POST-DIAPAUSE DEVELOPMENT OF *DELIA RADICUM* (DIPTERA: ANTHOMYIIDAE) AND HOST RANGE OF *ALEOCHARA BIPUSTULATA* (COLEOPTERA: STAPHYLINIDAE) FOR CLASSICAL BIOLOGICAL CONTROL IN CANADIAN CANOLA

By

Lars Andreassen

A thesis
submitted to the Faculty of Graduate Studies
in partial fulfillment of the requirements for the degree of

Master of Science

Department of Entomology
University of Manitoba
Winnipeg, MB

THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES

*****

COPYRIGHT PERMISSION

POST-DIAPAUSE DEVELOPMENT OF *DELIA RADICUM* (DIPTERA: ANTHOMYIIDAE) AND HOST RANGE OF ALEOCHARA *BIPUSTULATA* (COLEOPTERA: STAPHYLINIDAE) FOR CLASSICAL BIOLOGICAL CONTROL IN CANADIAN CANOLA

BY

Lars Andreassen

A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of Manitoba in partial fulfillment of the requirement of the degree

Master of Science

ACKNOWLEDGEMENTS

I would like to sincerely thank Dr. Holliday for guidance and encouragement during all stages of my project. Thanks also to Dr. Kuhlmann for input and assistance, especially while I was working in Switzerland. Dr. Roughley helped me to learn about identifying insects and non-target effects of biological control. Dr. Mason provided useful advice, particularly about host range testing, and Dr. Froese was very helpful when I was looking for areas to collect insects. Finally, Jay Whistlecraft was an extremely valuable resource for information about rearing insects.

I had a lot of help doing the experiments, from Jake Miall, Serge Hammerli, Brooke Bellefeuille, Jane Allison, Kathy Makela, and Basri Pulaj. Wade Jenner was also usually helpful, as long as the work did not smell too foul. Alicia Leroux has been extremely supportive over the past few years, with my experiments and otherwise.

Erich Staedler (Agroscope FAW, Waedenswil, Switzerland), Rosemary Collier (University of Warwick, Wellesbourne, UK), Rene Alfaro (Canadian Forest Service, Victoria), Ernst Gubler (Andermatt BioVet AG, Grossdietswil, Switzerland), Luisa Dindo (University of Bologna, Italy), Claude Wyss (Lausanne, Switzerland), Guenther Nentwig (Bayer CropScience, Germany), and Roger Moon (University of Minnesota, USA) provided non-target Diptera for host range testing. Julie Soroka (AAFC, Saskatoon) and Jay Whistlecraft (AAFC London) sent cabbage maggots to study spring emergence.

Knut Rognes and Bernhard Merz identified the Calliphoridae species. Graham Griffiths identified the *Pegomya* species. Adrian Pont identified the Muscidae species. Russell Bonduriansky identified *Stearibia nigriceps*. Stephen Marshall identified *Spelobia luteilabris*. Iain MacGowan identified the European Lonchaeidae.

Funding for this project was provided by the Canola Agronomic Research Program of the Canola Council of Canada, the Agronomic Research and Development Initiative of the Province of Manitoba, the Western Grains Research Foundations, and Agriculture and Agri-Food Canada. I received personal funding from the University of Manitoba, the Province of Manitoba, and the National Science and Engineering Research Council.

ABSTRACT

Aleochara bipustulata, a European natural enemy of *Delia radicum*, shows promise as a biological control agent in Canadian canola. Post-diapause development of *D. radicum* and *Aleochara bilineata* was studied in the laboratory. Prairie *D. radicum* developed more slowly than from Ontario, suggesting particular source populations of *A. bipustulata* may be better suited to western Canada than others. *Aleochara bilineata* develops too slowly for effective predation of early immature *D. radicum*. *Aleochara bipustulata*'s host range was studied in the laboratory and its habitat associations studied in Europe. Beneficial Diptera species were either unsuitable hosts, or for *Lonchaea corticis* found in habitats not visited by *A. bipustulata*. Suitable laboratory host species were relatively small or closely related to *D. radicum*. Species with unusual puparia were less likely to be accepted as hosts than *D. radicum*. Species which develop quickly in the pupal stage, or with relatively heavy puparia, were unsuitable hosts.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1. INTRODUCTION

Introducing natural enemies from one part of the world to another is a long-term and cost-effective strategy for pest control (DeBach 1964). It is however not uncommon for the introduction to fail, either because the introduced species does not establish or provides insignificant control of injury (Turnbull and Chant 1961; Beirne 1985). Introducing a well-synchronized population is recognized as one way to improve the likelihood of success. In addition, species moved outside of their native range can cause ecological problems (Elton 1958), and this applies to biological control agents as well (Howarth 1991). We can never be certain about the ecological risk introducing a species might carry with it, but several recent papers (*e.g.* van Lenteren et al. 2003, 2006a, 2006b) outline methods which should reduce the risk of intentional introduction to a minimum.

The cabbage maggot, *Delia radicum* (L.) (Diptera: Anthomyiidae), is an increasing problem as a pest of canola in Canada (Soroka et al. 2004). Agronomic practices can be adjusted to reduce losses due to injury caused by the cabbage maggot (Dosdall et al. 1998), but their adoption will depend on profitability, and control using these measures could be complemented with others. As *D. radicum* was introduced to North America from Europe, introducing European natural enemies is an option for its control (Biron et al. 2000; Soroka et al. 2002). *Aleochara bipustulata* L. (Coleoptera: Staphylinidae) is the most promising candidate for introduction (Hemachandra 2004). Adult *A. bipustulata* feed on immature *D. radicum*, and larvae of *A. bipustulata* parasitize *D. radicum* puparia.

This study was undertaken to improve the chance of success and determine if *A. bipustulata* can parasitize many species besides *D. radicum*. To improve the chance of

success, post-diapause development of *D. radicum* from the Canadian prairies was compared to a population from Ontario, and to a natural enemy already present in Canada, *Aleochara bilineata*, with the intention of using this information later to select an *A. bipustulata* population for introduction. The ability of *A. bipustulata* to parasitize species other than *D. radicum* was studied in the laboratory, and the likelihood of *A. bipustulata* doing so was assessed by studying what habitats it is found in where it is native, in Europe.

2. LITERATURE REVIEW

The cabbage maggot as a pest of canola

Cultural varieties, or cultivars, of *Brassica napus* L. and *B. rapa* L. (Brassicaceae) with less than two per cent erucic acid and less than 30 micromoles per gram of glucosinolates in oil-free meal from their seeds are called double low oilseed rape or canola (Gray et al. 2006). Although the term canola did not yet exist, the first cultivar to meet these specifications, Tower, was developed in 1974 at the University of Manitoba (Stefansson and Kondra 1975; Stefansson 1983). Since then, coordination by the Canola Council of Canada, research by university and government scientists, and increased involvement of the private sector have contributed to the development of 200 subsequent cultivars (Carew and Smith 2006; Gray et al. 2006). In 2005, about 5.2 million hectares of canola was harvested in Canada, with the vast majority grown in Alberta, Saskatchewan and Manitoba (Statistics Canada 2005). Farmers who integrate canola in their crop rotations benefit from increased net returns and decreased variability in annual income (Zentner et al. 1996). Threats to the yield of Canadian canola crops are therefore taken seriously.

Insect pests constitute one such threat. The species involved depend upon the geographical region, but generally all parts of the canola plant are fed upon by various insects wherever it is grown (Lamb 1989; Ekbom 1995). Furthermore, new potential pests of Canadian canola continue to appear. For example, *Contarinia nasturtii* (Kieffer) (Diptera: Cecidomyiidae) (Hallett and Heal 2001; Olfert et al. 2006) and *Meligethes viridescens* (Fabricius) (Coleoptera: Nitidulidae) (Mason et al. 2003) are both capable of spreading from eastern Canada to the prairies. In western Canada, seedlings are eaten by five species of flea beetles (Coleoptera: Chrysomelidae), the most important of which is

Phyllotreta cruciferae (Goeze) (Burgess 1977). Canola leaves are consumed by larvae of *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) (Palaniswamy et al. 1986), *Mamestra configurata* Walker (Lepidoptera: Noctuidae) (Mason et al. 1998), and especially in drier areas by certain species of grasshoppers (Orthoptera: Acrididae) (Olfert and Weiss 2002). Flowers are eaten by adult cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae) (Dosdall and Moisey 2004), *Lygus elisus* Van Duzee, *L. lineolaris* (Palisot), and *L. borealis* (Kelton) (Hemiptera: Miridae) (Butts and Lamb 1991a; Timlick et al. 1993). The fourth and fifth instars of *M. configurata* feed on pods (Mason et al. 1998), as do late instar *Lygus* spp. (Butts and Lamb 1991b), and the larvae of *C. obstrictus* develop inside the pods feeding on the seeds (Dosdall and Moisey 2004). Insignificant damage to the roots is caused by flea beetle larvae (Lamb 1989); more important are the root-feeding species of *Delia* Robineau-Desvoidy (Diptera: Anthomyiidae), and contributing to their control is the focus of this thesis.

The primary pests, species that can attack undamaged plants, are the cabbage maggot *Delia radicum* (L.), turnip maggot *Delia floralis* (Fallen), and radish maggot *Delia planipalpis* (Stein) (Liu and Butts 1982; Griffiths 1991a; Vernon and Broatch 1996; Broatch et al. 2006). The seedcorn maggot, *Delia platura* (Meigen), and tobacco maggot, *Delia florilega* (Zetterstedt), typically feed on tissue already invaded by the three primary pests (Brooks 1951). The seedcorn maggot is often the most abundant species trapped as adults in canola (Vernon and Broatch 1996; Broatch and Vernon 1997; Broatch et al. 2006). The turnip maggot is the predominant primary pest in northeastern Alberta and the agricultural region around the Peace River, where relatively high summer moisture deficits and low summer precipitation are typical (Griffiths 1986b). Notwithstanding, the most important root maggot pest of canola in Europe (Lamb 1984; Lerin 1995; Erichsen

and Huenmoerder 2005) and Canada (Turnock et al. 1992; Dosdall et al. 1994; Soroka et al. 2002; Broatch et al. 2006) is *D. radicum*.

The first to note root maggots infesting oilseed rape was B.R. Stefansson, who in 1958 discovered *D. radicum* damage to both *B. rapa* and *B. napus* in Manitoba (Allen 1964). Then in 1981 a survey in Alberta revealed that root maggot damage was widespread, particularly in the northern part of that province (Liu and Butts 1982). A survey in Manitoba from 1985 to 1988 again found percentage of roots infested per field to be higher in agricultural areas further north (Turnock et al. 1992). The percentage of roots infested per field and the average level of damage to plants increased in the time between the earlier studies and a survey across the three prairie provinces in 1996 and 1997 (Soroka et al. 2004). Reductions of yield due to root maggot infestation are estimated at $100 million during years favourable to the insects (Soroka et al. 2002; 2004). The majority of this damage has been attributed to *D. radicum*.

The genus *Delia* is in the dipteran suborder Muscomorpha (=Cyclorrapha), section Schizophora, subsection Calyptratae, superfamily Muscoidea, family Anthomyiidae (Huckett 1987; McAlpine 1989). The Anthomyiidae is distinguished from other muscoid families by continuously sclerotized connections between the cerci and inner surfaces of gonostyli (Griffiths 1982). Griffiths (1991a) provides ten characters common to members of the genus *Delia*, and additional characters for placing each of the 162 described Nearctic species in one of eight sections. The greatest diversity of *Delia* species is in the subarctic and subalpine, and the larval habitats are known for only about one fifth of these species (Griffiths 1991a; 1991b). The cabbage maggot is in the *D. radicum* section and *D. radicum* subsection. Other members of the *radicum* subsection are the two other primary

invaders of canola roots, *D. floralis* and *D. planipalpis*, and two species know only from a few specimens collected in the Canadian arctic (Griffiths 1991a).

The cabbage maggot is oviparous, laying elongate, white eggs in the soil (Brooks 1951; Miles 1952a). The larvae of *D. radicum* can be distinguished from those of other Diptera found around the roots of crucifers based on characters of the anterior spiracles, relative size of the head (Miles 1952b), structure of the cephalopharyngeal skeleton, and tubercles on the eighth abdominal segment (Brooks 1951; Miles 1952b). The three larval instars of *D. radicum* can be separated on the basis of spiracles, since the first instar has only posterior spiracles, the second instar anterior spiracles and posterior spiracles with two slits, and the third instar again with both anterior and posterior spiracles, but with three slits on the posterior pair (Brooks 1951). Like all cyclorraphous species, the larva pupariates, forming a hard puparium from the cuticle of the third instar (Fraenkel and Bhaskaran 1973). The larva detaches from the old cuticle and forms a larva-like cryptocephalic pupa, then a phanerocephalic pupa as the head evaginates, and finally a pharate adult before the adult fly emerges (Fraenkel and Bhaskaran 1973).

Delia radicum is distributed across the northern temperate parts of the world, from Morocco east to Irkutsk and north into Scandinavia in the Palearctic (CAB 1989). It came to North America in the 1800s (Schoene 1916; Griffiths 1991a), possibly as pupae in ship ballast (Schoene 1916). Analysis of egg micromorphology (Biron et al. 2000; Biron et al. 2003) and DNA (Biron et al. 2000) variation among different populations indicate a single introduction to eastern North America from northwestern Europe, followed by the spread of the founder population west across the rest of North America. In Canada, *D. radicum* is generally distributed where crops are cultivated, and absent in more natural

areas (Griffiths 1991a). In canola *D. radicum* can constitute all, some, or none of the root maggot community (Griffiths 1986b).

Phenology is the study of biological events which cycle (Gordh and Headrick 2001). For *D. radicum*, the events include emergence of adults, egg laying, larval and pupal development. The cycle may be interrupted by diapause, a programmed stoppage in development and growth (Danks 1987), depending on cues perceived by the insect from the environment. The cabbage maggot overwinters as a pupa inside the puparium (Schoene 1916). The environmental cues which induce diapause in *D. radicum* are temperature and photoperiod (Hughes 1960; Zabirov 1961; McLeod and Driscoll 1967; Read 1969; Soni 1976; Whistlecraft et al. 1985b). The number of cycles or generations completed each year depends on temperature during the interval between emergence of adults in spring and the induction of diapause in the larvae (Zabirov 1961).

In parts of North America three or four generations occur (Schoene 1916; Nair et al. 1973; Nair and McEwen 1975; Wyman et al. 1977; Jyoti et al. 2003), but the life history of *D. radicum* in the prairie provinces is most relevant to this study. In southern Alberta rutabaga, *Brassica napobrassica* Mill. (Brassicaceae), crops there are two peaks in oviposition, during the first week of June and in early September (Swailes 1958). Allen (1964) reported a similar two-cycle season in Manitoba, with puparia forming in rape during July and mid-October. Just north of Edmonton at Morinville Alberta, the *D. radicum* population in canola is predominately univoltine with adults emerging at the end of May, oviposition coincident with the onset of bolting of the crop in mid-June, and formation of puparia in mid-July (Griffiths 1986a). Rutabaga and canola crops in Manitoba experience two peak periods of adult *D. radicum* activity, during early June and mid-August (Bracken 1988; Turnock et al. 1992), and in rutabaga a third peak in some

years around mid-September (Bracken 1988). At Vegreville Alberta, emergence of overwintered *D. radicum* starts in May and peaks in mid-June (Dosdall et al. 1996b) and oviposition peaks in mid-June (Dosdall et al. 1996a). Broatch et al. (2006) found peaks in emergence of overwintering *D. radicum* and in activity in canola crops to be coincident over three years some time in June, and in two years of their three year study in the last week of June in Lacombe Alberta. In Carman and Altamont (Manitoba) canola crops, oviposition activity peaked in the third week of June and puparia formed toward the end of July, whereas these events occurred about one week later in Shellbrook and Melfort Saskatchewan and in Vegreville Alberta in 2000 (Hemachandra 2004).

Both Griffiths (1986a) and Broatch et al. (2006) noted a slight increase in adult activity during August, and a small proportion of puparia collected in canola at two sites in Manitoba in August were not in diapause (Hemachandra 2004). Selection is expected to favour minimizing the size of this potential second generation across the Canadian prairies, for the spring-planted canola will no longer support larval development, and the emerging adults will have no place to lay their eggs.

Adult *D. radicum* disperse upwind (Hawkes 1974; Finch and Skinner 1982). The process of selecting hosts is thought to involve three stages, which together are the basis of the appropriate-inappropriate landings theory (Finch and Collier 2000). In the first stage, the female is excited and stimulated to land by volatile chemicals from host plants (Traynier 1967a). For *D. radicum*, these are the products of hydrolysis of glucosinolates such as allylisothiocyanate (Nair and McEwen 1976). In the second stage the flies use visual stimuli to determine where to land. They prefer to land on green objects (Prokopy et al. 1982) and are just as likely to land on *Brassica*-shaped leaves as others (Kostal and Finch 1994; Degen and Staedler 1996). Having landed, female *D. radicum* make short

flights off the leaf and back (Kostal and Finch 1994; Morley et al. 2005). The third stage, a decision about laying an egg at the base of the plant, occurs as the female perceives chemical compounds from the leaf through her tarsi (Traynier 1967b; Roessingh et al. 1992). The chemicals are glucosinolates (Nair and McEwen 1976; Nair et al. 1976; Roessingh et al. 1992; Braven et al. 1996), phytoalexins (Baur et al. 1998), and thia-triaza-fluorenes (Baur et al. 1996; Roessingh et al. 1997; Gouinguene and Staedler 2005). If sufficient stimuli are accumulated in a series of successive landings, the female will lay an egg in soil at the base of the plant (Kostal and Finch 1994; Morley et al. 2005), but if she lands on a plant without the stimuli the process of accumulation starts anew (Morley et al. 2005).

To be part of *D. radicum*'s host range, a plant must stimulate oviposition according to the process in the preceding paragraph and be suitable for larval development. Plants that will do so in confined laboratory settings are part of its fundamental host range (Klinken and Heard 2000), and those which support development in nature are its ecological host range (Onstad and McManus 1996). In addition to canola and *Brassica* vegetables (Finch 1989), *D. radicum*'s ecological host range comprises several other plant species. For instance, *D. radicum* puparia have been collected around the roots of *Hesperis matronalis* L., *Barbarea vulgaris* R. Br., *Sinapis arvensis* L., *Lepidium densiflorum* Schrad., *Sisymbrium loeselii* L. (Nair et al. 1973), *Raphanus raphanistrum* L., *Sisymbrium officinale* (L.) Scop., and *Thlaspi arvense* L. (Finch and Ackley 1977) (Brassicaceae). Stinkweed, *T. arvense*, is an important alternative host in the Canadian prairies (Griffiths 1986a; 1991a).

The cabbage maggot damages canola when the larva feeds on the roots. Once the first instar has penetrated the periderm, the larva feeds on phloem, periderm and

secondary xylem, and creates vertical furrows in the root as a second and third instar (McDonald and Sears 1991; 1992). Feeding damage reduces root weight, dry matter content and sugar content of the roots (Hopkins et al. 1999). Damaged roots are more likely to be invaded by *Fusarium* species (Griffiths 1986b; 1986a; 1991c) but not by *Rhizoctonia solani* Kuehn (Klein-Gebbinck and Woods 2002). High levels of damage cause plants to lodge (Griffiths 1991c) or die (Griffiths 1986a).

The relationship between feeding damage to roots and reduction in yield is still ambiguous despite several attempts at characterization. In the laboratory, *D. radicum* feeding on roots of *B. rapa* reduce plant biomass, number of seeds per plant, number of racemes, and number of pods on axillary racemes (McDonald and Sears 1991). In field trials Griffiths (1991c) showed that root damage reduces the number of seeds and seed weight. When average damage to roots of *B. rapa* in 1 m^2 plots increases from zero to 50 per cent of the root surface, seed yield can be about 50 g/m^2 less, although the effect was only found in one year of a two year study (Dosdall 1998). Conversely, Klein-Gebbinck and Woods (2002) found plants with more damage have higher seed yield and plant biomass, and Soroka et al. (1999) found no significant effect of level of infestation on yield. However, the highest level of damage observed by Klein-Gebbinck and Woods (2002) was 32% of the root surface, and the greatest reduction in number of seeds per plant occurs when at least 25% of the surface is damaged (McDonald and Sears 1991; Dosdall 1998; Dosdall et al. 1998). Roots with 50-100% of the surface damaged are not uncommon across the prairies (Soroka et al. 2004), so even if economic reductions in yield were not demonstrated by Klein-Gebbinck and Woods, the large area planted to canola each year means small average losses on a farm scale combine for an expensive pest problem for western Canadian canola producers as a whole.

The categories of strategies outlined by Finch (1989) for control of *Delia* species in vegetable production can also be considered as they relate to canola in western Canada. These are chemical, cultural and biological control. Granules of cyclodienes applied in furrow at the time of seeding reduce damage to *B. rapa* by more than 90% (Allen 1964). Similar results are obtained by treating furrows with Counter, CGA 12223, and oftanol (Askew et al. 1976). Seed treatment of *B. napus* and *B. rapa* with oftanol or chlorpyrifos and terbufos granules all can protect roots and increase yield (Griffiths 1991c), and diazinon applied weekly as a soil drench reduces root damage (Ekuere et al. 2005). However, no insecticides are registered for *D. radicum* control in canola in Canada (Soroka et al. 2004), so chemical control will not be considered further.

That organisms are influenced by their environment, are tolerant of a finite range of various environmental factors, and thrive within more narrow limits is well known. Cultural control of pests involves activities which alter the environment to be outside the optimal range, or ideally outside the tolerable range, of one or more important environmental parameters. The options for cultural control are restricted by their influence on the crop and net return to the producer. Several strategies for cultural control of cabbage maggot in canola have been proposed. Decisions about implementing cultural controls in prairie canola based on the expected level of root maggot infestation are supported by a predictive model based on ecozone, canola species, and the previous season's rainfall and temperature (Soroka et al. 2004).

The selection of what to plant influences the level of *D. radicum* infestation. *Brassica napus* receives fewer eggs and less damage than *B. rapa* (Griffiths 1991c; Dosdall et al. 1994) and certain cultivars of both species are both more attractive for oviposition and more prone to damage (Dosdall et al. 1994; Dosdall et al. 2003). *Sinapis*

alba L. (Brassicaceae) plants are less preferred for oviposition (Dosdall et al. 1994) and less damaged than canola species (Dosdall et al. 1994; Dosdall et al. 2000). Certain hybrid accessions of *B. napus* and *S. alba* are also resistant (Dosdall et al. 2000; Ekuere et al. 2005) and the quantitative trait loci associated with this resistance have been identified with the intention of developing resistant cultivars (Ekuere et al. 2005).

Deciding when to plant is also important. Seeding canola in early June instead of mid-May will reduce damage by *D. radicum*, but negatively influences yield to the extent that it cannot be recommended (Dosdall et al. 1996a). Dormant seeding in the fall and seeding earlier in the spring sometimes (Dosdall et al. 2003) but not always (Clayton et al. 2004; Dosdall et al. 2006) influences the level of damage by root maggots, and since early spring seeding results in increased yield it is recommended (Clayton et al. 2004).

Decisions made about how to plant and manage the canola crop influence root maggot infestation further still. Seeding at a rate of 7–11 kg/ha reduces level of damage to roots relative to lower seeding rates (Dosdall et al. 1998; Hawkins-Bowman 2006). Spacing rows 17–25 cm apart reduces oviposition by the pest relative to narrower spacing and optimizes gross returns (Dosdall et al. 1998). Although reducing tillage increases the overwintering survival of *D. radicum* (Dosdall et al. 1996a) and may result in more damage to roots (Dosdall et al. 1998), this is not always the case (Hawkins-Bowman 2006) and reducing tillage increases gross margins of canola crops (Dosdall et al. 1998), reduces soil erosion, and uses less energy without affecting yield (Bortslap and Entz 1994). Delaying weed removal from when the crop has reached the two-leaf stage to the four-leaf stage reduces the severity of root maggot infestation and maintains yield as high as or higher than earlier weed removal (Dosdall et al. 2003). Planting larger seeds (Soroka and Elliott 2006) and applying fertilizer at recommended rates (Dosdall et al. 2002;

Clayton et al. 2004) are advocated in spite of neutral or even positive effects on root maggots due to other agronomic benefits.

The third category of control strategies listed by Finch (1989) is biological control. Biological control occurs when a pest population is regulated by its natural enemies (DeBach and Rosen 1991). There are several different types of biological control, and placement of a particular option into a category requires a geographical frame of reference. The frame of reference used here is the Canadian prairies.

Natural biological control is the reduction in the pest's population size by natural enemies without human intervention (DeBach and Rosen 1991). The natural enemies of *D. radicum* include parasitoids, predators and pathogens. Insect species whose larvae feed on and kill a single host, which typically is another insect, are parasitoids (Godfray 1994). Parasitoids of minor significance in the prairies are *Aleochara verna* Say (Coleoptera: Staphylinidae), *Phygadeuon* spp. (Hymenoptera: Ichneumonidae), *Aphaereta minuta* (Nees) (Hymenoptera: Braconidae) and *Trichopria* sp. (Hymenoptera: Proctotrupidae) (Hemachandra 2004). More important are *Aleochara bilineata* Gyllenhal (Coleoptera: Staphylinidae) and *Trybliographa rapae* (Westwood) (Hymenoptera: Eucoilidae) (Turnock et al. 1995; Hemachandra 2004).

In addition to the cabbage maggot, the ecological host range of *A. bilineata* includes *D. platura, D. floralis, D. florilega, D. planipalpis, D. antiqua* Meigen, and *Pegomya betae* Curtis (Maus et al. 1998). Eggs are laid in the soil near host puparia (Wadsworth 1915). The mobile, campodeiform larva that ecloses moves away from light (Wadsworth 1915) and locates a prospective host by randomly searching (Fuldner 1960). The larva attaches to a host using its pygopodium, an adhesive structure that telescopes from the tenth abdominal segment (Fuldner 1960), to secure itself as it chews an entrance

hole (Wadsworth 1915; Colhoun 1953; Fuldner 1960). The location of the hole is influenced by the relative size of transverse ridges along the puparium surface (Royer et al. 1998). The search for hosts may be random, but acceptance is not; the larva prefers to enter unparasitized over parasitized hosts (Royer et al. 1999), relatively large hosts (Ahlstrom-Olsson 1994), pupae in earlier stages of development (Fournet et al. 2004), and even hosts parasitized by more distantly related conspecifics over their siblings (Lize et al. 2006). Once inside the puparium the larva feeds for a while by puncturing the pupa (Fuldner 1960) and then returns to the hole to seal it (Wadsworth, 1915) with anal secretions (Wadsworth 1915; Colhoun 1953; Fuldner 1960). Hypermetamorphosis to a non-mobile second and third instar eruciform larva and pupation occur within the puparium (Wadsworth 1915), and then the adult emerges by chewing an opening (Sprague 1870). Adult *A. bilineata* feed on root maggot eggs and larvae (Fuldner 1960).

Female *T. rapae* are attracted to infested plants (Neveu et al. 2002) and oviposit in all three cabbage maggot larval instars, preferring later instars when given a choice (Neveu et al. 2000). The stimulus for females to probe with their ovipositor is perceived through the antennae, and although partly present in the host plant alone the stimulus is strengthened by the presence of larvae (Brown and Anderson 1999). Like *A. bilineata*, *T. rapae* larvae undergo hypermetamorphosis from a eucoiliform first instar to a polypodeiform second instar after the host forms a puparium (Wishart and Monteith 1954; Kacem et al. 1995). The third instar parasitoid chews out of the host pupa, and during the third and fourth instar feeds as an ectoparasitoid on the host, although still contained within the puparium (Wishart and Monteith 1954). The week-long pupal stage is also within the puparium, and then the adult wasp emerges after chewing for itself an exit hole (Wishart and Monteith 1954).

All developmental stages of the cabbage maggot are eaten by predators. Eggs and larvae are eaten by Carabidae, especially *Bembidion* and *Agonum* species (Wishart et al. 1956; Wright et al. 1960; Wyman et al. 1976; Andersen et al. 1983; Finch and Elliott 1992), staphylinid species of *Aleochara* and *Philonthus* (Wishart et al. 1956; Andersen et al. 1983), ants (Formicidae) and *Trombidium* spp. (Acarina: Trombidiidae) (Schoene 1916). Diptera species whose larvae prey on cabbage maggot larvae include *Platypalpus aequalis* Loew (Empididae) (Brooks 1951) and *Phaonia trimaculata* (Bouche) (Muscidae) (Finch and Collier 1984). Puparia are also eaten by carabid beetles (Block et al. 1987). Adult cabbage maggots are eaten by adult *Coenosia flavifrons* (Stein) (Diptera: Muscidae) (Schoene 1916) and *Scatophaga stercoraria* (Read 1958).

Entomopathogenic natural enemies of *D. radicum* have been identified as well. Epizootics caused by the fungi *Entomophthora muscae* (Cohn) Fresenius (Klingen et al. 2000) and *Strongwellsea castrans* Batko & Weiser (Zygomycota: Entomophthoraceae) (Griffiths 1985) have been reported. Adults are also sometimes infected with *Bacillus thuringiensis* (Firmicutes: Bacillaceae), *Cystospogenes deliaradicae* (Microspora: Glugeidae) (Eilenberg et al. 2000), *Entomophthora virulenta* Hall & Dunn, and *Conidiobolus coronatus* (Constantin) Batko (Zygomycota: Entomphthoraceae) (Matanmi et al. 1974). Finally, larvae are somewhat susceptible to nematodes, especially *Steinernema* species (Rhabdita: Steinernematidae) (Morris 1985; Bracken 1990; Royer et al. 1996).

Natural biological control by definition requires the involvement of another organism, the natural enemy, but natural mortality can also occur as a result of abiotic influences. For example, puparia that form in crowded conditions may be malnourished, and the pupa may die (Hughes and Mitchell 1960). Eggs and larvae may dry out (Schoene

1916), or an eclosed larva may not find the host plant (Hughes and Salter 1959; Mukerji 1971). Overwintering *D. radicum* can be malformed by cold injury and die (Turnock et al. 1990).

Conservation biological control is based on the ideas that certain species have become pests because their natural biological control has been disrupted, and that amendments can be made to improve the impact of natural enemies (DeBach and Rosen 1991). No conservation biological control strategies have been devised explicitly for control of *D. radicum* in canola in the prairies, although conventionally tilled plots have significantly more *Agonum placidum* Say (Coleoptera: Carabidae) than untilled plots (Hawkins-Bowman 2006) so the relative proportion of *D. radicum* eggs eaten may have been higher, although the untilled plots may have been more weedy, with a greater probability of 'inappropriate landing' (Finch and Collier 2000) and therefore fewer eggs to begin with. Modifications that increase the abundance of *D. radicum* predators will not necessarily result in improved control, as the predators can compete with and feed on one another (Prasad and Snyder 2004; 2006). Spreading mustard meal mulch around the base of canola plants increases the activity and prevalence of parasitism by *Aleochara bipustulata* (L.) (Coleoptera: Staphylinidae) (Riley et al. *In Press*), but as *A. bipustulata* is not present in North America (Hemachandra et al. 2005) there is no benefit to recommending Canadian canola growers spread the mulch.

Augmentation biological control is the release of particular natural enemy species in large numbers in places where they occur naturally, but in numbers insufficient for the desired level of control (DeBach 1964; DeBach and Rosen 1991). Rearing and releasing carabids for *D. radicum* control does not work because too many pest eggs are slightly below the soil surface and therefore not eaten (Finch and Elliott 1999). Methods

of mass producing *A. bilineata* for release exist (Adashkevich and Perekrest 1970; 1973; Adashkevich 1977; Whistlecraft et al. 1985a), and releasing two beetles per cabbage plant significantly reduces the proportion of *D. radicum* that complete development (Hartfield and Finch 2003), but production of sufficient *A. bilineata* to control *D. radicum* on even a portion of the five million hectares of canola in Canada is rather unrealistic. Augmenting *Steinernema* species does not sufficiently control *D. radicum* in cabbage (Nielsen and Philipsen 2004), and since an economic injury level, where the benefit of a control measure is greater than its cost (Gordh and Headrick 2001), for controlling *D. radicum* in canola with entomopathogenic nematodes has not been established there is no rational basis for decisions about their use in western Canada. Entomopathogenic fungi that effectively kill *D. radicum* larvae in the laboratory have been identified but not tested in field conditions (Bruck et al. 2005). No natural enemy of *D. radicum* is well-studied enough that augmenting populations in canola fields can be done with confidence that there will be improved control and increased net economic return.

Delia radicum larvae will infest canola roots as long as this crop is grown in western Canada. The agronomic practices outlined above will reduce the severity of these infestations, and the prospect for resistant cultivars (Ekuere et al. 2005) is promising. Other strategies to manage *D. radicum* should be compatible with these methods. One such strategy is classical biological control, where a natural enemy is imported from one region of the world to another (DeBach and Rosen 1991).

The classical approach has already been attempted. A survey of the parasitoids of *D. radicum* in Europe was conducted from 1949 to 1954 (Wilkes and Wishart 1953; Wishart et al. 1957). The species present in Europe were compared with those already in Canada (Wishart 1957) and several 'missing' species were introduced (McLeod 1962).

Misidentification of the natural enemies, a perennial problem in classical biological control (Gibson et al. 2005; Gillespie et al. 2006), meant that the species introduced were already in Canada (Turnbull and Chant 1961; McLeod 1962). Instability of *D. radicum* control, expansion into canola, and the misidentifications have led to calls for renewed effort (Turnock et al. 1995; Soroka et al. 2002), focusing on candidate species from northwestern Europe (Biron et al. 2000). The *D. radicum* problem in canola matches several of the criteria recommended for prioritizing biological control projects, including those related to biological control feasibility, economics, and inter-organization cooperation (Barbosa and Segarra-Carmona 1993). The next section describes the process of classical biological control in more detail and progress made in the renewed effort up to the initiation of my project.

Classical biological control and the second attempt against *Delia radicum*

In the past, entomophagous natural enemies introduced to Canada were more commonly targeting pests of orchard and forest systems than field crops (Turnbull and Chant 1961), perhaps in part because field crops are more frequently disturbed and rotated and therefore viewed as less hospitable (Turnock 1991). However, there is a precedent for successful use of introduced natural enemies in Canadian field crops. For instance, five natural enemy species were introduced to the United States in the 1960s against the European *Oulema melanopus* (L.) (Coleoptera: Chrysomelidae) (Dysart et al. 1973; Haynes and Gage 1981). The larval parasitoid *Tetrastichus julius* (Walker) (Hymenoptera: Eulophidae) followed *O. melanopus* into Ontario, where it contributes to reduction of pest density below economic levels (Ellis et al. 1978) as long as tillage is not so frequent as to destroy overwintering *T. julius* pupae (Ellis et al. 1988). The alfalfa

blotch leafminer, *Agromyza frontella* (Rondani) (Diptera:Agromyzidae), is another European insect targeted by classical biological control (Drea and Hendrickson 1986). Of the three natural enemies established, *Dacnusa dryas* (Nixon) (Hymenoptera: Braconidae) is the most important for control in Ontario (Harcourt et al. 1988). Damage by indirect pests, that do not feed on the marketable portion of the crop, is more likely to be successfully reduced by classical biological control than damage by direct pests (Turnbull and Chant 1961) – adequate control of damage from *D. radicum* by introducing natural enemies is therefore more probable in canola than rutabaga.

Before a natural enemy can be introduced, one or several candidates must be identified. The identification of candidates begins with exploratory surveys in an area where the target pest is native (Bellows and Legner 1993; Legner and Bellows 1999). The notion that all natural enemy species of even marginal significance should then be introduced (DeBach and Rosen 1991) is dated; the number of species introduced should be limited as far as possible to the most effective species, which is expected to improve control by reducing competitive interactions (Ehler and Hall 1982; Denoth et al. 2002).

The literature abounds in recommendations about how to develop a list of a few potential candidates from a large list of natural enemies. DeBach and Rosen (1991) suggest success is more likely when the introduced species is adapted to a wide range of environmental conditions, has a high reproductive capability relative to the host, is host specific, and detects the target at low densities. The most likely predictors of success in Kimberling's (2004) retrospective analysis are multivoltinism, monophagy, and parasitic rather than predaceous nutritional strategy. Natural enemies that occur at low density in the pest's native range can theoretically limit the population size of the target if they cause density-dependent mortality when the pest is at low density, or if their low density

is the result of limiting factors like interspecific competition from which the agent will be released in the introduced range (Myers et al. 1989). Life tables, where the number of individual pests surviving through each life stage is determined, can be used to compare natural enemies according to the degree of mortality they cause the pest (Bellows and Van Driesche 1999). The most promising species are then selected for further study, for example about the risk they pose to species besides the pest, the so-called non-target species.

For better or worse, the selection of candidate natural enemy species for introduction to Canada for the second attempt against *D. radicum* was more or less unencumbered by the various criteria suggested for choosing among agents. In 2000, samples of all immature stages of *D. radicum* were collected in canola fields at six locations in western Canada and reared for parasitoids (Hemachandra 2004). No egg parasitoids were found. The seven species of larval and pupal parasitoids collected were *A. bilineata, T. rapae,* two *Phygadeuon* species, *A. minuta*, *A. verna*, and a *Trichopia* species. In 2001 and 2002, similar collections and parasitoid identifications were made in canola and *Brassica* vegetables at 12 locations in Europe (Hemachandra 2004). Again, seven species were found: *T. rapae, A. bilineata, Phygadeoun trichops* Thomson and another *Phygadeuon* species, a *Trichopria* species, *Aleochara brevipennis* Gravenhorst and *A. bipustulata* (L.) (both Coleoptera: Staphylinidae). *Aleochara bipustulata* had already been reported in Canada, for instance in the survey for the first biological control attempt against *D. radicum* (Wishart 1957). However, conclusive separation of *A. bipustulata* and *A. verna* requires dissection and examination of genitalia, a process not possible prior to Lohse's (1986) key and made easier by the subsequent publication of well-illustrated keys (Maus 1996; 1998). All beetles collected in North America, held in

museums, and identified previously as *A. bipustulata* were examined and determined to be *A. verna* (Hemachandra et al. 2005). As the only parasitoid present in appreciable numbers that was not already in Canada, *A. bipustulata* became the candidate for introduction (Hemachandra 2004).

One distinct obstacle to successful pest control by introducing a natural enemy species is that relatively few establish viable populations (Turnbull 1967; Beirne 1975). Hypothesized explanations for failure of introduced species to establish were summarized by Ehler and Hall (1982): ecological requirements were lacking, too few individuals were released, strains adapted to laboratory culture were released, competitive exclusion occurred, or a poorly adapted species was introduced. The first explanation, the absence of ecological requirements, is rather vague and should rarely be a problem if the candidate has been studied sufficiently to suppose it has some potential as an agent of control. If too few individuals are released, there is potential for an Allee effect where individuals do not find mates and the population dies out (Beirne 1975; Hoy 1985; Hopper and Roush 1993). Mulch of mustard seed meal causes *A. bipustulata* to aggregate in an area (Riley et al. *In Press*) and could be used to increase the probability of individuals finding mates. The solution to problems associated with laboratory-adapted populations is perspicuous in theory, to release the agent shortly after the culture is started or refresh it regularly with wild individuals, but any number of practical complications can be imagined, especially related to the termination of funding (Beirne 1985), that would make this more difficult. Competitive exclusion, where two natural enemies have identical niches (Turnbull 1967; Ehler and Hall 1982) should rarely be a factor for if the target is in fact a pest it should be abundant enough in the environment that more than one natural enemy can exploit it (Keller 1984). With *D. radicum* in Canada, *A. bipustulata* is

expected to complement rather than compete with the naturalized parasitoids (Riley et al., *In Preparation*). Finally, a species or population could be poorly adapted to the new environment and fail to establish (Hoy 1985) or the genome of the population of individuals introduced may interact with the environment in the area of introduction to produce a population of supposed biological 'control' agents that are ineffective at reducing pest density (Caltagirone 1985).

Permanent establishment and the ability to multiply and spread independent of human intervention is a large part of the economical and practical attractiveness of pest control by natural enemy introductions (DeBach 1964; Beirne 1975; DeBach and Rosen 1991). However, these characteristics also can be harmful if the impact of the agent is not limited to the target pest. The potential exists for introduced entomophagous species to attack beneficial species and disrupt natural and applied biological control (Pimentel et al. 1984; Sands and Van Driesche 1999; Kuhlmann et al. 2006a), or benign native species (Howarth 1983; 1991; Simberloff and Stiling 1996; Hawkins and Marino 1997; Howarth 2000; Louda et al. 2003). For example, parasitic Hymenoptera species introduced to Guam attack native Lepidoptera and may have contributed to the extinction or extirpation of several native species (Nafus 1993).

In addition to direct attack, biological control agents can affect non-target species by indirect means, whether by competition with native natural enemies, alteration of habitat (Schellhorn et al. 2002), or via apparent competition wherein the introduced agent shares a natural enemy with a native species and causes the carrying capacity of this shared enemy to increase by its abundance, which then increases the density-dependent mortality of the native species by the surfeit of their shared natural enemy (Bonsall and Hassell 1997; Schellhorn et al. 2002). Thus *Trigonospila brevifacies* (Hardy) (Diptera:

Tachinidae), introduced to New Zealand to control an orchard pest, causes direct non-target effects by attacking native Lepidoptera (Munro 1998) and indirect non-target effects by competing with native parasitoids for these hosts (Munro and Henderson 2002). The probability of direct effects is reduced by selecting agents relatively specific to the target pest, and that of indirect effects by introducing only effective natural enemies which show functional and numerical responses to the density of the target species (Louda et al. 2003). Occasional attack on non-target species with negligible impact relative to the other sources of mortality is demonstrable in some cases (Barron et al. 2003; Johnson et al. 2005), but the potential for significant population-level impacts (Boettner et al. 2000; Kellogg et al. 2003) and especially the spectre of introduction-induced extinction (Howarth 1983; Gould 1991; Howarth 1991) have prompted discussion and development of ideas about increasing the safety of classical biological control.

From both an ethical standpoint (Delfosse 2005) and to fulfill the information requirements for introduction (Mason et al. 2005) it is therefore necessary to evaluate the environmental risk of each potential classical biological control agent rigorously. For non-indigenous natural enemies released for short-term control of a pest problem that are not meant to establish, it may suffice to base the environmental risk assessment on the likelihood of establishment and dispersal (van Lenteren et al. 2006a; 2006b). For most classical biological control projects however, including the introduction of *A. bipustulata* to Canada, establishment and self-dispersal of the agent is the desirable outcome and the principal component of the risk of direct and indirect effects on non-target species is determination of the candidate's host range (van Lenteren et al. 2003; 2005; 2006a; 2006b).

Host specificity testing starts in the laboratory, and requires a list of non-target species for testing. Before the list can be started, information about the candidate's ecology, reported host range, behavioural or other attributes that suggest limitations to its host range, and habitats is collected from the literature, consultation with taxonomic experts, and entomological museums (Sands 1997; Sands and Van Driesche 1999; Kuhlmann et al. 2005; 2006b). Negative evidence can be important at this stage, for example if a habitat has been extensively sampled without finding the candidate (Sands and Van Driesche 2004), or a species closely related to or in the same habitat as the target pest has been collected at an appropriate stage without evidence of parasitism by a candidate parasitoid (Nardo and Hopper 2004). Information is also required about what species are present and could be at risk in the area of intended introduction (Hoddle 2004). All species that are taxonomically or ecologically affiliated with the target are assembled in an initial list, to which species of conservation concern and beneficials are appended (Kuhlmann et al. 2005; 2006b). As this list will certainly contain too many species to test, the list is filtered to remove species based on attributes of the candidate's and non-targets' size, phenology, or spatiotemporal overlap (Kuhlmann et al. 2005; 2006b). A second filter is then applied to remove species that will be difficult to obtain in sufficient numbers for rigorous testing, until the list contains ten to twenty species (Kuhlmann et al. 2005; 2006b). As new information becomes available the list can be revised (Kuhlmann et al. 2005; 2006b).

