL	2.067 0.293	2.063 0.232	2.064 0.308
OSL	0.177 0.006	0.181 0.004	0.197 0.007
FFL	0.661 0.026	0.697 0.021	0.751 0.043
FTIL	0.663 0.024	0.698 0.023	0.734 0.036
FTAL	0.664 0.022	0.673 0.022	0.716 0.059
FSL	0.117 0.005	0.117 0.004	0.117 0.009
FSPINE	18.850 1.387	17.000 1.123	21.200 2.142
MFL	0.685 0.021	0.719 0.025	0.787 0.042
MTIL	0.716 0.024	0.748 0.030	0.824 0.036
MTAL	0.585 0.024	0.599 0.021	0.644 0.045
MSL	0.079 0.003	0.074 0.004	0.092 0.004
HFL	0.717 0.032	0.744 0.027	0.797 0.046
HTIL	0.891 0.036	0.947 0.036	1.028 0.055
HTAL	0.969 0.035	0.984 0.032	1.073 0.052
HSL	0.068 0.003	0.065 0.002	0.074 0.008
HW	0.579 0.021	0.582 0.029	0.623 0.046
AL1	0.159 0.005	0.170 0.006	0.185 0.009
AW1	0.052 0.001	0.053 0.001	0.054 0.003
AL2	0.158 0.006	0.166 0.006	0.181 0.008
AW2	0.052 0.001	0.053 0.001	0.054 0.003
SEG	17.150 0.366	17.300 0.470	17.050 0.224
MAX	0.426 0.017	0.444 0.013	0.508 0.025
LAB	0.138 0.008	0.148 0.009	0.164 0.010
MAND	0.178 0.006	0.184 0.007	0.191 0.009
WINGL	2.665 0.072	2.668 0.076	2.846 0.128
CSCL	1.078 0.033	1.087 0.036	1.188 0.048
CCW	0.252 0.013	0.274 0.013	0.277 0.016
BCW	0.052 0.004	0.053 0.001	0.054 0.006
TRACH	11.250 0.967	13.800 1.400	11.100 0.852
PIT	0.077 0.003	0.080 0.004	0.081 0.007

Variable	A. ervi (Kam)	A. ervi (Chwk)	A. ervi (Suss)
TL	0.959 ± 0.032	0.880 ± 0.037	0.925 ± 0.046
TW	0.498 0.027	0.473 0.027	0.475 0.024
PL	0.475 0.017	0.433 0.018	0.406 0.017
PW	0.273 0.018	0.249 0.015	0.248 0.022
AL	2.042 0.219	1.772 0.182	1.858 0.211
OSL	0.190 0.005	0.169 0.005	0.176 0.006
FFL	0.678 0.016	0.608 0.019	0.667 0.030
FTIL	0.680 0.018	0.625 0.021	0.663 0.025
FTAL	0.674 0.018	0.627 0.026	0.655 0.021
FSL	0.121 0.008	0.110 0.007	0.116 0.003
FSPINE	23.050 2.328	21.500 1.192	20.950 1.146
MFL	0.722 0.016	0.663 0.022	0.709 0.024
MTIL	0.744 0.018	0.697 0.020	0.720 0.021
MTAL	0.626 0.019	0.584 0.017	0.603 0.023
MSL	0.081 0.004	0.079 0.004	0.082 0.004
HFL	0.747 0.023	0.678 0.023	0.719 0.028
HTIL	0.932 0.020	0.856 0.028	0.913 0.033
HTAL	0.996 0.022	0.945 0.033	0.969 0.036
HSL	0.077 0.004	0.072 0.005	0.069 0.003
HW	0.613 0.021	0.588 0.015	0.583 0.023
AL1	0.167 0.003	0.157 0.004	0.163 0.006
AW1	0.054 0.002	0.051 0.001	0.051 0.001
AL2	0.167 0.003	0.152 0.005	0.159 0.006
AW2	0.056 0.003	0.052 0.001	0.052 0.001
SEG	16.500 0.513	16.750 0.444	17.000 0.000
MAX	0.455 0.014	0.400 0.023	0.443 0.018
LAB	0.158 0.008	0.117 0.006	0.140 0.007
MAND	0.185 0.007	0.179 0.008	0.176 0.007
WINGL	2.662 0.058	2.479 0.072	2.465 0.086
CSCL	1.090 0.031	1.007 0.023	0.992 0.036
CCW	0.299 0.009	0.243 0.011	0.263 0.012
BCW	0.064 0.005	0.061 0.004	0.053 0.003
TRACH	10.750 1.446	10.500 0.761	9.500 0.607
PIT	0.081 0.008	0.089 0.008	0.080 0.006