A sequence of tests has been proposed for testing the species on the filtered list (van Lenteren et al. 2003; 2006a). All species on the list are tested in the first step; non-target species that prove susceptible are carried to the next level, and those which are not are considered safe and not tested further. The first test is called a no-choice black box

test, where the candidate agent must either attack the non-target species or nothing at all (van Lenteren et al. 2003; 2005; 2006a; 2006b). It is important to consider how experimental design could influence the natural enemy and conduct the experiment so that maximum host range is expressed (Withers and Browne 2004; Withers and Mansfield 2005). Including appropriate controls is necessary at all stages of testing (van Lenteren et al. 2003; 2005; 2006a; 2006b). Subsequent tests in the recommended order are no-choice behavioural tests, tests in less confined conditions where the natural enemy is given a choice, and field tests (van Lenteren et al. 2003; 2005; 2006a; 2006b). Experiments about the suitability of non-target hosts for survival of the candidate over several generations (Van Driesche and Murray 2004) and other aspects of the candidate's natural history (Louda et al. 2003) can be used to complement the recommended sequence. The next section contains information about *A. bipustulata* and other *Aleochara* species relevant to its consideration as a candidate for introduction.

***Aleochara bipustulata*, a candidate for introduction to Canada**

Aleochara species have been introduced as classical biological control agents in the past. *Aleochara taeniata* Erichson was introduced to the United States from Jamaica in 1964 to control *Musca domestica* L. (Diptera: Muscidae) (White and Legner 1966). Collection of adult *A. taeniata* from dung (Klimaszewski 1984) indicates it has established, but there is no information about non-target effects or its impact on *M. domestica*. *Aleochara tristis* Gravenhorst was introduced from France to the United States in the 1960s to control the exotic face fly, *Musca autumnalis* De Geer (Drea 1966; Jones 1967; Wingo et al. 1967; Legner 1978). It has established (Hayes and Turner 1971; Wharton 1979; Drea 1981; Klimaszewski 1984; Cervenka and Moon 1991) and attacks both *M. autumnalis* and the non-target *Orthellia caesarion* (Meigen) (Diptera: Muscidae)

(Wingo et al. 1967; Wharton 1979). Parasitism of *O. caesarion* was predicted on the basis of host range testing in the laboratory (Drea 1966). *Aleochara tristis* is ineffective at controlling *M. autumnalis* (Drea 1981). Finally, *Aleochara bisolata* (Casey) was considered for introduction from Africa to Australia to control the Australian buffalo fly, *Haematobia irritans exigua* De Meijere (Diptera: Muscidae) (Wright and Muller 1989; Wright et al. 1989; Maus et al. 1998). Information about whether *A. bisolata* was introduced, and if so whether it established, was effective, or attacked non-target species does not exist explicitly in the literature. However, as its distribution is listed as Ethiopian by Maus et al. (1998), one can infer it was never introduced.

The genus *Aleochara* Gravenhorst is in the subfamily Aleocharinae, one of 23 subfamilies in the family Staphylinidae recognized in Canada (Klimaszewski 2000). *Aleochara* is in the tribe Aleocharini, the sister group of the tribe Hoplandriini (Klimaszewski 1984; 2000). The larvae of all *Aleochara* species are ectoparasitoids of Cyclorrapha (Diptera) species (Klimaszewski 1984; Maus et al. 1998) except the phylogenetically basal *A. clavicornis* Redtenbacher (Maus et al. 2001), whose larvae can complete development on meat, Diptera larvae or puparia (Maus et al. 1998). The subgenus *Coprochara* Mulsant & Rey, one of seven subgenera recognized by Klimaszewski (1984), contains *A. bipustulata* and 29 other species (Maus 1998); hosts are known for only twelve of these (Maus et al. 1998). The subgenus is monophyletic in both morphological (Klimaszewski 1984) and nucleic acid-based analyses (Maus et al. 2001). The validity of some of the other subgenera and the sister group of *Coprochara* are ambiguous on the basis of nucleic acid variation (Maus et al. 2001).

Two autapomorphies, or unique derived characters, distinguish the *Coprochara* from other species of *Aleochara*: two longitudinal rows of punctures on the pronotum

with a glabrous interspace between, and a coiled spermathecal duct in the females (Maus 1998). The external anatomy of *A. bipustulata* and *A. verna* are very similar, and these two are distinguishable from other *Coprochara* based on yellow or orange spots on the terminal portion of their elytra (Maus 1998). Distinguishing between these two species requires dissection and examination of the genitalia (Lohse 1986; Maus 1998). Females have 1-5 turns in the spermathecal duct in *A. bipustulata* and 6-18 in *A. verna* (Maus 1998). Male *A. bipustulata* have a subtriangular Z sclerite on the median lobe of the aedeagus, whereas in *A. verna* this sclerite is subrectangular (Maus 1998).

Aleochara bipustulata is distributed in the Oriental and Palearctic biogeographic regions (Maus 1998; Hemachandra et al. 2005). Both the genus *Aleochara* (Klimaszewski 1984; Maus et al. 1998) and subgenus *Coprochara* (Maus 1998) have species naturally distributed in all biogeographic regions but the Antarctic, so the centre of origin of the groups is uncertain. Specimens of *A. bipustulata* have been collected as far north as Fredrikstad in Norway, and as far south as Berguent, Algeria (Maus 1998).

The most complete information about the phenology of *A. bipustulata* is contained in a paper by Jonasson (1994b), who collected *A. bipustulata* in pitfall traps weekly from mid-May to September in a *Brassica* vegetable plot in Sweden. The beetles were already abundant by the first week of sampling, indicating *A. bipustulata* is active before the middle of May. There are four progressively smaller peaks in activity in southern Sweden: late May, mid-June to early July, late July, and early September. Oviposition by *D. radicum* in the Canadian prairies is often in mid-June (Swailes 1958; Griffiths 1986b; 1986a; Bracken 1988; Dosdall et al. 1996a) although it may be somewhat later (Broatch et al. 2006); the same is true in Sweden where *D. radicum* oviposition and the greatest activity of *A. bipustulata* coincide in mid-June (Jonasson 1994b). In Germany, a few *A.*

bipustulata adults are active in late April, and there are three periods of high activity: in late June, late July, and mid-September (Fuldner 1960). Although Fuldner (1960, p. 377) states *A. bipustulata* overwinters as a "first instar larva, or as pupa or adult" there are several indications that most if not all *A. bipustulata* overwinter in the adult stage. Puparia of *D. radicum* collected during the late fall or winter in areas where *A. bipustulata* is native (Ryan and Ryan 1980; Finch and Collier 1984; Turnock et al. 1985; Block et al. 1987; Reader and Jones 1990) contained *D. radicum*, *T. rapae,* and *A. bilineata* but never *A. bipustulata*. Further, soil samples collected during the winter in *Brassica* vegetable fields contained adult *A. bipustulata* (Finch and Collier 1984).

The ecological host range of an insect parasitoid is dictated by which hosts fulfill the requirements of each of five sequential steps: host habitat location, host location within the habitat, host acceptance, host regulation, and host suitability (Vinson 1976; Vinson and Iwantsch 1980). These two reviews deal with the first three steps as activities of a searching, female, adult insect, and the last two as those of an immature parasitoid. In *Aleochara*, however, the female lays eggs in the soil and the first instar larva must actively locate and accept hosts itself. Our knowledge about the processes of habitat and host location, host acceptance, host regulation, and host suitability in *Aleochara,* and when information is available for *A. bipustulata* in particular, are described below. Finally, the habitats from which *A. bipustulata* is recorded in the literature and, when applicable, information about what hosts were parasitized is discussed.

Although the final part of host location is completed by the larva, female parasitoids with mobile larvae frequently lay eggs near hosts and are therefore also involved in the location of hosts (Godfray 1994). Adult *Aleochara curtula* Goeze are most abundant around carrion at the active decay stage, when muscles are exposed; while

Calliphoridae (Diptera) larvae continue to develop, both sexes are abundant on the carcass, and after the mass exodus of mature Diptera larvae which will host the *A. curtula* larvae after pupariating in the soil, male *A. curtula* stay on the carcass and the females leave to oviposit (Peschke et al. 1987a; 1987b). The peak in *A. curtula* egg production occurs just after the calliphorid larvae migrate from the carcass, and most *A. curtula* larvae have hatched and are ready to parasitize as the puparia become optimally susceptible (Peschke et al. 1987b). Adult *A. bisolata* are attracted to cow dung during the first day after it is deposited (Wright and Muller 1989). In an olfactometer, adult *A. bilineata* prefer to move toward *D. radicum* larvae, frass, and host plants over clean air, and prefer infested host plants to uninfested ones (Royer and Boivin 1999). In laboratory arenas, female *A. bilineata* lay more eggs in the vicinity of a host plant inoculated with eggs or artificially buried *D. radicum* puparia than in sand (Fournet et al. 2001). When given a choice between a host plant inoculated with eggs and another cue, *A. bilineata* lay more eggs around damaged plants, fewer around an undamaged plant without eggs, and a similar number in the vicinity of buried host puparia (Fournet et al. 2001). They can detect the presence and parasitism status of host puparia, and lay more eggs around a damaged plant with puparia than a damaged plant alone, and more around a damaged plant with unparasitized puparia than around one with parasitized puparia (Fournet et al. 2001). Based on these studies, one expects female *A. bipustulata* are similarly involved in the location of hosts by laying eggs preferentially in certain areas, but no work has yet been published about oviposition site selection by *A. bipustulata.*

Once the egg hatches, the larva needs to locate a host. The probability of larvae of both *A. bilineata* and *A. bipustulata* locating hosts decreases with increasing distance the larvae are placed from puparia in Petri dish arenas (Fuldner 1960), suggesting chemical

cues from puparia do not guide them. However, Fuldner's experimental design did not investigate the possibility that parasitoid larvae follow a trail left by the migrating host larva, a phenomenon that occurs in *A. bisolata* (Wright and Muller 1989). Wingo et al. (1967) suggest the search may be random until the larva enters the threshold zone of some olfactory stimulus.

Acceptance of hosts by the larva must involve at least two steps: the acceptance of the puparium for chewing an entrance hole, and acceptance of the pupa within for feeding. Larvae of *A. bisolata* accept all ages of hosts when given no choice, but prefer the youngest when given a choice (Wright and Muller 1989). Larvae of *A. curtula* choose the location of their entrance hole on the basis of volatile chemicals emitted from stigmata on the puparium surface and puparium structure (Fuldner 1968), but will relocate if another larva has already entered in the preferred spot and plugged the hole (Fuldner and Wolf 1971). The location of the entrance hole in *D. radicum* made by *A. bilineata* is most often on the puparium's dorsal side, in the abdominal region where the ridges on the puparium surface are lowest (Royer et al. 1998). If the host has not yet formed a pupa within the puparium, the larva will wait on the puparium surface for it to do so (Peschke et al. 1987b). Larvae of both *A. bilineata* and *A. bipustulata* prefer to parasitize puparia with a pupa inside to one with a pharate adult fly (Fournet et al. 2004), and puparia not already occupied by another *Aleochara* larva (Royer et al. 1999). Given a choice, *A. bipustulata* larvae prefer smaller *D. radicum* puparia in laboratory arenas (Ahlstrom-Olsson 1994), and may do so also in nature (Jonasson 1994b), but as sample size increases this tendency is no longer apparent (Hemachandra 2004). After the hole is created, an *A. bisolata* larva may not start to feed, suggesting a feeding stimulant must be

present or an antifeedant must be absent for a host to be fully accepted (Wright et al. 1989).

Acceptance of a puparium by an *Aleochara* larva also depends on the host species. In laboratory arenas, *A. bipustulata* larvae accept *D. radicum* and *Delia antiqua* Meigen or *Delia platura* Meigen, but do prefer *D. radicum* to a *Lonchaea* species (Ahlstrom-Olsson 1994). Wright et al. (1989) determined that *A. bisolata* larva typically prefer one species to another when given a choice, and sometimes first attack one species, then reject it and attack another. The preference of *A. bisolata* for particular species is related to the mass of the puparia (Wright et al. 1989). In no-choice conditions, larvae of *A. tristis* accept puparia of *M. autumnalis* and *O. caesarion*, but not *M. domestica, Stomoxys calcitrans* (L.) (Jones 1967), *Mesembrina meridiana* L., *Morellia simplex* Loew., *Myospila meditabunda* (F.) (all Diptera: Muscidae), or *Scatophaga stercoaria* (L.) (Diptera: Scatophagidae) (Drea 1966). Clearly, the acceptance of a host by an *Aleochara* larva is an intricate process, and it is difficult to design experiments that could separate the demonstrably important effects due to host species, puparium mass, ridge size, and the presence of antifeedants or feeding stimulants together.

The suitability of accepted hosts for complete development is the next filter in the host range of *Aleochara*. Fuldner (1960) notes two important characteristics of the host in determining suitability. First, *Aleochara* larvae feed on the liquid haemolymph of the developing Diptera pupa, so species that develop from pupa to adult quickly provide less temporal availability of liquid food, and an adult fly emerges unharmed if the *Aleochara* larva enters the puparium too late. That puparia entered too late are less suitable has subsequently been demonstrated for *A. bipustulata* and *A. bilineata* (Fournet et al. 2004), *A. bisolata* (Wright and Muller 1989), *A. taeniata* (White and Legner 1966), and *A. tristis*

(Drea 1966; Wingo et al. 1967). Second, the cessation of feeding by the third instar *Aleochara* larva is based on some physiological clock, rather than how much of the pupa remains uneaten; if a lot of host material remains it will rot and result in the death of the immature parasitoid. Thus, survival of *A. bisolata* larvae decreases with increasing weight of host species (Wright et al. 1989).

Only one instance of an *Aleochara* larva regulating its host is recorded in the literature. In response to *Aleochara* larvae, face fly pupae are sometimes able to produce a "dark coriaceous spot on the membrane immediately under the puparium wall" (Drea 1966, p. 1372). The membrane is presumably part of the cuticle of the third larval instar which hardens to form the puparium (Fraenkel and Bhaskaran 1973). However, species in the *Musca* subgenus *Eumusca*, like the face fly, form their puparia by calcification rather than phenolic tanning of the cuticle (Fraenkel and Bhaskaran 1973) and this method of pupariation may result in a membrane and therefore defensive capability not available to other species of Cyclorrapha. It would be interesting to know how long the Diptera pupa survives the multiple punctures of its cuticle by an attacking *Aleochara* larva, and therefore how important host regulation is in determining the host range of species in this genus.

The final section of this literature review outlines the different habitats in which *A. bipustulata* has been reported and hosts it parasitized in those habitats. It is worth remembering Maus et al.'s (1998) *caveat* that records prior to Lohse (1986) cannot possibly have distinguished *A. verna* from *A. bipustulata*. Several *Aleochara* species are quite similar in external anatomy, with reddish spots on the elytra, and species like *A. bipustulata, A. verna,* and *A. binotata* Kraatz may be misidentified as one another (Maus

et al. 1998). However, the records may have been correct and it is worthwhile to assemble them in the context of assessing *A. bipustulata*'s host range.

The target habitat, broadly defined as cruciferous crops, has the greatest number of literature records about the presence of *A. bipustulata* and parasitism of Diptera species. Besides *D. radicum*, species that reportedly hosted *A. bipustulata* in cruciferous crops are *D. platura, D. floralis,* and *D. florilega* (references in Maus et al., 1998). These are all considered pests in cruciferous crops (Brooks 1951), and parasitism by *A. bipustulata* of these species in Canadian canola fields can only be considered beneficial. In reviews of this sort negative evidence, where parasitism was looked for but not found, can be useful (Nardo and Hopper 2004; Sands and Van Driesche 2004). The only negative evidence of parasitism in European cruciferous crops is (Jonasson 1994b) who collected an unspecified quantity of puparia of species in the families Agromyzidae, Drosophilidae, Fanniidae, and Muscidae, reared them out and found no *A. bipustulata.*

The second largest number of records about the habitat associations of *A. bipustulata* concerns its occurrence in dung. In France, *A. bipustulata* were collected in dung-baited pitfall traps and emerged from *Adia cinerella* (Fallen) (Diptera: Anthomyiidae) puparia that developed in cow dung, but not from species of Muscidae, Sepsidae, and Sphaeroceridae collected in the same pats (Kirk 1992). Other reliably determined *A. bipustulata* have been collected in cow dung (Jonasson 1994a; Vorst 2001), so it is doubtlessly a habitat of *A. bipustulata* at least occasionally. The reports of presence of *A. bipustulata* in horse (Sychevskaya 1972; Psarev 2002), yak and marmot (Sychevskaya 1972) dung are less reliable. Three species, *Ravinia pernix* Harris, *Sarcophaga* (*Helicophagella*) *gorodkovi* (Grunin) (as *Belleria gorodkovi* Grunin), and *Sarcophaga* (*Helicophagella*) *altitudinis* (Grunin) (as *B. rohdendorfi* Grunin; see Pape

1996) (Diptera: Sarcophagidae) reportedly host *A. bipustulata* in these sorts of dung, but since Sychevskaya also reports the overwintering of *A. bipustulata* in "early developmental stages" (p. 144), which does not agree with other evidence presented above, the reports of occurrence and parasitism may be misidentifications. *Physiphora demandata* F. (Diptera: Otitidae), *Lonchaea* sp. (Diptera: Lonchaeidae), and *M. domestica* puparia collected from the field reportedly host *A. bipustulata* (Fabritius 1981; Fabritius and Klunker 1991), but it is not clear whether the puparia were collected in cow dung or supralittoral algae, and *A. verna* is listed as a possible synonym of *A. bipustulata* (Fabritius and Klunker 1991), so the identity of the emerged beetles in not clear. Finally, reliably identified *A. bipustulata* adults emerged from puparia of unidentified Diptera species collected in manure piles in Kazakhstan (R. Moon, University of Minnesota, personal communication, December 2006).

Parasitism of the wheat bulb fly, *Delia coarctata* (Fallen) (Diptera: Anthomyiidae), has been reported several times. The wheat bulb fly, like *D. radicum*, is a European species now in North America (McAlpine and Slight 1981). Eggs are laid on bare soil, and *D. coarctata* is a pest of winter wheat, potato, and sugar beets. Dobson (1961) found two and eight per cent of *D. coarctata* puparia in two wheat fields supported development of *A. bipustulata*. Puparia only hosted *A. bipustulata* occasionally in two German studies (Sol 1972; Roloff and Wetzel 1989), and it is not clear if the *D. coarctata* hosts from which *A. bipustulata* emerged were collected in sugar beets, potatoes, or both in either study. All three records of development in *D. coarctata* puparia may have been misidentifications. Another host record from the sugar beet habitat concerns one or more species of *Pegomya* Robineau-Desvoidy, but since the species concepts in this genus were recently revisited (Griffiths 1982), it is difficult to know which species was hosting

the *Aleochara*. *Pegomya betae* Curtis and *Pegomya hyoscyami* (Panzer) are not synonyms as suggested by Maus et al. (1998) (Griffiths 1982), so the development of *A. bipustulata* reported by Hille Ris Lambers (1932) may have been in puparia of either or both of these. Of course, the "*A. bipustulata*" may have been another *Aleochara* species as well. A Polish survey of parasitoids of *P. betae* found *A. bilineata* but not *A. bipustulata* (Miczulski and Pawelska 1964).

The only European record of *A. bipustulata* in the carrion habitat is Peschke et al. (1987b). Puparia of *Lucilia sericata* (Meigen) were parasitized by *A. bipustulata* in an open area but not the forest, and puparia of *Calliphora vicina* Robineau-Desvoidy were parasitized only by *A. curtula* in both habitats. Reference to Peschke et al. (1987b) is not made in Maus et al. (1998) even though Peschke is an author of both papers, so perhaps the *Aleochara* identifications in the earlier paper were recognized as mistaken.

In bean fields, *A. bipustulata* has been recorded as a parasitoid of *D. platura* and *D. florilega*. These records are suspect though, as Dinther (1953) apparently assumed puparia with *Aleochara*-like exit holes had been caused by *A. bipustulata*, and Miles (1948) did not specify if the parasitized puparia had been collected in cabbage or bean fields. Finally, up to 26% of *D. platura* puparia were parasitized by *A. bipustulata* in a Hungarian study (Darvas and Kozma 1982), and beans are mentioned along with several other crops, but it is not clear what crop was sampled to assess the level of parasitism.

In addition to these reported natural hosts, two other species are within *A. bipustulata*'s fundamental host range. *Piophila casei* (L.) (Diptera: Piophilidae) (Fabritius 1981) and *D. antiqua* (Ahlstrom-Olsson 1994) support complete development in the laboratory.

The presence of *A. bipustulata* has also been recorded in diverse habitats without any indication about why it was there. One beetle was collected in a *Formica rufa* L. (Hymenoptera: Formicidae) nest (Sieber 1982), and it is reportedly common in pea fields (Zatjamina 1971). One adult was found under bark of a *Betula* stump, and another under the bark of a dead, standing *Betula* (Vorst 2001; Vorst, personal communication, March 2006). On nine occasions small collections have been made from flood refuse (Vorst 2001), presumably including things like seaweed. Pitfall traps in carrot fields (Ramert et al. 2001) and apple and pear orchards (Balog et al. 2003) catch *A. bipustulata*. Emergence traps in oat fields (Jones 1965) and sticky traps in onion fields do likewise (Fuldner 1960). Along rivers in Scotland *A. bipustulata* occurs most frequently in dry open sites and disturbed sites, and less frequently in areas with trees and dense vegetation (Eyre et al. 2001). In Scottish moors, *A. bipustulata* is found most frequently in grassy areas without heather (*Calluna vulgaris* L. (Ericaceae)) (Eyre et al. 2003). Along coastal salt marshes, *A. bipustulata* is found associated with *Juncus gerardii* Loisel (Juncaceae) (Irmler and Heller 2002). All of the information presented above about the biology of *A. bipustulata* must be considered in the context of what is known about biological control by the introduction of natural enemies and the risks this practice poses to non-target species in order to design appropriate experiments and increase the likelihood of providing a safe and effective control strategy for *D. radicum* to Canadian canola producers.

Conclusions and research objectives

As the area Canadian farmers devoted to the production of canola increased over the past 30 years, so did their problems with insect pests. Many of these are not native to North America, and introducing natural enemies is an option for their control. The

cabbage maggot is one of several non-indigenous insect species that may be controlled by this method, and in its case in particular alternative control measures are not available. A candidate for introduction, *A. bipustulata*, has been identified (Hemachandra et al. 2005).

The rates of establishment and effective control by classical biological control agents have historically been rather low. Poor adaptation to the environment in the area of introduction decreases the likelihood of permanent colonization (Hoy 1985) and effective control (Caltagirone 1985). Understanding the phenology of natural enemies already present helps to predict and improve the success of prospective candidates (Hoddle 2004), and a more complete understanding of the pest can only do likewise. The first objective of this research is to compare the thermal response to temperature for spring emergence of *D. radicum* populations from western Canada with an established natural enemy and a cabbage maggot population from another part of Canada. This information will aid in selecting a well-adapted *A. bipustulata* population for eventual introduction.

Risk to non-target species is also a concern when introducing natural enemies. According to the literature, *A. bipustulata*'s ecological host range includes fourteen species with larvae in several different types of habitats. Two additional species are suitable hosts in the laboratory. One's first impression may reasonably be that the host range is too broad for an introduction to be considered environmentally responsible. Four of the recorded hosts, however, are pest species in the target habitat, and several of the others are pests as well. Further, some of the records may have mistaken another *Aleochara* species for *A. bipustulata*. The second objective of this research is to do laboratory experiments about the fundamental host range of *A. bipustulata*.

3.1 TEMPERATURE RESPONSE OF POST-DIAPAUSE DEVELOPMENT OF *DELIA RADICUM* AND OF ITS NATURAL ENEMIES

Introduction

The larvae of five species of *Delia* Robineau-Desvoidy (Diptera: Anthomyiidae) are known to develop feeding on the roots of Canadian cruciferous crops (Brooks 1951). Three species are common in canola. Larvae of the cabbage maggot, *Delia radicum* (L.), and turnip maggot, *Delia floralis* (Fallen), feed on healthy root tissue (Brooks 1951), the former dominating areas with higher summer rainfall (Griffiths 1986b). Both species overwinter as pupae in puparia (Griffiths 1991a). Emergence of adult *D. radicum* begins earlier than *D. floralis* , but the peak in activity of the two species is in mid-June (Griffiths 1986b) during the crop's bud stage when the main stem grows and the flies lay their eggs (Griffiths 1986a). The larvae feed while the crop is flowering, and pupariate around the end of July (Griffiths 1986a). The seedcorn maggot, *Delia platura* (Meigen), generally requires roots infested by other species for its larvae to feed (Brooks 1951) and is frequently quite common in canola fields (Vernon and Broatch 1996; Broatch and Vernon 1997; Broatch et al. 2006).

Canola is planted during the spring in the three Canadian prairie provinces because this is less risky, higher yielding, and more economically competitive than planting in the fall (Clayton et al. 2004; O'Donovan et al. 2005; Upadhyay et al. 2005). The optimum seeding date depends on many factors, including the year and location, but falls somewhere in late April or early May (Clayton et al. 2004; Johnson et al. 2004; Upadhyay et al. 2005). The seeds germinate to become plants, which pass through the following growth stages: seedling, rosette, bud, flower, and ripening (Harper and Berkenkamp 1975). The onset and duration of the various growth stages vary in time, but

typically the seedling stage is in late May, the rosette and bud stages in June, flowering in July, and ripening in August (Thomas, 1984). If periods of high *D. radicum* activity can reasonably be assumed to represent when eggs are laid by the overwintered generation, oviposition in *Brassica* vegetables in the prairies (Bracken 1988) is about two weeks earlier than in canola (Broatch et al. 2006). The date the mature crop is harvested also depends on many factors, but generally will be some time from mid-August onward (Thomas 1984).

Injury to roots from larval feeding reduces the number of seeds (Griffiths 1991c; McDonald and Sears 1991), number of racemes and pods (McDonald and Sears 1991), and the weight of seeds produced per unit area (Griffiths 1991c; Dosdall 1998), particularly when at least about half the root surface is damaged (Dosdall 1998; Dosdall et al. 2003). Across the prairies, nearly every canola field shows evidence of root maggot infestation, and the percentage of plants infested per field and average level of damage to individual plants are increasing (Soroka et al. 2004). Root maggot management strategies available to growers are to seed earlier, delay herbicide application (Dosdall et al. 2003), space rows about 20 cm apart (Dosdall et al. 1998), increase seeding rate to about 7 kg/ha (Dosdall et al. 1996a; Dosdall et al. 1998; Dosdall et al. 2006), and plant less susecptible cultivars (Dosdall et al. 1994); the extent to which these measure are adopted will depend on their impacts on yield and net economic return. An additional option to complement these strategies is the importation and release of non-indigenous natural enemies — classical biological control.

The turnip maggot is native to North America (Griffiths 1991a) but the cabbage maggot is not (Biron et al. 2000). Classical biological control of *D. radicum* in Canada was attempted in the 1950s but failed because the parasitoids introduced from Europe

were already present (Turnbull and Chant 1961; McLeod 1962; Soroka et al. 2002). The most important parasitoids already in Canada are *Aleochara bilineata* (Gyllenhal) (Coleoptera: Staphylinidae) and *Trybliographa rapae* (Westwood) (Hymenoptera: Eucoilidae) (Wishart 1957; Nair and McEwen 1975; Turnock et al. 1995; Hemachandra 2004). *Aleochara bilineata* adults can feed on root maggot eggs and larvae; *A. bilineata* lay their eggs in the soil (Wadsworth 1915; Colhoun 1953; Fuldner 1960), and the mobile larvae locate and enter host puparia, then develop as parasitoids of the pupal stage (Sprague 1870; Wadsworth 1915; Fuldner 1960; Read 1962); however, the adults emerge too late in spring to be effective egg predators (Read 1962; Bondarenko 1982; Whistlecraft et al. 1985a; Jonasson 1994b; Fournet et al. 2000), levels of parasitism can be low in cool years (Turnock et al. 1995), and in Canada it is poorly synchronized as a parasitoid (Hemachandra 2004). Adult *T. rapae* females oviposit in *D. radicum* larvae and adults emerge from puparia (Wishart and Monteith 1954); although better synchronized (Hemachandra 2004) its prevalence in host puparia is consistently low across the prairies (Wishart 1957; Turnock et al. 1995; Hemachandra 2004), never greater than 21% at a location. The increasing root maggot problem in canola (Soroka et al. 2004) and inability of established parasitoids to regulate *D. radicum* density (Turnock et al. 1995) prompted interest in searching for additional species of parasitoids (Turnock et al. 1995; Soroka et al. 2002), especially in north western Europe where the *D. radicum* introduced to North America originated (Biron et al. 2000; Biron et al. 2003).

The search is newly complete and *Aleochara bipustulata* (L.) (Coleoptera: Staphylinidae) has been identified as a candidate for introduction (Hemachandra 2004; Hemachandra et al. 2005). The life cycle of *A. bipustulata* is similar to *A. bilineata*: adults can feed on the root maggot eggs and larvae, and *A. bipustulata* larvae develop as

parasitoids inside dipteran puparia (Fuldner 1960). The prevalence of *A. bipustulata* in *D. radicum* puparia in Europe varies among locations, years (Wilkes and Wishart 1953; Wishart et al. 1957; Hughes and Mitchell 1960), and host generation (Hughes and Mitchell 1960). For example, while it was nearly absent in puparia collected in Norway, 41% of *D. radicum* puparia in a Scottish sample were parasitized by *A. bipustulata* (Wishart et al. 1957), as were up to 45 per cent of *D. radicum* in French oilseed rape crops (Brunel et al. 1999). In European *Brassica* vegetable fields *A. bipustulata* adults appear at the same time *D. radicum* starts to lay eggs in the spring (Jonasson 1994b), implying a community of Canadian natural enemies which includes *A. bipustulata* may better reduce the number of *D. radicum* larvae that reach the canola roots. In its native range, *A. bipustulata* will parasitize *D. radicum* in fields of summer canola (Hemachandra 2004). However, parasitized puparia occur in European summer canola crops from mid-June to the first week of July (Hemachandra 2004), and the *D. radicum* in Canadian canola form puparia towards the end of July (Griffiths 1986a). If *A. bipustulata* adapted to host puparia available in late June are introduced to the Canadian prairies, and they do not quickly change their phenology to parasitize hosts in late July, they will be poorly synchronized with the pest against which they were introduced.

Classical biological control projects in Canada historically have had an unenviable rate of success, largely due to failure of the introduced species to establish, and then failure of the species that do establish to control the pest (Turnbull and Chant 1961; Beirne 1975; Turnock 1991). Synchronization of parasitoid biological control agents with their hosts is one of several desirable characteristics to select for in choosing prospective agents for improved probability of establishment and effective control (Messenger and Bosch 1971; Messenger et al. 1976), and lack of synchronization frequently explains

failed projects (Messenger and Bosch 1971; Hagvar 1991; Stiling 1993). A parasitoid is synchronized with its host when the relationship between density of vulnerable hosts and density of searching parasitoids is constant over the entire period that vulnerable hosts are found (MacDonald and Cheng 1970). Synchronization is not always necessary for a parasitoid to contribute an economically significant level of control, particularly if several generations of parasitoid can be produced per generation of host (Murdoch et al. 1984; Murdoch et al. 1985). However, poor synchronization between indigenous parasitoids and non-indigenous pests has been adduced to explain outbreaks of these pests (Coote and Ellis 1986; Grabenweger 2004; Girardoz et al. 2006), natural biological control can break down and result in outbreaks if environmental factors disrupt synchronization (Sunose 1985), poorly synchronized biological control agents often contribute minimally to pest control (Schlinger and Hall 1961; Weseloh 1976; Muller et al. 1990; Kuhar et al. 2001), and the introduction of well synchronized natural enemies has often resulted in an economically significant reduction in pest density (Dowell and Horn 1977; Harcourt et al. 1988).

Aleochara bipustulata will be synchronized as a parasitoid with *D. radicum* in the prairies if the number of searching *A. bipustulata* larvae divided by the number of puparia suitable for attack remains constant over the period puparia form, typically in late July. As a predator, *A. bipustulata* will be synchronized with *D. radicum* if adults are in the fields feeding on eggs starting about the middle of June and continue to feed on larvae until puparia are formed.

Aleochara bipustulata is distributed across the Palearctic and Oriental biogeographical regions (Maus 1998). Populations of some widely distributed natural enemies are adapted to local environments (Caltagirone 1985; Ruberson et al. 1989), and

it is reasonable to expect some populations of *A. bipustulata* will be better suited than others for control of *D. radicum* in western Canada. To identify such a population, a method must be used that can estimate when *D. radicum* eggs will appear around canola roots in the Canadian prairies and characterize different populations of *A. bipustulata* according to their activity during the *D. radicum* oviposition period. Determining the thermal accumulation requirements for spring emergence of the pest is an appropriate method in this context.

The cabbage maggot overwinters in the pupal stage (Schoene 1916) in diapause (Hughes 1960; Zabirov 1961; Soni 1976), a physiological state where development stops and cannot resume until it is completed, often associated with increased tolerance of cold (Andrewartha 1952; Tauber and Tauber 1976; Danks 1987). Between the termination of diapause and normal growth and development is a period of postdiapause development (Tauber and Tauber 1976; Danks 1987); for *D. radicum* postdiapause development is over when an adult fly emerges from a puparium. The duration of postdiapause development is most influenced by temperature and the conditions experienced during diapause development (Tauber and Tauber 1976). Many studies have been done on the thermal accumulation requirement for spring emergence of *D. radicum*, both in the laboratory and the field.

Temperature influences the duration of the post-diapause period by controlling the rate of development (Wigglesworth 1972). The most straightforward method of relating rate of insect development to temperature is by linear regression (Andrewartha and Birch 1954; Campbell et al. 1974). From the linear regression equation it is possible to determine a theoretical lower temperature threshold and a thermal constant, most commonly in day degrees Celsius, both of which are useful in applied entomology

(Andrewartha and Birch 1954). However, development proceeds more rapidly at temperatures near the developmental threshold than predicted by linear regression (Andrewartha and Birch 1954; Wigglesworth 1972; Campbell et al. 1974), a consideration of particular importance when studying development in spring, which led to the application of logistic regression to describe the influence of temperature on developmental rate (Davidson 1944). Also, development proceeds more slowly than predicted by linear regression at temperatures above a certain limit (Andrewartha and Birch 1954; Wigglesworth 1972; Campbell et al. 1974), which can be described by a polynomial model (Logan et al. 1976). By adding a parameter to the polynomial model, a developmental threshold can be estimated (Lactin et al. 1995). In common with the logistic and polynomial equations, Taylor's (1981) truncated normal distribution method of relating developmental rate to temperature can accurately describe development at relatively high and low temperatures. I selected it to use in this study because the developmental threshold and day degree requirements can be estimated (Lamb 1992), and because it has been used to characterize Canadian populations of *D. radicum* in the past (Turnock and Boivin 1997).

Postdiapause development of *D. radicum* is slow at temperatures below 10°C (Read 1962). In the laboratory, 135 day degrees above 6.1°C ($DDC_{6.1}$) accumulate before the first *D. radicum* emerge (Eckenrode and Chapman 1971a) and 160 DDC_4 are required for 50 per cent emergence (Collier and Finch 1985). Populations from Geneva and Highland, New York and Fletcher, North Carolina require 170 to 184 DDC_4 for 50 per cent emergence, whereas *D. radicum* from Scaly Mountain, North Carolina require an average of 232 DDC_4 (Walgenbach et al. 1993). At Wellesbourne England, five per cent of *D. radicum* adults emerge in the field after about 143 $DDC_{5.6}$ have accumulated in the

air (as 368 DD above 42°F) (Coaker and Wright 1963), and 50 per cent emerge after 179 DDC_4 have accumulated in the soil (Collier and Finch 1985) starting 1 February. In the field 251 DDC_4 accumulate in New York (Jyoti et al. 2003), 330 $DDC_{4.3}$ in Oregon (Dreves et al. 2006) in the air for 50 per cent spring emergence, and at Lacombe, Alberta 325 DDC_4 measured in the soil (Broatch et al. 2006). In Wisconsin, the first *D. radicum* emerge after about 167 (Eckenrode and Chapman 1972; Wyman et al. 1977) to 200 $DDC_{6.1}$ (Eckenrode and Chapman 1971b; 1972) have accumulated, but a second peak in spring emergence at around 396 $DDC_{6.1}$ (Eckenrode and Chapman 1972) or a protracted period of emergence (Wyman et al. 1977) are observed in some years. The first emergence in Guelph, Ontario during spring is likewise quite predictable after about 97 $DDC_{6.1}$ accumulate, but emergence is protracted and the peak in spring emergence is poorly predicted by accumulated thermal units (Nair and McEwen 1975). The unpredictable, protracted pattern of spring emergence was attributed to cool spring temperatures in those years.

A new perspective emerged later. Finch and Collier (1983) showed that while some *D. radicum* complete postdiapause development within 14 days at 20°C, others develop at a similar rate but the onset of their development is delayed, extended cold treatment does not enable this second group to start development sooner, across England the proportion of a population with delayed development is quite variable but not related to latitude, and finally that the development pattern can be selected for within one generation. Similar variation among populations in the proportion of *D. radicum* that complete diapause within 14 days at 20°C exists across Europe (Finch et al. 1985) and Canada (Turnock and Boivin 1997), and even within a few kilometres (Finch et al. 1986). Even though the rate of development is the same for the late emerging flies after the

delay, the pattern of emergence of a population with both types of *D. radicum* is not bimodal but protracted (Finch and Collier 1983). There are no differences among diapausing, nondiapausing, postdiapausing early phenotype, or late phenotype in supercooling point, water content, or the level of cryoprotectants (Collier et al. 1988), but the rate of respiration increases and physical signs of development start the same number of days before the emergence of adult flies (Collier et al. 1989b) so the late phenotype is hypothesized to require a second phase of diapause equivalent to 280 DDC_7 before postdiapause development can start (Collier et al. 1989a). The temperature- and light-induced winter diapause, common to both phenotypes, need not be experienced for the late phenotype to develop more slowly than the early (Biron et al. 1998) and the other life cycle stages develop at the same rate for both phenotypes (Biron et al. 2002). The progeny of two late phenotype parents require more time to emerge as adults at 20°C, and their emergence is more protracted than flies with one late parent (Walgenbach et al. 1993). The early phenotype is less likely to aestivate at temperatures above 21°C (Biron et al. 2002). It is not possible to breed the early phenotype out of a late population in three years, suggesting the two phenotypes are not two alleles for the same locus, but rather that late can only be expressed when early, the dominant allele, is in the recessive state (Biron et al. 2002).

The criterion to separate the two phenotypes has been variously defined as 224 DDC_4 (Finch and Collier 1983), 320 DDC_4 (Collier et al. 1989a; 1989b), and 256 DDC_4 (Turnock et al. 1985; Turnock and Boivin 1997). By any of these definitions, a large proportion of the *D. radicum* populations studied so far from Alberta (Broatch et al. 2006), Saskatchewan (Hemachandra 2004), and Manitoba (Turnock and Boivin 1997) are

the late phenotype. The late phenotype therefore is important in determining the seasonal activity of *D. radicum* in canola crops in western Canada.

The thermal accumulation requirements for spring emergence of *D. radicum*'s natural enemies have not been well studied. Read (1962) showed *A. bilineata* develops more slowly than *D. radicum* at low temperatures, more quickly at high temperatures, and suggests the developmental threshold is around 10°C. In Ontario, the peak spring emergence of *A. bilineata* is about three weeks after the peak spring emergence of *D. radicum* (Nair and McEwen 1975). The objectives of this study were to compare the thermal accumulation requirements of *D. radicum* from western Canada to a population from London, learn more about the nature of the late phenotype, and determine the temperature response of an *A. bilineata* population from Winnipeg. This information will assist in selecting an *A. bipustulata* population well suited to the Canadian prairies for introduction.

Materials and Methods

Experimental Insects

In 2004–5 and 2005–6, experiments were performed in which five populations of insects (three *D. radicum* populations, one *A. bilineata* population, and one *A. bipustulata* population) were exposed to different post-diapause temperature regimes to allow assessments of development rate. Larvae and puparia of *D. radicum* for the experiment were collected in the fall of 2004 and 2005. The type of crop and collection date for each population is shown in Table 1. The *A. bilineata* population was from a laboratory colony maintained at Agriculture and Agri-Food Canada's Southern Crop Protection and Food Research Centre in London, Ontario. The colony was started with *A. bilineata* collected in Manitoba in 2002. Adult *A. bipustulata* and parasitized *D. radicum* puparia were

collected in broccoli, cabbage, and cauliflower fields at various locations in southern Sweden from 17 to 24 June 2004 and from a cauliflower field at Killebackstorp, Sweden 7 to 14 July 2005. Both *Aleochara* species were maintained in plastic containers with expanded clay granules (Hertveldt et al. 1984), 9 cm high and 3.5 cm diameter. Adults were fed *D. radicum* pupae with the puparium removed, and parasitoid larvae parasitized *D. radicum* puparia.

Diapause induction and development

The different insect populations arrived at the University of Manitoba at different times, and some of the *D. radicum* were still larvae when they arrived. As the *D. radicum* were collected from the field in the fall as either late instar larvae or puparia, diapause development was assumed to have been induced. In 2004, as the material arrived puparia were buried individually in 14 mL plastic vials half full of sand and vermiculite and then kept in environmental cabinets at 7°C with no light until all material was assembled. Diapause was induced in the *A.bilineata* by exposing diapausing *D. radicum* puparia from a laboratory colony (Whistlecraft et al. 1985a) to *A. bilineata* larvae for 18 to 21 days at 14°C and no light (Whistlecraft et al. 1985b). In 2004 an attempt to induce *A. bipustulata* to diapause was made by exposing postdiapause *D. radicum* pupae to *A. bipustulata* larvae for five days at 20°C and natural light, then five days at 14°C and 16:8 light dark photoperiod for five days, then 10°C and 13:11 for five days, and finally 5°C and total darkness. The environmental chambers were then set to 1°C, where the insects were kept for 16 weeks. One week before the cold treatment was over, the depth of substrate was reduced to about 5 mm to make emerging adults easier to see.

In the 2005–6 experiment all *D. radicum* were kept at 1°C for 22 weeks in 2005–2006. The same vials were used as in 2004, but the puparia were placed at 1°C as soon as

they arrived or formed, and the volume of substrate was not reduced. Diapause induction in both *Aleochara* species in 2005 followed the same procedure as was used for *A. bilineata* in 2004. The two *Aleochara* populations were split in two groups. One was kept at 1°C for 12 weeks and the other was at 1°C for 22 weeks.

Temperature treatments

In both years, each of the five populations was divided into equal groups and one group was placed at each of five temperature treatments to estimate rate of post-diapause development. In the 2004–5 experiment the vials were moved from 1°C to the treatment temperatures in steps of 5°C every two days. There were 16 hours of light per day in the environmental chambers during all steps and subsequent temperature treatments. The final temperatures in 2004–5 were 13.0, 16.0, 19.0, 22.0, and 24.0°C.

In the 2005–6 experiment, insects were moved directly from 1°C to the treatment temperatures, and a lower range of temperatures was used. The temperature treatments were 8.2, 12.2, 14.6, 17.0 and 20.0°C. The two *Aleochara* species were divided into ten groups, one for each temperature treatment after 12 or 22 weeks at 1°C. The three *D. radicum* populations were divided into seven groups, one for each temperature treatment and one that was kept at 12 or 15°C for the equivalent of 280 DDC_7, then moved to 17°C.

In both 2004–5 and 2005–6 the vials were checked daily for emergence. Two Hobo dataloggers in each environmental cabinet were checked twice per week to make sure the temperature was as constant as possible, and the temperature control on the cabinets adjusted as necessary. Some of the puparia became rotten or desiccated and flat during the cold treatment, so the number of *D. radicum* puparia assigned to the temperature treatments was lower than the number collected (Table 1). This was also a problem with the *A. bipustulata* population; in the 2004–5 experiment only 69% of the

856 *A. bipustulata* puparia appeared healthy enough to contain an insect by the time the vials were moved from 1°C to the treatment temperatures.

Analysis of data

The per cent emergence for each population at each of the temperature treatments was calculated as the number of insects emerging divided by the number in each treatment, multiplied by 100; for the field-collected *D. radicum* the number of parasitoids that emerged was subtracted from the divisor. To determine the per cent emergence at each temperature, the two groups in each *D. radicum* population that started at 12.2 and 14.6°C and were then moved to 17°C were included with the 12.2 or 14.6°C treatment groups.

The relationship between rate of insect development and temperature for the 2005–6 experiment was fitted to Taylor's (1981) truncated normal model. This model estimates parameters for a Gaussian distribution; its equation is:

$$R(T) = R_m * \exp\left[-1/2\left(\frac{T-T_m}{T_\sigma}\right)^2\right]$$

Where R(T) is the rate of development (1/days) at temperature T°C, R_m is the maximum rate of development which occurs at temperature T_m, and T_σ describes the spread of the normal curve. The simple model, as shown above, was estimated for the *Aleochara* species. For *D. radicum*, the 2005–6 data were used to estimate parameters of a model which allowed the three populations different criteria in DDC_4, or 'breakpoints', to separate the early and late phenotypes, different parameter values (R_m, T_m, T_σ) for the two phenotypes, and different parameters for both phenotypes for the three populations. The full model therefore was:

$$R(T) = R_{mle} * \exp(-1/2 * ((T-T_{mle})/T_{\sigma le})^2) * (DDC4 \leq Breakpoint_{London})$$

$$+ R_{mll} * \exp(-1/2 * ((T-T_{mll})/T_{\sigma ll})^2) * (DDC4 > Breakpoint_{London})$$
$$+ R_{mse} * \exp(-1/2 * ((T-T_{mse})/T_{\sigma se})^2) * (DDC4 \leq Breakpoint_{Shellbrook})$$
$$+ R_{msl} * \exp(-1/2 * ((T-T_{msl})/T_{\sigma sl})^2) * (DDC4 > Breakpoint_{Shellbrook})$$
$$+ R_{mce} * \exp(-1/2 * ((T-T_{mce})/T_{\sigma ce})^2) * (DDC4 \leq Breakpoint_{Carman})$$
$$+ R_{mcl} * \exp(-1/2 * ((T-T_{mcl})/T_{\sigma cl})^2) * (DDC4 > Breakpoint_{Carman})$$

Where the parameter R_{mij} is for the ith population (c=Carman, l=London, s=Shellbrook) and jth phenotype (e=early, l=late).

Breakpoints were initially estimated for each population individually and, as the distribution of DDC_4 values is discontinuous and non-integratable, they were estimated by manual iteration. The most appropriate breakpoint for each population was a DDC_4 value within the range of 200 to 320, including the published values 256 DDC_4 (Turnock and Boivin 1997), 320 DDC_4 (Collier et al. 1989a), and 224 DDC_4 (Finch and Collier 1983). An F-ratio test of error mean squares was used to determine whether including separate parameters and breakpoints for the different populations significantly improved the fit of the model (Gallant 1987). Lamb's (1992) methods of estimating the developmental threshold temperature and day degree requirement were followed: the developmental threshold is $TH_{08} = T_m - 2.23\ T_\sigma$, and the day degree requirement $DD_{80} = T_\sigma / 0.483R_m$.

The effectiveness of the model was tested by comparing the observed days to emergence with those predicted by the model. The number of days required for emergence was frequently not normally distributed for particular combinations of population and temperature treatment, so for each combination of population, phenotype, and year the predicted days to emergence was compared to the median observed days for each temperature treatment by linear regression. Data from the 2004–5 experiment could not be directly fitted to a model because of the complexity introduced by the stepped

temperature increase, so they were analyzed by first determining the amount of development that occurred as the insects were gradually brought to the final treatment temperatures using the appropriate parameters derived from the 2005–6 experiment. The estimated rate of development was used to find the predicted days to complete development at the final temperature, which was then regressed on the observed median number of days. If the calculated intercept was not statistically different from zero, and the slope not statistically different from one, the estimated parameters were considered unbiased (Lactin et al. 1995). The days to emergence of *D. radicum* from Fort Whyte, which emerged in spring 2005, were compared to predicted days based on the model developed for the *D. radicum* from Carman. When the estimates were biased, or poorly predicted the median days required as indicated by the adjusted multiple r^2 ($r^2 < 0.80$), the observed and predicted values were plotted together to identify possible explanations.

To aid in identification of explanations for bias, particularly for *D. radicum* in the 2004–5 experiment, data from Hemachandra (2004) were reanalyzed. Hemachandra collected *D. radicum* puparia from canola fields at Shellbrook in October 2000, kept them for 21 weeks at 1°C, and then transferred them in groups to 5, then 10, 15, and finally 20°C. Each group spent one, two, four, or six days at each intermediate temperature, and emergence was checked daily. To reexamine his data, each *D. radicum* was designated as early or late phenotype according to the appropriate criterion for Shellbrook populations. For each warming period duration and phenotype, the median observed days to emergence at 20°C was compared with the predicted number of days. Predicted days were calculated the same way as data from the 2004–5 experiment.

A two-sample Kolmogorov-Smirnov test was used to determine if the hypothesis that *D. radicum* of the late phenotype pass through a second phase of diapause and

thereafter develop at the same rate as the early phenotype described the pattern of emergence of the three Canadian *D. radicum* populations. The *D. radicum* from the three populations that were kept at 12.2 or 14.6°C for the equivalent of 280 DDC_7 and then moved to 17°C were classified individually as early or late according to the appropriate criterion for their population in DDC_4. The DDC_7 to emergence was calculated for each *D. radicum*, and for the late phenotype 280 DDC_7 subtracted from this total. The test compared DDC_7 to emergence of the early phenotype with the adjusted value for the late phenotype. If the hypothesis fits the Canadian *D. radicum*, the test would conclude the two samples are from the same population (Daniel 1990).

Results

No *A. bipustulata* emerged in the 2004–5 or 2005–6 experiments. The per cent emergence of the other populations in the different temperature treatments is shown in Figure 1. The emergence of both Shellbrook and Fort Whyte *D. radicum* populations was poor at 24°C, but it was also poor for Shellbrook at intermediate temperatures in the 2005–6 experiment. The emergence of *A. bilineata* was poor in both years, and with both durations of exposure to 1°C, especially at the lower treatment temperatures. As the fit of a model describing *A. bilineata*'s rate of development in the 2005–6 experiment was not improved by separate parameters for the 12 and 22 week cold treatments at 1°C (combined $SS_{Error} = 0.000167287$, $df_{Error} = 36$; separate $SS_{Error} = 0.000151942$, $df_{Error} = 33$; $F_{3,33} = 1.1$, $P = 0.36$), the rate of development of both groups was the same.

In developing a model to relate *D. radicum*'s rate of development to temperature, it was clear that for all populations there were two phenotypes. If the *D. radicum* from Carman, London, and Shellbrook were considered as a single population, the breakpoint between the two phenotypes which gave the highest mean corrected r^2 was 255 DDC_4.

Estimating separate developmental parameters (R_m, T_m, T_σ) for the two phenotypes significantly improved the fit of the model (Table 2a; $F_{4, 573} = 772.8$, $P < 0.001$). However, in terms of both the best breakpoint for separating the phenotypes, and the developmental parameters, the two prairie populations which were collected from canola, from Shellbrook and Carman, were the same as one another and different from the London population which developed on *Brassica* vegetables.

Considering the three populations independently, the model fit the *D. radicum* from London with distinct parameters for two phenotypes, separated at 255 DDC_4, better than a model with only one phenotype (Table 2b; $F_{4, 217} = 97.2$, $P < 0.001$); however the highest r^2 was obtained when the two phenotypes were separated at 224 DDC_4, and this improved the fit of the model relative to the 255 DDC_4 breakpoint ($F_{1, 217} = 22.0$, $P < 0.001$). The population from Shellbrook fit a model with two phenotypes separated at 255 DDC_4 better than a model with no separation (Table 2c; $F_{4, 118} = 254.5$, $P < 0.001$), but the optimal breakpoint was 280 DDC_4, which when used was a better fit to the data than 255 ($F_{1, 119} = 6.0$, $P < 0.05$). The Carman population was the same, where separate parameters for two phenotypes separated at 255 DDC_4 was a better model than one with one phenotype (Table 2d; $F_{4, 224} = 298.9$, $P < 0.001$), but the r^2 was highest when 280 DDC_4 was used, which improved the model relative to a model with phenotypes separated at 255 DDC_4 ($F_{1, 119} = 9.4$, $P < 0.05$).

Considering the three populations combined, a model with separate parameter estimates for each population based on a breakpoint of 255 DDC_4 was not as good a fit to the data as a model using the same parameter estimates but the most appropriate breakpoint for each population (Table 2e; $F_{2, 559} = 5.2$, $P < 0.05$). The point of separation

was therefore not the same for all populations; for the prairie populations it was 280 DDC_4, and for the London population 224.

A significantly better fit was achieved by estimating three parameters for each population to describe the developmental rate of the late phenotype, compared to estimating a set of parameters common to all populations (Table 2f; $F_{6,559} = 9.16$, $P < 0.001$). However, estimating separate parameters for the late phenotype for the two prairie populations was not significantly better than using combined estimates for these populations ($F_{3,559} = 0.35$, $P = 0.79$). Similarly, separate parameters for each population for the early phenotype improved the model's fit relative to using a single set of early phenotype parameters (Table 2g; $F_{6,562} = 51.10$, $P < 0.001$), but not compared to using a single set for the two prairie populations ($F_{3,562} = 2.12$, $P = 0.11$). Thus the two prairie populations had common breakpoints and developmental parameters for both phenotypes, which were significantly different from those of the London population. The estimated parameters for *D. radicum* and *A. bilineata* are shown in Table 3.

The developmental threshold temperature of the early phenotype was nearly the same for the London and prairie *D. radicum* populations, but the day-degree requirement of the prairie *D. radicum* was higher by about 50 (Table 3). The developmental threshold of the late phenotype from London was nearly 1°C higher than the prairie *D. radicum* (Table 3), making direct comparison of the day-degree requirement of this phenotype more difficult. However the late *D. radicum* appear to require the accumulation of more heat for post-diapause development. Function plots relating the rate of *D. radicum* development to temperature are in Figure 2. The *A. bilineata* from Manitoba had a higher day-degree requirement than any of the *D. radicum*.

The estimated days to emergence were biased for four combinations of year, population, and phenotype (Table 4). For *A. bilineata* from the 2004–5 experiment, the lack of fit seemed to be at 13 and 16°C, at which temperatures relatively few emerged (Figure 3). For the early phenotype from Fort Whyte (Figure 4) and Shellbrook (Figure 7) in the 2004–5 experiment, the parameters estimated for the prairie populations consistently underestimated days to emergence. The late phenotype from London in the 2004–5 was the most poorly predicted of all populations studied, particularly at 24°C where the days to emergence was over-predicted by about 100 (Figure 6).

For two populations, unbiased estimates of days to emergence were calculated, but the r^2 was relatively low. Days to emergence of the late phenotype in the 2004–5 experiment from Fort Whyte (Figure 5) and Shellbrook (Figure 8) were under-predicted at 13°C and over-predicted at 24°C.

The rate of development for the early phenotype *D. radicum* from Shellbrook was well-predicted by the model when one day was spent at each of 5, 10, and 15°C before a final temperature of 20°C, but when two, four, or six days were spent at each intermediate temperature, days to emergence at 20°C was under-predicted by about two days (Figure 9). For late phenotype *D. radicum*, days to emergence was over-predicted for all warming period durations, but when six days were spent at each intermediate temperature the over-prediction was slightly more than one day (Figure 10).

On the basis of *D. radicum* that did emerge and the criterion of emergence up to 224 DDC_4, the early phenotype was 71% of 210 in 2004–5 and 89% of 224 in 2005–6 of the London population. The Shellbrook population in 2004–5 was 32% of 183 early emergers, up to 280 DDC_4, and 45% of 124 in 2005–6. Of the 234 *D. radicum* from Fort

Whyte in the 2004–5 experiment, 31% were the early phenotype. The Carman population in the 2005–5 experiment had the smallest proportion of early emergers, with 23% of 230.

Of the *D. radicum* kept at 12.2 or 14.6°C for 280 DDC_7 then moved to 17°C that emerged, 13 of 92 from London, 11 of 54 from Shellbrook, and 65 of 76 from Carman were the late phenotype. All of the late *D. radicum* from London, 6 from Shellbrook, and 27 from Carman emerged at the first temperature, prior to completing 280 DDC_7. For all three *D. radicum* populations studied in 2005–6, the accumulated DDC_7 for emergence of the early phenotype was significantly different than the hypothesized DDC_7-280 DDC_7 for the late phenotype (K-S, $P < 0.001$).

Discussion

The Canadian prairies were originally quite a different ecosystem for insects, and relatively few native species have adapted to the foreign plants grown as crops (Turnock 1977). Many of the insect pests of the prairies are, like *D. radicum* (Schoene 1916), non-indigenous — but have adapted to the plants, the seasonal availability of food and periods of adverse weather conditions in the new habitat. The synchronization of insects with seasonal events in their environment is most strongly achieved by diapause-associated processes (Tauber and Tauber 1976; 1981). Species are known to vary in the timing of their seasonal cycles on both the geographical level, where a population from a specific location is better adapted to that area than another, and at the intra-population level where a population shows a range of responses to seasonal change (Danilevsky et al. 1970; Tauber and Tauber 1981). For instance, the post-diapause development rate of *Tetrastichus julius* (Walker) (Hymenoptera: Eulophidae) shows geographical variation which may be related to the seasonal availability of it host, *Oulema melanopus* (L.) (Coleoptera: Chrysomelidae) (Nechols et al. 1980), and populations of *Rhagoletis pomonella* (Walsh) (Diptera: Tephritidae) contain individuals that

develop at different rates, which serves to time emergence in the spring with the availability of different host plants (Oatman 1964; Bush 1969). Emergence of a species after diapause can be synchronous, or protracted as a strategy of spreading risk (Danks 2006). Thus arctic Chironomidae emerge over a very short period early in the season (Danks and Oliver 1972), whereas *Malacasoma americanum* (F.) (Lepidoptera: Lasiocampidae) eggs hatch over a considerable period, spreading risk between mortality caused by late spring frost and natural enemies (Neal et al. 1997). Post-diapause development of *D. radicum* is variable at the both intra-population and geographical levels.

Two *D. radicum* phenotypes are recognized, an 'early phenotype' which emerges rather synchronously, and a 'late phenotype' with protracted emergence (Finch and Collier 1983). Phenotypes of *D. radicum* with rapid, intermediate, and particularly slow rates of development can readily be selected in the laboratory (Finch and Collier 1983; Walgenbach et al. 1993; Biron et al. 1998). The evolutionary argument for maintaining two phenotypes is essentially that the early phenotype can complete more generations in warm years, whereas the late is safer in case of extreme spring weather events (Finch and Collier 1983; Walgenbach et al. 1993; Biron et al. 1998); it is also thought to synchronize emergence in spring with host plant availability (Finch et al. 1986).

A variety of criteria to separate the two phenotypes have been used, but these results are the first to show the most appropriate definition depends on the location. Also, it was clear that *D. radicum* populations in the Canadian prairies are similar in measures of post-diapause development and much different than a population from Ontario which developed on roots of vegetable *Brassica* plants. Early phenotype *D. radicum* from Manitoba have a higher day degree requirement than early phenotypes from other locations, and the late phenotype a relatively low day degree requirement compared with late phenotype *D. radicum* from Prince Edward Island and England (Turnock and Boivin 1997). This may be a common

feature of the *D. radicum* from the Canadian prairies. It is perhaps not too surprising, then, that emergence of the late *D. radicum* studied here was not well explained as a second phase of diapause lasting 280 DDC_7, followed by development at the same rate as the early phenotype (Collier et al. 1989a). The rate of development is clearly not the same for the two phenotypes from a given location (Figure 8). The early phenotype *D. radicum* did not develop at the same rate as the late phenotype if 280DDC_7 were subtracted from the late individuals' developmental times, and at least half of the late individuals actually emerged before 280DDC_7 had passed. The increasing *D. radicum* problem in prairie canola (Soroka et al. 2004) may be due to *D. radicum* becoming adapted to its seasonal availability as a host plant.

The emergence of *D. radicum* in the 2004–5 experiment was not always well-explained by the model developed using data from 2005–6, and there are reasonable explanations besides inadequacy of the model. The data from Hemachandra (2004) indicate that for the early phenotype *D. radicum*, if two days are spent at each intermediate temperature as happened in the 2004–5 experiment, days to emergence is under-predicted by about two days (Figure 9). This effect is largely independent of cold treatment duration, as 21 were used in 2000–1 and 22 weeks in 2005–6, when data were collected to develop the model. Under-predicted days to emergence of the early phenotype in 2004–5 were observed for Fort Whyte (Figure 4) and Shellbrook (Figure 7). The effect of gradual warming on the late phenotype was over-prediction of days to emergence of about 2.5 days (Figure 10); days were over-predicted at higher temperatures for the late phenotype from all three populations, but the over-prediction was often greater than 2.5 days. In addition, duration of the 1°C cold treatment for diapause development was not the same in the two experiments, 16 weeks in 2004–5 and 22 weeks in 2005–6. Diapause is complete at 0°C in about 60 per cent of *D. radicum* individuals after 16 weeks, and is maximum after 22 (Collier and Finch 1983). Incomplete diapause would cause the days to development to be under-predicted. This

occurred in the 2004–5 data for the early Fort Whyte *D. radicum* (Figure 4), the late Fort Whyte at 13°C (Figure 5), the late London at 16 and 19°C (Figure 6), and both Shellbrook phenotypes, particularly at 13 and 16°C (Figures 7 and 8). As well, in the 2004–5 experiment 22 and 24°C were two of the treatment temperatures, and temperatures above 21°C are unfavourable for *D. radicum* pupae, causing delayed development or death (Finch and Collier 1985; Johnsen et al. 1990), although this phenomenon seems to be specific to certain populations (Turnock and Boivin 1997). If mortality was an important factor, the most rapidly developing individuals would emerge and give the impression that developmental time had been over-predicted. This was observed in the 2004-5 experiment for the late phenotype from Fort Whyte (Figure 5), London (Figure 6), and Shellbrook (Figure 8). All of the early phenotype *D. radicum* from Shellbrook in the 2004-5 experiment at 24°C may have died of heat injury (Figure 7). Also, no data collected above 20°C were used in the actual development of the model. Over-prediction due to extrapolation of developmental rate at 22 and 24°C, as opposed to heat injury, is a reasonable explanation for the *A. bilineata* in the 2004-5 experiment (Figure 3), since survival of *A. bilineata* was higher at higher temperatures (Figure 1).

Turnock and Boivin (1997) studied *D. radicum* from the Canadian prairies and London using very similar methods of experimentation and analysis of data to those used here, although their prairie population developed on vegetable *Brassica* plants. The developmental threshold (TH_{08} = 3.0) and day-degree requirement (TH_{08} = 237) of my early *D. radicum* from the prairies is very similar to their early *D. radicum* from Winnipeg (TH_{08} = 3.3, DD_{80} = 246). My late prairie phenotype, however, had a higher developmental threshold (TH_{08} = 5.1) and day-degree requirement (TH_{08} = 371) than the late *D. radicum* from Winnipeg in their study (TH_{08} = 4.4, 316). Whether prairie *D. radicum* are becoming better adapted with time to the availability of canola, or if this resulted from different criteria for

separating the phenotypes is difficult to say, as many of their 'late' *D. radicum* would have been 'early' in my analysis. Although the late prairie *D. radicum* studied have a similar estimated developmental threshold to late *D. radicum* from England (TH_{08} = 5.0, TH_{08} = 538) and Prince Edward Island (TH_{08} = 5.0, TH_{08} = 530), the day-degree requirement is much lower. The late *D. radicum* from the prairies therefore are not as late as in some populations, and are similar to North Carolina (Walgenbach et al. 1993) and certain English (Finch et al. 1986) populations. Studying a *D. radicum* population under the assumption that each individual will fall into one of two well-defined and universal phenotypes is a good place to start, but is no doubt an oversimplification.

Aleochara bilineata emerges in spring about two or three weeks after the peak emergence of *D. radicum* under field conditions (Nair and McEwen 1975), and post-diapause development takes 22–30 days at 20°C in the laboratory (Turnock et al. 1985). Activity of *A. bilineata* is highest later in the season, from mid-July onwards (Read 1962). Read (1962) states development of *A. bilineata* is slower than *D. radicum* at low temperatures, and more rapid at higher temperatures. The *D. radicum* Read studied were entirely late phenotype, with a comparatively high thermal accumulation requirement (Turnock and Boivin 1997). The *A. bilineata* from Manitoba agree with Read's conclusions with respect to late prairie *D. radicum*, but not the early prairie nor either London phenotypes (Figure 8). In European crops *A. bipustulata* is more active than *A. bilineata* while the over-wintered generation of *D. radicum* is ovipositing, and therefore *A. bipustulata* has more potential as an early season predator (Jonasson 1994b). Assuming peaks in oviposition and flight in a crop occur at the same time, and that the *D. radicum* are similar across prairie Canada, the oviposition is typically around mid- to late June (Broatch et al. 2006). If the temperature at 1 cm below the soil surface dictates the rate of development of *A. bilineata*, and a temperature profile from a field near Winnipeg can be extrapolated very liberally to cover three provinces, then the

developmental threshold of *A. bilineata* is reached about the first of May, the average temperature during May is about 10°C, in June 15°C, and July 17°C (Reimer and Shaykewich 1980). By these temperature estimates and the DD_{80} estimated in the model, *A. bilineata* will emerge at the beginning of July. This estimate is consistent with the literature and implies the potential impact of *A. bilineata* as an egg predator in Canadian canola is small.

If adult *Aleochara* are to eat *D. radicum* eggs and early instar larvae in Canadian canola crops, they will have to be from a population that moves into fields around the middle of June. Unfortunately it is not yet possible to identify whether a population of *A. bipustulata* with these characteristics exists on the basis of post-diapause thermal accumulation requirements. The conditions that induce diapause in *A. bilineata* (Whistlecraft et al. 1985a) fail to do so for *A. bipustulata*. *Aleochara bipustulata* is thought to overwinter as an adult (Jonasson 1994b), although no data support this. Insects which diapause in the adult stage typically delay reproductive maturation and instead build up reserves of fat and storage proteins (Denlinger 2002); it may be possible to determine if *A. bipustulata* overwinters as an adult by catching them in the late fall and observing how far the reproductive organs have developed. Trying to collect *A. bipustulata* during the winter could complement this approach. Cues that induce an insect to take the diapause development pathway are usually perceived well in advance of diapause itself (Danks 1987). Work toward identifying a well-suited population of *A. bipustulata* to introduce to the Canadian prairies must wait until first the stage at which it overwinters, and then cues that will induce diapause, are understood. Once it is possible to induce diapause in *A. bipustulata*, the methods used to determine the rate of postdiapause development of *D. radicum* and *A. bilineata* can be applied to several populations of *A. bipustulata*, and the most appropriate one selected.

In addition to identifying an *A. bipustulata* population for introduction, several other research directions can follow from this experiment. Only one *A. bilineata* population was

characterized. Additional *A. bilineata* populations could be studied, particularly from areas where the early *D. radicum* phenotype predominates, to see if the rate of *A. bilineata*'s post-diapause development changes with that of its host. This information would be valuable in predicting how much variation to expect in different populations of *A. bipustulata*. Also, despite all the work that has been done about it, the 'late phenotype' of *D. radicum* is still incompletely understood. The late phenotype was a large proportion of the prairie populations studied here, and although the developmental parameters for this phenotype were found to be the same in prairie populations, the day degree requirements of the late *D. radicum* were considerably less than have been reported elsewhere. The 'obvious' explanation is that this intermediate thermal accumulation requirement serves *D. radicum* to adapt to the phenology of its principal prairie host plant, canola. However, it usually pays to consider alternative explanations (Gould and Lewontin 1979; Mayr 1983). Perhaps the response of the late phenotype to temperature, as protracted as it can be, is an unavoidable correlate of selection to better exploit canola nutritionally. Alternatively, the late phenotype may be associated with greater coldhardiness. The supercooling point and level of cryoprotectants of the phenotypes are not different (Collier et al. 1988), but this is not necessarily the best measure of coldhardiness (Turnock and Fields 2005). Winnipeg *D. radicum* are more coldhardy than some other populations based on non-freezing cold injury (Turnock et al. 1990; Turnock et al. 1998).

The *D. radicum* in prairie canola is different in its spring emergence biology from populations that exploit vegetable *Brassica* crops. Introducing a natural enemy is an option for controlling this non-indigenous pest, and *A. bipustulata* shows great potential as the candidate for introduction. However, it is not yet possible to identify a population of *A. bipustulata* synchronized with the prairie *D. radicum*, which would increase the probability of establishment and adequate control.

Table 1. Origin and crop of sampled *Delia radicum* populations, studied to determine thermal response of post-diapause development, and the per cent of puparia collected that were healthy at the end of cold treatment.

Population	Crop sampled	Date of collection	Number collected	% Healthy
Fort Whyte, MB	rutabaga, broccoli, cabbage	8-11 October 2004	573	98
Carman, MB	canola	14-31 October 2005	539	100
Shellbrook, SK	canola	30 September – 6 October 2004	384	96
		29 September 2005	523	99
London, ON	rutabaga	14 November 2004	417	97
		8 November 2005	442	100

Table 2. Error sum of squares (SS_{Error}) and degrees of freedom (df_{Error}) for models relating rate of development (1/days) of *Delia radicum* and *Aleochara bilineata* to temperature. The SS_{Error} values were used in likelihood ratio tests to determine whether a model better fit the data with (a) two *D. radicum* phenotypes; (b-e) population-specific definitions of the phenotypes; and (f-g) population-specific model parameters.

	Model	SS_{Error}	df_{Error}
a	All *D. radicum*, one phenotype	0.253156	577
	Early and late phenotypes separated at 255 DDC_4	0.039589	573
b	London, one phenotype	0.043392	221
	breakpoint 255 DDC_4	0.017123	218
	breakpoint 224 DDC_4	0.015544	217
c	Shellbrook, one phenotype	0.026400	122
	breakpoint 255 DDC_4	0.002882	119
	breakpoint 280 DDC_4	0.002742	118
d	Carman, one phenotype	0.044375	228
	breakpoint 255 DDC_4	0.007295	225
	breakpoint 280 DDC_4	0.007001	224
e	All *D. radicum*, breakpoint 255 DDC_4, population-specific parameters	0.027299	561
	breakpoint specific to populations, parameters same as above	0.026797	559
f	All *D. radicum*, breakpoint and parameters specific to populations	0.025287	559
	common parameters for late phenotype	0.027773	565
	common parameters for late phenotypes from prairies	0.025335	562
g	All *D. radicum*, breakpoint and early parameters specific to populations, common for late prairies	0.025335	562
	same parameters for early phenotype	0.039156	568
	common parameters for early phenotype from prairies	0.025664	565

Table 3. Estimated parameters for a model describing post-diapause development of *Delia radicum* populations from Shellbrook and Carman ('Prairies') and London and an *Aleochara bilineata* population, developmental threshold temperature, and day-degree requirement.

	definition (DDC_4)	R_m (s.e.)	T_m (s.e.)	T_σ (s.e.)	TH_{08}	DD_{80}
London, early	≤ 224	0.1246 (0.0144)	28.0343 (2.4896)	11.1942 (1.1317)	3.1	186
Prairies, early	≤ 280	0.0841 (0.0061)	24.4501 (1.7393)	9.6243 (0.9631)	3.0	237
London, late	> 224	0.0429 (0.0027)	15.6767 (0.4065)	4.3857 (0.5340)	5.9	212
Prairies, late	> 280	0.0302 (0.0007)	17.1913 (0.2267)	5.4145 (0.2777)	5.1	371
Aleochara bilineata		0.0349 (0.0021)	22.5083 (1.2976)	7.4820 (0.8420)	5.8	444

Table 4. Statistics for regression of predicted on observed days to emergence, for N different temperature treatments.

Population	Year	Phenotype	adjusted multiple r^2	N	Intercept (SEM)	P^a	Slope (SEM)	P^b	F(df)
Aleochara bilineata									
Manitoba	2004–5		0.962	5	9.57 (3.01)	NS	0.69 (0.07)	*	101.4 (1, 3)
	2005–6		0.999	5	0.94 (0.57)	NS	0.99 (0.01)	NS	25252.6 (1, 3)
Delia radicum									
Fort Whyte	2004–5	early	0.996	5	-0.10 (0.44)	NS	0.82 (0.03)	*	1028.1 (1, 3)
		late	0.774	5	-5.84 (12.83)	NS	1.16 (0.30)	NS	14.71 (1, 3)
Carman	2005–6	early	0.997	5	2.10 (0.74)	NS	0.88 (0.06)	NS	1287.6 (1, 3)
		late	0.999	5	-1.09 (1.31)	NS	1.00 (0.02)	NS	2833.7 (1, 3)
London	2004–5	early	0.993	5	-1.20 (0.50)	NS	0.89 (0.04)	NS	559.2 (1, 3)
		late	0.568	5	123.73 (32.07)	*	-2.42 (0.97)	*	6.25 (1, 3)
	2005–6	early	0.999	5	0.10 (0.35)	NS	1.01 (0.02)	NS	4122.4 (1, 3)
		late	0.832	5	-16.70 (17.03)	NS	1.70 (0.44)	NS	14.87 (1, 3)
Shellbrook	2004–5	early	0.994	4	1.67 (0.77)	NS	0.71 (0.04)	*	310.8 (1, 2)
		late	0.541	5	0.89 (22.46)	NS	0.97 (0.51)	NS	3.53 (1, 3)
	2005–6	early	0.984	5	1.69 (1.92)	NS	0.90 (0.06)	NS	194.1 (1, 3)
		late	0.993	5	1.59 (2.90)	NS	0.95 (0.04)	NS	542.0 (1, 3)

[a] t-test, N-2 df; * significant at 0.05 level, NS is not significantly different from 0
[b] t-test, N-2 df; * significant at 0.05 level, NS is not significantly different from 1

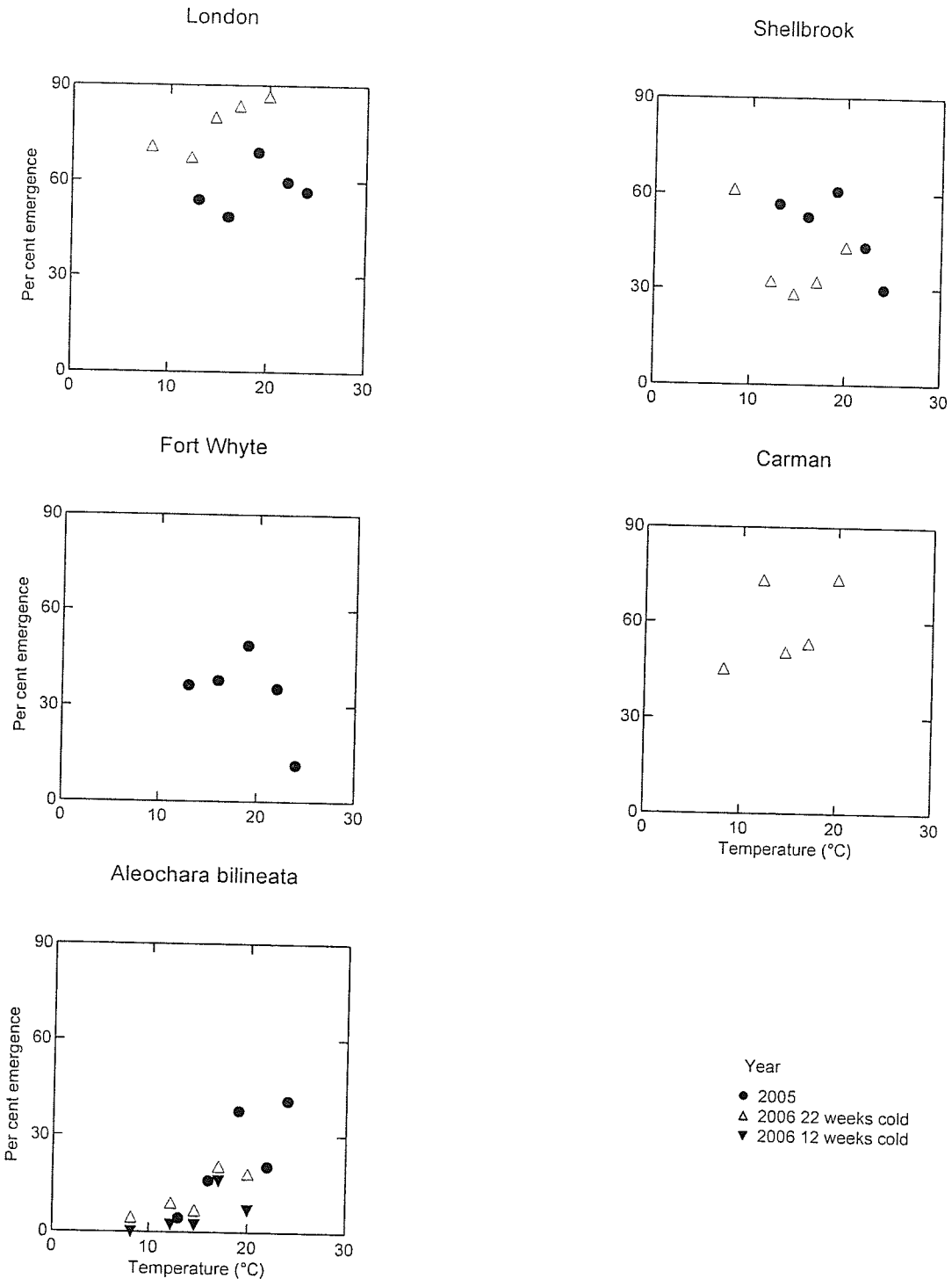

Figure 1. Percentage of four *Delia radicum* populations, and an *Aleochara bilineata* population with two durations of cold treatment, that emerged at different treatment temperatures.

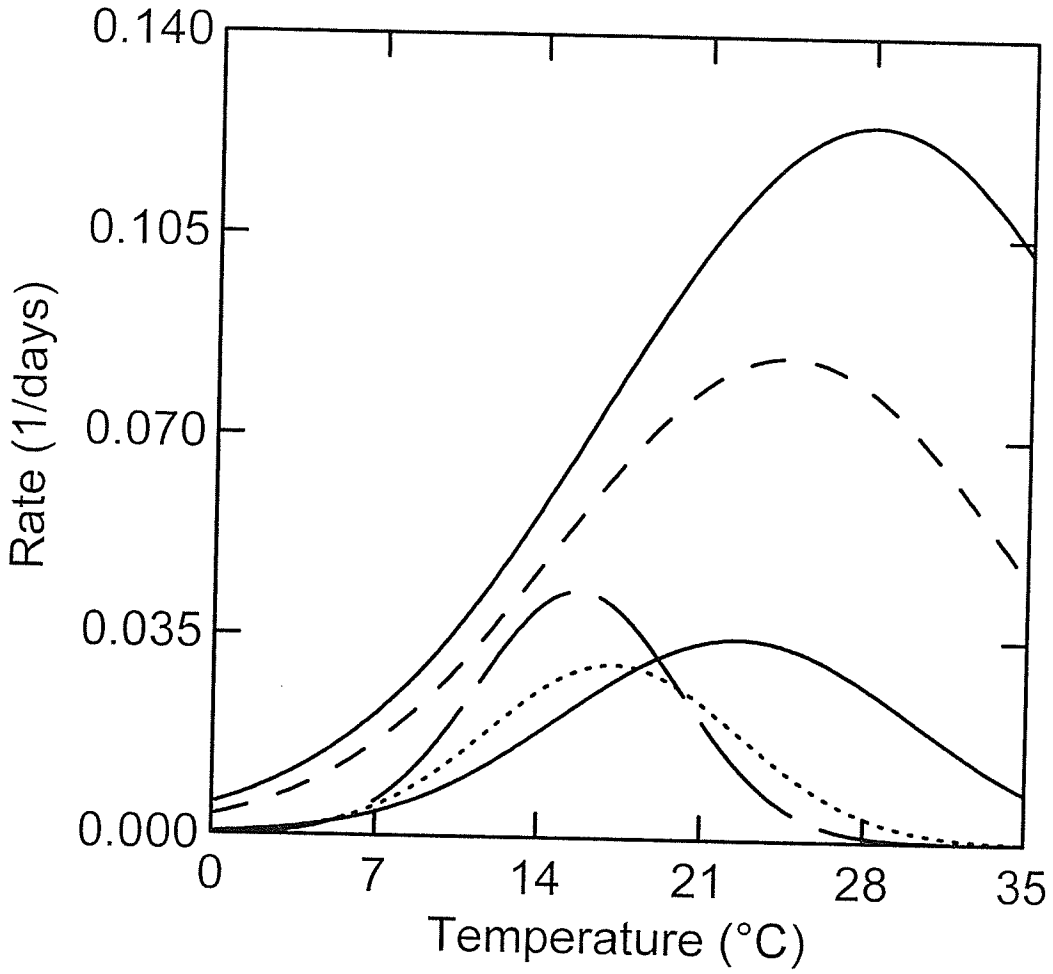

Figure 2. Rate of post-diapause development as a function of temperature for *Delia radicum* early phenotype from London (upper solid line), late phenotype from London (long dashes), early phenotype from the prairies (short dashes), late phenotype from the prairies (dots), and *Aleochara bilineata* from Manitoba (lower solid line).

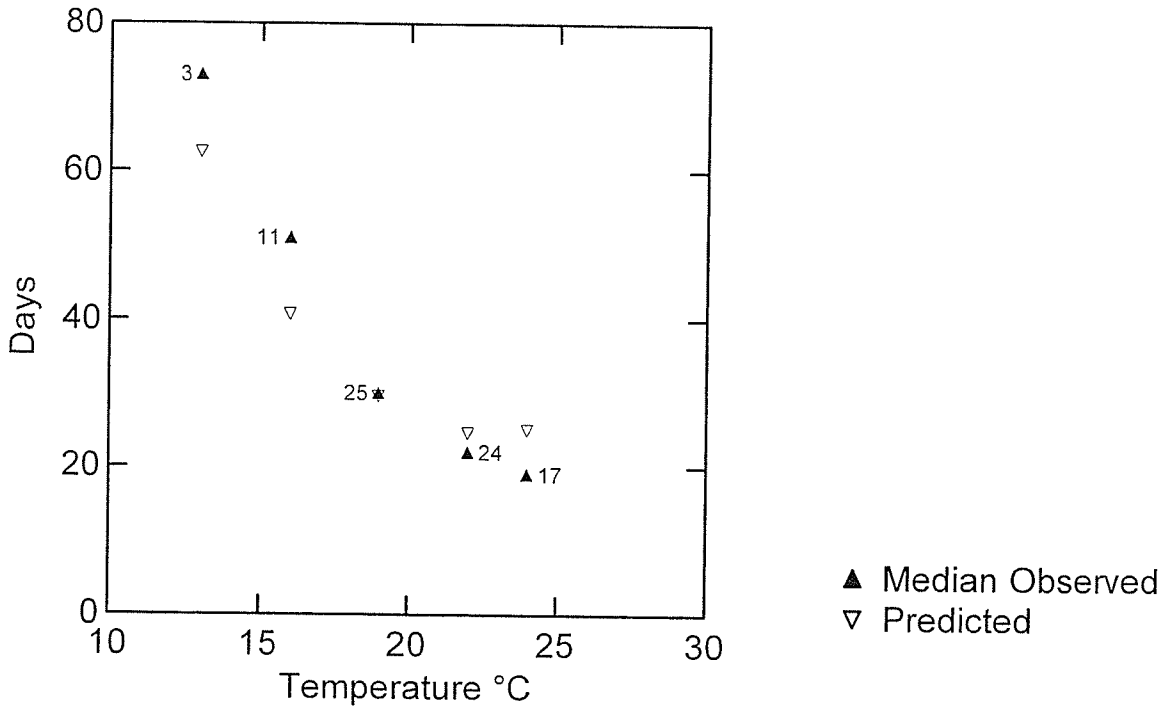

Figure 3. Predicted and median observed days to emergence of *Aleochara bilineata* in spring 2005. Numbers beside observed days indicate the number that emerged at that temperature.

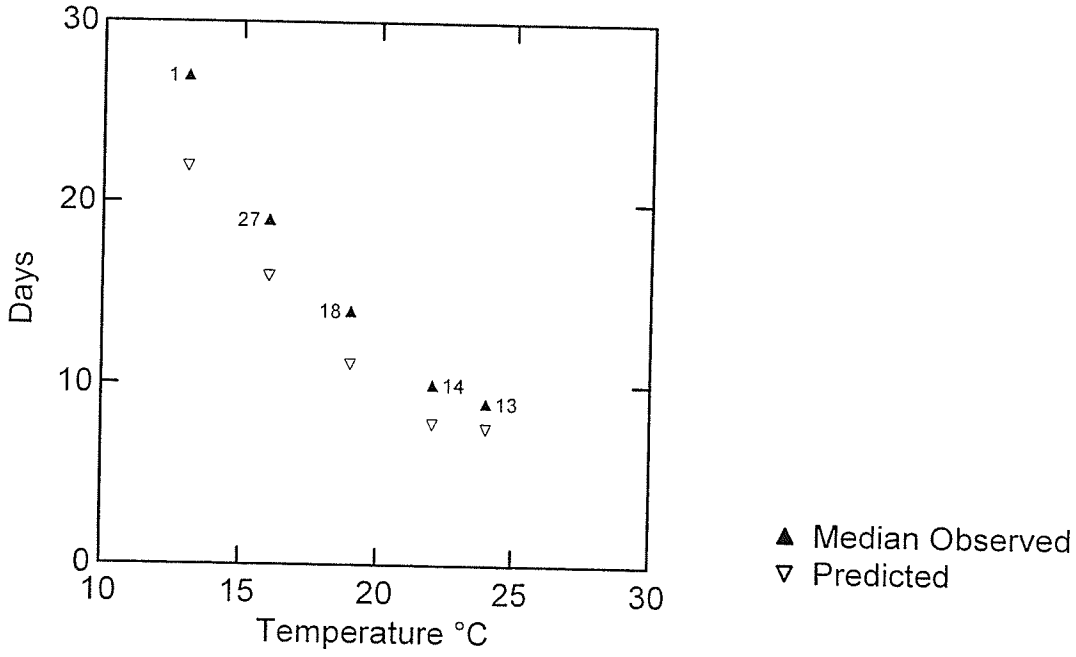

Figure 4. Predicted and median observed days to emergence of *Delia radicum* early phenotype from Fort Whyte in spring 2005. Numbers beside observed days indicate the number that emerged at that temperature.