Variable	*P. pequodorum* (Kam)	*P. pequodorum* (Chwk)	*P. pequodorum* (Sus)
TL	0.824 ± 0.030	0.832 ± 0.023	0.833 ± 0.033
TW	0.295 0.020	0.325 0.023	0.315 0.018
PL	0.221 0.026	0.234 0.019	0.212 0.023
PW	0.235 0.015	0.218 0.021	0.223 0.016
AL	1.724 0.123	1.709 0.119	1.653 0.098
OSL	0.189 0.008	0.202 0.006	0.187 0.012
FFL	0.658 0.037	0.709 0.033	0.655 0.031
FTIL	0.737 0.029	0.766 0.039	0.725 0.033
FTAL	0.596 0.025	0.617 0.029	0.600 0.022
FSL	0.085 0.005	0.092 0.005	0.085 0.005
FSPINE	14.950 1.191	14.750 0.639	13.950 0.887
MFL	0.656 0.036	0.723 0.040	0.648 0.039
MTIL	0.763 0.050	0.828 0.033	0.753 0.033
MTAL	0.459 0.028	0.496 0.024	0.478 0.026
MSL	0.065 0.005	0.070 0.005	0.066 0.004
HFL	0.646 0.051	0.707 0.050	0.582 0.044
HTIL	0.898 0.059	0.988 0.042	0.936 0.041
HTAL	0.811 0.035	0.887 0.047	0.800 0.043
HSL	0.077 0.005	0.081 0.006	0.078 0.004
HW	0.483 0.021	0.510 0.029	0.515 0.031
AL1	0.196 0.007	0.205 0.008	0.188 0.007
AW1	0.039 0.001	0.040 0.001	0.040 0.001
AL2	0.143 0.006	0.150 0.006	0.133 0.005
AW2	0.039 0.001	0.039 0.001	0.039 0.001
SEG	18.450 0.510	19.000 0.324	18.900 0.553
MAX	0.445 0.018	0.488 0.021	0.454 0.016
LAB	0.140 0.008	0.150 0.008	0.142 0.008
MAND	0.182 0.006	0.191 0.007	0.174 0.008
WINGL	2.428 0.080	2.581 0.080	2.481 0.085
CSCL	0.972 0.029	0.996 0.033	0.939 0.032
CCW	0.226 0.009	0.239 0.015	0.220 0.014
BCW	0.078 0.006	0.079 0.005	0.069 0.005
TRACH	4.950 0.224	5.500 0.513	5.050 0.224
PIT	0.054 0.003	0.056 0.005	0.059 0.005

ERRATA

TABLE VI:

Column 1: PIELL should read 9.40 ± 0.92

Column 2: MEANEGGS should read 1.54 ± 0.03

TABLE VII:

Column 1: PIELL should read 5.17 ± 0.30

NESCAPE should read 42.33 ± 4.56

NWASTE should read 84.00 ± 11.47

TABLE VIII:

Column 2: SUPER should read 0.36 ± 0.03

TABLE IX:

Column 1: MEANEGGS should read 1.54 ± 0.03

MEANDAY should read 61.53 ± 1.63

Column 2: MEANDAY should read 55.29 ± 2.01

Column 3: NWASTE should read 175.67

TABLE X:

Column 1: PIELL should read 9.40 ± 0.92

PIELFEC should read 708.80

MEANEGGS should read 1.85 ± 0.11

Column 2: PIELL should read 5.17 ± 0.30

NESCAPE should read 42.33 ± 4.56

NWASTE should read 84.00 ± 11.47

MEANEGGS should read 1.22 ± 0.06

Column 3: MEANEGGS should read 1.10 ± 0.06

Column 4: PIELL should read 8.46 ± 0.58

NAPHIDS should read 300.92 ± 23.73

NESCAPE should read 37.54 ± 6.29

TABLE XI:

Column 1: PIELFEC should read 557.83 ± 49.41