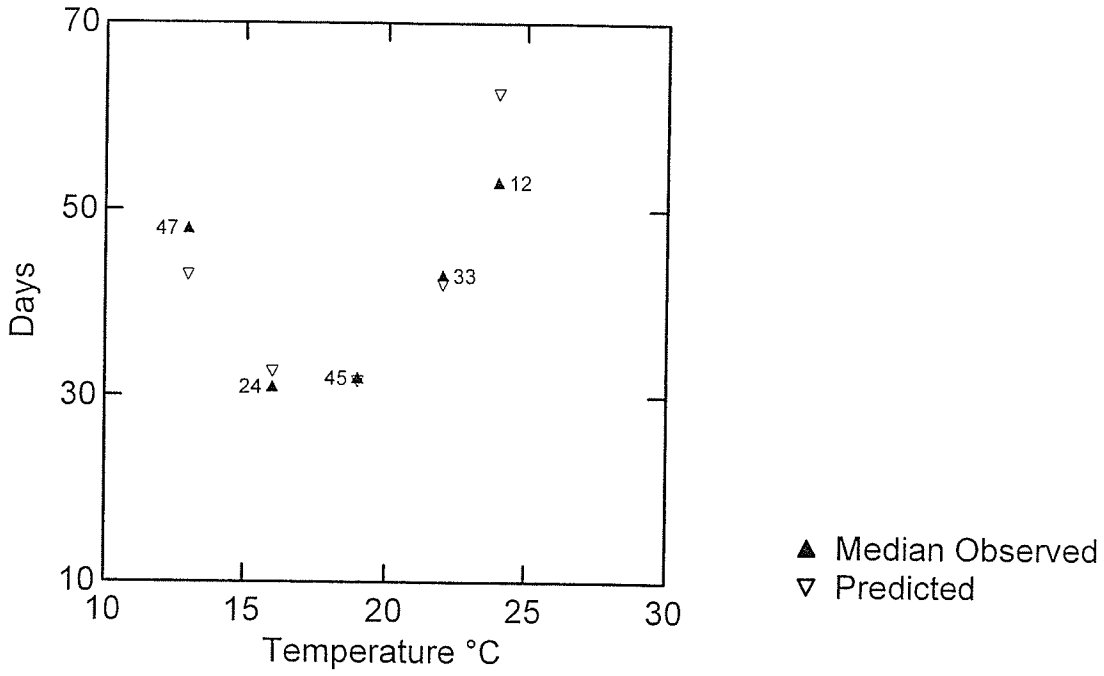

Figure 5. Predicted and median observed days to emergence of *Delia radicum* late phenotype from Fort Whyte in spring 2005. Numbers beside observed days indicate the number that emerged at that temperature.

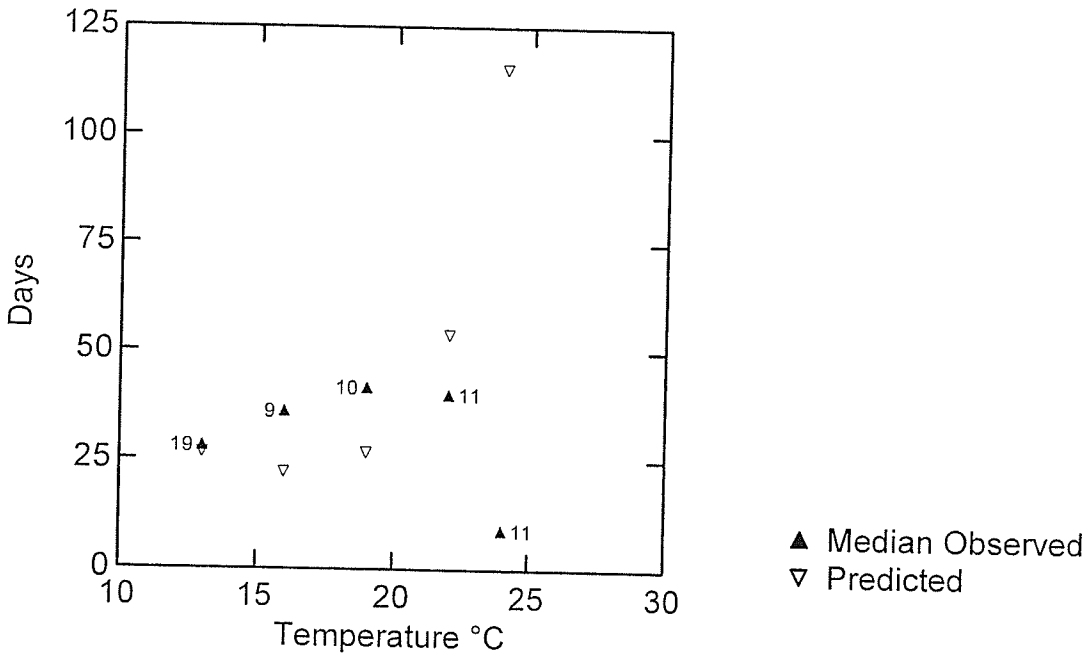

Figure 6. Predicted and median observed days to emergence of *Delia radicum* late phenotype from London in spring 2005. Numbers beside observed days indicate the number that emerged at that temperature.

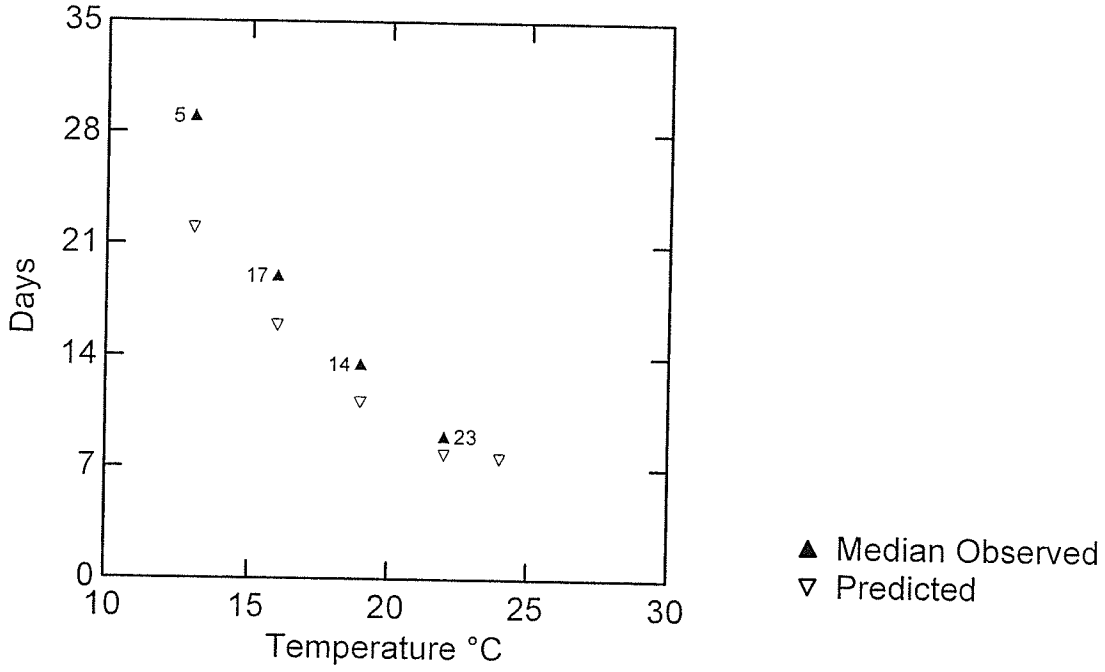

Figure 7. Predicted and median observed days to emergence of *Delia radicum* early phenotype from Shellbrook in spring 2005. Numbers beside observed days indicate the number that emerged at that temperature.

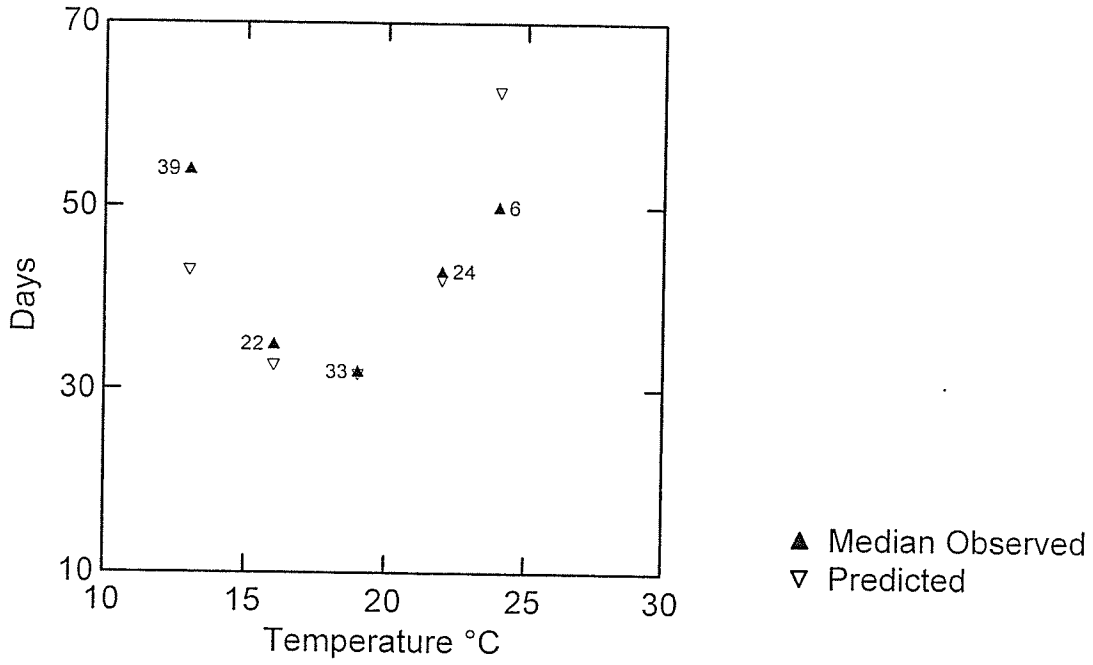

Figure 8. Predicted and median observed days to emergence of *Delia radicum* late phenotype from Shellbrook in spring 2005. Numbers beside observed days indicate the number that emerged at that temperature.

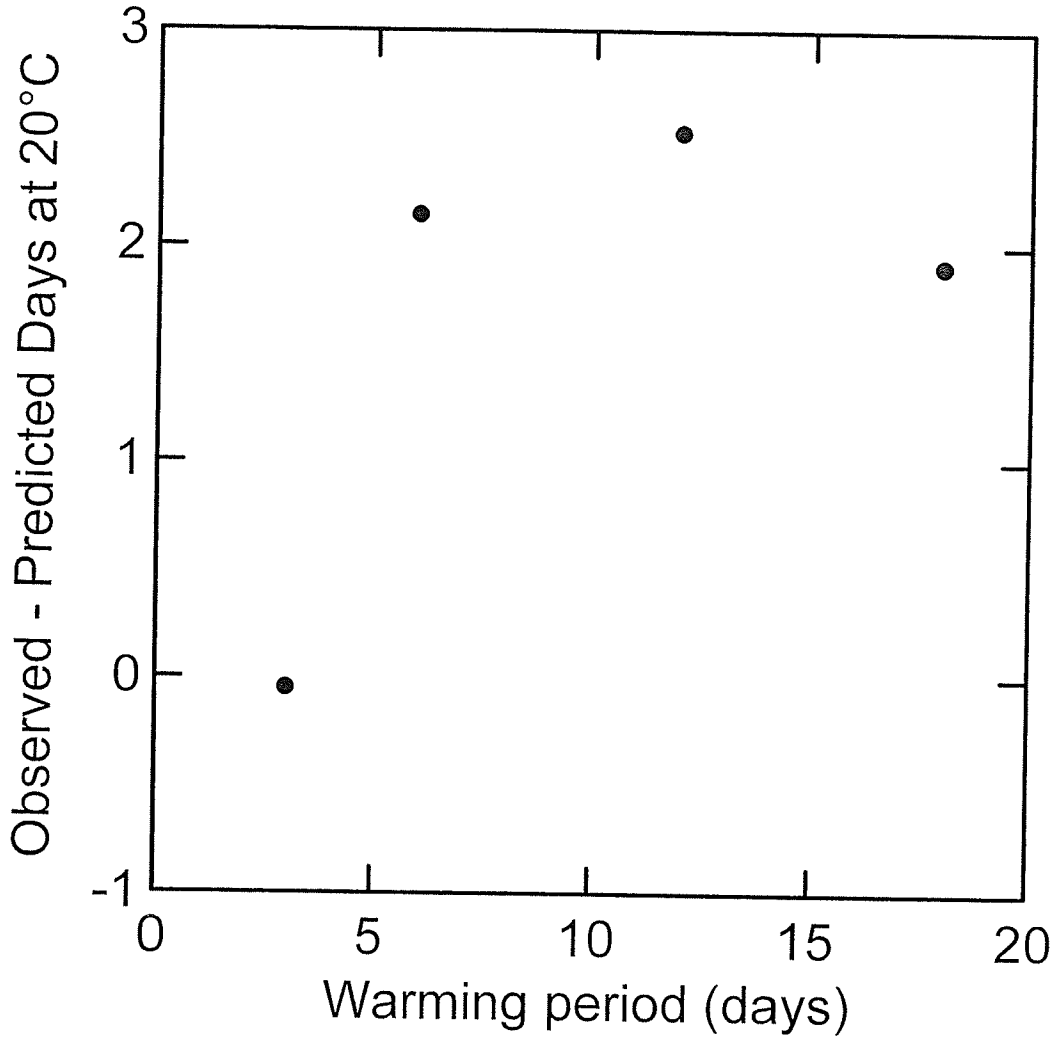

Figure 9. Difference between observed and predicted days to emergence of early phenotype *Delia radicum* collected at Shellbrook in 2000 and moved from 1 to 20°C over 3, 6, 12, or 18 days.

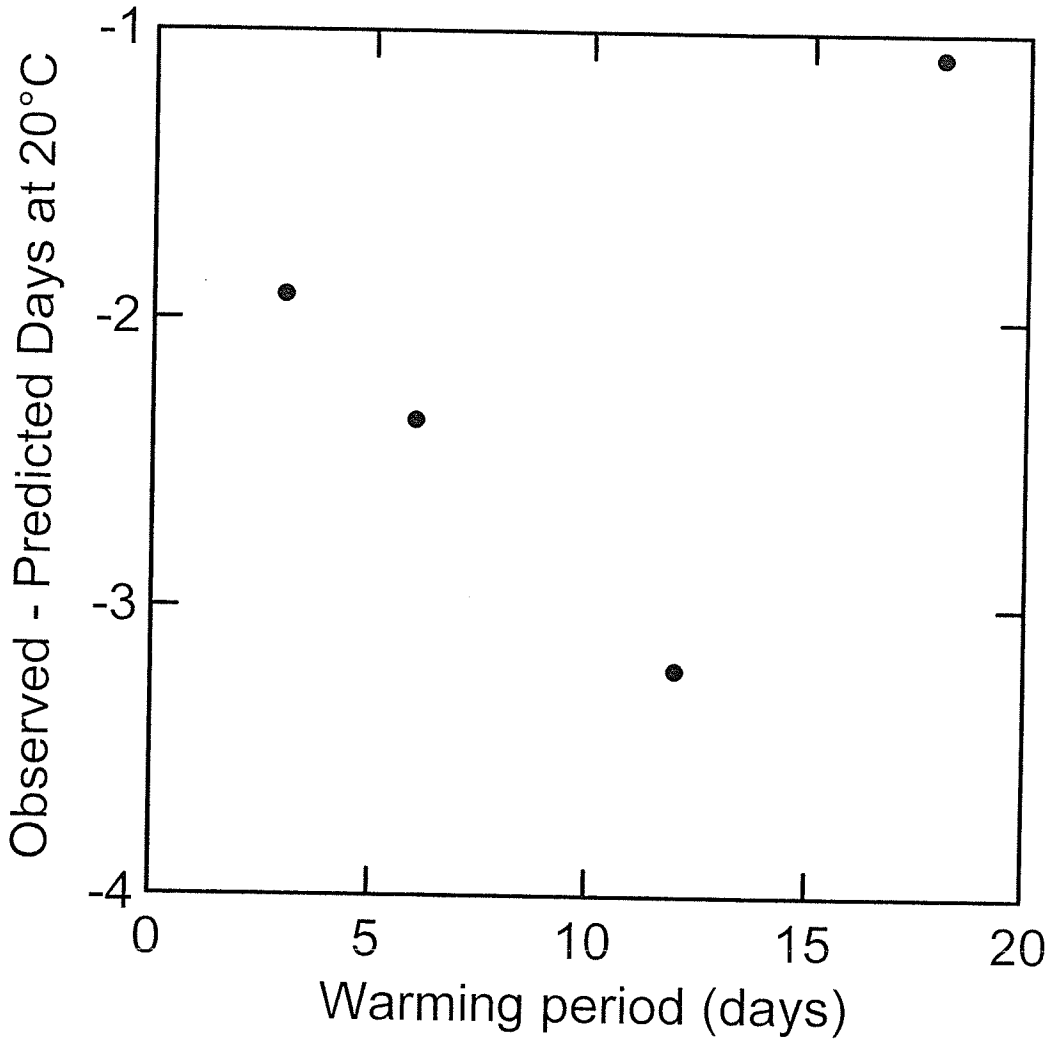

Figure 10. Difference between observed and predicted days to emergence of late phenotype *Delia radicum* collected at Shellbrook in 2000 and moved from 1 to 20°C over 3, 6, 12, or 18 days.

3.2 HOST RANGE ASSESSMENT FOR INTRODUCING A EUROPEAN NATURAL ENEMY OF *DELIA RADICUM*

Introduction

There are environmental risks associated with introducing natural enemies from one part of the world to another (Howarth 1983; 1991; Lockwood 1993b; 1993a; Simberloff and Stiling 1996; Louda et al. 1997; Samways 1997; Lockwood et al. 2001), as there are with all forms of pest control (Pimentel et al. 1984). The practice of introducing polyphagous species should stop, and each prospective biological control agent should be tested to determine its host range (Louda et al. 2003).

Delia radicum (L.) (Diptera: Anthomyiidae) is a target for classical biological control in Canada. Larvae of *D. radicum* feed on the roots of cruciferous crops (Schoene 1916) including canola (Liu and Butts 1982). The levels of infestation and damage to canola roots have increased over the past couple of decades (Soroka et al. 2004). Infested canola roots are more likely to be infected with pathogens (Griffiths 1986b; 1986a; 1991c). Feeding damage can reduce seed yield (McDonald and Sears 1991; Dosdall 1998). Puparia of *D. radicum* are attacked by the parasitoids *Aleochara bilineata* Gyllenhal and *A. bipustulata* L. (Coleoptera: Staphylinidae) (Fuldner 1960). *Aleochara bilineata* is already part of the Canadian fauna (Colhoun 1953; Wishart 1957; Read 1962). *Aleochara bipustulata* is found only in Europe and Asia (Maus 1998; Hemachandra 2004; Hemachandra et al. 2005) and is the most promising candidate for introduction (Hemachandra 2004). To assess potential impacts to Canadian species the host range of *A. bipustulata* must be studied.

Before host range testing can start, a list of species to be tested must be assembled (Kuhlmann et al. 2005; 2006b). First, information about the ecological host range, the

species reported to be attacked in natural settings, of the candidate for introduction and its relatives is examined. This information is used to identify number of species about which to be concerned, whether because they are closely related or ecologically similar to the target pest, or because they represent beneficial or species of conservation significance. It is expected that this initial list will be impractically large. A refined list of species for testing is made by dropping from consideration those species unlikely to be available in sufficient quantities and the species which for some reason or other are not expected to be at risk. The particular information of use for identifying species unlikely to be at risk will depend on the species involved, but could for example include considering a non-target species unlikely to come into contact with the biological control agent. For practical reasons, the list will eventually contain 10–20 species, and can be revised as new information becomes available. All of the species on the list are then tested in conditions designed for maximum expression of the candidate's host range; species not attacked are considered safe and tested no further, and species that are attacked are tested under increasingly natural conditions (van Lenteren et al. 2003; 2005; 2006a; 2006b). Information about a natural enemy's host range can be supplemented with studies of its behaviour (Booth et al. 1995), habitat associations (Benson et al. 2003; Yong and Hoffmann 2006), and coldhardiness (Hatherly et al. 2005) to develop a more complete picture of risk to non-target species.

Adults of *Aleochara* Gravenhorst species are commonly associated with the eggs and larvae of Cyclorrapha (Diptera) species, on which they feed (Klimaszewski 1984). *Aleochara* larvae search for and enter puparia of cyclorraphous Diptera by chewing a hole, then feed on the fly pupa inside as ectoparasitoids (Maus et al. 1998). The reported hosts of *A. bipustulata* during the larval parasitic stage comprise 15 species in seven

families: *Physiphora demandata* (Fabricius) (Ulidiidae); *Piophila casei* (L.) (Piophilidae); a unidentified species of *Lonchaea* Fallen (Lonchaeidae); *Delia radicum* (L.), *D. platura* (Meigen), *D. antiqua* (Meigen), *D. floralis* (Fallen), *D. florilega* (Zetterstedt), *D. coarctata* (Fallen), *Adia cinerella* (Fallen), *Pegomya betae* (Curtis) (Anthomyiidae); *Musca domestica* L. (Muscidae); *Lucilia sericata* (Meigen) (Calliphoridae); and *Sarcophaga* (*Helicophagella*) *gorodkovi* (Grunin), *Sarcophaga* (*Helicophagella*) *rohdendorfi* (Grunin), and *Ravinia pernix* (Harris) (Sarcophagidae) (Maus et al. 1998). All these species are reported as hosts of *A. bipustulata* in the field except *D. antiqua*.

The ecological host range of *A. bipustulata* is limited by several factors. First, it is limited by habitat associations, since *A. bipustulata* larvae can only develop in puparia they contact. Literature reports about habitat associations prior to Lohse's (1986) paper about distinguishing *A. bipustulata* from structurally similar *Aleochara* species should be interpreted cautiously (Maus et al. 1998). The greatest number of literature reports is from cruciferous crops (Maus et al. 1998). However, *A. bipustulata* has also been reported from dung of cows (Kirk 1992; Jonasson 1994a; Vorst 2001), horses (Sychevskaya 1972; Psarev 2002), yaks and marmots (Sychevskaya 1972). Puparia collected in supra-littoral algae may have yielded *A. bipustulata*, but the puparia may have come from dung, and *A. verna* Say is listed as a synonym of *A. bipustulata* (Fabritius 1981; Fabritius and Klunker 1991) although it is not (Lohse 1986; Maus 1998), so *A. bipustulata* may not be associated with algae at all. Reliably identified *A. bipustulata* have been collected from flood refuse, though, which may have included seaweed (Vorst 2001). Single records report *A. bipsustulata*'s occurrence in carrion (Peschke et al. 1987b), ant nests (Sieber 1982), wheat (Dobson 1961) and oat fields (Jones 1965), pea fields (Zatjamina 1971),

carrot fields (Ramert et al. 2001), apple and pear orchards (Balog et al. 2003), and onion fields (Fuldner 1960). Two reliably-identified *A. bipustulata* were collected under bark of *Betula*, one a stump and the other a dead, standing tree (Vorst 2001; Vorst, personal communication March 2006). Several older reports exist of *A. bipustulata* in fields of beans (Miles 1948; Dinther 1953; Darvas and Kozma 1982). Finally, *A. bipustulata* is reported from either potato or sugar beet fields, or possibly both (Sol 1972; Roloff and Wetzel 1989). Diptera species in the same habitats as *A. bipustulata* are at greater risk than those species which are not.

Not all species with which *A. bipustulata* larvae come into contact are suitable hosts, so additional factors must be at play in dictating a particular species' acceptability and suitability as a host. For example, no adult *A. bipustulata* emerged from puparia of species of Agromyzidae, Faniidae, Drosophilidae, and Muscidae collected from the same cruciferous crops with *D. radicum* which were parasitized (Jonasson 1994b). Similarly, dung pats with *A. cinerella* parasitized by *A. bipustulata* also contained puparia of species of Muscidae, Sepsidae, and Sphaeroceridae which were not (Kirk 1992). Entrance holes on puparia made by *A. bilineata* are most often where the ridges on the puparium are smallest (Royer et al. 1998), so puparium structure could be an important determinant of host susceptibility for *A. bipustulata*. There is evidence that *A. bipustulata* prefer puparia of a certain mass (Ahlstrom-Olsson 1994) or width (Jonasson 1994b), so the importance of puparium size in determining host acceptability is worth consideration. Excess pupal material remaining after an *Aleochara* larva finishes feeding may rot and kill the immature parasitoid (Fuldner 1960). The duration of the pupal stage of different host species might be important, as survival of *A. bipustulata* is higher in *D. radicum* puparia containing pupae which develop relatively slowly (Fournet et al. 2004), and survival

decreases with host puparium age for the larvae of *Aleochara bisolata* Casey (Wright and Muller 1989), *A. taeniata* Erichson (White and Legner 1966), and *A. tristis* Gravenhorst (Wingo et al. 1967). Given a choice, both *A. bipustulata* and *A. bilineata* prefer to enter puparia in which the pupa is in the phanerocephalic stage over puparia containing a pharate adult (Fournet et al. 2004).

This study is the first part of an attempt to determine the environmental risk of introducing *A. bipustulata* to the Canadian prairies to control *D. radicum*. The first objective was to study *A. bipustulata*'s habitat associations to clear up some uncertainty in the literature and predict what Diptera species *A. bipustulata* will likely encounter. The second objective was to study *A. bipustulata*'s fundamental host range, the range of hosts which are suitable in an artificial laboratory setting (Klinken and Heard 2000). The relevance of the host's weight and time required to complete the pupal stage were also studied. Explicit hypotheses about the importance of puparial structure were not tested, but some Diptera with unusual structure were exposed to *A. bipustulata* larvae. To allow for maximum expression of host range, the parasitoid larvae were exposed to puparia and decisions made by a foraging adult female *A. bipustulata* removed from consideration.

Selection of Species

Methods

Diptera species were selected for testing according to the methods of Kuhlmann et al. (2005; 2006b), with some necessary modifications. As the recorded hosts of *A. bipustulata* are in seven families, the first step was to find information about every Nearctic, Palaearctic, and Holarctic species from these seven families whose larvae develop in at least one of the habitats from which *A. bipustulata* is recorded. This search yielded more than 400 species. Much of the information used to compile this list is found

in Ferrar (1987), which those interested in constructing a list of non-target Cyclorrapha species should consult first; however, this book was not found until most of the information was gathered from the primary literature. The next step should have been to remove species at little risk of attack for a relevant reason, such as size outside the suitable range, disparate geographical distribution or climatic requirements, and asynchronous seasonal cycles. However, the likely geographical distribution and seasonal cycle of *A. bipustulata* in North America have not yet been explored. Also, although it was known that size and structure of the puparium and duration of the pupal stage were likely important, there was not enough information to apply these criteria to a Diptera species and assert that the species is unlikely to be attacked. Further, the size and pupal duration were unknown for the majority of the species on the initial list. Instead of applying the first filter as prescribed, certain species were selected instead to represent groups of ecologically or taxonomically related species. After applying the second filter, removing species expected to be difficult to obtain, there was a list of 14 species. Safeguard species of conservation concern could not be included because contact with Diptera taxonomists at the Canadian National Collection and insect conservation workers revealed that there are no lists of threatened Diptera in Canada. Beneficial species and species with remarkable puparial structure were also considered for inclusion. The list of species actually used for testing is not the same as the original list, as I was fortunate to get some extras, but unable to find others.

Puparia of each species were weighed individually on a Mettler AE 160 electronic balance to the nearest 0.1 mg to determine the mean mass for a species. The duration of the pupal stage in days at 20°C was determined by checking developing larvae daily for pupariation, holding puparia at 20°C for emergence of adults, and checking emergence

daily. The individuals used to determine duration of the pupal stage were those not exposed to *A. bipustulata* (see 'Testing of Fundamental Host Range').

Results

The species which were tested, the mean puparium weight and pupal duration of each is in Table 5.

Discussion

The infraorder Cyclorrapha, or Muscomorpha, contains two sections, the Aschiza and Schizophora (McAlpine 1989). *Episyrphus balteatus* (De Geer) (Diptera: Syrphidae) was included in the filtered list as a representative of the Aschiza. It also represents the family Syrphidae and their atypical puparia, which are humped anteriorly rather than barrel-shaped (Ferrar 1987). *Episyrphus balteatus* was selected over other syrphids because it was available commercially. All other species tested are in the subgroup Schizophora.

The Schizophora contains two subsections, the Acalyptratae and Calyptratae (McAlpine 1989). The Acalyptratae contains between eight and ten superfamilies (McAlpine 1989), three of which contain the five acalyptrate species I tested. *Psila rosae* (Fabricius) (Diptera: Psilidae) is the only representative of the Diopsoidea superfamily. This species was the obvious choice as a representative from carrot fields, a reported habitat of *A. bipustulata*. Like the other acalyptrates I tested, *P. rosae* also represents species with relatively small puparia (Table 5). The only *Aleochara* species known to attack *P. rosae* is *A. sparsa* Heer (Wright et al. 1946; Maus et al. 1998).

Spelobia luteilabris (Rondani) (Diptera: Sphaeroceridae) was included to represent the smallest cyclorrapheous species; its puparium weighs less than 1 mg. It is the only representative of the superfamily Sphaeroceroidea. The only record of an

Aleochara species attacking a sphaerocerid is *Copromyza marginata* Adams, which supports complete development of *A. bisolata*. Larvae of *S. luteilabris* develop feeding on fungi (Hayashi and Tuno 1998) dead molluscs and small mammalian carrion (Buck 2001), and carrion is a reported habitat of *A. bipustulata*. The other three acalyptrates are in the superfamily Tephritoidea.

Carrion passes through stages as it decays, and each stage has certain arthropod groups associated with it (Chapman and Sankey 1955; Payne 1965; Tullis and Goff 1987). The larvae of Piophilidae are a major part of the Diptera fauna of the advanced decay stage, which follows the active decay stage and its accompanying exodus of calliphorid larvae (Payne 1965; Anderson and VanLaerhoven 1996). *Stearibia nigriceps* (Meigen) (Diptera: Piophilidae) was included to represent the fauna of the late decay stage.

The two other acalyptrates have larvae under bark, a reported habitat of *A. bipustulata* and a habitat typical of *Lonchaea* larvae (Diptera: Lonchaeidae) (McAlpine 1964; Kovalev 1973; 1975; 1976; 1977; 1979; 1981; 1984). *Lonchaea* species are found under the bark of deciduous and coniferous trees, and individual species lives are confined to one or the other (Ferrar 1987). *Lonchaea fugax* Becker and *L. scutellaris* Rondani, which could not be separated as larvae, were tested together as representatives of the *Lonchaea* from dead deciduous trees, where they feed on dead insects (Kovalev 1977). *Lonchaea corticis* Taylor was selected to represent the species from coniferous trees. It is also a safeguard species, as its larvae feed on pupae of the pest *Pissodes strobi* Peck (Coleoptera: Curculionidae) (Harman and Wallace 1971; Alfaro and Borden 1980; Hulme 1989; 1990).

The other selected species are all Calyptratae. There are three calyptrate superfamilies, the Hippoboscoidea, Muscoidea, and Oestroidea (McAlpine 1989). Three muscoid families were included on the filtered list, the Anthomyiidae, Fanniidae, and Muscidae, as were three oestroid families, the Calliphoridae, Sarcophagidae, and Tachinidae.

Pegomya hyoscyami (Panzer) and *P. flavifrons* (Walker) (Diptera: Anthomyiidae) were tested as one species, since they were indistinguishable as larvae. Their inclusion was by chance, as when I tested them I hoped they were *Delia echinata* (Seguy) (Diptera: Anthomyiidae), which would have represented the *cardui* subsection of the *radicum* section of the genus *Delia* (Griffiths 1991a). Both species are leafminers of Caryophyllaceae species, and *P. hyoscyami* also mines Solanaceae leaves (Griffiths 1982). *Pegomya hyoscyami* is a reported host of *A. bipustulata* (Maus et al. 1998).

The only Fanniidae species tested was *Fannia scalaris* (Fabricius). This species was included to represent the family, with its unusual puparium structure. Puparia of Fanniidae are covered in tubercles, as are the larvae, whereas the typical puparium is relatively smooth (Ferrar 1987). Larvae of *F. scalaris* are known to develop in garbage, dung, fungi, nests of Hymenoptera, mammal and bird nests, dead molluscs, and vertebrate carrion (Ferrar 1987; Horsfield et al. 2005). Only one *Aleochara* species in known to parasitize *Fannia* species, *Aleochara castaneipennis* Mannerheim (Moore and Legner 1971).

About one third of the 400 species on the initial list were from the family Muscidae, and six were tested. An effort was made to include representatives from the subfamilies with the greatest number of species on the initial list. The Muscini tribe of Muscinae (Skidmore 1985) is represented by *Musca domestica* L. and *M. autumnalis* De

Geer. In addition to having larvae in dung, *M. autumnalis* was appropriate for inclusion as a representative of the subgenus *Eumusca*, whose puparia harden by calcification rather than by phenolic tanning (Ferrar 1987). Maus et al. (1998) include *M. domestica* as a host of *A. bipustulata*. The Muscinae tribe Mesembriini is represented by *Polietes domitor* (Harris), whose larvae are known primarily from the horse dung (Skidmore 1985; Ferrar 1987).

The subfamily Reinwardtiinae includes *Muscina levida* (Harris), a species with similar larval pabula to *F. scalaris* (Skidmore 1985). *Muscina levida* was also included to represent the *Muscina* species with larvae around the roots of Canadian cruciferous crops (Brooks 1951). Finally, *M. levida* is relatively common around the area where the study was to take place (Cuny 1978).

The final two muscid species were included to represent the subfamily Azeliinae (Skidmore 1985), although their correct taxonomic placement is not clear (Schuehli et al. 2004). More than 20 *Hydrotaea* species are known to have larvae in the habitats from which *A. bipustulata* is reported, particularly carrion and dung, and *H. ignava* (Harris) was tested as their representative. It is primarily a forest species, with larvae in carrion and dung (Martinez-Sanchez et al. 2000; Buck 2001). *Ophyra aenescens* (Wiedemann) larvae develop in carrion (Wells and Greenberg 1994) and dung as facultative predators (Skidmore 1985). This is a beneficial species, as it is used to control *M. domestica* larvae in livestock production (Farkas et al. 1998; Hogsette and Jacobs 1999; Hogsette et al. 2002).

The four remaining species are all in the superfamily Oestroidea (McAlpine 1989). Two Calliphoridae species were used to represent the Diptera fauna of carrion in the fresh, bloat, and active stages of decay, when calliphorid larvae are the dominant

larval Diptera (Anderson and VanLaerhoven 1996). Larvae of calliphorid species occupy a variety of niches, feeding on living and dead animal material (Shewell 1987; Rognes 1998). *Calliphora vicina* (Meigen) was tested as a representative of the cosmopolitan (Rognes 1998) subfamily Calliphorinae. *Lucilia sericata* (Meigen) represents the temperate (Rognes 1998) subfamily Luciliinae. *Calliphora vicina* is a recorded host of 12 *Aleochara* species, and *L. sericata* is a recorded host of even more, including *A. bipustulata* (Maus et al. 1998). In addition, both were known to occur in the study area (Cuny 1978).

Agria mamillata (Pandelle) (Diptera: Sarcophagidae) was included in the filtered list to represent the subfamily Paramacronychinae; the recorded sarcophagid hosts of *A. bipustulata* are in the subfamily Sarcophaginae (Pape 1996). *Agria mamillata* is not found in North America, but *Agria housei* Shewell is; this species is often called *Pseudosarcophaga affinis* (Fallen) in the literature (Shewell 1971). *Agria mamillata* is intended to satisfy safeguard criteria as a proxy for *A. housei*, a natural enemy of *C. fumiferana* (Wilkes et al. 1949) and other forestry pests (Shewell 1971; Sabrosky and Reardon 1976; Nealis 1991). Larvae of *A. mamillata* are predators of *Yponomeuta* species pupae (Kuhlmann 1995). Its availability was also a consideration.

The final species on the filtered list was *Exorista larvarum* (L.) (Diptera: Tachinidae). Its inclusion was foremost to satisfy safeguard criteria, as all tachinid species are parasitoids in their larval stage, and many are important agents for control of pests (Stireman et al. 2006). *Exorista larvarum* is a polyphagous Palaearctic species deliberately introduced to North America for control of *Lymantria dispar* L. (Lepidoptera: Lymantriidae) (Sabrosky and Reardon 1976). If *A. bipustulata* is introduced to Canada, it will be in the same habitat as *Exorista mella* (Walker), a parasitoid of

Mamestra configurata Walker (Lepidoptera: Noctuidae) (Wylie and Bucher 1977). Also, *E. larvarum* was available from a laboratory colony.

Testing of Fundamental Host Range

Insect Rearing

A colony of *A. bipustulata* was maintained according to the methods described by Hertveldt et al. (1984). The bottom of a 6 cm by 3.5 cm diameter clear plastic pill container was removed, and a disc of 1 mm mesh glued at a 30° angle across the middle of the vial approximately halfway up. The top of this container was half filled with light expanded clay aggregate (LECA) pellets. Ten to 20 adult beetles were kept in the top of the container and fed three times per week with two *D. radicum* pupae from which the puparial case had been removed. Eggs were collected three times per week by washing water through the LECA onto a flat-bottomed coffee filter in a Buchner funnel. Eggs were transferred with a fine paint brush from the coffee filter to a moist filter paper in a 5 cm diameter tightly-sealed Petri dish and held for eclosion of larvae. For colony maintenance, about 40 larvae were added to a 9 cm loosely-sealed Petri dish where the same number of *D. radicum* puparia sat on a moist mixture of sand and vermiculite. After the larvae were added the puparia were covered with another layer of the same substrate. The colony was started with free-living adult beetles, and adults emerged from *D. radicum* puparia, both collected around the roots of *Brassica* vegetables in southern Sweden in 2004. These were supplemented with beetles collected in the same manner in southern Sweden in 2005, and Galmiz, Switzerland in 2005 and 2006. During the winter the colony was held in a quarantine facility at the University of Manitoba Department of Entomology at 21°C, 16:8 h light:dark, and 80% RH. During the summer the containers

were kept on the laboratory bench at CABI Europe Swiss Centre at room temperature with natural daylight.

Delia radicum for experimental controls and for rearing *A. bipustulata* were reared according to Whistlecraft et al. (1985b). For non-target species tested in Winnipeg (*L. corticis*, *M. autumnalis*), rearing was done in an environmental chamber at 21°C and 16:8 L:D. Controls for testing the remaining species were reared at ambient room temperatures (18–32°C) with 16:8 photoperiod. Adults were provided water, unrefined sugar, yeast, and milk powder for food and rutabaga, kohlrabi, or white radish for oviposition and larval rearing.

Puparia of *E. balteatus* were purchased from Koppert Biological Systems. Adults were reared at ambient temperatures at 16:8 L:D in a 78 by 41 by 41 cm wooden frame cage with 1 mm plastic mesh sides and top and a wooden bottom. Adults received crushed "Pure Honey Bee Pollen" (Springfield Apiaries, Anola, Manitoba), sugar cubes and water from a cotton wick, all placed on a stand in the middle of the cage, 30 cm from the cage bottom, meant to facilitate mating (Frazer 1972). A diverse assortment of aphids was offered daily for oviposition in 9 cm diameter Petri dishes with a moist filter paper in the bottom. One or two *E. balteatus* larvae were reared per Petri dish, and more aphids were added as necessary.

A culture of *P. rosae* was started with pupae from Agroscope FAW in Wadenswil, Switzerland and reared according to Staedler (1971), at ambient room temperature (18–32°C) and 16:8 L:D. Adults were provided with water and a paste of unrefined sugar, honey and yeast hydrolysate. Eggs were collected using a black cloth disc over a sponge, with a carrot top inserted in the middle. The sponge was fitted into a 9 cm diameter plastic dish to retain water, and a circular nylon mesh was attached to the top of the cloth

with elastic bands to simulate the texture of soil. Eggs were washed into a 30 by 30 by 20 cm ceramic tray half filled with moist sand, whole carrots with green tops, and carrot seedlings. Larvae were collected five weeks after the eggs were added to the trays and kept in 5 cm diameter Petri dishes with sand and a small piece of carrot until puparia formed.

Adults of *S. luteilabris* were captured in vials as they visited a bait of perch fillets outside the CABI centre in Delémont on 20 June 2006. These adults were kept in a square plastic box at ambient room temperatures (18–32°C) and 16:8 L:D. Unrefined sugar, water, yeast hydrolysate, milk powder, crushed bee pollen and honey were provided for the adults. Eggs were collected and larvae reared in 9 cm Petri dishes with pig kidney pieces on moist sand.

Larvae of *S. nigriceps* were collected 20 July 2006 from the paste-like remains of a pig at the advanced decay stage at a sewage treatment plant in Lausanne, Switzerland. Thousands of larvae were collected, and about 100 were moved each day to ambient temperatures in a 10 by 10 by 10 cm clear plastic box with screen on top for ventilation and 2 cm sawdust substrate for pupation. The remaining larvae were kept at 2°C until needed, and did not seem ill-affected by up to two weeks at this temperature.

Larvae of *L. fugax* and *L. scutellaris* ('*Lonchaea* spp.') were collected under the bark of a dead, fallen *Populus* at Gletterens, Switzerland on 8 May 2006. The larvae were kept in Petri dishes with moist filter paper for about one month at 10°C, and then moved to ambient room temperature (18–32°C) and 16:8 L:D for formation of puparia.

Lonchaea corticis larvae were collected by members of the Pacific Forestry Centre who obtained terminal leaders of *Picea sitchensis* (Bong.) Carr. (Pinaceae) infested with *Pissodes strobi* Peck (Coleoptera: Curculionidae) from Jordan River, British

Columbia on 1 February 2005 and 25 January 2006. The leaders were shipped to Winnipeg where the bark was peeled away and the *L. corticis* larvae transferred to 9 cm loosely-sealed Petri dishes with a moist filter paper and *P. strobi* pupae for food. The dishes were kept in the same environmental chamber as the *A. bipustulata* until puparia formed.

Larvae of *P. hyoscyami* and *P. flavifrons* ('*Pegomya* spp.') were collected from mined spinach leaves in a greenhouse at the CABI centre between 11 and 20 July 2006. They were kept in Petri dishes with a filter paper lined bottom and provided with spinach leaves until puparia formed. The leaves were checked daily and replaced as required.

Fannia scalaris adults were captured in a blowfly trap, a rectangular screen cage with a funnel in the bottom suspended over pig kidney bait, in a meadow near the CABI centre on 14 June 2006. Methods for rearing were the same as for *S. luteilabris*.

Puparia to start the *M. domestica* colony were obtained from Bayer CropScience and reared according to Frings (1948). Adults were provided unrefined sugar, water, and milk powder. The oviposition substrate and larval rearing medium were dog biscuits soaked in water with a small amount of brewers' yeast.

A colony of *M. autumnalis* was started with puparia from the University of Minnesota, and maintained according to Knapp (1985). Adult flies were kept in a clear plexiglass-sided cubic cage with a sleeve at 27°C and 16:8 L:D, and provided with water in a beaker with a paper towel wick and a dry diet of 50% sucrose, 25% dried egg powder, and 25% non-fat milk powder. Eggs were collected by providing adults with a 500 mL plastic container filled with cow dung, which had been frozen while less than 3 h old. After the container had been in the adult cage 24 hours, it was removed to the same

chamber as the *A. bipustulata* for larval development. Mature larvae left the container to pupate in a tray with sand upon which the larval rearing container sat.

Larvae of *P. domitor* were collected in pastures outside Saignelegier, Switzerland between 7 and 26 July 2006 by digging through pats of horse dung. The larvae were taken to the laboratory and kept at ambient room temperature (18–32°C) and 16:8 L:D in square plastic boxes half filled with previously frozen but fresh-collected horse dung. It was necessary to freeze fresh dung to avoid contaminating the culture with predators.

Muscina levida adults to start a colony were collected 21 May 2006 with the same trap in the same location as was used for *F. scalaris*. *Hydrotaea ignava* adults to start a colony were collected on the same date, using the same method, as *S. luteilabris*. Rearing methods and conditions for both species were the same as for *S. luteilabris*.

Puparia from Andermatt BioVet AG were used to start the colony of *O. aenescens*. Adults were given water, yeast hydrolysate and unrefined sugar in separate containers for food, and a black cloth wrapped around a ball (~2 cm diameter) of artificial diet for oviposition. The artificial diet was made as close as possible to the specifications of Farkas et al. (1998): 125 g rolled oats, 75 g dry rabbit food, 50 g corn meal, and 50 g dry cat food, moistened to a paste with water. Eggs were transferred from the cloth to a square box with 2 cm sand in the bottom and about 50 g of diet every two days with a moistened paintbrush, and the larvae developed in the box until puparia formed. Rearing was done at ambient room temperature (18–32°C) and 16:8 L:D.

The *C. vicina* colony was started by placing a wire cage over a Petri dish with beef liver resting on moist sand under a bush at Delémont, Switzerland from 26 to 29 May 2005. Adult flies were kept in cubic cages at ambient room temperature (18–32°C) and 16:8 L:D, and provided with water, unrefined sugar, honey and yeast hydrolysate in

separate containers, and a piece of beef liver in a square box with a base of sand for oviposition. The boxes were recovered every two days, and liver added as necessary until puparia formed. Three adult *L. sericata* females were caught in the act of ovipositing into the larval rearing boxes for *C. vicina* on 27 July 2005 and these were used to establish a colony. The rearing methods and conditions were the same as those used for *C. vicina*.

Larvae of *A. mamillata* were obtained by collecting tents of *Yponomeuta evonymellus* L. (Lepidoptera: Yponomeutidae) on *Prunus padus* L. (Rosaceae) trees near Muenster, Switzerland on 22 July 2005 and 17 July 2006. The cocoons were dissected and *A. mamillata* larvae kept in 9 cm Petri dishes with moist filter paper and some *Y. evonymellus* pupae for food until puparia formed.

Exorista larvarum was obtained from a colony at the University of Bologna, Italy. Adults were kept in a square plastic cage at 25°C and 16:8 L:D, and provided with sugar cubes and water. Three times per week mature *Galleria mellonella* (L.) (Lepidoptera: Pyralidae) larvae were removed from freshly-spun cocoons and placed in the cage with the adult tachinids. After half an hour the larvae were removed and kept without food in loosely sealed urine cups in the same environmental conditions as the adult flies until the formation of puparia. *Galleria mellonella* were reared on an artificial diet at 30°C in darkness. The diet was the same as the one used at the University of Bologna: 1 kg corn flour, 1 kg brown flour, 2 kg white flour, 1 kg milk powder, 900 kg bee wax, 1 kg glycerine, 0.5 kg brewer's yeast, and 2 kg honey.

Testing

Experiments to test *A. bipustulata*'s fundamental host range were based on the 'no-choice black box test' (van Lenteren et al. 2003; 2005; 2006a; 2006b). The age, rather than physiological stage, of each puparium was controlled, as only puparia 3–4 days old

were used. Each replicate consisted of four plastic vials, 4.5 cm tall and 2.2 cm diameter, about half full of a moistened mixture of sand and vermiculite. Two of the vials each had one *D. radicum* puparium buried to half the depth of the substrate, and the other two each had a puparium of the non-target species to be tested. An *A. bipustulata* larva not more than two days old was added with a moistened paintbrush to one of the *D. radicum* vials and one of the non-target vials. All of the vials were then kept at 20°C and 16:8 L:D. After five days, the volume of substrate in the vials was reduced to about 5 mm to make it easier to determine the date of emergence, and the puparia that were exposed to the *A. bipustulata* larvae were checked for host acceptance. A host was considered to have been accepted if an entrance hole or parasitoid larva was visible under a microscope after moistening the puparium with water and drying it on paper towel. Puparia were kept at 20°C and monitored daily for at least 45 days after the *A. bipustulata* larva was added for emergence of adult insects, which was monitored daily. Puparia from which nothing emerged were dissected. The number of emerging parasitoids relative to the number of attacked puparia was considered to be a measure of host suitability. Healthy *A. bipustulata* adults inside dissected puparia were included with the number of emerging parasitoids.

There were some deviations from the above standard protocol. In the first 100 replicates with *L. corticis*, during winter 2005, the vial with *D. radicum* alone was not included. The *A. mamillata* puparia exposed to *A. bipustulata* in summer of 2005 were kept through the winter in a subterranean insectary, and the *A. mamillata* which emerged in the spring were counted as having emerged. In 2006, the *A. mamillata* puparia were dissected and healthy pupae were scored as emerged. The two vials with *D. radicum* were often used as controls for replicates of several different non-target species, but one pair of

D. radicum vials was not used more than once for a particular non-target species. The vials were arranged to get maximum replication from the *Aleochara bipustulata* larvae available, so that the first *D. radicum* exposed in a day to *Aleochara bipustulata* was often the controls for more non-target species than the final pair of *D. radicum*.

Voucher specimens of all non-target species were deposited at the J.B. Wallis Museum at the University of Manitoba. Additional voucher specimens of some species were also kept at CABI in Delémont. If the identity of a species was not known for certain, it was checked with a taxonomic specialist for the group.

Analysis of Data

For each non-target species, the proportion of replicates in which *D. radicum* and the non-target emerged from the negative controls, and the number of puparia attacked, supporting development of *A. bipustulata*, and producing an adult fly from the positive controls and test vial were calculated (van Lenteren et al. 2006b). A 95% confidence interval was calculated for each of the proportions.

A 2 X 2 contingency table was used to determine if each non-target species was accepted as a host as often as *D. radicum*. Because the expected frequency of acceptance for some species was small, Fisher's Exact Test was used (Daniel 1990). The same test was used to determine if each non-target species was as suitable a host as *D. radicum*. Suitability relative to *D. radicum* was tested by comparing the number of puparia accepted from which a parasitoid emerged and the number of puparia accepted from which no parasitoid emerged between a particular non-target species and the *D. radicum* controls. Fisher's Exact Test was also used to determine if the number of adult flies emerging from puparia exposed to *A. bipustulata* was different between *D. radicum* and

each non-target species, and if survival of *D. radicum* was independent of exposure to *A. bipustulata*. An alpha level of 0.05 was used as the criterion of significance.

The approach used to determine the importance of mass of host puparia and duration of the pupal stage on host acceptance and suitability of each non-target species was based on Wright et al. (1989). For each species, a standardized value for host acceptance was calculated as the proportion of non-target puparia accepted by the *A. bipustulata* larvae divided by the proportion of *D. radicum* accepted: values < 1.0 indicated that the non-target was less accepted than *D. radicum*. Similarly, a standardized survival value was calculated based on the relative proportions of non-target and target accepted puparia from which *A. bipustulata* emerged. These values, including 1.0 values for *D. radicum*, were plotted against the mean duration of the pupal stage and mean puparium weight of each species.

Results

The proportion of *D. radicum* puparia which were not exposed to *A. bipustulata* and produced a healthy adult was variable, ranging from 0.36–0.88 in the controls for the different non-target species (Table 8). The proportion of *D. radicum* puparia accepted as hosts, 0.33–0.83 (Table 6), and proportion of accepted puparia supporting complete parasitoid development, 0.14–0.84, were likewise variable (Table 7). For most of the tests for non-target species, exposing the *D. radicum* controls to an *A. bipustulata* larva significantly reduced the proportion that produced an adult *D. radicum* ($P \leq .05$). The proportion of *D. radicum* emerged was not significantly different for the *E. balteatus* test ($P = .64$) and was not quite significant for the controls for *M. domestica* ($P = .06$). Only 11 replicates were done with *E. balteatus* (Table 6).

Of the 18 non-target species exposed to *A. bipustulata*, the puparia of 15 were accepted as hosts and entered by *A. bipustulata* larvae (Table 6). Of these 15, six were suitable for complete development of *A. bipustulata* adults: *Pegomya* spp., *Lonchaea* spp., *S. nigriceps*, *P. rosae*, *L. corticis*, and *A. mamillata* (Table 7). Seven non-target species were as likely to be accepted as hosts as *D. radicum*, and the others were less likely (Table 6). There was no relationship between duration of the pupal stage and host acceptance (Figure 11). With the exception of *L. sericata*, whose puparia weighed over 30 mg, the species accepted to an appreciable extent weighed less than about 15 mg (Figure 12). Puparia of non-target species with higher standardized acceptance than *D. radicum* were between about 2 and 4 mg (Figure 11).

Six of the fifteen species accepted were significantly less suitable hosts than *D. radicum* (Table 7). The duration of the pupal stage was greater than 9.5 days for all suitable host species (Figure 13). There was a clear relationship between puparium weight and suitability, where suitable species were relatively light (Figure 14). Non-target species more suitable than *D. radicum* for complete parasitoid development weighed between 2 and 8 mg (Figure 14).

The proportion of puparia not exposed to *A. bipustulata* which produced adult flies was greater than 0.50 for all non-target species except *M. autumnalis* (Table 8). Of the six non-target species which were suitable hosts, only *A. mamillata* had a greater probability of surviving exposure to *A. bipustulata* larvae than *D. radicum* (Table 8). Puparia of some species that were entered by *A. bipustulata* still produced an adult fly, and this phenomenon seemed to be species specific. Thus 95% of the *O. aenescens* puparia which were accepted still produced a fly, whereas only 4% of the *L. corticis* did the same. Data about the tendency of accepted puparia to survive are necessarily

fragmentary, as many species were not accepted often, but what information there is is presented in Table 9. The number of days between when the *A. bipustulata* larva was exposed to the puparium to emergence of an adult *A. bipustulata* was longer for *D. radicum* (31.2 d, S.D. = 3.2) than *L. corticis* (27.6 d, S.D. = 2.7) ($t = 8.88$, df = 205, $P < 0.001$).

As many of the species were collected as larvae for use in the experiments, they were exposed to their own natural enemies. Unidentified parasitic Hymenoptera emerged from four puparia of the *L. corticis* exposed to *A. bipustulata*, three unexposed and one exposed *Pegomya* spp., two unexposed and four exposed *A. mamillata*, one exposed *S. nigriceps,* three unexposed and two exposed *P. domitor*. Also, *Trybliographa rapae* (Westwood) (Hymenoptera: Eucoilidae) emerged from five of the unexposed *D. radicum* control puparia for testing *O. aenescens*, the first species tested in Switzerland; the *D. radicum* larvae were subsequently protected from parasitoids by a cage and no more were parasitized. Finally, although reared indoors, one *E. balteatus* puparium exposed to *A. bipustulata* was parasitized by an unidentified wasp.

Discussion

Lonchaea species are known to support complete development of *A. bipustulata* in the laboratory (Ahlstrom-Olsson 1994), so the suitability of the *Lonchaea* I tested was not unexpected. Numerous other species are reported to host *A. bipustulata* in the literature, and much of the research I did was to evaluate the accuracy of these reports. The piophilid *P. casei* is one example (Fabritius 1981) where it was not certain whether the beetle species hosted was really *A. bipustulata*, but as *S. nigriceps* was an entirely suitable laboratory host it is clear that puparia of at least some species of Piophilidae will support development of *A. bipustulata* larvae if the two are brought together. Another is *P.*

hyoscyami, which reportedly hosts *A. bilineata* in crops (Hille Ris Lambers 1932), but Maus et al. (1998) believe actually hosted *A. bipustulata* in the earlier report. Complete development in *Pegomya* species was confirmed.

In other cases the literature records were brought into question. Adult *A. bipustulata* reportedly emerged from 11, 2, and 3 % of *L. sericata* puparia whose larvae developed feeding on three dead rabbits in a grassy clearing in Germany, and no *A. bipustulata* emerged from *L. sericata* from seven rabbits exposed in a forest (Peschke et al. 1987b). I did 91 trials with *L. sericata*, and although the hosts were accepted, no *A. bipustulata* emerged (Table 7). Neither *Aleochara verna* Say nor *A. binotata* Kraatz were among the carrion fauna recorded by Peschke et al. (1987), although both are structurally similar to *A. bipustulata* and could be mistaken for one another (Maus 1998; Maus et al. 1998). *Lucilia sericata* is a recorded host of *A. binotata* (Maus et al. 1998), so the *Aleochara* which emerged from *L. sericata* may not have been *A. bipustulata*. Carrion is a reported habitat for both *A. binotata*, *A. bipustulata* (Maus et al. 1998) and *A. verna* (Klimaszewski 1984; Tomberlin and Adler 1998).

The house fly, *M. domestica*, is also a recorded host of *A. bipustulata*, both in natural settings and the laboratory, and the laboratory-reared beetles are certainly *A. bipustulata* (Maus et al. 1998). However, I did 32 replicates and *M. domestica* was seldom accepted and never suitable as a host (Table 7). Perhaps the *M. domestica* I offered, which on average weighed 18 mg, were too large; by limiting the larvae's food *M. domestica* puparia as small as 4 mg can be obtained (Wright et al. 1989). Also, *M. domestica* pupae develop quickly (Table 5), and may have been no longer suitable when the 3–4 day old puparia were offered. Survival of *A. bipustulata* is higher in *D. radicum* puparia of a phenotype which develops relatively slowly (Fournet et al. 2004).

Duration of the pupal stage, average puparium mass, and other attributes of the non-target species contributed to their acceptance and suitability. Most of the non-target puparia offered were accepted, but the abnormally shaped *E. balteatus,* the very small *S. luteilabris*, and calcareous the *M. autumnalis* puparia were not (Table 6). Heavier puparia were accepted to a relatively small degree, as were the abnormally shaped *F. scalaris* (Table 6). Puparium structure (Fuldner 1968; Royer et al. 1998) and a chemical signature from the puparium's prothorax region (Fuldner 1968) are known to influence the location of *Aleochara* entrance holes. Experimentally blocking the chemical and offering mock-puparia made from wax of different shapes both alter the sequence of orientation behaviour of the larva prior to starting a hole (Fuldner 1968). Low host acceptance of abnormally-shaped puparia could be an indication that *A. bipustulata* larvae did not recognize some species as potential hosts. More speculatively, puparia of some species may be too hard or thick for the larva to penetrate.

The duration of the pupal stage was most clearly a determinant at the level of host suitability. Puparia of *D. radicum* which take longer to develop are more suitable hosts for *A. bipustulata* (Fournet et al. 2004). Survival of other *Aleochara* species decreases in older puparia (White and Legner 1966; Wingo et al. 1967; Wright and Muller 1989). *Musca autumnalis* pupae inside puparia attacked by *A. tristis* can sometimes actively defend themselves, sealing the entrance hole or somehow isolating the parasitoid larva (Drea 1966), perhaps by the same means as it seals the hole fastening the larva to the inner surface of the puparium. If a pupa's ability to defend itself changes over its development, species which develop more slowly may spend more time in a susceptible state. Also, *Aleochara* larvae entering older puparia may not have time to feed enough to

stop the host pupa developing and adult fly emerging (Wright and Muller 1989).The species I tested which develop most quickly were unsuitable hosts.

The importance of puparium weight was also evident. When calculated as the proportion of accepted hosts which supported development of *A. bipustulata,* the suitability of *A. mamillata*, which weighed 17.7 mg, is relatively high (Table 7) but acceptance is very low (Table 6). Species accepted and supporting development more than once weighed in the range of 2.2–12.4 mg. Heavy puparia contain more host material than the developing *A. bipustulata* can consume, and the excess rots, killing the immature parasitoid (Fuldner 1960; Wright et al. 1989). However, *Aleochara* can develop in a wide range of sizes of a particular host species (Jones 1967), and *A. bipustulata* can develop in puparia of *Delia floralis* Fallen, which is larger than *D. radicum* (Andersen 1982).

Additional factors not investigated in detail were also at work. Most of the *O. aenescens* attacked also survived, and many of the entrance holes were not sealed. A similar phenomenon occurs with other *Aleochara* species, possibly because some hosts do not stimulate the parasitoid larva to feed (Wright et al. 1989). When an *A. bisolata* larva accepts a puparium and then dies, death usually happens before the larva moults to the second instar (Wright et al. 1989). This suggests that while incomplete ingestion and rotting of heavy species may influence success, the incompletely understood interaction between parasitoid larva and host pupa at its early stages is more important in determining if an attempted parasitism event is successful (Wright et al. 1989).

Habitat Use by *Aleochara bipustulata*

Methods

Pitfall traps were used in summer 2005 to assess *A. bipustulata*'s habitat associations. Four sites in Switzerland were selected based on their having a cruciferous crop, a forest, and other habitats of interest. The habitats studied at the Courtemaiche site (Figure 15), in canton Jura, had winter canola, winter wheat, and forest. The dominant trees in the Courtemaiche forest were *Carpinus betulus* L., *Corylus avellana* L. (Betulaceae), *Fagus sylvatica* L. (Fagaceae), *Abies alba* P. Mill. (Pinaceae), and *Cornus sanguinea* L. (Cornaceae). The Galmiz site (Figure 16), in canton Fribourg, had cabbage, carrots, onion, leek, rhubarb, and forest. Dominant trees in the Galmiz forest were *Picea abies* L. (Pinaceae), *Acer pseudoplatanus* L (Aceraceae), *Fraxinus excelsior* L. (Oleaceae), and *Prunus* sp. (Rosaceae). The Jerisberghof site (Figure 17), in canton Bern, had cabbage, potato, and forest. Dominant trees in the forest at Jerisberghof were *F. sylvatica, A. alba, F. excelsior,* and *Pinus strobus* L. (Pinaceae). The Lordel site (Figure 18), in canton Neuchatel, had winter canola, peas, winter wheat, and forest. Dominant trees at the Lordel site were *A. alba, P. abies, C. avellana,* and *F. sylvatica.*

In each habitat eight pitfall traps were placed in two rows of four. The pitfall traps were at least 8 m from one another. When possible, traps were at least 20 m from the edge of a habitat; this was not possible for the onion and carrot fields at Galmiz and the cabbage field in Jerisberghof because the fields were too small. The traps were two 500 mL plastic cups, one inside the other, with salt water as preservative. Each trap was covered by a 30 by 30 cm wooden sheet to reduce effects of rain and sun on the catch. Four traps in each habitat were baited with 20 g of defatted mustard seed meal (Kräuterpflug, Kiel, Germany), known to attract *A. bipustulata* (Riley et al. *In Press*). The other traps were left unbaited, and arranged so baited traps were not adjacent to other baited traps. The bait was held in a gauze bag stapled under a wooden sheet cover.

Traps were monitored weekly as long as possible, but the duration each habitat was monitored depended on when the crop was harvested. Beetles that could be *A. bipustulata* based on external morphology were dissected to compare their genitalia with the illustrations in Maus (1998) and with mounted genitalia of *A. bipustulata* determined by J. Klimaszewski of the Laurentian Forestry Centre. Male *Aleochara* are beyond my ability to identify, so all males were assumed to be *A. bipustulata*. The genitalia of a few beetles were lost while dissecting, and these were assumed to be *A. bipustulata* as well.

In summer of 2006 sentinel puparia, rather than pitfall traps, were used to study habitat associations. Four sites were used, again selected on the basis of each having a cruciferous crop, a forest, and several additional habitats. The Galmiz site was used again, with cabbage, pasture, forest, rhubarb, leek and barley habitats. The Jerisberghof site was also used again, with cabbage, forest, beans, pasture and potato habitats. The Alle site, in canton Jura, had winter canola, *Vicia faba* L. (Legumaceae), wheat, forest and a *Prunus* orchard. Dominant trees at Alle were *F. sylvatica, C. betulus, A. alba, P. abies,* and *F. excelsior.* The Fahy site, in canton Jura, had clover, winter wheat, a *Prunus* orchard, pasture, winter canola, peas, and forest. Dominant trees at Fahy were *A. alba, F. sylvatica,* and *Alnus incana* L. (Betulaceae).

In each habitat eight groups of ten *D. radicum* sentinel puparia were set out using a technique developed to study predation by carabid beetles (Raworth et al. 2004). Groups were at least 8 m apart and at least 20 m from the edge when possible. In the pasture habitats the puparia were placed just outside the fence line to avoid damage from grazing animals. Each group of puparia was fastened to a 15 cm long Post-It sticky note. The puparia and note were buried 1 cm below the soil surface with the puparia under the note. The note was trimmed into an L shape so it could be bent to have part sticking

above the ground. The same 30 by 30 cm wooden covers were placed over the groups of puparia, but this time 11 mm wire mesh was stapled around the four sides to create a cage to keep out vertebrate predators. Half the covers were baited with mustard seed meal as in 2005. The puparia were left out for six days, as a preliminary experiment determined the post-diapause puparia took seven days on average to pass through the vulnerable phanerocephalic stage. At each location the experiment was repeated three times; weekly cabbage or canola root samples and pitfall trap samples from the cruciferous crop habitat were used to time deployment of the sentinel puparia to be synchronized with natural formation of puparia and abundance of *A. bipustulata*. The puparia were recollected at Fahy and Alle on 29 May, 3 July, and 12 July; at Jerisberghof on 31 May, 28 June, and 27 July; and at Galmiz on 12 June, 27 July, and 3 August. Each group of puparia was held for at least 45 days in a plastic vial with moistened sand and vermiculite for emergence of adult *A. bipustulata*; after 45 days all puparia were dissected.

Data from the pitfall traps were analyzed by nonparametric methods, as the data did not satisfy the assumptions for analysis of variance (Daniel 1990). Catch per four traps per week was calculated for each combination of site, habitat, and baited or not with mustard meal. Catch per week was compared between forest and other habitats using a Mann-Whitney test. Among the crops, catch per week was compared between the target habitat (*Brassica* crops), suspected habitat (*Allium* crops), and all other crops, where the association of *A. bipustulata* was unknown, using the Kruskall-Wallis Test. Not enough *A. bipustulata* emerged from the sentinel puparia to warrant further statistical analysis.

Results

No *A. bipustulata* were trapped in the forest, where the sampling effort was the greatest (Table 10). Catch per week was significantly higher in habitats other than forest

than in the forest (Mann Whitney U = 168, $P < 0.001$). There were also no *A. bipustulata* in traps in the carrot field at Galmiz (Table 9), which was separated from the cabbage field by a small road (Figure 16). The relative frequency of *A. bipustulata* in baited and unbaited traps in the 'target' and 'non-target' habitats was significantly different ($\chi^2 = 5.5$, d.f. = 1, $P < 0.05$), so although the rhubarb and leek fields at Galmiz and potato field at Jerisberghof trap catches were relatively high, most of the beetles were in traps baited with mustard meal (Table 10). The high catch in the leek field was strongly influenced by one week's catch, 5–12 July, when 44 *A. bipustulata* were caught in two baited traps. Some time during that week leek field A was harvested and five of the traps were found, properly deployed, at the southern edge of leek field B (Figure 16). The leek fields were noticeably infested with Diptera larvae, probably *Pytomyza gymnostoma* Loew (Diptera: Agromyzidae); fallen and rotting leaves of rhubarb were being consumed by larvae which looked similar to *M. levida*; no Diptera larvae or puparia were noticed in the potato or wheat fields. There was no significant difference among the three types of crop habitat in catch per week of *A. bipustulata* (K-W = 1.19, $P = 0.57$).

Generally, at least 30 of the 80 sentinel puparia deployed in each habitat in 2006 were healthy and appeared capable of hosting *A. bipustulata* (Table 11). One *A. bipustulata* emerged, from the pasture margin habitat at Jerisberghof. This puparium was collected on 28 June.

Discussion

Pitfall traps catch more *A. bipustulata* in plots of canola with mustard seed meal mulch applied to the ground than plots without the mulch (Riley et al. *In Press*). The activity of *Aleochara*, as measured by pitfall traps, is higher among turnips heavily infested with *D. radicum* than in less infested broccoli less than one metre away (Rousse

et al. 2003). The mustard meal bait I used was meant to mimic damaged *Brassica* plants and attract *A. bipustulata* already in the habitat being studied to the traps. An equal number of unbaited as baited traps were used in each habitat to provide information about whether catch in baited traps is indicative of *A. bipustulata* activity in a habitat, or rather if *A. bipustulata* were drawn into a habitat they would not normally occur by the bait. This could be suggested if catch was entirely in baited traps in a habitat. The higher catches in baited traps in non-target habitats like leek and rhubarb are probably indicative that the plan to attract nearby *A. bipustulata* into the traps worked, rather than that *A. bipustulata* were attracted from outside the habitat to the traps. Reliable inferences about *A. bipustulata*'s activity in wheat fields cannot be made on the basis of my data, since activity at Lordel and Courtemaiche was generally low, but in another study only 14 of about 11,000 staphylinids trapped in 42 wheat fields in Germany were *A. bipustulata* (Clough et al. 2007).

Adult *A. bipustulata* have been reported from a variety of open habitats but never from dense forests. Adult *A. bipustulata* were found twice under bark of dead *Betula* in a forest clearing (Vorst 2001; Vorst personal communication, March 2006), and *A. bipustulata* is one of the most widespread and abundant staphylinid species in apple and pear orchards in Hungary (Balog et al. 2003). On the basis of my results and the literature, *A. bipustulata* is not found in forests. I expected to find *A. bipustulata* in the carrot field, as it can be one of the most abundant staphylinids in this habitat (Ramert et al. 2001). The finding that *A. bipustulata* is one of the most abundant staphylinids in pea crops (Zatjamina 1971) also was not supported by my data from Lordel, although the activity of *A. bipustulata* at this site was overall quite low. Older plants are sometimes (Rousse et al. 2003) but not always (McDonald and Sears 1992) less suitable for *D.*

radicum, and the canola at Lordel and Courtemaiche were at or near flowering by the time my traps were first deployed, which may have influenced the activity of *A. bipustulata* at these sites. In another study, the activity of *A. bipustulata* among six different field crops was not different over several years (Andersen and Eltun 2000). It seems *Aleochara bipustulata* can be, but is not always, active in a variety of open habitats.

Activity in a variety of open habitats does not mean the soil in all open habitats is full of *A. bipustulata* larvae seeking hosts, as only one sentinel puparium yielded an adult *A. bipustulata*. From research about *A. bilineata*, we know adult *Aleochara* orient towards cues indicative of the presence of hosts (Royer and Boivin 1999) and lay eggs preferentially in areas where their progeny are most likely to find suitable hosts (Fournet et al. 2001). Also, *A. bipustulata* eggs require an average of seven days at 20°C before they hatch (Fournet et al. 2000), so even assuming eggs were laid the duration the puparia were exposed to *A. bipustulata* was probably too short. The duration of exposure could not be extended, limited as it was by how long the *D. radicum* pupae took to become pharate. Non-target Canadian Diptera species which do not provoke *A. bipustulata* to oviposit by providing the necessary cues, whatever these turn out to be, will not be exposed to *A. bipustulata* larvae and will not be at risk of parasitism.

General Discussion

If complete development of *A. bipustulata* on one of the 49 exposed *A. mamillata* can safely be considered a laboratory artefact, then there are three remaining groups of non-target species to be concerned about. The first is *L. corticis*, which was an even more suitable host in the laboratory than *D. radicum*. A predator of *P. strobi* pupae (Harman and Wallace 1971; Alfaro and Borden 1980), *L. corticis* is generally the most abundant

natural enemy associated with the weevil (Harman and Kulman 1968; Alfaro et al. 1985), and is important in regulating *P. strobi* populations (Hulme 1989; 1990; Nealis 1998; Lavallee et al. 2001). Still, the risk of disrupting natural control of *P. strobi* is low for several reasons. The *P. strobi* feeding ring is at the top of the tree, and *L. corticis* completes its lifecycle, including the pupal stage, under bark above the ring (Harman and Wallace 1971). Puparia form in late April and early May in British Columbia (Alfaro and Borden 1980), which is likely before *A. bipustulata* forages for hosts, although this remains to be conclusively determined, and in the United States puparia can form during the summer (Harman and Wallace 1971; Aukema et al. 2004). Finally, although *L. corticis* may (Harman and Kulman 1968) or may not (Lavallee et al. 2001) be more abundant in stands with a dense overstory, it is a forest species, and based on my pitfall trap data *A. bipustulata* is not found in forests, even when mustard meal bait is used. In my opinion, no more research is needed about the risk to *L. corticis*.

The second group of non-target species to be concerned about is species whose puparia weigh 2–4 mg; in my study, these are represented by *P. rosae*, *S. nigriceps*, and the three *Lonchaea* species, all of which were suitable hosts. Many if not most acalyptrate species probably have puparia around this weight. In choice tests, *D. radicum* puparia 4–8 mg are preferred by *A. bipustulata* larvae for host acceptance over 13–17 mg puparia, but *D. radicum* puparia 3–7 mg are preferred to *Lonchaea* puparia of similar weight (Ahlstrom-Olsson 1994). However, the smaller the puparium of the host, the smaller the adult *Aleochara* will be (Langlet et al. 1998). Larger females of species which mature eggs over their lifetime, like *A. bipustulata*, tend to produce more eggs than smaller females (Rosenheim and Rosen 1991) and have more favourable measures of other fitness components like travelling speed and longevity (Godfray 1994). Conversely, the

development time of *A. bipustulata* in *L. corticis* puparia is less than in *D. radicum*, which could affect the rate of increase. The fitness consequences of *A. bipustulata*'s host choices would be an interesting area for further study and would likely contribute some predictions about its ecological host range, but the cues *A. bipustulata* adults use in selecting habitats and oviposition sites are not sufficiently understood to make any statement about how often *A. bipustulata* will be forced to make decisions about the size of host to exploit. Comparing the fitness of *A. bipustulata* from different host species should be the next step concerning the risk to the relatively small species.

The third group of non-target species to be concerned about are those most closely related to *D. radicum*. Complete development in the *Pegomya* species suggests most Anthomyiidae species will be suitable hosts of *A. bipustulata* in the laboratory. Many *Delia* species are pests, but most of the 162 Nearctic species are not (Griffiths 1991a). About one quarter are known only from two mountain ranges in the Yukon (Griffiths 1991a); assuming *A. bipustulata* will not enter the forest, these are protected by several hundred kilometres of boreal forest. I do not think van Lenteren et al.'s (2003, 2005, 2006a, 2006b) suggested approach of proceeding to experiments where *A. bipustulata* is given a choice of hosts is appropriate to determine the risk to members of the Anthomyiidae family. Non-target species to use in experiments would likely take years to obtain and be difficult to rear as their larval life histories are largely unknown. It makes more sense to study *A. bipustulata* further and determine how specific its host seeking behaviour is to potential hosts in the target habitat. Experiments of this sort should be done to determine the risk to Canadian species closely related to *D. radicum*.

The approach I used to study *A. bipustulata*'s host range was appropriate given what was already known about *A. bipustulata* and what information was required, but

there were areas where potentially useful information was not gathered. Between *A. bipustulata* larvae accepting a host and successfully completing development, the weight and duration of the pupal stage of the host clearly were important. However, some non-target species were not hosts although, on the basis of weight and duration were expected to be suitable; the mechanism allowing *O. aenescens* to avoid stimulating parasitoid feeding and continue development would be helpful to understand in the context of *A. bipustulata*'s host range. Second, although the pitfall traps provided a clear indication about *A. bipustulata* not venturing into the forest, its use of more open habitats remains equivocal. Finally, species that would have been nice to test, like representative Ulidiidae and Sarcophagidae with dung-feeding larvae, could not be found.

This study has identified some questions for future research, but its purpose was to determine *A. bipustulata*'s host range in the context of the safety of introducing a biological control agent to Canada. The risk of parasitism to beneficial Canadian species is small, as *L. corticis* occurs in a different habitat, *A. mamillata* was a very marginal host, and *O. aenescens* and the representative Tachinidae and Syrphidae did not support *A. bipustulata*'s complete development. Ideally, smaller tachinid and syrphid species would have been tested. As *L. sericata* is not an appropriate host, and a single record exists of its occurrence in the well-studied carrion habitat, Canadian Diptera with larvae in carrion should also be safe. More research is required about the risk of parasitism to the more anthropologically neutral species non-target species, and I believe the best way to do this is to fill in the knowledge gap at levels above host acceptance, such as host location and stimuli for oviposition. Finally, before *A. bipustulata* can be introduced its host range as a predator must be investigated.

Table 5. Mean puparium weight and duration of pupal stage of Diptera species exposed to *Aleochara bipustulata* larvae. Species were included based on taxonomic (T), or ecological (E) relationships to reported hosts, as beneficial species (B), or as representatives with unusual puparia (P)

Section	Subsection	Superfamily	Family	Species	Puparium weight (mg) $\bar{x}$ ±SE (N)	Duration at 20°C (days) $\bar{x}$ ±SE (N)	Justification
Aschiza		Syrphoidea	Syrphidae	*Episyrphus balteatus*	27.9±1.10 (25)	7.7±0.29 (7)	B,P
Schizophora	Acalyptratae	Diopsoidea	Psilidae	*Psila rosae*	3.2±0.06 (200)	26.9±1.75 (11)	E
		Sphaeroceroidea	Sphaeroceridae	*Spelobia luteilabris*	<1	7.6±0.14 (13)	E
		Tephritoidea	Piophilidae	*Stearibia nigriceps*	2.8±0.04 (102)	9.5±0.26 (34)	E,T
			Lonchaeidae	*Lonchaea* spp.	2.2 ±0.11 (32)	11.9±0.43 (14)	T
				Lonchaea corticis	3.7±0.10 (100)	11.6±0.10 (153)	T,B
	Calyptratae	Muscoidea	Anthomyiidae	*Pegomya* spp.	7.5±0.32 (65)	17.6 ±0.26 (17)	T,E
				Delia radicum	12.4±0.29 (130)	19.3±0.44 (638)	
			Fanniidae	*Fannia scalaris*	11.6±0.12 (100)	9.5±0.13 (60	E,P
			Muscidae	*Musca domestica*	18.0±0.23 (100)	8.7±0.21 (28)	T,E
				Musca autumnalis	25.1±0.30 (200)	11.6±0.14 (37)	T,E,P
				Polietes domitor	12.3±0.48 (59)	8.9±0.22 (22)	T,E
				Muscina levida	36.6±0.66 (100)	10.0±0.12 (59)	T,E
				Hydrotaea ignava	17.2±0.44 (100)	13.0±0.20 (22)	T,E
				Ophyra aenescens	13.7±0.13 (200)	11.0±0.24 (98)	T,E,B
		Oestroidea	Calliphoridae	*Calliphora vicina*	59.2±0.68 (200)	12.5±0.09 (88)	T,E
				Lucilia sericata	31.3±0.26 (200)	9.5±0.25 (88)	T,E
			Sarcophagidae	*Agria mamillata*	17.7±0.52 (71)	†	T,B
			Tachinidae	*Exorista larvarum*	38.2±1.43 (104)	13.2±0.20 (64)	B

† duration of *A. mamillata*'s pupal stage was not calculated as it is an obligate univoltine species, overwintering as a pupa

Table 6. Proportion (95 % confidence interval) of *Delia radicum* and non-target species puparia accepted as a host by *Aleochara bipustulata* larvae in N replicates, and probability that acceptance is independent of host species. Standardized acceptance (SA) is proportion of non-target puparia accepted over *D. radicum* controls accepted.

Non-target species	N	Proportion entered by parasitoid			SA
		Delia radicum	Non-target	*P*	
Episyrphus balteatus	11	0.64 (.28)	0.00 (.00)	< 0.01	0.00
Psila rosae	18	0.72 (.21)	0.56 (.23)	0.489	0.78
Spelobia luteilabris	25	0.56 (.19)	0.00 (.00)	< 0.001	0.00
Stearibia nigriceps	37	0.37 (.15)	0.46 (.16)	0.486	1.24
Lonchaea spp.	18	0.33 (.22)	0.61 (.23)	0.181	1.85
Lonchaea corticis	173	0.73 (.07)	0.80 (.06)	0.160	1.10
Pegomya spp.	29	0.52 (.18)	0.31 (.17)	0.182	0.60
Fannia scalaris	67	0.72 (.11)	0.03 (.04)	< 0.001	0.04
Musca domestica	32	0.56 (.17)	0.06 (.08)	< 0.001	0.11
Musca autumnalis	115	0.65 (.09)	0.00 (.00)	< 0.001	0.00
Polietes domitor	30	0.60 (.18)	0.37 (.17)	0.120	0.62
Muscina levida	100	0.63 (.10)	0.02 (.03)	< 0.001	0.03
Hydrotaea ignava	39	0.59 (.15)	0.03 (.05)	< 0.001	0.05
Ophyra aenescens	102	0.76 (.08)	0.36 (.09)	< 0.001	0.47
Calliphora vicina	100	0.83 (.07)	0.04 (.04)	< 0.001	0.05
Lucilia sericata	91	0.54 (.10)	0.43 (.10)	0.179	0.80
Agria mamillata	49	0.63 (.14)	0.04 (.05)	< 0.001	0.06
Exorista larvarum	83	0.63 (.10)	0.19 (.08)	< 0.001	0.30

Table 7. Proportion (95 % confidence interval) of *Delia radicum* and non-target species puparia suitable as a host for *Aleochara bipustulata* larvae of N puparia accepted, and probability that suitability is independent of host species. Standardized suitability (SS) is proportion of non-target puparia accepted which were suitable, over suitability of *D. radicum* controls.

Non-target species	*Delia radicum*		Non-target species		*P*	SS
	N accepted	proportion suitable	N accepted	proportion suitable		
Episyrphus balteatus	7	0.14 (.25)	0	0.00 (.00)	†	0.00
Psila rosae	13	0.46 (.27)	10	0.50 (.31)	1.00	1.09
Spelobia luteilabris	14	0.50 (.26)	0	0.00 (.00)	†	0.00
Stearibia nigriceps	21	0.38 (.21)	17	0.29 (.22)	0.73	0.76
Lonchaea spp.	6	0.67 (.38)	11	0.64 (.28)	1.00	0.96
Lonchaea corticis	127	0.74 (.08)	139	0.81 (.07)	0.18	1.09
Pegomya spp.	15	0.60 (.25)	9	0.67 (.31)	1.00	1.11
Fannia scalaris	48	0.46 (.14)	2	0.00 (.00)	< 0.001	0.00
Musca domestica	18	0.22 (.19)	2	0.00 (.00)	1.00	0.00
Musca autumnalis	75	0.84 (.08)	0	0.00 (.00)	†	0.00
Polietes domitor	18	0.39 (.23)	11	0.00 (.00)	< 0.05	0.00
Muscina levida	63	0.52 (.12)	2	0.00 (.00)	0.24	0.00
Hydrotaea ignava	23	0.22 (.17)	1	0.00 (.00)	1.00	0.00
Ophyra aenescens	78	0.54 (.11)	37	0.00 (.00)	< 0.001	0.00
Calliphora vicina	83	0.77 (.09)	88	0.00 (.00)	< 0.01	0.00
Lucilia sericata	49	0.67 (.13)	39	0.00 (.00)	< 0.001	0.00
Agria mamillata	31	0.65 (.17)	2	0.50 (.00)	1.00	0.77
Exorista larvarum	52	0.40 (.13)	16	0.00 (.00)	< 0.001	0.00

† test was not done as no non-target puparia were accepted

Table 8. Proportion (95 % confidence interval) of adult *Delia radicum* and non-target Diptera species emerging in N replicates, and probability that survival after exposure to *Aleochara bipustulata* larvae is independent of host species.

		Proportion of hosts emerging in absence of parasitoid		Proportion of hosts emerging in presence of parasitoid		
Non-target species	N	*Delia radicum*	Non-target	*Delia radicum*	Non-target	*P*
Episyrphus balteatus	11	0.64 (.19)	0.52 (.20)	0.18 (.23)	0.73 (.26)	< 0.05
Psila rosae	18	0.44 (.16)	0.62 (.15)	0.11 (.14)	0.11 (.14)	1.00
Spelobia luteilabris	25	0.60 (.10)	0.59 (.06)	0.16 (.14)	0.36 (.19)	0.20
Stearibia nigriceps	37	0.78 (.10)	0.90 (.07)	0.19 (.13)	0.41 (.16)	0.07
Lonchaea spp.	18	0.46 (.16)	0.92 (.09)	0.06 (.11)	0.17 (.17)	0.60
Lonchaea corticis	173	0.88 (.06)	0.88 (.06)	0.11 (.05)	0.18 (.06)	0.09
Pegomya spp.	29	0.42 (.10)	0.97 (.04)	0.28 (.16)	0.40 (.18)	0.41
Fannia scalaris	67	0.83 (.17)	0.61 (.23)	0.09 (.07)	0.96 (.05)	< 0.001
Musca domestica	32	0.47 (.17)	0.88 (.11)	0.22 (.14)	0.88 (.11)	< 0.001
Musca autumnalis	115	0.62 (.09)	0.32 (.09)	0.05 (.08)	0.32 (.09)	< 0.001
Polietes domitor	30	0.75 (.08)	0.96 (.04)	0.20 (.14)	0.60 (.18)	< 0.01
Muscina levida	100	0.57 (.18)	0.73 (.16)	0.12 (.06)	0.55 (.14)	< 0.001
Hydrotaea ignava	39	0.66 (.17)	0.59 (.18)	0.21 (.13)	0.56 (.16)	< 0.01
Ophyra aenescens	102	0.69 (.13)	0.73 (.14)	0.14 (.07)	0.92 (.05)	< 0.001
Calliphora vicina	100	0.48 (.11)[1]	0.88 (.05)	0.12 (.06)	0.82 (.08)	< 0.001
Lucilia sericata	91	0.39 (.23)	0.78 (.19)	0.07 (.05)	0.75 (.09)	< 0.001
Agria mamillata	49	0.71 (.10)	0.77 (.09)	0.10 (.08)	0.67 (.13)	< 0.001
Exorista larvarum	83	0.36 (.28)	0.64 (.28)	0.13 (.07)	0.64 (.10)	< 0.001

[1] out of 73, since the *Delia radicum* alone treatment was done only in winter 2006

Table 9. Percentage of puparia accepted by *Aleochara bipustulata* larvae as hosts which survived to produce adult flies.

Species	Number of Puparia Entered	Entered Puparia Yielding Fly	%
Psila rosae	10	0	0
Stearibia nigriceps	17	2	12
Lonchaea spp.	11	0	0
Lonchaea corticis	139	5	4
Pegomya spp.	9	2	22
Fannia scalaris	2	2	100
Musca domestica	2	1	50
Polietes domitor	11	1	9
Muscina levida	2	0	0
Hydrotaea ignava	1	0	0
Ophyra aenescens	37	35	95
Calliphora vicina	4	3	75
Lucilia sericata	39	24	64
Exorista larvarum	16	5	31
Agria mamillata	2	1	50
Delia radicum	741	17	2

Table 10. Pitfall trap catches of *Aleochara bipustulata* in different habitats at four sites in Switzerland in 2005.

Site	Habitat	Collection Period	Weeks	Number of *Aleochara bipustulata*			
				Unbaited Traps	Baited Traps	Total	Per week (S.E.)
Courtemaiche	Canola	8vi – 25vii	7	2	0	2	0.3 (.18)
	Forest	8vi – 1viii	8	0	0	0	–
	Wheat	8vi – 5ix	13	0	0	0	–
Jerisberghof	Cabbage	9vi – 6ix	13	1	4	5	0.4 (0.22)
	Potato	9vi – 5vii; 19vii – 6ix	8	9	14	23	2.9 (1.37)
	Forest	14vi – 6ix	12	0	0	0	–
Galmiz	Cabbage	12vii – 6ix	8	17	30	47	5.9 (2.4)
	Carrot	19vii – 9viii	3	0	0	0	–
	Forest	21vi – 6ix	11	0	0	0	–
	Leek	28vi – 6ix	10	4	55	59	6.6 (4.25)
	Onion	9vi – 28vi	3	0	8	8	2.7 (2.19)
	Rhubarb	9vi – 6ix	9	11	24	35	3.9 (1.09)
Lordel	Canola	9vi – 30viii	12	1	1	2	0.1 (0.11)
	Forest	9vi – 6ix	13	0	0	0	–
	Peas	16vi – 19vii	5	2	2	4	0.8 (0.37)
	Wheat	9vi – 6ix	13	2	2	4	0.4 (0.24)

Table 11. Number of *Delia radicum* sentinel puparia recovered, of 80 deployed, at four sites to assess habitat associations of *Aleochara bipustulata*.

Site	Habitat	Recovery		
		First	Second	Third
Alle	feverole	37	27	43
	wheat	5	44	40
	orchard	52	54	53
	canola	44	3	5
	forest	39	13	61
Fahy	grass	50	–	–
	wheat	31	37	16
	canola	55	37	16
	orchard	40	43	56
	pasture	37	64	78
	forest	31	43	56
	peas	34	65	65
Galmiz	rhubarb	47	58	62
	cabbage	50	61	67
	barley	39	–	–
	forest	43	41	60
	pasture	54	69	79
	leek	–	66	79
Jerisberghof	beans	61	48	65
	cabbage	68	49	72
	forest	36	60	33
	potato	61	57	58
	pasture	34	62	42

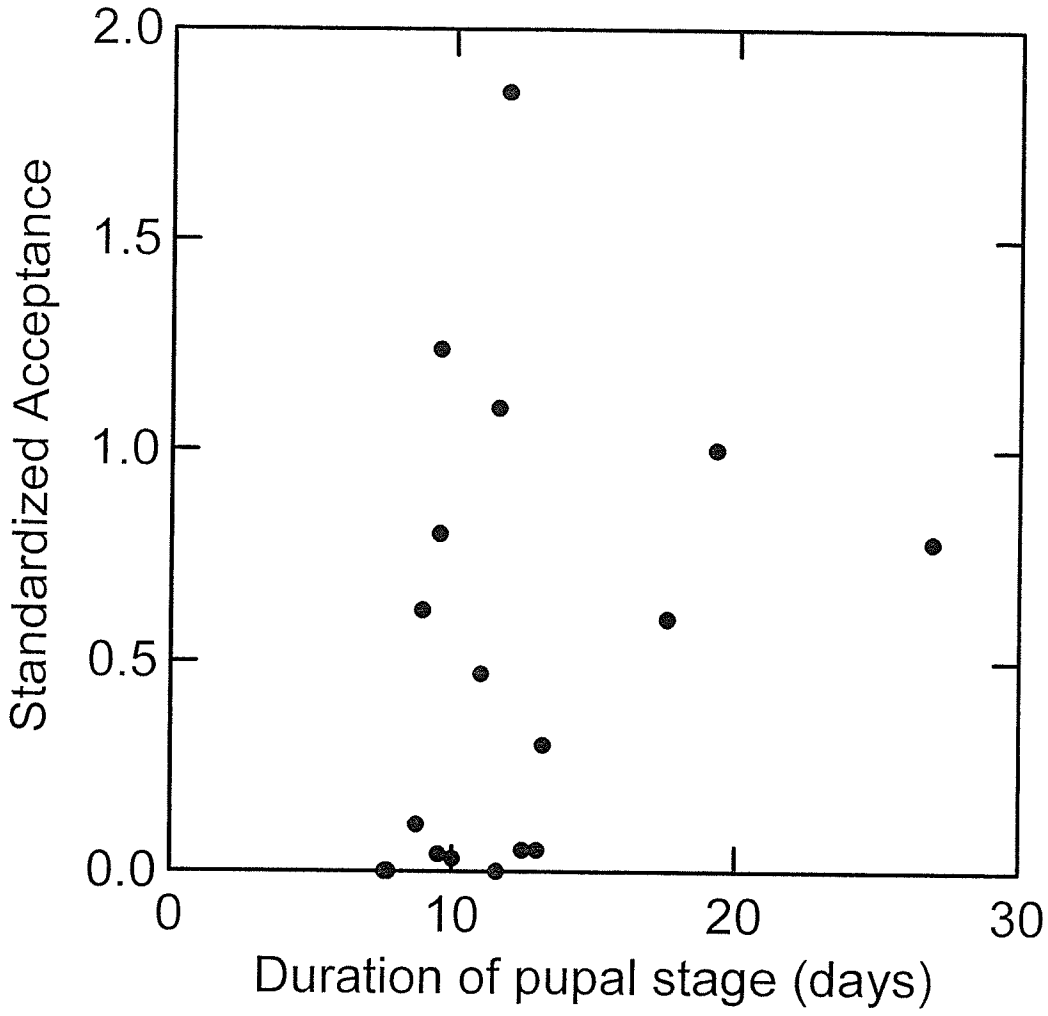

Figure 11. Proportion of non-target Diptera puparia accepted as hosts relative to *Delia radicum* (proportion = 1.0) as a function of mean duration of the pupal stage.

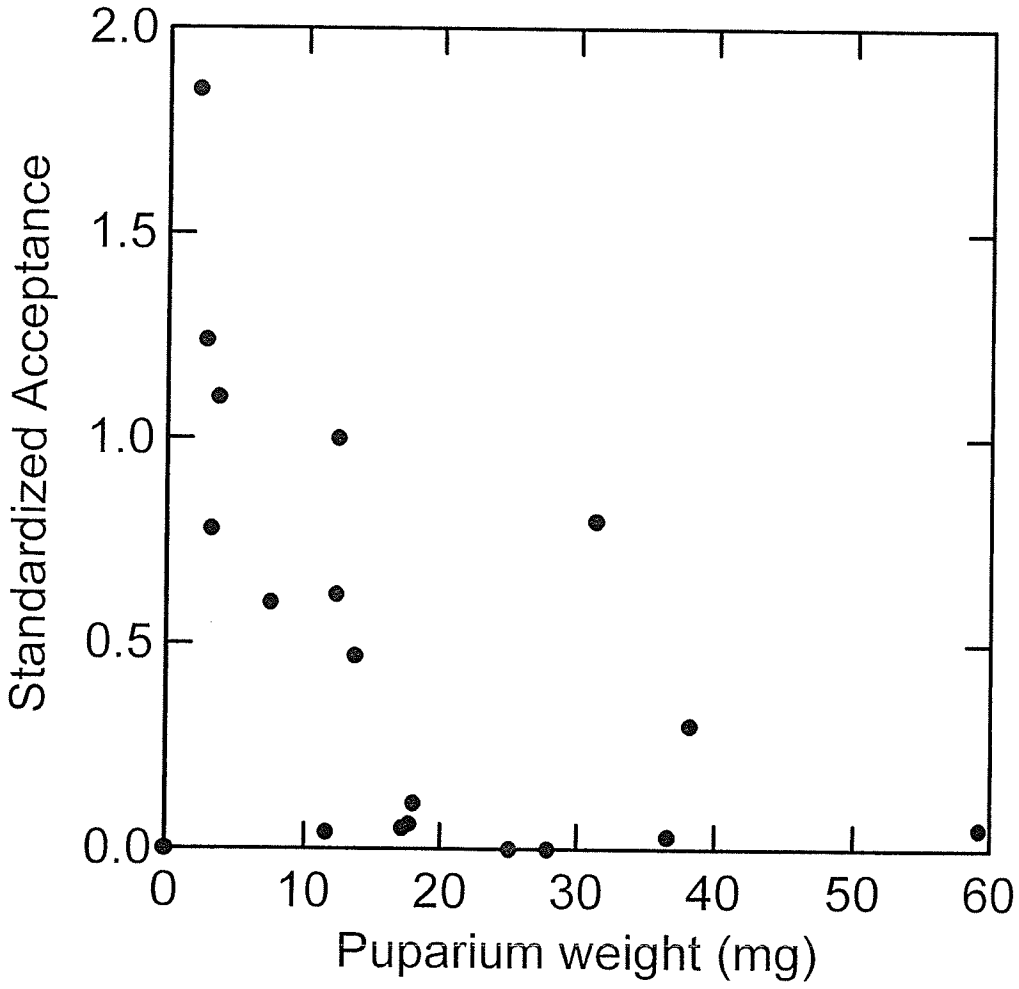

Figure 12. Proportion of non-target Diptera puparia accepted as hosts relative to *Delia radicum* (proportion = 1.0) as a function of mean puparium weight.

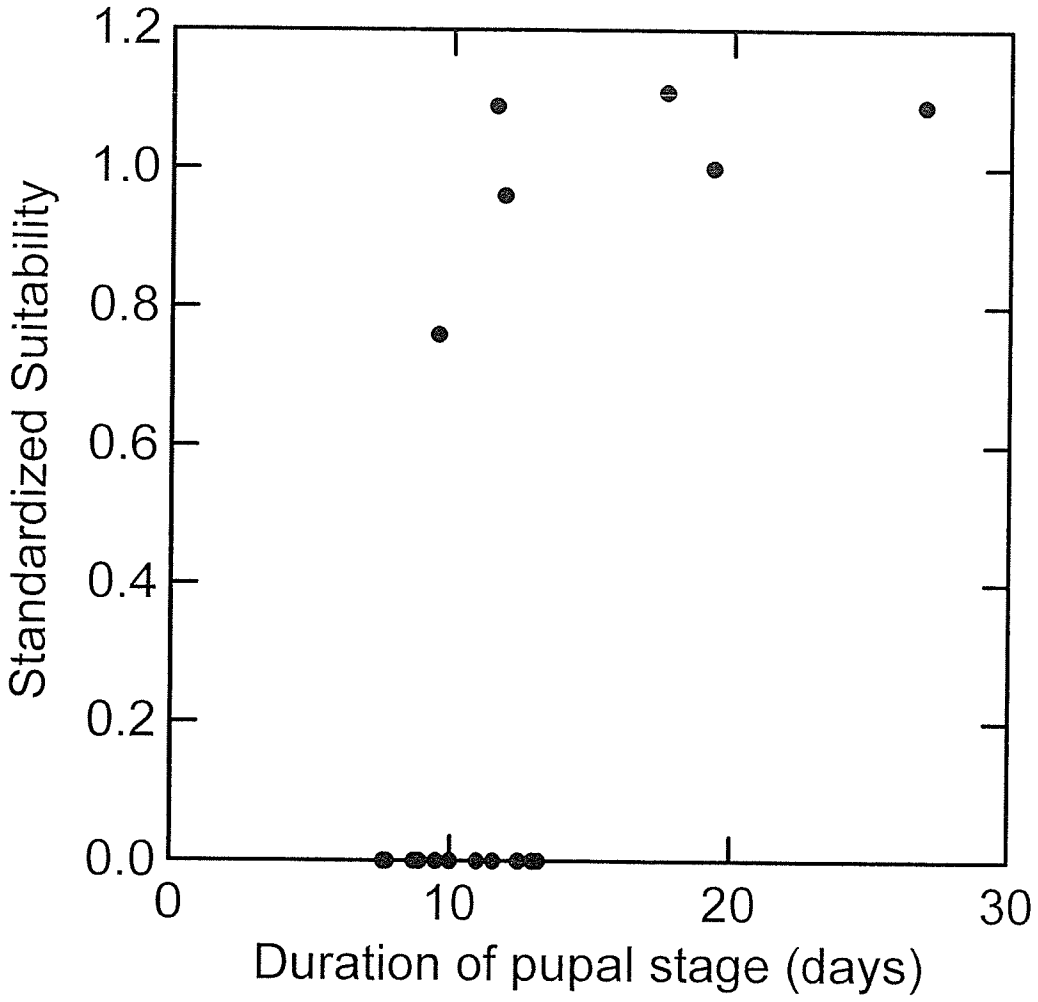

Figure 13. Proportion of non-target Diptera puparia suitable as hosts relative to *Delia radicum* (proportion = 1.0) as a function of mean duration of the pupal stage.

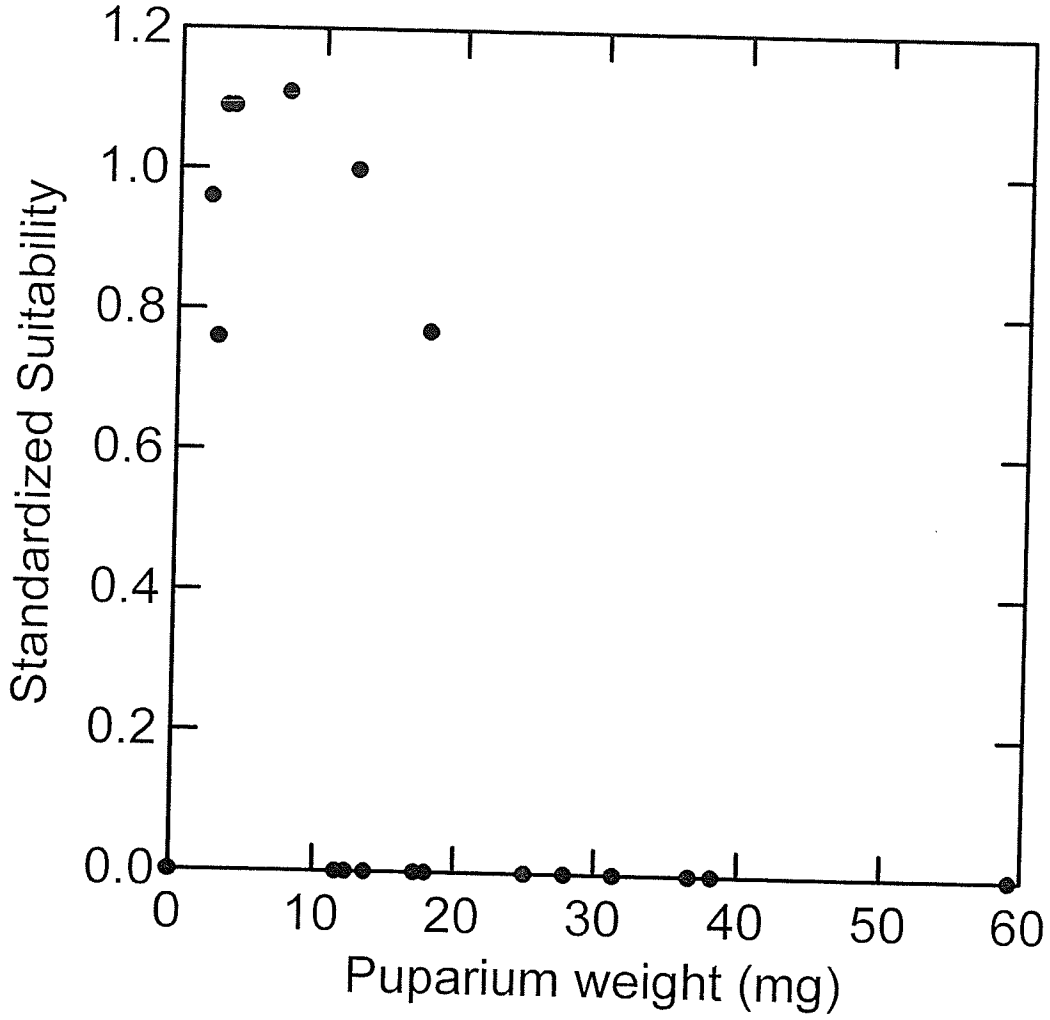

Figure 14. Proportion of non-target Diptera puparia suitable as hosts relative to *Delia radicum* (proportion = 1.0) as a function of mean puparium weight.

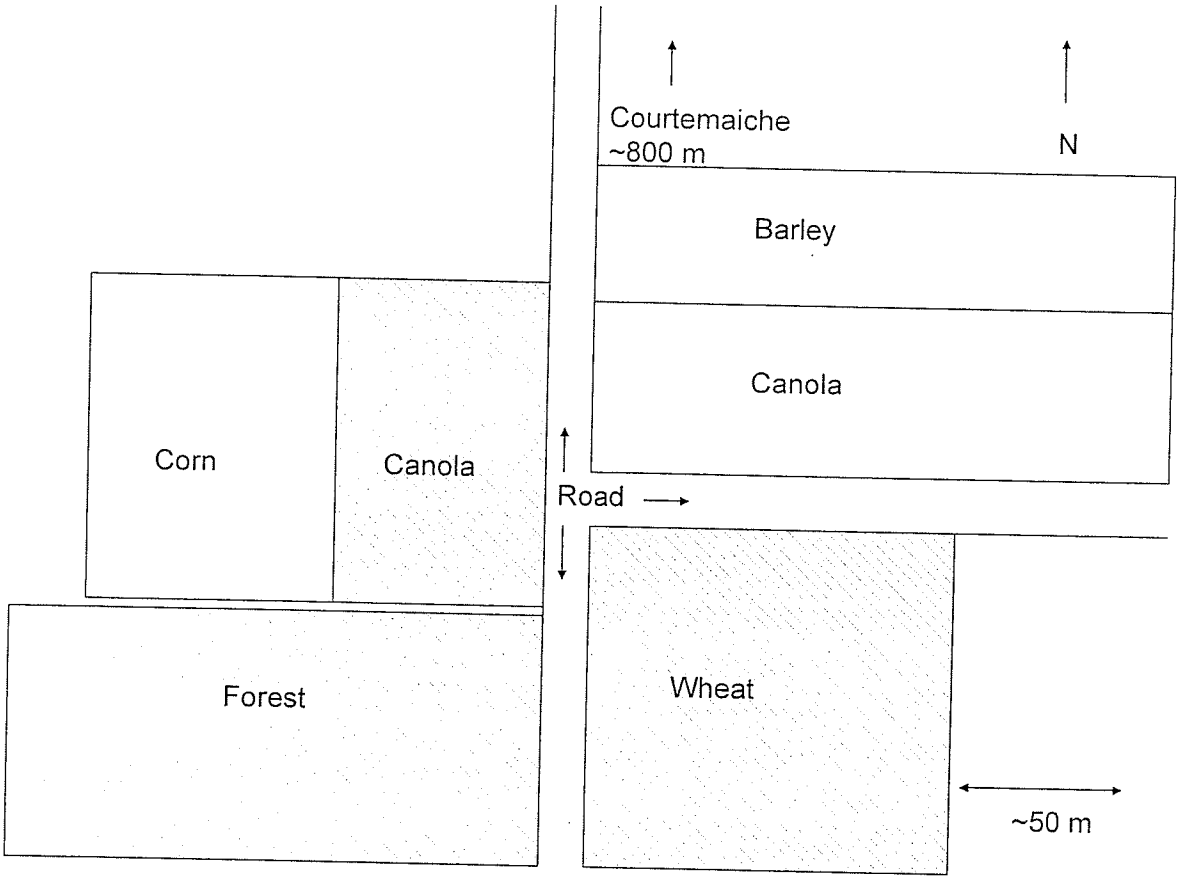

Figure 15. Map of Courtemaiche site sampled with pitfall traps for adult *Aleochara bipustulata*; hatched habitats were sampled.

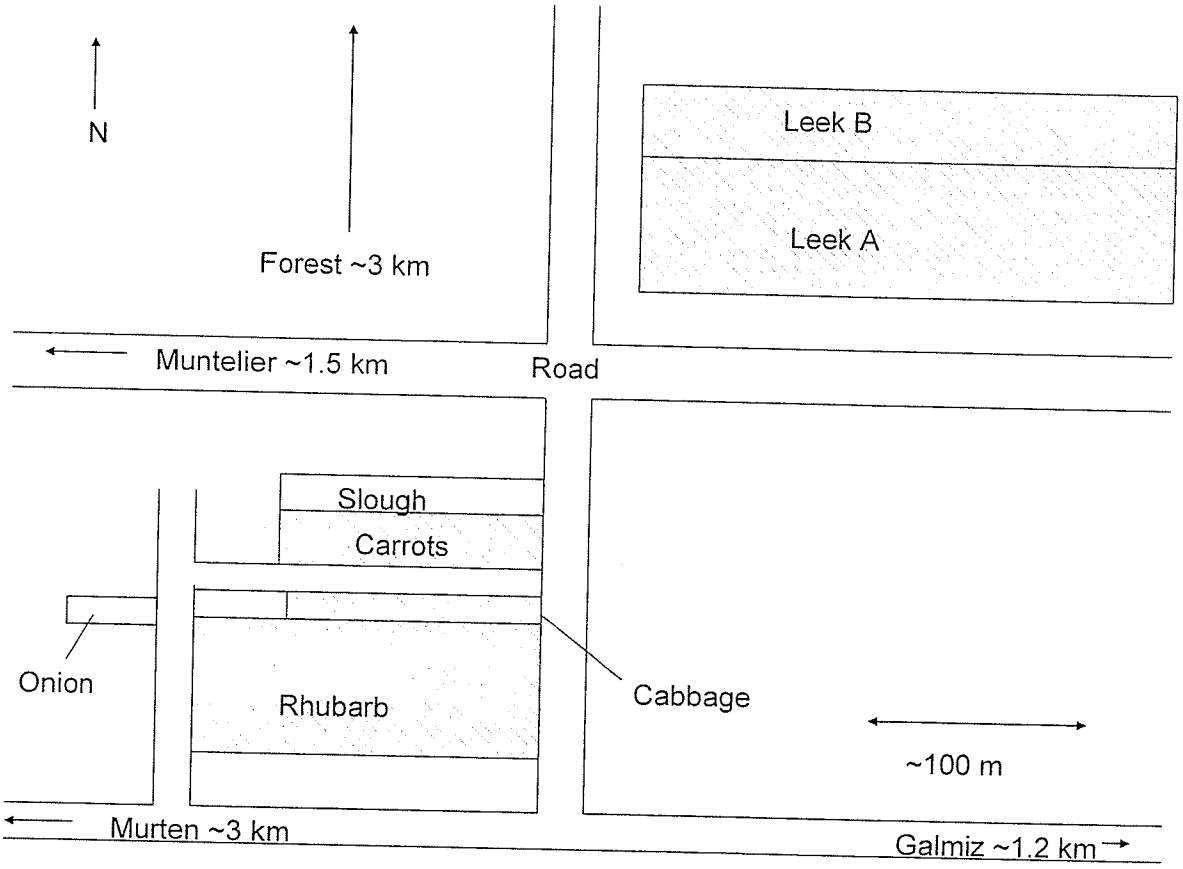

Figure 16. Map of Galmiz site sampled with pitfall traps for adult *Aleochara bipustulata*; hatched habitats were sampled.

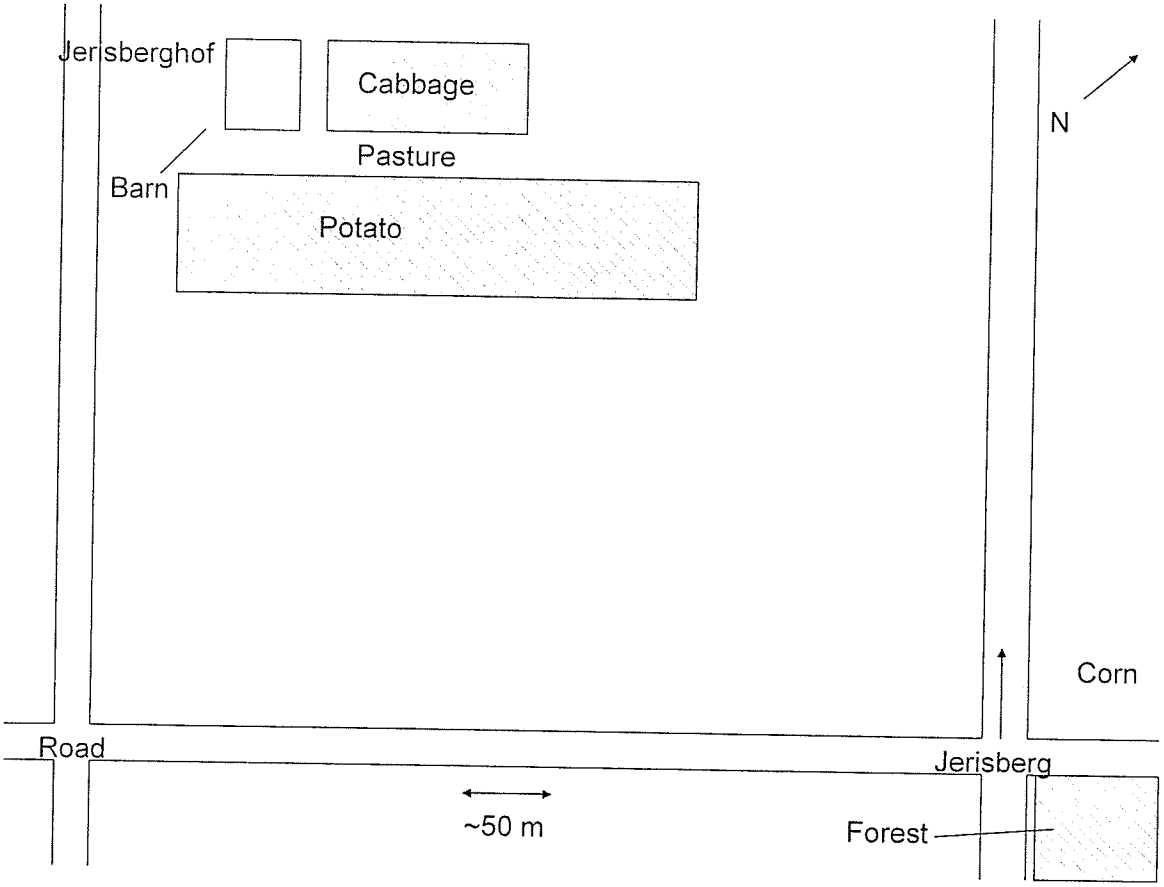

Figure 17. Map of Jerisberghof site sampled with pitfall traps for adult *Aleochara bipustulata*; hatched habitats were sampled.

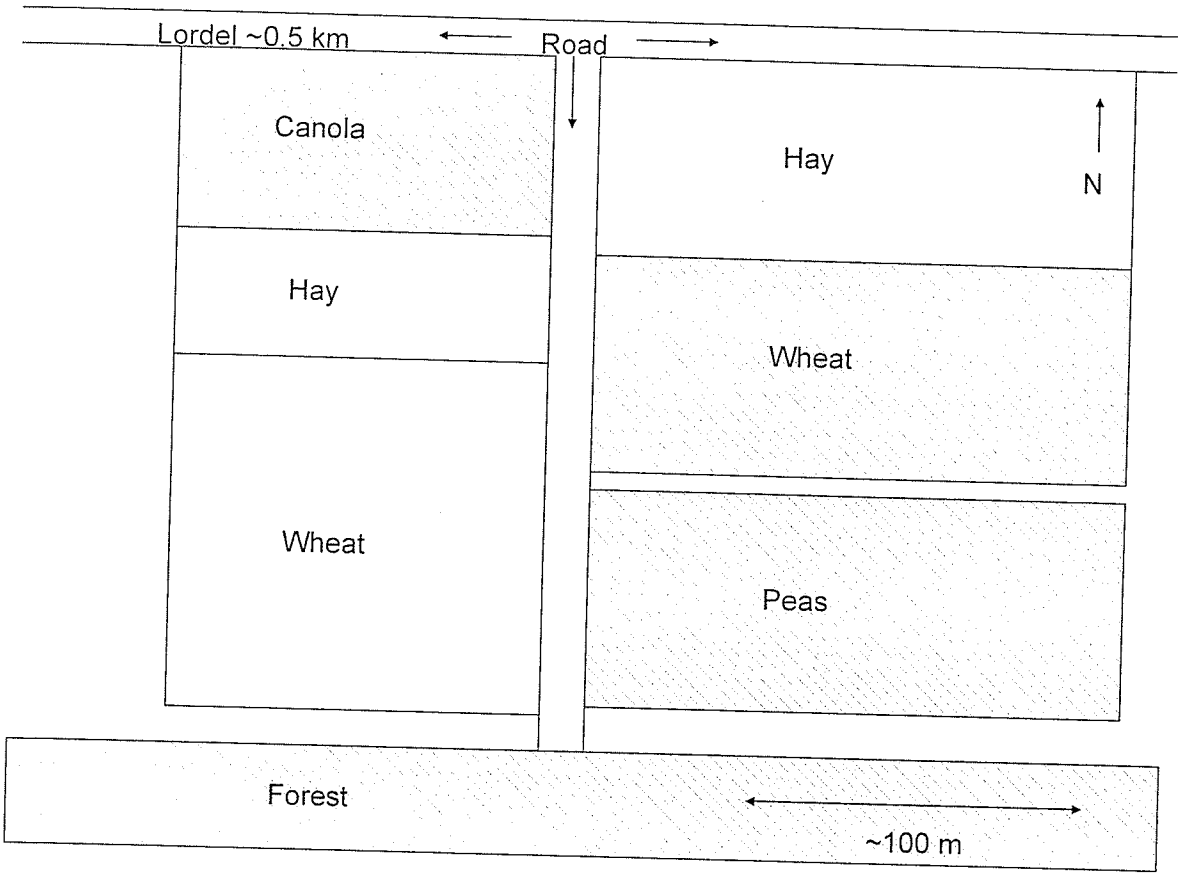

Figure 18. Map of Lordel site sampled with pitfall traps for adult *Aleochara bipustulata*; hatched habitats were sampled.

4. GENERAL DISCUSSION

The yield of Canadian canola crops is reduced by herbivory from numerous species of insects, including *Delia radicum* (L.) (Diptera: Anthomyiidae) (Lamb 1989). Over the past few decades the damage caused by *D. radicum* has increased (Soroka et al. 2004). One strategy to increase mortality of *D. radicum* is to introduce natural enemy species from Europe (Turnock et al. 1995; Soroka et al. 2002). The species with the greatest potential in this regard is *Aleochara bipustulata* L. (Coleoptera: Staphylinidae) (Hemachandra 2004). Puparia of *D. radicum* around the roots of canola plants in France are often highly parasitized by *A. bipustulata* (Brunel et al. 1999), and predation of immature *D. radicum* by *A. bipustulata* is probably more extensive than by other species already present in Canada (Jonasson 1994b).The research reported in this thesis is a contribution to this effort to provide Canadian canola producers with a cost-effective and long-term reduction in yield lost to *D. radicum*.

The first objective was related to selecting a well-synchronized population of *A. bipustulata*. The *D. radicum* in prairie canola crops were different in their spring emergence biology than *D. radicum* from vegetable *Brassica* crops in Ontario, suggesting that synchronization will be an issue when selecting an appropriate *A. bipustulata* population for introduction. Are there other characteristics which could improve the likelihood of establishment and effective control? In the biological control literature, characteristics supposed to be good predictors of success include high search capacity, density-dependent attack rate, high potential rate of increase, ability to survive in the environment of introduction (Bennett 1974; Gerling et al. 2004), host-specificity (Bennett 1974; Kimberling 2004) and multiple generations per year (Kimberling 2004). Information about this combination of characteristics will likely remain imperfect, but

does provide a starting point. Insights from outside biological control may prove helpful as well, and the recently increasing study of invasive alien species may be particularly informative.

Invasive alien species have been called 'biological pollution' (Britton 2004) and 'unwanted biological contamination' (Samways 1997). However, species introduced for biological control have been labelled 'intended biological contamination' (Samways 1997). Information about classical biological control has been used to gain insight into invasions (Elton 1958; Williamson 1996; Williamson and Fitter 1996a; 1996b). Although parallels between invasive species and biological control agents have made biological control more difficult to practice (Messing and Wright 2007) the possibility remains to learn from the burgeoning field of invasive species research and apply its findings to the improvement of introduction strategies (Crawley 1987; 1989; Grevstad 1999b).

Aspects of the invading species and invaded environment, and the fit between the two, are all important (Elton 1958; Smith et al. 1999). Identifying predictors of invasiveness is more informative if the process is viewed as a series of stages (Richardson et al. 2000; Kolar and Lodge 2001; Williamson 2006). A model developed with a focus on invasive plants starts with immigration, then independent growth of at least one individual, increase in population size to the 'minimum viable population', and then colonization of new areas (Heger and Trepl 2003). In the invasive plant literature, a species which grows independently is a casual, one which reaches the minimum viable population size is naturalized, and one spreading to new areas is a colonizer (Richardson et al. 2000). In biological control, immigration would happen by intentional introduction by humans, and the other steps are desirable. Ideally the agent will not only spread, but have a significant impact on the target pest and a minimum effect on the rest of the

environment, although a trade-off between the two is not unusual (Ehler 2000). Also, one would hope that biological control practitioners working to introduce a species will have a reasonable idea about what the minimum viable population size is, and release populations of an appropriate size.

In Heger and Trepl's (2003) scheme, whether a species becomes a casual depends on obstacles confronting individual organisms. These obstacles can be abiotic like unfavourable conditions, interspecific biotic like competition and predation, and intraspecific biotic, in particular the inability to find mates (Crawley 1987; Heger and Trepl 2003). Habitats characterized by relatively harsh abiotic conditions, like salt marshes and arid areas, tend to have relatively few non-native plant species (Alpert et al. 2000). Conversely, non-native plants are often at a competitive advantage over the native members of the communities when resources are abundant (Alpert et al. 2000). Competition in disturbed communities may be less, making communities prone to certain disturbances more hospitable to invaders (Alpert et al. 2000). For example, there are more exotic plant species on prairie that is grazed than ungrazed, but fewer on prairie that is frequently burned than unburned (Smith and Knapp 1999). It makes sense that competition from species already present in an area could prevent the establishment of new species (Elton 1958), but at least for plants the areas most hospitable to invaders do not have fewer species (Lonsdale 1999). Previous invaders may alter the environment to make it more favourable to subsequent invaders (Simberloff 2006). Exotic carabid beetles on the Canary Islands may have been aided in establishment by occupying vacant trophic niches and thereby avoiding competition (Arndt 2006). A population of a colonizing species which reproduces sexually cannot survive more than one generation if individuals do not find one another and mate.

Aspects of a species which could facilitate an individual to overcome the barriers to reaching casual status include defensive mechanisms, competitive ability, and broad ecological tolerance (Crawley 1986; Heger and Trepl 2003; Devin and Beisel 2007). Defensive mechanisms are expected to be particularly effective if they are something to which the natural enemies have not previously been exposed, like the toxins of the invasive *Homalodisca coagulata* (Say) (Homoptera: Cicadellidae) and their effect on native spiders in French Polynesia (Suttle and Hoddle 2006). The competitive ability and invasive impact of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) are due in part to more rapid development to aggressive instars and more aggressive behaviour relative to native coccinellid species (Labrie et al. 2006). The importance of broad ecological tolerance is illustrated by the many exotic aphids with relatively wide ranges of host plants each can exploit (Mondor et al. 2007). Wide distribution in the native range (Goodwin et al. 1999) and commonness in the native range (Crawley 1987) are probably indicative of broad ecological tolerance, and seem to be the best predictors of invasiveness of plants.

Whether a casual population becomes naturalized is believed to depend on obstacles confronting the population, as opposed to the individual (Heger and Trepl 2003). These obstacles include demographic and environmental stochasticity, Allee effects (Grevstad 1999b; Heger and Trepl 2003), and a lack of suitable sites near the casual individuals (Heger and Trepl 2003). Demographic stochasticity, the variation in growth rates among different generations, is predicted to have a minimum impact on its own, but can be important when the environment is relatively variable (Grevstad 1999b). Allee effects are when individual fitness increases, for example by collective modification of the environment or reduction in inbreeding, with increasing number or density of

conspecifics (Stephens et al. 1999). When an invading population is affected by Allee effects, a population must be larger than a theoretical threshold to establish (Grevstad 1999b) and even above this threshold can suffer non-critical ecological consequences like a slow rate of spread (Taylor and Hastings 2005). A casual cannot become naturalized if the resources it requires to do so are not present.

Characteristics of species thought to favour population growth and naturalization include a relatively high intrinsic rate of increase and genetic variability (Heger and Trepl 2003). Mortality caused by natural enemies can reduce the effect of high rate of increase, and it may be important for an invader to be less attacked or have a higher rate of increase than native species with which it shares natural enemies (Lawton and Brown 1986; Settle and Wilson 1990). Species with high intrinsic rates of increase but narrow ecological tolerances, while theoretically capable of rapidly increasing in population size and spreading if they become casuals, are unlikely to fulfill the earlier stages of invasion (Crawley 1986; Devin and Beisel 2007). It is not always true that invasive species have higher genetic variability than conspecific populations in the native range or native species in the introduced range (Gray 1986), but the genetic bottleneck created by a colonization can reduce genetic variability in the founding population, which could have consequences for inbreeding depression and potential for adaptation (Sakai et al. 2001).

In the fourth and final stage, a naturalized species colonizes new areas. Obstacles include the availability of suitable sites to spread to, given their distance and the species' ability to disperse (Heger and Trepl 2003). Theoretically, the more suitable sites there are within dispersing distance of a population of an invasive species, the fewer individuals will be lost to mortality associated with dispersal and the greater the potential population density in the invaded area (Barlow and Kean 2004). A species will be more likely to find

suitable sites the more broad its ecological tolerances are (Heger and Trepl 2003). There is often a trade-off in different strategies to locate new sites, where a species is adept at locating new sites but has relatively few dispersers, or has a large number of dispersers which end up in suitable areas by chance (Barlow and Kean 2004).

All of these characteristics listed above about invasible areas and invasiveness of species are probably better viewed as explanations than predictors, as biological invasions cannot be predicted with much certainty (Lawton and Brown 1986; Williamson 2006) and many invasive species do not match the prediction characteristics (Goodwin et al. 1999; Williamson 2006). The characteristics are mediated by 'propagule pressure', the number and size of introductions (Williamson 1996). The more often an area is visited by people, the more non-native species are brought with them there and establish (Lonsdale 1999).

Research about invasive species has intensified in recent years, and much of the work has focused on predicting invasions. Most of the generalizations and patterns have already been incorporated into introduction strategies for biological control. Matching climates has long been encouraged for selecting agents to introduce (Harris 1973; Wapshere 1985). The importance of sufficient propagule pressure is also well-known, and large increases are recommended (Beirne 1985; Hopper and Roush 1993), if possible into many different areas to minimize the risks of environmental stochasticity (Grevstad 1999a; 1999b). The option might not always exist of selecting agents on the basis of defensive mechanisms, competitive abilities, and high intrinsic rates of increase, but if it does it should be utilized. Selecting agents with broad ecological tolerances over others may mean selecting those less specific to the target (Ehler 2000), and decisions will have to be made about specific situations. Finally, the enemy release hypothesis, often used to explain the greater size or abundance of an invasive species in its introduced range

(Torchin et al. 2002), can be turned around and used to select agents that suffer from natural enemies or competition and release them from this pressure, resulting in less restricted growth and effective biological control (Myers et al. 1989).

If invasive species and biological control agents require similar characteristics for success, as they seem to do, there are several reasons to suspect *A. bipustulata* will be successful if introduced to North America. Local population densities of *A. bipustulata* can be increased with mustard seed meal (Riley et al. *In Press*). High densities will make it more likely that mates will find one another. *Aleochara bipustulata* is distributed across Europe and Asia (Maus 1998), and wide distribution is supposed to indicate broad ecological tolerance of invasive species. My own research was about selecting an appropriate population, and it is likely *A. bipustulata* populations exist which are capable of eventually surviving in agricultural areas from the Peace to the Red River valleys. Nothing is known about the natural enemies of *A. bipustulata* in its native range, and it would be difficult to predict how establishment and population densities of *A. bipustulata* in Canada might be affected by things like predation. Competition with natural enemies of *D. radicum* in Canada could in theory prevent its establishment and effectiveness, but this is not likely. In Europe, *A. bipustulata, A. bilineata* Gyllenhal (Coleoptera: Staphylinidae), and *Trybliographa rapae* (Westwood) (Hymenoptera: Eucoilidae) coexist as the major parasitoids of *Delia radicum* (Wishart et al. 1957; Hemachandra 2004). Competitive interactions between *A. bilineata* and *A. bipustulata* may be reduced by preference for hosts of different sizes (Ahlstrom-Olsson 1994; Jonasson 1994b), differences in phenology (Jonasson 1994b), and developmental rate (Ahlstrom-Olsson 1995). None of these factors eliminate overlap completely though, and the two species occur together in the same fields for most of the season (Jonasson 1994b; Brunel et al.

1999; Fournet and Brunel 1999). Larvae of both species tend to avoid entering puparia where other larvae are already present (Royer et al. 1999) and the level of parasitism is higher in systems with both species present than equivalent numbers of one or the other, suggesting they complement one another as biological control agents (Riley et al. *In Preparation*). It remains only to select an appropriate population for there to be a good potential for successful control.

The second objective was related to assessing *A. bipustulata*'s host range. The steps for successful parasitism are host habitat location, host location, host acceptance, host suitability, and host regulation (Vinson 1976). If the five steps are met, a species is in *A. bipustulata*'s ecological host range. Useful information about *A. bipustulata*'s habitat associations was gathered, but it is not yet possible to state for certain much more than *A. bipustulata* is not found in forests but is found to a greater or lesser extent in various crops habitats. Focusing on host acceptance and host suitability, a more complete picture was assembled about *A. bipustulata*'s fundamental host range. From the perspective of assessing risk to non-target Canadian Diptera, species of Acalyptratae with small puparia and Anthomyiidae species are the two groups where non-target effects might be predicted. Understanding the risk to these groups better will require more research about host habitat location, host location, and host acceptance by *A. bipustulata*.

Particularly at Galmiz, where pitfall trap catches indicated *A. bipustulata* was present in the cabbage, the sentinel puparia might have yielded some *A. bipustulata*. Assuming larvae were present in the soil, they were not attracted to the puparia. Searching larvae of some *Aleochara* species are known to follow the trail made by the host larva to find a puparium (Wright and Muller 1989). As the puparia were placed in the field by hand without the trail, which may be important, was missing. Without a trail,

larvae of *A. bipustulata* can find host puparia from up to 10 cm away in Petri dishes, whether by wandering randomly or following a cue from the puparium (Fuldner 1960). If larvae are attracted to something given off by the puparium itself, they then did not venture close enough to the sentinel puparia. Perhaps eggs are laid close to damaged plants, so the larva has not far to wander. If eggs are laid by *A. bipustulata* only near damaged Brassicaceae plants, which is by no means certain, then the risk to non-target Canadian species is probably quite small.

The range of habitats in which an insect parasitoid is found has obvious consequences for its ecological host range, as hosts cannot be attacked if they live in a habitat the parasitoid never visits. Habitats used are sometimes preferred on the bases of things like temperature, humidity, light intensity and wind (Vinson 1976). For example, the *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) parasitoids *Itoplectis conquisitor* (Say) and *Theronia atalantae* (Poda) (Hymenoptera: Ichneumonidae) forage preferentially in the open and shade, respectively (Campbell 1963). Chemical cues also guide parasitoids to the habitats of their hosts (Vinson 1976). The absence of *A. bipustulata* from forests likely has more to do with environmental variables than chemical cues. In the pre-agricultural period during which *A. bipustulata* evolved, differentiating between forest and not forest may have been sufficient at the landscape scale to locate hosts, so we should perhaps be not too surprised to find somewhat ambiguous habitat associations when these are studied in their contemporary form. The monophyly of the *Aleochara* subgenus *Coprochara* is well supported based on analysis of genetic variation among species, but which species are most closely related to *A. bipustulata* depends on the method used to analyze the genetic variability (Maus et al. 2001). The ecological host range of *Coprochara* species, however, seems principally to comprise Diptera species

developing in dung, carrion, and roots of *Allium* (Liliaceae) and Brassicaceae species (Maus et al. 1998). Given my results concerning the occurrence of *A. bipustulata* in carrion, and the fact that Diptera pests of *Allium* roots are not in the reported ecological host range of *A. bipustulata* (Maus et al. 1998), perhaps it is reasonable to suggest *A. bipustulata* arose from an evolutionary lineage of species whose larvae parasitized puparia around wild Brassicaceae plants and dung. At least 48 wild Brassicaceae species will support development of *D. radicum* in the laboratory (Finch and Ackley 1977). Generally, Brassicaceae species are found in dry, open areas, and forest is not listed as habitat for any of the potential host plants of *D. radicum* (Clapham et al. 1962). In open habitats, *A. bipustulata* might use chemical cues to locate host habitats at a more refined scale.

Vinson's (1976) stepwise scheme is a very useful heuristic tool, but at the host location and host acceptance stages we find the path through the steps is not always direct. Adult *Aleochara* locate hosts within the host's habitat, and then accept them by laying an egg. The *Aleochara* larva which hatches must then do some host location of its own, to find a host puparium, and then accept a host by chewing for itself an entrance hole, feeding, and sealing the hole. Of these four steps, my study about *A. bipustulata*'s fundamental host range looked only at the last. In fact, detailed observations were made only about the creation of an entrance hole, and subsequent suitability of each host. The host range of other species with initially-mobile, parasitic larvae are known to be restricted by host location activities of the adult stage. For instance, *Pheropsophus aequinoctialis* L. (Coleoptera: Carabidae), whose larvae feed on eggs of *Scapteriscus* species (Orthoptera: Gryllotalpidae), oviposits preferentially in real over artificial tunnels, suggesting a semiochemical in natural tunnels guides placement of *P. aequinoctialis* eggs

(Weed and Frank 2005). Oviposition by *A. bilineata* is also higher near suitable hosts (Fournet et al. 2001). I believe our knowledge about risk to non-target species could be refined considerably by investigating the three steps prior to host acceptance by the larva, particularly the steps involving the adult stage.

Additional species of natural enemies are required if *D. radicum* is to be controlled biologically in Canadian canola (Soroka et al. 2002) and the partnership between the University of Manitoba, CABI Switzerland Centre, and Agriculture and Agri-Food Canada has resulted in considerable progress towards this end. Dr. K.S. Hemachandra (2004) discovered that *A. bipustulata* is the most promising candidate for introduction. Two findings by K. Riley were also important. First, *A. bipustulata* is likely to complement the parasitoids already present in Canada, adding to rather than replacing mortality of *D. radicum* pupae. Second, mustard seed meal is an effective attractant of *A. bipustulata* adults and could be used to create high densities of introduced *A. bipustulata* to encourage mate finding and establishment. My work builds on their efforts.

My first objective was to compare the thermal response for spring emergence of *D. radicum* populations from western Canada with an established natural enemy and a *D. radicum* population from another part of Canada. I found that the spring emergence biology of *D. radicum* in canola crops in the prairies is different than a population from vegetable *Brassica* crops in Ontario, which means certain *A. bipustulata* populations might be more appropriate for introduction than others. I also found that *A. bilineata* emerges in spring too late to be an effective predator of early immature stages of *D. radicum*, even when these occur as late as they do in canola in prairie Canada.

My second objective was to determine *A. bipustulata*'s host range. I determined that relatively small species of Cyclorrapha (Diptera) and those relatively closely related

to *D. radicum* are the most suitable hosts in the laboratory. By combining these results with studies about *A. bipustulata*'s habitat use, I determined that the risk to beneficial species like *Lonchaea corticis* is small.

Future research about *A. bipustulata* could follow any of several directions, but from the perspective of progress towards determining its suitability for introduction the most pressing area is further research about risk to non-target species. The recommended next step would be further testing with the species which supported development, with the species on their host plants (van Lenteren et al. 2006a; 2006b). However, many of the suitable hosts were found in the first place by luck, and may not be available a second time, and all of them are difficult or impossible to maintain over several generations in the laboratory. Testing with *L. corticis* cannot be 'scaled up' as it is not found in Europe and its hosts are found in mature trees. As noted above, experiments about host selection by adult *A. bipustulata* are more appropriate.

Perhaps more important is the need to determine *A. bipustulata*'s predatory host range. Adult *A. bipustulata* are known to feed on *D. radicum* eggs and larvae (Coaker and Williams 1963), but the breadth of their diet is incompletely understood. Testing should follow the same stepwise protocol that I used to determine *A. bipustulata*'s fundamental host range, with modifications as appropriate to studies about predation. Testing will start in the laboratory, but experiments will probably have to be done in the field or field cages to determine what *A. bipustulata* adults eat in nature. With this information in hand, it is likely that enough will be known about *A. bipustulata* to decide if its introduction to Canada can proceed.

Literature Cited

Adashkevich BP. 1977. Rearing of *Aleochara bilineata* and calculating its effectiveness (Biological control of vegetable pests). Zashchita Rastenii 6:29–30.

Adashkevich BP, Perekrest ON. 1970. Breeding of *Aleochara bilineata* (Col., Staphylinidae) in the laboratory. Zoologicheskij Zhurnal 49:1081–1083.

Adashkevich BP, Perekrest ON. 1973. Mass rearing of *Aleochara bilineata* in the laboratory. Zoologicheskij Zhurnal 52:1705–1709.

Ahlstrom-Olsson M. 1994. Host preference of *Aleochara bilineata* and *A. bipustulata* (Coleoptera: Staphylinidae) in relation to host size and host. Norwegian Journal of Agricultural Sciences 16:283–291.

Ahlstrom-Olsson M. 1995. Naturally occurring predators and parasitoids of brassica root flies: *Aleochara* spp. (Coleoptera: Staphylinidae). Nordisk Jordbrugsforskning Utredning/Rapport 107:135–138.

Alfaro RI, Borden JH. 1980. Predation by *Lonchaea corticis* (Diptera: Lonchaeidae) on the white pine weevil, *Pissodes strobi* (Coleoptera: Curculionidae). The Canadian Entomologist 112:1259–1270.

Alfaro RI, Hulme MA, Harris JWE. 1985. Insects associated with the sitka spruce weevil, *Pissodes strobi* [Col.: Curculionidae] on sitka spruce, *Picea sitchensis* in British Columbia, Canada. Entomophaga 30:415–418.

Allen WR. 1964. The occurrence of cabbage maggot on rape in Manitoba and evaluation of insecticides for control. Proceedings of the Entomological Society of Manitoba 20:54–58.

Alpert P, Bone E, Holzapfel CM. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology, Evolution and Systematics 3:52–66.

Andersen A. 1982. *Aleochara bipustulata* (L.) (Col., Staphylinidae) parasitizing *Delia floralis* Fallen (Dipt., Anthomyiidae). Fauna Norvegica Series B 29:46–47.

Andersen A, Eltun R. 2000. Long-term developments in the carabid and staphylinid (Col., Carabidae and Staphylinidae) fauna during conversion from convetional to biological farming. Journal of Applied Entomology 124:51–56.

Andersen A, Hansen AG, Rydland N, Oyre G. 1983. Carabidae and Staphylinidae (Col.) as predators of eggs of the turnip root fly *Delia floralis* Fallen (Diptera, Anthomyiidae) in cage experiments. Zeitschrift fur Angewandte Entomologie 95:499–506.

Anderson GS, VanLaerhoven SL. 1996. Initial studies on insect succession on carrion in southwestern British Columbia. Journal of Forensic Science 41:617–625.

Andrewartha HG. 1952. Diapause in relation to the ecology of insects. Biological Reviews 27:50–107.

Andrewartha HG, Birch LC. 1954. The distribution and abundance of animals. Chicago: The University of Chicago Press. 782 p.

Arndt E. 2006. Niche occupation by invasive ground-dwelling predator species in Canarian laurel forests. Biological Invasions 8:893–902.

Askew WL, Westdal PH, Romanow W, Stefansson BR. 1976. Control of flea beetles and cabbage maggots on rape with insecticides, and effect on yield of rapeseed. Ottawa: Canada Committee on Pesticide Use in Agriculture. p 131–132.

Aukema BH, Richards GR, Krauth SJ, Raffa KF. 2004. Species assemblage arriving at and emerging from trees colonized by *Ips pini* in the Great Lakes Region: partitioning by time

since colonization, season, and host species. Annals of the Entomological Society of America 97:117–129.
Balog A, Marko V, Kutasi C, Adam L. 2003. Species composition of ground dwelling staphylinid (Coleoptera: Staphylinidae) communities in apple and pear orchards in Hungary. Acta Phytopathologica et Entomologica Hungarica 38:181–198.
Barbosa P, Segarra-Carmona A. 1993. Criteria for the selection of pest arthropod species as candidates for biological control. In: Van Driesche RG, Bellows TS, editors. Steps in classical arthropod biological control. Lanham: Entomological Society of America. p 5–23.
Barlow ND, Kean JM. 2004. Resource abundance and invasiveness: a simple model. Biological Invasions 6:261–268.
Barron MC, Barlow ND, Wratten SD. 2003. Non-target parasitism of the endemic New Zealand red admiral butterfly (*Bassaris gonerilla*) by the introduced biological control agent *Pteromalus puparum*. Biological Control 27:329–335.
Baur R, Birch ANE, Hopkins RJ, Griffiths DW, Simmonds MSJ, Staedler E. 1996. Oviposition and chemosensory stimulation of the root flies *Delia radicum* and *D. floralis* in response to plants and leaf surface extracts from resistant and susceptible *Brassica* genotypes. Entomologia Experimentalis et Applicata 78:61–75.
Baur R, Staedler E, Monde K, Taksugi M. 1998. Phytoalexins from *Brassica* (Cruciferae) as oviposition stimulants for the cabbage root fly, *Delia radicum*. Chemoecology 8:163–168.
Beirne BP. 1975. Biological control attempts by introductions against pest insects in the field in Canada. The Canadian Entomologist 107:225–236.
Beirne BP. 1985. Avoidable obstacles to colonization in classical biological control of insects. Canadian Journal of Zoology 63:743–747.
Bellows TS, Legner EF. 1993. Foreign exploration. In: Dreische RG, van, Bellows TS, editors. Steps in classical biological control. Lanham: Entomological Society of America. p 25–41.
Bellows TS, Van Driesche RG. 1999. Life table construction and analysis for evaluating biological control agents. In: Bellows TS, Fisher TW, editors. Handbook of biological control. San Diego: Academic Press. p 199–224.
Bennett FD. Criteria for determination of candidate hosts and for selection of biotic agents. In: Maxwell FG, Harris FA, editors; 1974; Jackson, Mississippi. University of Mississippi Press. p 87–96.
Benson J, Pasquale A, Van Driesche RG, Elkinton J. 2003. Assessment of risk posed by introduced braconid wasps to *Pieris virginiensis,* a native woodland butterfly in New England. Biological Control 26:83–93.
Biron DG, Coderre D, Boivin G, Brunel E, Nenon JP. 2002. Genetic variability and expression of phenological and morphological differences in populations of *Delia radicum* (Diptera: Anthomyiidae). The Canadian Entomologist 134:311–327.
Biron DG, Landry BS, Nenon JP, Coderre D, Boivin G. 2000. Geographical origin of an introduced pest species, *Delia radicum* (Diptera: Anthomyiidae), determined by RAPD analysis and egg micromorphology. Bulletin of Entomological Research 90:23–32.
Biron DG, Langlet X, Boivin G, E. B. 1998. Expression of early and late-emerging phenotypes in both diapausing and non-diapausing *Delia radicum* L. pupae. Entomologia Experimentalis et Applicata 87:119–124.

Biron DG, Nenon JP, Coderre D, Boivin G. 2003. Intra- and interspecific variation on chorionic ultrastructures of *Delia* eggs (Diptera: Anthomyiidae). Annals of the Entomological Society of America 96:245–249.

Block W, Turnock WJ, Jones TH. 1987. Cold resistance and overwintering survival of the cabbage root fly, *Delia radicum* (Anthomyiidae), and its parasitoid, *Trybliographa rapae* (Cynipidae), in England. Oecologia 71:332–338.

Boettner GH, Elkinton JS, Boettner CJ. 2000. Effects of a biological control introduction on three nontarget native species of saturniid moths. Conservation Biology 14:1798–1806.

Bondarenko N. 1982. Prospects of biological control of pests in cruciferous vegetable crops in the USSR. Acta Entomologica Fennica 40:3–5.

Bonsall MB, Hassell MP. 1997. Apparent competition structures ecological assemblages. Nature 388:371–373.

Booth RG, Cross AE, Fowler SV, Shaw RH. 1995. The biology and taxonomy of *Hyperaspis pantherina* (Coleoptera: Coccinellidae) and the classical biological control of its prey, *Orthezia insignis* (Homoptera: Ortheziidae). Bulletin of Entomological Research 85:307–314.

Bortslap S, Entz MH. 1994. Zero-tillage influence on canola, field pea and wheat in a dry subhumid region: agronomic and physiological responses. Canadian Journal of Plant Science 74:411–420.

Bracken GK. 1988. Seasonal occurrence and infestation potential of cabbage maggot, *Delia radicum* (L.) (Diptera: Anthomyiidae), attacking rutabaga in Manitoba as determined by captures of females in water traps. The Canadian Entomologist 120:609–614.

Bracken GK. 1990. Susceptibility of first-instar cabbage maggot, *Delia radicum* (L.) (Anthomyiidae: Diptera), to strains of the entomopathogenous nematodes *Steinernema feltiae* Filipjev, *S. bibionis* (Bovien), *Heterorhabditis bacteriophora* Poinar, and *H. heliothidis* (Khan, Brooks, and Hirschmann). The Canadian Entomologist 122:633–639.

Braven J, Chilcott NP, Hawkes C. 1996. Structure-activity relationship in glucosinolates and other compounds stimulating oviposition in the cabbage root fly (*Delia radicum*). Journal of Chemical Ecology 22:1567–1578.

Britton KO, editor. 2004. Biological pollution: an emerging global menace. St. Paul: The American Phytopathological Society. 113 p.

Broatch JS, Dosdall LM, Clayton GW, Harker KN, Yang RC. 2006. Using degree-day and logistic models to predict emergence pattern and seasonal flights of the cabbage maggot and seed corn maggot (Diptera: Anthomyiidae) in canola. Environmental Entomology 35:1166–1177.

Broatch JS, Vernon RS. 1997. Comparison of water pan traps and sticky traps for monitoring *Delia* spp. (Diptera: Anthomyiidae) in canola. The Canadian Entomologist 129:979–984.

Brooks AR. 1951. Identification of the root maggots (Diptera: Anthomyiidae) attacking cruciferous garden crops in Canada, with notes on biology and control. The Canadian Entomologist 83:109–120.

Brown PE, Anderson M. 1999. Factors affecting ovipositor probing in *Trybliographa rapae*, a parasitoid of the cabbage root fly. Entomologia Experimentalis et Applicata 93:217–225.

Bruck DJ, Snelling JE, Dreves AJ, Jaronski ST. 2005. Laboratory bioassays of entomopathogenic fungi for control of *Delia radicum* (L.) larvae. Journal of Invertebrate Pathology 89:179–183.

Brunel E, Fournet S, Langlet X. 1999. Variation in the rate of parasitism of *Delia radicum* in the west of France. IOBC/WPRS Bulletin 22:103–107.

Buck M. 2001. Protogyny, protandry, and bimodal emergence patterns of necrophagous Diptera. The Canadian Entomologist 133:521–531.
Burgess L. 1977. Flea beetles (Coleoptera: Chrysomelidae) attacking rape crops in the Canadian prairie provinces. The Canadian Entomologist 109:21–32.
Bush GL. 1969. Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). Evolution 23:237–251.
Butts RA, Lamb RJ. 1991a. Pest status of lygus bugs (Hemiptera: Miridae) in oilseed *Brassica* crops. Journal of Economic Entomology 84:1591–1596.
Butts RA, Lamb RJ. 1991b. Seasonal abundance of three *Lygus* species (Heteroptera: Miridae) in oilseed rape and alfalfa in Alberta. Journal of Economic Entomology 84:450–456.
1989. Distribution maps of pests No. 83 *Delia radicum* (L.). London: CAB International.
Caltagirone LE. 1985. Identifying and discriminating among biotypes of parasites and predators. In: Hoy MA, Herzog DC, editors. Biological control in agricultural IPM systems. Orlando: Academic Press. p 189–200.
Campbell A, Frazer BD, Gilbert N, Gutierrez AP, Mackauer M. 1974. Temperature requirements of some aphids and their parasites. The Journal of Applied Ecology 11:431–438.
Campbell RW. 1963. Some ichneumonid-sarcophagid interactions in the gypsy moth *Porthetria dispar* (L.) (Lepidoptera: Lymantriidae). The Canadian Entomologist 95:337–345.
Carew R, Smith EG. 2006. Assessing the contribution of genetic enhancements and fertilizer application regimes on canola yield and production risk in Manitoba. Canadian Journal of Agricultural Economics 54:215–226.
Cervenka VJ, Moon RD. 1991. Arthropods associated with fresh cattle dung pats in Minnesota. Journal of the Kansas Entomological Society 64:131–145.
Chapman RF, Sankey JHP. 1955. The larger invertebrate fauna of three rabbit carcasses. Journal of Animal Ecology 24:395–402.
Clapham AR, Tutin TG, Warburg EF. 1962. Flora of the British Isles. Cambridge: University Press. 1269 p.
Clayton GW, Harker KN, O'Donovan JT, Blackshaw RE, Dosdall LM, Stevenson FC, Ferguson T. 2004. Fall and spring seeding date effects on herbicide-tolerant canola (*Brassica napus* L.) cultivars. Canadian Journal of Plant Science 84:419–430.
Clough Y, Kruess A, Tscharntke T. 2007. Organic versus conventional arable farming systems: functional grouping helps understand staphylinid response. Agriculture, Ecosystems and Environment 118:285–290.
Coaker TH, Williams DA. 1963. The importance of some Carabidae and Staphylinidae as predators of the cabbage root fly, *Erioschia brassicae* (Bouche). Entomologia Experimentalis et Applicata 6:156–164.
Coaker TH, Wright DW. 1963. The influence of temperature on the emergence of the cabbage root fly (*Eriochia brassicae* (Bouche)) from overwintering pupae. Annals of Applied Biology 52:337–343.
Colhoun EH. 1953. Notes on the stages and the biology of *Baryodma ontarionis* Casey (Coleoptera: Staphylinidae), a parasite of the cabbage maggot, *Hylemya brassicae* Bouche (Diptera, Anthomyiidae). The Canadian Entomologist 85:1–8.
Collier RH, Finch S. 1983. Effects of temperature and duration of low temperatures in regulating diapause development of the cabbage root fly (*Delia radicum*). Entomologia Experimentalis et Applicata 34:193–200.

Collier RH, Finch S. 1985. Accumulated temperatures for predicting the time of emergence in the spring of the cabbage root fly, *Delia radicum* (L.) (Diptera: Anthomyiidae). Bulletin of Entomological Research 75:395–404.
Collier RH, Finch S, Anderson M. 1989a. Laboratory studies on late-emergence in the cabbae root fly (*Delia radicum*). Entomologia Experimentalis et Applicata 50:233–40.
Collier RH, Finch S, Anderson M. 1989b. Oxygen uptake by pupae of early- and late-emerging biotypes of the cabbage root fly *Delia radicum* L. Functional Ecology 3:613-616.
Collier RH, Worland MR, Block W, Anderson M. 1988. Sugar and polyol content of cabbage root fly pupae. Cryo-letters 9:256–265.
Coote LD, Ellis CR. 1986. Parasites of the alfalfa blotch leafminer, *Agromyza frontella* (Diptera: Agromyzidae), near Guelph, Ontario. Proceedings of the Entomological Society of Ontario 117:21–27.
Crawley MJ. 1986. The population biology of invaders. Philosophical Transaction of the Royal Society of London. Series B 314:711–731.
Crawley MJ. 1987. What makes a community invasible? In: Gray AJ, Crawley MJ, Edwards PJ, editors. A Symposium of the British Ecological Society. Oxford: Blackwell Scientific Publications. p 429–453.
Crawley MJ. 1989. The successes and failures of weed biocontrol using insects. Biocontrol News and Information 10:213–223.
Cuny R. 1978. Muscidae and Calliphoridae (Insecta: Diptera) der Laegern (Schweiz: Jura). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 51:377–394.
Daniel WW. 1990. Applied nonparametric statistics. Boston: PWS-Kent Publishing Company. 635 p.
Danilevsky AS, Goryshin NI, Tyshchenko VP. 1970. Biological rythyms in terrestrial arthropods. Annual Review of Entomology 15:201–244.
Danks HV. 1987. Insect dormancy: an ecological perspective: Biological Survey of Canada (Terrestrial Arthropods). 439 p.
Danks HV. 2006. Insect adaptations to cold and changing environments. The Canadian Entomologist 138:1–23.
Danks HV, Oliver DR. 1972. Seasonal emergence of some high arctic Chironomidae (Diptera). The Canadian Entomologist 104:661–686.
Darvas B, Kozma E. 1982. A fesuslabu viraglegy, *Delia platura* Meigen (Diptera: Anthomyiidae) morfologiaja, biologiaja, es parazitai. Novenyvedelem 18:145–156.
Davidson J. 1944. On the relationship between temperature and rate of development of insects at constant temperatures. The Journal of Animal Ecology 13:26–38.
DeBach P. 1964. Biological control of insect pests and weeds. London: Chapman & Hall. 844 p.
DeBach P, Rosen D. 1991. Biological control by natural enemies. Cambridge: Cambridge University Press. 440 p.
Degen T, Staedler E. 1996. Influence of natural leaf shapes on oviposition in three phytophagous flies: a comparative study. Entomologia Experimentalis et Applicata 80:97–100.
Delfosse ES. 2005. Risk and ethics in biological control. Biological Control 35:319–329.
Denlinger DL. 2002. Regulation of diapause. Annual Review of Entomology 47:93–122.
Denoth M, Frid L, Myers JH. 2002. Multiple agents in biological control: improving the odds? Biological Control 24:20–30.
Devin S, Beisel JN. 2007. Biological and ecological characteristics of invasive species: a gammarid study. Biological Invasions 9:13–24.

Dinther JBM, van. 1953. Biology and control of the bean seed flies *H. cana* Macq. and *H. liturata* Meig. (In Dutch). Tijdschrift over Plantenziekten 59:217–232.
Dobson RM. 1961. Observations on natural mortality, parasites and predators of wheat bulb fly, *Leptohylemyia coarctata* (Fall.). Bulletin of Entomological Research 52:281–291.
Dosdall LM. 1998. Incidence and yield impact of root maggots in canola. Vegreville: Alberta Research Council. Report nr 96M980. 42 p.
Dosdall LM, Clayton GW, Harker KN, O'Donovan JT, Stevenson FC. 2003. Weed control and root maggots: making canola pest management strategies compatible. Weed Science 51:576–585.
Dosdall LM, Clayton GW, Harker KN, O'Donovan JT, Stevenson FC. 2006. Effects of fall and spring seeding date and other agronomic factors on infestations of root maggots, *Delia* spp. (Diptera: Anthomyiidae), in canola. Journal of Economic Entomology 99:1655–1674.
Dosdall LM, Florence LZ, Conway PM, Cowle NT. 1998. Tillage regime, row spacing, and seeding rate influence infestations of root maggots (*Delia* spp.) (Diptera: Anthomyiidae) in canola. Canadian Journal of Plant Science 78:671–681.
Dosdall LM, Good A, Keddie BA, Ukuere U, Stringam G. 2000. Identification and evaluation of root maggot (*Delia* spp.) (Diptera: Anthomyiidae) resistance within Brassicaceae. Crop Protection 19:247–253.
Dosdall LM, Herbut MJ, Cowle NT. 1994. Susceptibilities of species and cultivars of canola and mustard to infestation by root maggots (*Delia* spp.) (Diptera: Anthomyiidae). The Canadian Entomologist 126:251–260.
Dosdall LM, Herbut MJ, Cowle NT, Micklich TM. 1996a. The effect of seeding date and plant density on infestations of root maggots, *Delia* spp. (Diptera: Anthomyiidae), in canola. Canadian Journal of Plant Science 76:169–177.
Dosdall LM, Herbut MJ, Cowle NT, Micklich TM. 1996b. The effect of tillage regime on emergence of root maggots (*Delia* spp.) (Diptera: Anthomyiidae) from canola. The Canadian Entomologist 128:1157–1165.
Dosdall LM, Moisey DWA. 2004. Developmental biology of the cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Coleoptera: Curculionidae), in spring canola, *Brassica napus*, in western Canada. Annals of the Entomological Society of America 97:458–465.
Dosdall LM, Yang RC, Conway PM. 2002. Do applications of sulfur or sulfate influence infestations of root maggots (*Delia* spp.) (Diptera: Anthomyiidae) in canola? Canadian Journal of Plant Science 82:599–610.
Dowell RV, Horn DJ. 1977. Adaptive strategies of larval parasitoids of the alfalfa root weevil (Coleoptera: Curculionidae). The Canadian Entomologist 109:641–648.
Drea JJ, Jr. 1966. Studies of *Aleochara tristis* (Coleoptera: Staphylinidae), a natural enemy of the face fly. Journal of Economic Entomology 59:1368–1373.
Drea JJ, Jr. The coordination of scientific and commercial aspects of biological control of filth breeding flies. In: Patterson RS, editor; 1981; University of Florida Gainesville. USDA. p 1–4.
Drea JJ, Jr., Hendrickson RM, Jr. 1986. Analysis of a successful classical biological control project: the alfalfa blotch leafminer (Diptera: Agromyzidae) in the northeastern United States. Environmental Entomology 15:448–455.
Dreves AJ, Dalthorp D, Stone AG, Fisher G. 2006. Spring emergence and seasonal flight of *Delia radicum* L. (Diptera: Anthomyiidae) in western Oregon. Environmental Entomology 35:465–477.

Dysart RJ, Maltby HL, Brunson MH. 1973. Larval parasites of *Oulema melanopus* in Europe and their colonization in the United States. Entomophaga 18:133–167.
Eckenrode CJ, Chapman RK. 1971a. Effect of various temperatures upon rate of development of the cabbage maggot under artificial conditions. Annals of the Entomological Society of America 64:1079–1083.
Eckenrode CJ, Chapman RK. 1971b. Observations on cabbage maggot activity under field conditions. Annals of the Entomological Society of America 64:1226–1230.
Eckenrode CJ, Chapman RK. 1972. Seasonal adult cabbage maggot populations in the field in relation to thermal-unit accumulation. Annals of the Entomological Society of America 65:151–156.
Ehler LE. 2000. Critical issues related to nontarget effects in classical biological control of insects. In: Follett PA, Duan JJ, editors. Nontarget Effects of Biological Control. Norwell, Massachusetts: Kluwer Academic Publishers. p 3–13.
Ehler LE, Hall RW. 1982. Evidence for competitive exclusion of introduced natural enemies in biological control. Environmental Entomology 11:1–4.
Eilenberg J, Damgaard PH, Hansen BM, Pedersen JC, Bresciani J, Larsson R. 2000. Natural coprevalences of *Strongwellsea castrans, Cystosporongenes deliaradicae,* and *Bacillus thuringensis* in the host, *Delia radicum*. Journal of Invertebrate Pathology 75:69–75.
Ekbom B. 1995. Insect pests. In: Kimber DS, McGregor DI, editors. *Brassica* oilseeds: production and utilization. Oxon: CAB International. p 141–152.
Ekuere UU, Dosdall LM, Hills M, Keddie AB, Kott L, Good A. 2005. Identification, mapping, and economic evaluation of QTLs encoding root maggot resistance in *Brassica*. Crop Science 45:371–378.
Ellis CR, Harcourt DG, Dubois-Martin D. 1978. The current status in Ontario of *Tetrastichus julius* (Hymenoptera: Eulophidae), a parasitoid of the cereal leaf beetle. Proceedings of the Entomological Society of Ontario 109:23–26.
Ellis CR, Kormos B, Guppy JC. 1988. Absence of parasitism in an outbreak of the cereal leaf beetle, *Oulema melanopus* (Coleoptera: Chrysomelidae), in the central tobacco growing area of Ontario. Proceedings of the Entomological Society of Ontario 119:43–46.
Elton CS. 1958. The ecology of invasions by animals and plants. London: Methuen and Co. Ltd. 181 p.
Erichsen E, Huenmoerder S. 2005. Kohlfliegenaugtreten im raps. Gesunde Pflanzen 57:149–157.
Eyre MD, Lott DA, Luff ML. 2001. The rove beetles (*Coleoptera, Staphylinidae)* of exposed riverine sediments in Scotland and northern England: habitat classification and conservation aspects. Journal of Insect Conservation 5:173–186.
Eyre MD, Luff ML, Woodward JC. 2003. Grouse moor management: habitat conservation implications for invertebrates in southern Scotland. Journal of Insect Conservation 7:21–32.
Fabritius K. 1981. Uber das naturliche vorkommen und den wirtskreis von parasiten synanthroper fliege. Zietschrift fur Angewandte Zoologie 68:139–149.
Fabritius K, Klunker R. 1991. Die larven- und puparienparasitoide von synanthropen fliegen in Europa. Angewandte Parasitologie 32:1–24.
Farkas R, Hogsette JA, Borzsonyi L. 1998. Development of *Hydrotaea aenescens* and *Musca domestica* (Diptera: Muscidae) in poultry and pig manures of different moisture content. Environmental Entomology 27:695–699.
Ferrar P. 1987. A guide to the breeding habits and immature stages of Diptera Cyclorrhapha. Lyneborg L, editor. Copenhagen: E.J. Brill/ Scandinavian Science Press. 907 p.

Finch S. 1989. Ecological considerations in the management of *Delia* pest species in vegetable crops. Annual Review of Entomology 34:117–137.
Finch S, Ackley CM. 1977. Cultivated and wild host plants supporting populations of the cabbage root fly. Annals of Applied Biology 85:13–22.
Finch S, Bromand B, Brunel E, Bues M, Collier RH, Dunne R, Foster G, Freuler J, Hommes M, Keymeulen M, van and others. Emergence of cabbage root flies from puparia collected throughout northern Europe. In: Cavalloro R, Pelerents C, editors; 1985 20-22 November; Rennes. Commission of the European Communities. p 33–36.
Finch S, Collier RH. 1983. Emergence of flies from overwintering populations of cabbage root fly pupae. Ecological Entomology 8:29–36.
Finch S, Collier RH. 1984. Parasitism of overwintering pupae of cabbage root fly, *Delia radicum* (L.) (Diptera: Anthomyiidae), in England and Wales. Bulletin of Entomological Research 74:79–86.
Finch S, Collier RH. 1985. Laboratory studies on aestivation in the cabbage root fly (*Delia radicum*). Entomologia Experimentalis et Applicata 38:137–43.
Finch S, Collier RH. 2000. Host-plant selection by insects - a theory based on 'appropriate-inappropriate landings' theory by pest insects of cruciferous crops. Entomologia Experimentalis et Applicata 96:91–102.
Finch S, Collier RH, Skinner G. 1986. Local population differences in emergence of cabbage root flies from south-west Lancashire: implications for pest forecasting and population divergence. Ecological Entomology 11:139–145.
Finch S, Elliott MS. 1992. Predation of cabbage root fly eggs by Carabidae. IOBC/WPRS Bulletin 15:176–183.
Finch S, Elliott MS. 1999. Predation of cabbage root fly eggs by carabid ground beetles- fact or fantasy? Antenna- London 23:228–232.
Finch S, Skinner G. 1982. Trapping female cabbage root flies (*Delia radicum* (L.)) (Diptera: Anthomyiidae) with allylisothiocyanate traps. Bulletin of Entomological Research 72:165–73.
Fournet S, Astier N, Cortesero AM, Biron DG. 2004. Influence of a bimodal emergence strategy of a Dipteran host on life-history traits of its main parasitoids. Ecological Entomology 29:685–691.
Fournet S, Brunel E. 1999. A hypothesis to explain the competition between two staphylinid parasitoids of *Delia radicum*. IOBC/WPRS Bulletin 22:113–116.
Fournet S, Poinsot D, Brunel E, Nenon JP, Cortesero AM. 2001. Do female coleopteran parasitoids enhance their reproductive success by selecting high-quality oviposition sites? Journal of Animal Ecology 70:1046–1052.
Fournet S, Stapel JO, Kacern N, Nenon JP, Brunel E. 2000. Life history comparison between two competitive *Aleochara* species in the cabbage root fly, *Delia radicum*: implications for their use in biological control. Entomologia Experimentalis et Applicata 96:205–211.
Fraenkel G, Bhaskaran G. 1973. Pupariation and pupation in cyclorrhaphous flies (Diptera): terminology and interpretation. Annals of the Entomological Society of America 66:418–422.
Frazer BD. 1972. A simple and efficient method of rearing aphidophagous hoverflies (Diptera: Syrphidae). Journal of the Entomological Society of British Columbia 69:23–24.
Frings H. 1948. Rearing houseflies and blowflies on dog biscuit. Science 107:629–630.

Fuldner D. 1960. Beitrage zur morphologies und biologies von *Aleochara bilineata* Gyll. und *A. bipustulata* L. (Coleoptera: Staphylinidae). Zeitschrift fur Morphologie und Okologie der Tiere 48:312–386.
Fuldner D. 1968. Experimentelle analyse des orientierungsverhaltens der eilarve von *Aleochara curtula* Goeze (Coleoptera: Staphylinidae) am wirt. Journal of Comparative Physiology A: Neuroethology, Sensory, Neural and Behavioral Physiology 61:298–354.
Fuldner D, Wolf H. 1971. Staphyliniden-larven beeinflussen chemisch das orientierungsverhalten ihrer konkurrenten. Naturwissenschaften 58:418.
Gallant AR. 1987. Nonlinear statistical models. New York: John Wiley & Sons. 610 p.
Gerling D, Rottenberg O, Bellows TS. 2004. Role of natural enemies and other factors in the dynamics of field populations of the whitefly *Siphoninus phillyreae* (haliday) [Sic.] in introduced and native environments. Biological Control 31:199–209.
Gibson GAP, Baur H, Ulmer B, Dosdall L, Muller F. 2005. On the misidentification of chalcid (Hymenoptera: Chalcidoidea) parasitoids of the cabbage seedpod weevil (Coleoptera: Curculionidae) in North America. The Canadian Entomologist 137:381–403.
Gillespie DR, Mason PG, Dosdall LM, Bouchard P, Gibson GAP. 2006. Importance of long-term research in classical biological control: an analytical review of a release against the cabbage seedpod weevil in North America. Journal of Applied Entomology 130:401–409.
Girardoz S, Kenis M, Quicke DLJ. 2006. Recruitment of native parasitoids by an exotic leaf miner, *Cameria ohridella*: host-parasitoid synchronization and influence of the environment. Agricultural and Forest Entomology 8:49–56.
Godfray HCJ. 1994. Parasitoids: behavioural and evolutionary ecology. Princeton: Princeton University Press. 473 p.
Goodwin BJ, McAllister AJ, Fahrig L. 1999. Predicting invasiveness of plant species based on biological information. Conservation Biology 13:422–426.
Gordh G, Headrick D. 2001. A dictionary of entomology. Wallingford, UK: CABI Publishing. 1032 p.
Gouinguene SPD, Staedler E. 2005. Comparison of the sensitivity of four *Delia* species to host and non-host plant compounds. Physiological Entomology 30:62–74.
Gould SJ. 1991. Unenchanted evening. Natural History 100:4–9.
Gould SJ, Lewontin RC. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proceedings of the Royal Society of London. Series B 205:581–598.
Grabenweger G. 2004. Poor control of the horse chestnut leafminer, *Cameraria ohridella* (Lepidoptera: Gracillariidae), by native European parasitoids: a synchronization problem. European Journal of Entomology 101:189–192.
Gray AJ. 1986. Do invading species have definable genetic characteristics. Philosophical Transaction of the Royal Society of London. Series B 314:655–674.
Gray R, Malla S, Phillips PWB. 2006. Product innovation in the Canadian canola sector. Supply Chain Management 11:65–74.
Grevstad FS. 1999a. Experimental invasions using biological control introductions: the influence of release size on the chance of population establishment. Biological Invasions 1:313–323.
Grevstad FS. 1999b. Factors influencing the chance of population establishment: implications for release strategies in biocontrol. Ecological Applications 9:1439–1447.
Griffiths GCD. 1982. Anthomyiidae. Cyclorrhapha II (Schizphora: Calyptratae). Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung (Naegele u. Obermiller). p 1–160.

Griffiths GCD. 1985. *Hypogastrura succinea* (Collembola: Hypogastruridae) dispersed by adults of the cabbage maggot, *Delia radicum* (Diptera: Anthomyiidae), infected with the parasitic fungus *Strongwellsea castrans* (Zygomycetes: Entomophthoraceae). The Canadian Entomologist 117:1063–1064.
Griffiths GCD. 1986a. Phenology and dispersion of *Delia radicum* (L.) (Diptera: Anthomyiidae) in canola fields at Morinville, Alberta. Quaestiones Entomologicae 22:29–50.
Griffiths GCD. 1986b. Relative abundance of the root maggots *Delia radicum* (L.) and *D. floralis* (Fallen) (Diptera: Anthomyiidae) as pests of canola in Alberta. Quaestiones Entomologicae 22:253–60.
Griffiths GCD. 1991a. Anthomyiidae. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung (Naegele u. Obermiller). p 953–1048.
Griffiths GCD. 1991b. Anthomyiidae. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung (Naegele u. Obermiller). p 1049–1240.
Griffiths GCD. Economic assessment of cabbage maggot damage in canola in Alberta; 1991c; Saskatoon. p 528–535.
Hagvar EB. 1991. Ecological problems in the establishment of introduced predators and parasites for biological control. Acta Entomologica Bohemoslov 88:1–11.
Hallett RH, Heal JD. 2001. First Nearctic record of the swede midge (Diptera: Cecidomyiidae), a pest of cruciferous crops in Europe. The Canadian Entomologist 133:713–715.
Harcourt DG, Guppy JC, Meloche F. 1988. Population dynamics of the alfalfa blotch leafminer, *Agromyza frontella* (Diptera: Agromyzidae), in eastern Ontario: impact of the exotic parasite *Dacnusa dryas* (Hymenoptera: Braconidae). Environmental Entomology 17:337–343.
Harman DM, Kulman HM. 1968. Biology and natural control of the white-pine weevil in Virginia. Annals of the Entomological Society of America 61:280–185.
Harman DM, Wallace JB. 1971. Description of the immature stages of *Lonchaea corticis*, with notes on its role as a predator of the white pine weevil, *Pissodes strobi*. Annals of the Entomological Society of America 64:1221–1226.
Harper FR, Berkenkamp B. 1975. Revised growth-stage key for *Brassica campestris* and *B. napus*. Canadian Journal of Plant Science 55:657–658.
Harris P. 1973. The selection of effective agents for the biological control of weeds. The Canadian Entomologist 105:1495–1503.
Hartfield C, Finch S. 2003. Releasing the rove beetle *Aleochara bilineata* in the field as a biological agent for controlling the immature stages of the cabbage root fly, *Delia radicum*. IOBC/WPRS Bulletin 26:127–133.
Hatherly IS, Hart AJ, Tullett AG, Bale JS. 2005. Use of thermal data as a screen for the establishment potential of non-native biological control agents in the UK. BioControl 50:687–698.
Hawkes C. 1974. Dispersal of adult cabbage root fly (*Erioischia brassicae* (Bouche)) in relation to a brassica crop. Journal of Applied Ecology 11:83–93.
Hawkins BA, Marino PC. 1997. The colonization of native phytophagous insects in North America by exotic parasitoids. Oecologia 112:566–571.
Hawkins-Bowman AK. 2006. The effect of tillage and seeding rate on infestations of cabbage root maggots, *Delia radicum* (L.) (Diptera: Anthomyiidae) in canola, *Brassica napus* (L.), in Manitoba [MSc.]. Winnipeg: University of Manitoba. 90 p.
Hayashi T, Tuno N. 1998. Notes on the lesser dung flies emerged from fungi in Japan (Diptera, Sphaeroceridae). Medical Entomology and Zoology 49:357–359.

Hayes CG, Turner EC, Jr. 1971. Field and laboratory evaluation of parasitism of the face fly in Virginia. Journal of Economic Entomology 64:443–448.
Haynes DL, Gage SH. 1981. The cereal leaf beetle in North America. Annual Review of Entomology 26:259–287.
Heger T, Trepl L. 2003. Predicting biological invasions. Biological Invasions 5:313–321.
Hemachandra KS. 2004. Parasitoids of *Delia radicum* (Diptera: Anthomyiidae) in canola: assessment of potential agents for classical biological control [PhD]. Winnipeg: University of Manitoba. 264 p.
Hemachandra KS, Holliday NJ, Klimaszewski J, Mason PG, Kuhlmann U. 2005. Erroneous records of *Aleochara bipustulata* from North America: an assessment of the evidence. The Canadian Entomologist 137:182–187.
Hertveldt L, Keymeulen M, Van, Gillard A. 1984. Simple techniques for handling adults and collecting eggs of *Musca domestica* (Diptera: Muscidae) and *Aleochara bilineata* (Coleoptera: Staphylinidae). Journal of Economic Entomology 77:267–70.
Hille Ris Lambers D. 1932. Gegevens over biologie en bestrijding der bietenvlieg. Meded. Inst. Suikerbietenteelt 2:164–214.
Hoddle MS. 2004. Analysis of fauna in the receiving area for the purpose of identifying native species that exotic natural enemies may potentially attack. In: Van Driesche RG, Reardon R, editors. Assessing host ranges for parasitoids and predators used for classical biological control: a guide to best practice. Morgantown: USDA Forest Service. p 24–39.
Hogsette JA, Farkas R, Coler RR. 2002. Development of Hydrotaea aenescens (Diptera: Muscidae) in manure of unweaned dairy calves and lactating cows. Journal of Economic Entomology 95:527–530.
Hogsette JA, Jacobs RD. 1999. Failure of *Hydrotaea aenescens,* a larval predator of the housefly, *Musca domestica*, to establish in wet poultry manure on a commercial farm in Florida, U.S.A. Medical and Veterinary Entomology 13:349–354.
Hopkins RJ, Griffiths DW, McKinlay RG, Birch ANE. 1999. The relationship between cabbage root fly (*Delia radicum*) larval feeding and the freeze-dried matter and sugar content of *Brassica* roots. Entomologia Experimentalis et Applicata 92:109–17.
Hopper KR, Roush RT. 1993. Mate finding, dispersal, number released, and the success of biological control introductions. Ecological Entomology 18:321–331.
Horsfield D, MacGowan I, Rotheray G. 2005. Breeding site and host plant relationships of saproxylic calyptrate Diptera in Britain. Studia Dipterologica 12:209–221.
Howarth FG. 1983. Classical biocontrol: panacea or Pandora's box. Proceedings of the Hawaiian Entomological Society 24:239–244.
Howarth FG. 1991. Environmental impacts of classical biological control. Annual Review of Entomology 36:485–509.
Howarth FG. 2000. Non-target effects of biological control agents. In: Gurr G, Wratten S, editors. Biological Control: Measures of Success. Norwell, Massachusetts: Kluwer Academic Publishing. p 369–403.
Hoy M. 1985. Improving establishment of arthropod natural enemies. In: Hoy MA, Herzog DC, editors. Biological control in IPM systems. Orlando: Academic Press. p 151–166.
Huckett HC. 1987. Anthomyiidae. In: McAlpine JF, editor. Manual of Nearctic Diptera. Ottawa: Biosystematics Research Institute. p 1099–1114.
Hughes RD. 1960. Induction of diapause in *Erioschia brassicae* Bouche (Dipt., Anthomyiidae). Journal of Experimental Biology 37:218–223.

Hughes RD, Mitchell B. 1960. The natural mortality of *Erioschia brassicae* (Bouche) (Dipt., Anthomyiidae): life tables and their interpretation. Journal of Animal Ecology 29:359–374.

Hughes RD, Salter DD. 1959. Natural mortality of *Erioshia brassicae* (Bouche) (Diptera, Anthomyiidae) during the immature stages of the first generation. The Journal of Animal Ecology 28:231–241.

Hulme MA. 1989. Laboratory assessment of predation by *Lochaea coriticis* (Diptera: Lochaeidae) on *Pissodes strobi* (Coleoptera: Curculionidae). Environmental Entomology 18:1011–1014.

Hulme MA. 1990. Field assessment of predation by *Lochaea corticis* (Diptera: Lochaeidae) on *Pissodes strobi* (Coleoptera: Curculionidae) in *Picea sitchensis*. Environmental Entomology 19:54–58.

Irmler Uv, Heller K. 2002. Zonierung der Staphylinidae in einem salzgruenland der schleswig-holsteinischen nordseekueste 1. Faunistisch-Okologische Mitteilungen 8:219–229.

Johnsen S, Gutierrez AP, Freuler J. 1990. The within season population dynamics of the cabbage root fly (*Delia radicum* [L.]). A simulation model. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 63:451–463.

Johnson EN, Miller PR, Blackshaw RE, Gan Y, Harker KN, Clayton GW, Kephart KD, Wichman DM, Topinka K, Kirkland KJ. 2004. Seeding date and polymer seed coating effects on plant establishment and yield of fall-seeded canola in the Northern Great Plains. Canadian Journal of Plant Science 84:955–963.

Johnson MT, Follett PA, Taylor AD, Jones VP. 2005. Impacts of biological control and invasive species on a non-target native Hawaiian insect. Oecologia 142:529–540.

Jonasson T. 1994a. Kortvingen *Aleochara verna* (Coleoptera, Staphylinidae) ny for Sverige. Entomologiske Tidskrift 225:173–174.

Jonasson T. 1994b. Parasitoids of *Delia* root flies in brassica vegetable crops: coexistence and niche separation in two *Aleochara* species (Coleoptera: Staphylinidae). Norwegian Journal of Agricultural Sciences Supplement 16:379–86.

Jones CM. 1967. *Aleochara tristis,* a natural enemy of face fly I. Introduction and laboratory rearing. Journal of Economic Entomology 60:816–817.

Jones MG. 1965. The effects of some insecticides on populations of frit fly (*Oscinella frit*) and its enemies. The Journal of Applied Ecology 2:391–401.

Jyoti JL, Shelton AM, Barnard J. 2003. Evaluation of degree-day and Julian-day logistic models in predicting cabbage maggot (Diptera: Anthomyiidae) emergence and flight in upstate New York. Journal of Entomological Science 38:525–532.

Kacem N, Neveu N, Nenon JP. 1995. Development of *Trybliographa rapae*, a larval parasitoid of the cabbage root fly *Delia radicum*. IOBC/WPRS Bulletin:156–161.

Keller MA. 1984. Reassessing evidence for competitive exclusion of introduced natural enemies. Environmental Entomology 13:192–195.

Kellogg SK, Fink LS, Brower LP. 2003. Parasitism of native luna moths, *Actias luna* (L.) (Lepidoptera: Saturniidae) by introduced *Compsilura concinnata* (Meigen) (Diptera: Tachinidae) in central Virginia, and their hyperparasitism by trigonalid wasps (Hymenoptera: Trigonalidae). Environmental Entomology 32:1019–1027.

Kimberling DN. 2004. Lessons from history: predicting successes and risks of intentional introductions for arthropod biological control. Biological Invasions 6:301–318.

Kirk AA. 1992. The effect of the dung pad fauna on the emergence of *Musca tempestiva* (Dipt.: Muscidae) from dung pads in southern France. Entomophaga 37:507–514.

Klein-Gebbinck HW, Woods DL. 2002. Yield loss assessment in canola: effects of brown girdling root rot and maggot damage on single plant yield. Plant Disease 86:1005–1010.
Klimaszewski J. 1984. A revision of the genus *Aleochara* Gravenhorst of America north of Mexico (Coleoptera: Staphylinidae, Aleocharinae). Memoirs of the Entomological Society of Canada 129:211.
Klimaszewski J. 2000. Diversity of the rove beetles in Canada and Alaska (Coleoptera Staphylinidae). Memoires de la Societe royale belge d'Entomologie. Brussels. p 126.
Klingen I, Meadow R, Eilenberg J. 2000. Prevalence of fungal infections in adult *Delia radicum* and *Delia floralis* captured on the edge of a cabbage field. Entomologia Experimentalis et Applicata 97:265–274.
Klinken RD, van, Heard TA. 2000. Estimating fundamental host range: a host-specificity study of a potential biocontrol agent for *Prosopis* species (Leguminosae). Biocontol Sciece and Technology 10:331–342.
Knapp FW. 1985. *Musca autumnalis*. In: Singh P, Moore RF, editors. Handbook on insect rearing: Elsevier. p 125–128.
Kolar CS, Lodge DM. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution 16:199–204.
Kostal V, Finch S. 1994. Influence of background on host-plant selection and subsequent oviposition by the cabbage root fly (*Delia radicum*). Entomologia Experimentalis et Applicata 70:153–63.
Kovalev VG. 1973. Descriptions of new and little-known species of flies of the genus *Lochaea* Fll. (Diptera, Lonchaeidae) from the southern primor'ye. Entomological Review 52:145–155.
Kovalev VG. 1975. Palearctic species of the *Lochaea corticis* group (Diptera, Lonchaeidae). Zoologicheskii Zhurnal 54:1648–1655.
Kovalev VG. 1976. Data on the fauna and ecology of flies of the genus *Lonchaea* Diptera Lonchaeidae form the Tuva–ASSR USSR. Entomologicheskoe Obozrenie 55:934–935.
Kovalev VG. 1977. Faunistic and ecological material on flies of the genus *Lochaea* (Diptera, Lochaeidae) from Tuva. Entomological Review 55:141–148.
Kovalev VG. 1979. New and little-known species of Lochaeidae (Diptera) from the Moscow region. Entomological Review 57:131–139.
Kovalev VG. 1981. On European species of the group *Lonchaea peregrina* (Diptera, Lonchaeidae). Zoologicheskii Zhurnal 60:221–228.
Kovalev VG. 1984. On finnish and some other species of *Lochaea* Fallen (Diptera, Lonchaeidae). Annales Entomologici Fennici 50:17–20.
Kuhar TP, Youngman RR, Laub CA. 2001. Alfalfa weevil (Coleoptera: Curculionidae) phenology with its host crop and parasitoids in Virginia. Journal of Entomological Science 36:352–365.
Kuhlmann U. 1995. Biology and predation rate of the sarcophagid fly, *Agria mamillata*, a predator of European small ermine moths. International Journal of Pest Management 41:67–73.
Kuhlmann U, Mason PG, Hinz HL, Blossey B, Clerck-Floate RA, De, Dosdall LM, McCaffrey JP, Schwaerzlaender M, Olfert O, Brodeur J and others. 2006a. Avoiding conflicts between insect and weed biological control: selection of non-target species to assess host specificity of cabbage seedpod weevil parasitoids. Journal of Applied Entomology 130:129–141.

Kuhlmann U, Schaffner U, Mason PG. Selection of non-target species for host specificity testing of entomophagous biological control agents. In: Hoddle MS, editor; 2005; Davos, Switzerland. USDA Forest Service. p 566–583.
Kuhlmann U, Schaffner U, Mason PG. 2006b. Selection of non-target species for host specificity testing. In: Bigler F, Babendreier D, Kuhlmann U, editors. Environmental Imapct of Invertebrates in Biological Control of Arthropods: Methods and Risk Assessment. Wallingford, UK: CAB International. p 15–37.
Labrie G, Lucas E, Coderre D. 2006. Can developmental and behavioral characteristics of the multicolored Asian lady beetle *Harmonia axyridis* explain its invasive success. Biological Invasions 8:743–754.
Lactin DJ, Holliday NJ, Johnson DL, Craigen R. 1995. Improved rate model of temperature–dependent development by arthropods. Environmental Entomology 24:68–75.
Lamb DJ. 1984. The potential of oilseed rape as a host for the first generation of cabbage root fly, *Delia radicum* (L.). Crop Research 24:61–63.
Lamb RJ. 1989. Entomology of oilseed *Brassica* crops. Annual Review of Entomology 34:211–229.
Lamb RJ. 1992. Developmental rate of *Acyrthosiphon pisum* (Homoptera: Aphididae) at low temperatures: implications for estimating rate parameters for insects. Environmental Entomology 21:10–19.
Langlet X, Boivin G, Brunel E, Nenon JP. 1998. Variation in weight of *Aleochara bilineata* (Coleoptera: Staphylinidae) in relation to host size and reproduction. The Canadian Entomologist 130:257–265.
Lavallee R, Daoust G, Mauffette Y, Audet G, Coulombe C. 2001. Feeding, ovipostition, and emergence of the white pine weevil (*Pissodes strobi* (Peck)) under a pioneer broad-leaved forest canopy. The Forestry Chronicle 77:885–892.
Lawton JH, Brown KC. 1986. Population and community ecology of invading insects. Philosophical Transaction of the Royal Society of London. Series B 314:607–617.
Legner EF. Natural enemies imported in California for the biological control of face fly, *Musca autumnalis* De Geer, and horn fly, *Heamatobia irritans* (L.). In: Grant CD, editor; 1978; Yosemite, California. CMVCA Press. p 77–79.
Legner EF, Bellows TS. 1999. Exploration for natural enemies. In: Bellows TS, Fisher TW, editors. Handbook of biological control. San Diego: Academic Press. p 87–102.
Lerin J. 1995. Assessment of yield losses caused by insects in winter oilseed rape, a critical review. Bulletin OILB/SROP 18:95–101.
Liu HJ, Butts RA. 1982. *Delia* spp. (Diptera: Anthomyiidae) infesting canola in Alberta. The Canadian Entomologist 114:651–653.
Lize A, Carval D, Cortesero AM, Fournet S, Poinsot D. 2006. Kin discrimination and altruism in the larvae of a solitary insect. Proceedings of the Royal Society of London. Series B 273:2381–2386.
Lockwood JA. 1993a. Benefits and costs of controlling rangeland grasshoppers (Orthoptera: Acrididae) with exotic organisms: search for a null hypothesis and regulatory compromise. Environmental Entomology 22:904–914.
Lockwood JA. 1993b. Environmental issues involved in biological control of rangeland grasshoppers (Orthoptera: Acrididae) with exotic agents. Environmental Entomology 22:503–518.

Lockwood JA, Howarth FG, Purcell MF. 2001. Balancing nature: assessing the impact of importing non-native biological control agents (an international perspective). Lanham, Maryland: Entomolological Society of America. 130 p.
Logan JA, Wollkind DJ, Hoyt SC, Tanigoshi LK. 1976. An analytic model for description of temperature dependent rate phenomena in arthropods. Environmental Entomology 5:1133–1140.
Lohse GA. 1986. *Aleochara*-studien II *) Die rotgeflecken arten der untergattung *Coprochara* Mulsant, Rey. Verhandlungen des Vereins vaturw fur naturissenschaftliche Heimatforschung, Hamburg 39:95–98.
Lonsdale WM. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536.
Louda SM, Kendall D, Simberloff D. 1997. Ecological effects of an insect introduced for the biological control of weeds. Science 277:1088–1090.
Louda SM, Pemberton RWJ, Johnson MT, Follett PA. 2003. Nontarget Effects – The Achilles' heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. Annual Review of Entomology 48:365–396.
MacDonald PDM, Cheng L. 1970. A method of testing for synchronization between host and parasite populations. The Journal of Animal Ecology 39:321–331.
Martinez-Sanchez A, Rojo S, Maros-Garcia MA. 2000. Annual and spatial activity of dung flies and carrion in a Mediterranean holm-oak pasture ecosystem. Medical and Veterinary Entomology 14:56–63.
Mason PG, Arthur AP, Olfert OO, Erlandson MA. 1998. The Bertha armyworm (*Mamestra configurata*) (Lepidoptera: Noctuidae) in western Canada. The Canadian Entomologist 130:321–336.
Mason PG, Flanders RG, Arrendondo-Bernal HA. How can legislation facilitate the use of biological control of arthropods in North America. In: Hoddle MS, editor; 2005; Davos, Switzerland. USDA Forest Service. p 701–714.
Mason PG, Olfert O, Sluchinsski L, Weiss RM, Boudreault C, Grossrieder M, Kuhlmann U. 2003. Actual and potential distribution of an invasive canola pest, *Meligethes viridescens* (Coleoptera: Nitidulidae), in Canada. The Canadian Entomologist 135:405–413.
Matanmi BA, Libby JL, Maxwell DP. 1974. Two phycomycetes infecting root maggot adults in Wisconsin. Environmental Entomology 3:1030–1031.
Maus C. 1996. Taxonomische und phylogenetisch-systematische untersuchungen zur untergattung *Coprochara* Mulsant and Rey 1874 der Gattung *Aleochara* Gravenhorst 1802 (Coleoptera, Staphylinidae).
Maus C. 1998. Taxonomical contributions to the subgenus *Coprochara* Mulsant and Rey, 1874 of the genus *Aleochara* Gravenhorst, 1802. Koleopterologische Rundschau 68:81–100.
Maus C, Mittmann B, Peschke K. 1998. Host records of parasitoid *Aleochara* Gravenhorst species (Coleoptera, Staphylinidae) attacking puparia of cyclorrhapheous Diptera. Deutsche Entomologische Zeitschrift 45:231–254.
Maus C, Peschke K, Dobler S. 2001. Phylogeny of the genus *Aleochara* inferred from mitochondrial cytochrome oxidase sequences (Coleoptera: Staphylinidae). Molecular Phylogenetics and Evolution 18:202–216.
Mayr E. 1983. How to carry out the adaptationist program? The American Naturalist 121:324–334.
McAlpine JF. 1964. Descriptions of new Lonchaeidae (Diptera) II. The Canadian Entomologist 96:701–757.

McAlpine JF. 1989. Phylogeny and Classification of the Muscomorpha. In: McAlpine JF, editor. Manual of Nearctic Diptera. Ottawa: Biosystematics Research Centre. p 1397–1518.
McAlpine JF, Slight C. 1981. The wheat bulb fly, *Delia coarctata*, in North America (Diptera: Anthomyiidae). The Canadian Entomologist 113:615–621.
McDonald RS, Sears MK. 1991. Effects of root damage by cabbage maggot, *Delia radicum* (L.) (Diptera: Anthomyiidae), on yield of canola, *Brassica campestris* L., under laboratory conditions. The Canadian Entomologist 123:861–867.
McDonald RS, Sears MK. 1992. Assessment of larval feeding damage of the cabbage maggot (Diptera: Anthomyiidae) in relation to oviposition preference on canola. Journal of Economic Entomology 85:957–962.
McLeod DGR, Driscoll GR. 1967. Diapause in the cabbage maggot, *Hylemya brassicae* (Diptera: Anthomyiidae). The Canadian Entomologist 99:890–893.
McLeod JH. 1962. Root maggots - *Hylemya* spp. In: McLeod JH, editor. A review of the biological control attempts against insects and weeds in Canada. Farnham Royal: CAB. p 6–7.
Messenger PS, Bosch R, van den. 1971. The adaptability of introduced biological control agents. In: Huffaker CB, editor. Biological control. New York: Plenum Press. p 68–92.
Messenger PS, Wilson F, Whitten MJ. 1976. Variation, fitness, and adaptability of natural enemies. In: Huffaker CB, Messenger PS, editors. Theory and practice in biological control. New York: Academic Press. p 209–232.
Messing RH, Wright MG. 2007. Biological control of invasive species: solution of pollution? Frontiers in Ecology and Evolution 4:132–140.
Miczulski B, Pawelska K. 1964. Przyczynek do znajomosci pasozytow smietki ewiklanki-*Pegomyia hyoscami* (Panzer) (Dipt., Muscidae). Polskie Pismo Entomologiczne 1–2:71–77.
Miles M. 1948. Field observations on the bean seed fly (seed corn maggot) *Chortophila cilicura,* Rond., and *C. trichodactyla,* Rond. Bulletin of Entomological Research 38:559–574.
Miles M. 1952a. Further observations on the biology of the cabbage root fly, *Erioschia brassicae* Bche. Annals of Applied Biology 39:385–391.
Miles M. 1952b. Studies on British anthomyiid flies III. Immature stages of *Delia cilicrura* (Rond.), *D. trichodactyla* (Rond.), *Erioschia brassicae* (Bch.), *E. floralis* (Fall.) and *Pegohylemyia fugax* (Mg.). Bulletin of Entomological Research 43:83–90.
Mondor EB, Tremblay MN, Messing RH. 2007. Morphological and ecological traits promoting aphid colonization of the Hawaiian islands. Biological Invasions 9:87–100.
Moore I, Legner EF. 1971. Host records of parasitic staphylinids of the genus *Aleochara* in America (Coleoptera: Staphylinidae). Annals of the Entomological Society of America 64:1184–1185.
Morley K, Finch S, Collier RH. 2005. Companion planting - behaviour of the cabbage root fly on host plants and non-host plants. Entomologia Experimentalis et Applicata 117:15–25.
Morris ON. 1985. Susceptibility of 31 species of agricultural insects to the entomopathogenous nematodes *Steinernema feltiae* and *Heterorhabditis bacteriophora*. The Canadian Entomologist 117:401–417.
Mukerji MK. 1971. Major factors in survival of the immature stages of *Hylemya brassicae* (Diptera: Antomyiidae) on cabbage. The Canadian Entomologist 103:717–728.
Muller H, Nuessly GS, Goeden RD. 1990. Natural enemies and host-plant asynchrony contributing to the failure of the introduced moth, *Coleophora parthenica* Meyrick

(Lepidoptera: Coleophoridae), to control Russian thistle. Agriculture, Ecosystems and Environment 32:133–142.
Munro VMW. 1998. A retrospective analysis of the establishment and dispersal of the introduced parasitoids *Xanthopimpla rhopaloceros* (Krieger) (Hymenoptera: Ichneumonidae) and *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae) within New Zealand. Biocontrol Sciece and Technology 8:559–571.
Munro VMW, Henderson IM. 2002. Nontarget effect of entomophagous biocontrol: shared parasitism between native lepidopteran parasitoids and the biocontrol agent *Trigonospila brevifacies* (Diptera: Tachinidae) in forest habitats. Environmental Entomology 31:388–396.
Murdoch WW, Chesson J, Chesson PL. 1985. Biological control in theory and practice. The American Naturalist 125:344–366.
Murdoch WW, Reeve JD, Huffaker CB, Kennett CE. 1984. Biological control of olive scale and its relevance to ecological theory. The American Naturalist 123:371–392.
Myers JH, Higgins C, Kovacs E. 1989. How many insect species are necessary for the biological control of insects? Environmental Entomology 18:541–547.
Nafus DM. 1993. Movement of introduced biological control agents onto nontarget butterflies, *Hypolimnas* spp. (Lepidoptera: Nymphalidae). Environmental Entomology 22:265–272.
Nair KSS, McEwen FL. 1975. Ecology of the cabbage maggot, *Hylemya brassicae* (Diptera: Anthomyiidae), in rutabaga in southwestern Ontario, with some observations on other root maggots. The Canadian Entomologist 107:343–354.
Nair KSS, McEwen FL. 1976. Host selection by the adult cabbage maggot, *Hylemya brassicae* (Diptera: Anthomyiidae): effect of glucosinolates and common nutrients on oviposition. The Canadian Entomologist 108:1021–1030.
Nair KSS, McEwen FL, Alex JF. 1973. Oviposition and development of *Hylemya brassicae* (Bouche) (Diptera: Anthomyiidae) on cruciferous weeds. Proceedings of the Entomological Society of Ontario 104:11–15.
Nair KSS, McEwen FL, Snieckus V. 1976. The relationship between glucosinolate content of cruciferous plants and oviposition preferences of *Hylemya brassicae*. The Canadian Entomologist 108:1031–1036.
Nardo EAB, De, Hopper KR. 2004. Using literature to evaluate parasitoid host ranges: a case study of *Macrocentrus grandii* (Hymenoptera: Braconidae) introduced into North America to control *Ostrinia nubilalis* (Lepidoptera: Crambidae). Biological Control 31:280–295.
Neal JW, Chittams JL, Bentz JO. 1997. Spring emergence by larvae of the eastern tent caterpillar (Lepidoptera: Lasiocampidae): a hedge against high-risk conditions. Annals of the Entomological Society of America 90:596–603.
Nealis VG. 1991. Parasitism in sustained and collapsing populations of the jack pine budworm, *Choristoneura pinus pinus* Free. (Lepidoptera: Tortricidae), in Ontario, 1985–1987. The Canadian Entomologist 123:1065–1075.
Nealis VG. 1998. Population dynamics of the white pine weevil, *Pissodes strobi*, infesting jack pine, *Pinus banksiana*, in Ontario, Canada. Ecological Entomology 23:305–313.
Nechols JR, Tauber MJ, Helgesen RG. 1980. Environmental control of diapause and postdiapause development in *Tetrastichus julius* (Hymenoptera: Eulophidae), a parasite of the cereal leaf beetle, *Oulema melanopus* (Coleoptera: Chrysomelidae). The Canadian Entomologist 112:1277–1284.

Neveu N, Grandgirard J, Nenon JP, Cortesero AM. 2002. Systemic release of herbivore-induced plant volatiles by turnips infested by concealed root-feeding larvae *Delia radicum* L. Journal of Chemical Ecology 28:1717–1732.

Neveu N, Krespi L, Kacem N, Nenon JP. 2000. Host-stage selection by *Trybliographa rapae*, a parasitoid of the cabbage root fly *Delia radicum*. Entomologia Experimentalis et Applicata 96:231–237.

Nielsen O, Philipsen H. 2004. Occurrence of *Steinernema* species in cabbage fields and the effect of inoculated *S. feliae* on *Delia radicum* and its parasitoids. Agricultural and Forest Entomology 6:25–30.

Oatman ER. 1964. Apple maggot emergence and seasonal activity in Wisconsin. Journal of Economic Entomology 57:676–679.

O'Donovan JT, Otani J, Clayton GW, Soon YK. 2005. Effect of fall and spring seeding on canola productivity in the Peace River region of northern Alberta. Canadian Journal of Plant Science 85:641–644.

Olfert O, Hallett R, Weiss RM, Soroka J, Goodfellow S. 2006. Potential distribution and relative abundance of swede midge, *Contarinia nasturtii*, an invasive pest in Canada. Entomologia Experimentalis et Applicata 120:221–228.

Olfert O, Weiss RM. 2002. Impact of grasshopper feeding on selected cultivars of cruciferous oilseed crops. Journal of Orthoptera Research 11:83–86.

Onstad DW, McManus ML. 1996. Risks of host range expansion by parasites of insects. Bioscience 46:430–436.

Palaniswamy P, Gillott C, Slater GP. 1986. Attraction of diamondback moths, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), by volatile compounds of canola, white mustard, and faba bean. The Canadian Entomologist 118:1279–1285.

Pape T. 1996. Catalogue of the Sarcophagidae of the world (Insecta: Diptera). Memoirs on Entomology International. p 558.

Payne JA. 1965. A summer carrion sutdy of the baby pig *Sus scrofa* Linnaeus. Ecology 64:592–602.

Peschke K, Hahn P, Fuldner D. 1987a. Adaptations of the blow fly parasitoid *Aleochara curtula* (Coleoptera, Staphylinidae) to the temporal availability of hosts at carrion. Zoologische Jahrbuecher Abteilung fuer Systematik Oekologie und Geographia der Tiere 114:471–486.

Peschke K, Krapf D, Fuldner D. 1987b. Ecological separation, functional relationships, and limiting resources in a carrion insect community. Zoologische Jahrbuecher Abteilung fuer Systematik Oekologie und Geographia der Tiere 114:241–265.

Pimentel D, Glenister C, Fast S, Gallahan D. 1984. Environmental risks of biological pest controls. Oikos 42:283–290.

Prasad RP, Snyder WE. 2004. Predator interference limits fly egg biological control by a guild of ground-active beetles. Biological Control 31:482–437.

Prasad RP, Snyder WE. 2006. Polyphagy complicates conservation biological control that targets generalist predators. Journal of Applied Ecology 43:343–352.

Prokopy RJ, Collier RH, Finch S. 1982. Leaf color used by cabbage root flies to distinguish among host plants. Science 221:190–192.

Psarev AM. 2002. Succession in a insects community inhabiting horse dung. Russian Entomological Journal 11:297–290.

Ramert B, Ehnstrom B, Lundberg S. 2001. Inverkan av marktackning och samodling pa forekomst av jordlopare och kortvingar (Coleoptera: Carabidae och Staphylinidae) i morotsodlingar. Entomologiske Tidskrift 122:177–187.

Raworth DA, Robertson MC, Bittman S. 2004. Effects of dairy slurry applications on carabid beetles in tall fescue, British Columbia, Canada. Agriculture, Ecosystems and Environment 103:527–534.

Read DC. 1958. Notes on *Scatophaga stercoraria* (L.) (Diptera: Anthomyiidae), a predator of the cabbage maggot, *Hylemya brassicae* (Bouche). The Canadian Entomologist 90:376.

Read DC. 1962. Notes on the life history of *Aleochara bilineata* (Gyll.) (Coleoptera: Staphylinidae), and on its potential value as a control agent for the cabbage maggot, *Hylemya brassicae* (Bouche) (Diptera: Anthomyiidae). The Canadian Entomologist 94:417–424.

Read DC. 1969. Rearing the cabbage maggot with and without diapause. The Canadian Entomologist 101:725–737.

Reader PM, Jones TH. 1990. Interactions between an eucoilid (Hymenoptera) and a staphylinid (Coleoptera) parasitoid of the cabbage root fly. Entomophaga 35:241–246.

Reimer A, Shaykewich CF. 1980. Estimation of Manitoba soil temperatures from atmospheric meteorological measurements. Canadian Journal of Soil Science 60:299–309.

Richardson DM, Pysek P, Rejmanek M, Barbour MG, Panetta FD, West CJ. 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6:93–107.

Riley KJ, Kuhlmann U, Mason PG, Whistlecraft J, Donald LJ, Holliday NJ. *In Press*. Can mustard seed meal increase attacks by *Aleochara* spp. on *Delia radicum* in oilseed rape? Biocontol Sciece and Technology.

Roessingh P, Staedler E, Baur R, Hurter J, Ramp T. 1997. Tarsal chemoreceptors and oviposition behaviour of the cabbage root fly (*Delia radicum*) sensitive to fractions and new compounds of host-leaf surface extracts. Physiological Entomology 22:140–148.

Roessingh P, Staedler E, Fenwick GR, Lewis JA, Nielsen JK, Hurter J, Ramp T. 1992. Oviposition and tarsal chemoreceptors of the cabbage root fly are stimulated by glucosinolates and host plant extracts. Entomologia Experimentalis et Applicata 65:267–282.

Rognes K. 1998. Family Calliphoridae. In: Papp L, Darvas B, editors. Contributions to a manual of Palaearctic Diptera. Budapest: Science Herald. p 617–648.

Roloff B, Wetzel T. 1989. Untersuchungen zur parasitierung und pradation von puparien der brachfliege (Delia coarctata (Fall.)). Archiv fur Phytopathologie und Pflanzenschutz 25:481–86.

Rosenheim JA, Rosen D. 1991. Foraging and oviposition decisions in the parasitoid *Aphytis lingnanensis*: distinguishing the influences of egg load and experience. Journal of Applied Ecology 60:873–893.

Rousse P, Fournet S, Porteneuve C, Brunel E. 2003. Trap cropping to control *Delia radicum* populations in cruciferous crops: first results and future applications. Entomologia Experimentalis et Applicata 109:133–138.

Royer L, Belair G, Boivin G, Fournier Y. 1996. Attractiveness of cabbage maggot (Diptera: Anthomyiidae) to entomopathogenic steinernematid nematodes. Journal of Economic Entomology 89:614–620.

Royer L, Boivin G. 1999. Infochemicals mediating the foraging behavious of *Aleochara bilineata* Gyllenhal adults: sources of attractants. Entomologia Experimentalis et Applicata 90:199–205.
Royer L, Fournet S, Brunel E, Boivin G. 1999. Intra- and interspecific host discrimination by host-seeking larvae of coleopteran parasitoids. Oecologia 118:59–68.
Royer L, Lannic JL, Nenon JP, Boivin G. 1998. Response of first-instar *Aleochara bilineata* larvae to puparium morphology of its dipteran host. Entomologia Experimentalis et Applicata 87:217–220.
Ruberson JR, Tauber MJ, Tauber CA. 1989. Intraspecific variation in hymenopteran parasitoids: comparative studies on two biotypes of the egg parasitoid *Edovum puttleri* (Hymenoptera: Eulophidae). Journal of the Kansas Entomological Society 62:189–202.
Ryan J, Ryan MF. 1980. Observations on the natural mortality of the overwintering pupa of the cabbage root fly, *Delia brassicae* (Wiedemann), in Ireland. Plant Pathology 29:38–44.
Sabrosky CW, Reardon RC. 1976. Tachinid parasites of the gypsy moth, *Lymantria dispar,* with keys to adults and puparia. Miscellaneous Publications of the Entomological Society of America 10:1–80.
Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC and others. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics 32:305–332.
Samways MJ. 1997. Classical biological control and biodiversity conservation: what risks are we prepared to accept. Biodiversity and Conservation 6:1309–1316.
Sands DPA. 1997. The 'safety' of biological control agents: Assessing their impact on beneficial and other non-target hosts. Memoirs of the Museum of Victoria 56:611–615.
Sands DPA, Van Driesche RG. Evaluating the Host Range of Agents for Biological Control of Arthropods: Rationale, Methodology and Interpretation. In: Van Driesche RG, Heard T, McClay A, Reardon R, editors. Proceedings of Session: Host Specificity Testing of Exotic Arthropod Biological Control Agents - The Biological Basis for Improvement in Safety; 1999; Bozeman, Montana, USA. USDA Forest Service. p 84–95.
Sands DPA, Van Driesche RG. 2004. Using the scientific literature to estimate the host range of a biological control agent. In: Van Driesche RG, Reardon R, editors. Assessing host ranges for parasitoids and predators used for classical biological control: a guide to best practice. Morganton, West Virginia: USDA Forest Service. p 15–23.
Schellhorn NA, Kuhman TH, Olson AC, A.R. Ives AR. 2002. Competition between native and introduced parasitoids of aphids: nontarget effects and biological control. Ecology 83:2745–2757.
Schlinger EI, Hall JC. 1961. The biology, behavior, and morphology of *Trioxys (Trioxys) utilis,* an internal parasite of the spotted aflalfa aphid, *Therioaphis maculata* (Hymenoptera: Braconidae, Aphidiinae). Annals of the Entomological Society of America 54:34–45.
Schoene WJ. 1916. The cabbage maggot: its biology and control. New York Agricultural Station Bulletin 419:99–160.
Schuehli GSE, Carvalho CJB, De, Wiegmann BM. 2004. Regarding the taxonomic status of *Ophyra* Robineau-Desvoidy (Diptera: Muscidae): a molecular approach. Zootaxa 712:1–12.
Settle WH, Wilson LT. 1990. Invasion by the variegated leafhopper and biotic interactions: parasitism, competition, and apparent competition. Ecology 71:1461–1470.
Shewell GE. 1971. On the type of *Agria,* with description of a new Nearctic species (Diptera: Sarcophagidae). The Canadian Entomologist 103:1179–1191.

Shewell GE. 1987. Calliphoridae. In: McAlpine JF, editor. Manual of Nearctic Diptera. Ottawa: Biosytematics Research Centre. p 1133–1146.
Sieber M. 1982. Results of sampling by sifting to determine the quantitiative proportion of Coleoptera in nests of *Formica rufa*. Entomologische Nachrichten und Berichte 26:137–138.
Simberloff D. 2006. Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? Ecology Letters 9:912–919.
Simberloff D, Stiling P. 1996. How risky is biological control? Ecology 77:1965–1974.
Skidmore P. 1985. The biology of the Muscidae of the world. Spencer KA, editor. Dordrecht: Dr. W. Junk Publishers. 550 p.
Smith CS, Lonsdale WM, Fortune J. 1999. When to ignore advice: invasion predictions and decision theory. Biological Invasions 1:89–96.
Smith MD, Knapp AK. 1999. Exotic plant species in a C4-dominated grassland: invasibility, disturbance, and community structure. Oecologia 120:605–612.
Sol R. 1972. Beitrag zur frage einiger begrenzungsfaktoren des massenwechsels der brachfliege (*Phorbia coarctata* Fall.). Anzeiger fur Schadlinskunde Pflanzenshutz umwelschutz 45:20–24.
Soni SK. 1976. Effect of temperature and photoperiod on diapause induction in *Erioschia brassicae* (Bch.) (Diptera, Anthomyiidae) under controlled environmental conditions. Bulletin of Entomological Research 66:125–131.
Soroka J, Dosdall L, Olfert O. 1999. Occurrence and damage potential of root maggots in canola. Agriculture and Agri-Food Canada. Report nr CA96–16. 77 p.
Soroka JJ, Dosdall LM, Olfert OO, Seidle E. 2004. Root maggots (*Delia* spp., Diptera: Anthomyiidae) in prairie canola (*Brassica napus* L. and *B. rapa* L.): spatial and temporal surveys of root damage and prediction of damage levels. Canadian Journal of Plant Science 84:1171–1182.
Soroka JJ, Elliott RH. 2006. Size doesn't matter: the effects of seed size and seeding rate on injury by root maggots (*Delia* spp., Diptera: Anthomyiidae) to canola (*Brassica rapa* L. and *B. napus* L.). Canadian Journal of Plant Science 86:907–909.
Soroka JJ, Kuhlmann U, Floate KD, Whistlecraft J, Holliday NJ, Boivin G. 2002. *Delia radicum* (L.), Cabbage Maggot (Diptera: Anthomyiidae). In: Mason PG, Huber JT, editors. Biological Control Programmes in Canada: CABI Publishing. p 99–104.
Sprague PS. 1870. A new rove-beetle parasitic on the cabbage maggot. American Entomologist 2:370.
Staedler E. 1971. An improved mass-rearing method of the carrot rust fly, *Psila rosae* (Diptera: Psilidae). The Canadian Entomologist 103:1033–1038.
Statistics Canada. 2005. November estimates of production of principal field crops, Canada, 2005. 1–22 p.
Stefansson BR. 1983. The development of improved rapeseed cultivars. In: Kramer JKG, Sauer FD, Pigden WJ, editors. High and low erucic acid rapeseed oils. Toronto: Academic Press. p 144–161.
Stefansson BR, Kondra ZP. 1975. Tower summer rape. Canadian Journal of Plant Science 55:343–344.
Stephens PA, Sutherland WJ, Freckleton RP. 1999. What is an Allee effect? Oikos 87:185–190.
Stiling P. 1993. Why do natural enemies fail in classical biological control programs. American Entomologist 39:31–37.

Stireman JO, III, O'Hara JE, Wood DM. 2006. Tachinidae: Evolution, behavior, and ecology. Annual Review of Entomology 51:525–555.
Sunose T. 1985. Population regulation of the euonymus gall midge *Masakimyia pustulae* Yukawa and Sunose (Diptera: Cecidomyiidae) by hymenopterous parasitoids. Researches in Population Ecology 27:287–300.
Suttle KB, Hoddle MS. 2006. Engineering enemy-free space: an invasive pest that kills its predators. Biological Invasions 8:639–649.
Swailes GE. 1958. Periods of flight and oviposition of the cabbage maggot, *Hylemya brassicae* (Bouche) (Diptera: Anthomyiidae), in southern Alberta. The Canadian Entomologist 90:434–435.
Sychevskaya VI. 1972. Aleocharinae (Coleoptera, Staphylinidae) as natural enemies of synanthropic flies of the family sarcophagidae in Central Asia. Zool. Zhourn. 51:142–144.
Tauber CA, Tauber MJ. 1981. Insect seasonal cycles: genetics and evolution. Annual Review of Ecology and Systematics 12:281–308.
Tauber MJ, Tauber CA. 1976. Insect seasonality: diapause maintenance, termination, and postdiapause development. Annual Review of Entomology 21:81–107.
Taylor CM, Hastings A. 2005. Allee effects in biological invasions. Ecology Letters 8:895–908.
Taylor F. 1981. Ecology and evolution of physiological time in insects. The American Naturalist 117:1–23.
Thomas PT. 1984. Canola council of Canada - Canola growers manual.
Timlick BH, Turnock WJ, Wise IL. 1993. Distribution and abundance of *Lygus* spp. (Heteroptera: Miridae) on alfalfa and canola in Manitoba. The Canadian Entomologist 125:1033–1041.
Tomberlin JK, Adler PH. 1998. Seasonal colonization and decomposition of rat carrion in water and on land in an open field in South Carolina. Journal of Medical Entomology 35:704–709.
Torchin ME, Lafferty KD, Kuris AM. 2002. Parasites and marine invasions. Parasitology 124:S137–S151.
Traynier RMM. 1967a. Effect of host plant odour on the behaviour of the adult cabbage root fly, *Erioschia brassicae*. Entomologia Experimentalis et Applicata 10:321–328.
Traynier RMM. 1967b. Stimulation of oviposition by the cabbage root fly *Erioschia brassicae*. Entomologia Experimentalis et Applicata 10:401–412.
Tullis K, Goff ML. 1987. Arthropod succession in exposed carrion in a tropical rainforest on O'ahu Island, Hawai'i. Journal of Medical Entomology 24:332–339.
Turnbull SA. 1967. Population dynamics of exotic insects. Bulletin of the Entomological Society of America 13:333–337.
Turnbull SA, Chant DA. 1961. The practice and theory of biological control of insects in Canada. Canadian Journal of Zoology 39:697–753.
Turnock WJ. 1977. Adaptability and stability of insect pest populations in prairie agricultural ecosystems. In: Kulman HM, Chiang HC, editors. University of Minnesota Agriculture Experiment Station Bulletin 310. p 89–101.
Turnock WJ. Biological control of insect pests of field crops. In: McClay AS, editor; 1991 October 11–12, 1990; Calgary. Alberta Environment Centre. p 9–14.
Turnock WJ, Boivin G. 1997. Inter- and intra-population differences in the effects of temperature on postdiapause development of *Delia radicum*. Entomologia Experimentalis et Applicata 84:255–265.

Turnock WJ, Boivin G, Ring RA. 1998. Interpopulation differences in the coldhardiness of *Delia radicum* (Diptera: Anthomyiidae). The Canadian Entomologist 130:119–129.
Turnock WJ, Boivin G, Whistlecraft JW. 1995. Parasitism of overwintering puparia of the cabbage maggot *Delia radicum* (L.) (Diptera: Anthomyiidae), in relation to host density and weather factors. The Canadian Entomologist 127:535–542.
Turnock WJ, Fields PG. 2005. Winter climates and coldhardiness in terrestrial insects. European Journal of Entomology 102:561–576.
Turnock WJ, Jones TH, Reader PM. 1985. Effects of cold stress during diapause on the survival and development of *Delia radicum* (Diptera: Anthomyiidae) in England. Oecologia 67:506–510.
Turnock WJ, Reader PM, Bracken GK. 1990. A comparison of the cold hardiness of populations of *Delia radicum* (L.) (Diptera: Anthomyiidae) from southern England and the Canadian Prairies. Canadian Journal of Zoology 68:830–835.
Turnock WJ, Timlick BH, Galka BE, Palaniswamy P. 1992. Root maggot damage to canola and the distribution of *Delia* spp. (Diptera: Anthomyiidae), in Manitoba. The Canadian Entomologist 124:49–58.
Upadhyay BM, Smith EG, Clayton GW, Harker KN, O'Donovan JT, Blackshaw RE. 2005. Economic evaluation of seeding decisions in hybrid and open-pollinated herbicide-resistant canola (*Brassica napus*). Canadian Journal of Plant Science 85:761–769.
Van Driesche RG, Murray TJ. 2004. Overview of testing schemes and designs used to estimate host ranges. In: Van Driesche RG, Reardon R, editors. Assessing host ranges for parasitoids and predators used for classical biological control: a guide to best practice. Morgantown: USDA Forest Service. p 68–99.
van Lenteren JC, Babendreier D, Bigler F, Burgio G, Hokkanen HMT, Kuske S, Loomans AJM, Menzler-Hokkanen I, van Rijn PCJ, Thomas MB and others. 2003. Environmental risk assessment of exotic natural enemies used in inundative biological control. BioControl 48:3–38.
van Lenteren JC, Bale J, Bigler F, Hokkanen HMT, Loomans AJM. 2006a. Assessing risks of releasing exotic biological control agents of arthropod pests. Annual Review of Entomology 51:609–634.
van Lenteren JC, Cock MJ, Hoffmeister TS, Sands DPA. Host ranges of natural enemies as an indicator of non-target risk. In: Hoddle MS, editor; 2005; Davos, Switzerland. USDA Forest Service. p 584–592.
van Lenteren JC, Cock MJ, Hoffmeister TS, Sands DPA. 2006b. Host specificity in arthropod biological control, methods of testing and interpretation of the data. In: Bigler F, Babendreier D, Kuhlmann U, editors. Environmental impact of invertebrates for biological control of arthropods - methods and risk assessment. Wallingford: CABI Publishing. p 38–63.
Vernon RS, Broatch JS. 1996. Responsiveness of *Delia* spp. (Diptera: Anthomyiidae) to colored sticky traps in flowering and rosette stage canola. The Canadian Entomologist 128:1077–1085.
Vinson SB. 1976. Host selection by insect parasitoids. Annual Review of Entomology 21:109–133.
Vinson SB, Iwantsch GF. 1980. Host suitability for insect parasitoids. Annual Review of Entomology 25:397–419.
Vorst O. 2001. Twee *Aleochara*-soorten niew voor de Nederlandse fauna (Coleoptera: Staphylinidae). Entomologische Berichten 61:37–41.

Wadsworth JT. 1915. On the life-history of *Aleochara bilineata,* Gyll., a staphylinid parasite of *Chortophila brassicae,* Bouche. Jounal of Economic Biology 10:1–17.
Walgenbach JF, Eckenrode CJ, Straub RW. 1993. Emergence patterns of *Delia radicum* (Diptera: Anthomyiidae) populations from North Carolina and New York. Environmental Entomology 22:559–66.
Wapshere AJ. 1985. Effectiveness of biological control agents for weeds: present quandries. Agriculture, Ecosystems and Environment 13:261–280.
Weed AS, Frank JH. 2005. Oviposition behavior of *Pheropsophus aequinoctialis* L. (Coleoptera: Carabidae): a natural enemy of *Scapteriscus* mole crickets (Orthoptera: Gryllotalpidae). Journal of Insect Behavior 18:707–723.
Wells JD, Greenberg B. 1994. Resource use by an introduced and native carrion flies. Oecologia 99:181–187.
Weseloh RM. 1976. Reduced effectiveness of the gypsy moth parasite, *Apanteles melanoscelus*, in Connecticut due to poor seasonal synchronization with its host. Environmental Entomology 5:743–746.
Wharton RA. 1979. Some predators and parasitoids of dung-breeding Diptera from central California. The Pan-Pacific Entomologist 55:181–186.
Whistlecraft JW, Harris CR, Tolman JH, Tomlin AD. 1985a. Mass-rearing technique for *Aleochara bilineata* (Coleoptera: Staphylinidae). Journal of Economic Entomology 78:995–997.
Whistlecraft JW, Tolman JH, Harris CR. 1985b. *Delia radicum.* In: Singh P, Moore RF, editors. Handbook of insect rearing: Elsevier. p 67–73.
White EB, Legner EF. 1966. Notes on the life history of *Aleochara taeniata*, a staphylinid parasite of the house fly, *Musca domestica.* Annals of the Entomological Society of America 59:573–577.
Wigglesworth VB. 1972. Water and temperature. The principles of insect physiology. 7th ed. London: Chapman & Hall. p 663–699.
Wilkes A, Coppel HC, Mathers WG. 1949. Notes on the insect parasites of the spruce budworm *Choristoneura fumiferana* (Clem.) in British Columbia. The Canadian Entomologist 80:138–155.
Wilkes A, Wishart G. 1953. Studies on parasites of root maggots (*Hylemya* spp.; Diptera: Antomyiidae) in the Netherlands in relation to their control in Canada. Tijdschrift over Plantenziekten 59:185–188.
Williamson M. 1996. Biological invasions. Usher MB, editor. London: Chapman & Hall. 244 p.
Williamson M. 2006. Explaining and predicting the success of invading species at different stages of invasion. Biological Invasions 8:1561–1568.
Williamson M, Fitter A. 1996a. The varying success of invaders. Ecology 77:1661–1666.
Williamson MH, Fitter A. 1996b. The characters of successful invaders. Biological Conservation 78:163–170.
Wingo CW, Thomas GD, Nelms NM. 1967. Laboratory evaluation of two aleocharine parasites of the face fly. Journal of Economic Entomology 60:1514–1517.
Wishart G. 1957. Surveys of parasites of *Hylemya* spp. (Diptera: Anthomyiidae) that attack cruciferous crops in Canada. The Canadian Entomologist 89:450–454.
Wishart G, Colhoun EH, Monteith AE. 1957. Parasites of *Hylemya* spp. (Diptera: Anthomyiidae) that attack cruciferous crops in Europe. The Canadian Entomologist 89:510–517.
Wishart G, Doane JF, Maybee GE. 1956. Notes on beetles as predators of eggs of *Hylemya brassicae* (Bouche) (Diptera: Anthomyiidae). The Canadian Entomologist 88:634–639.

Wishart G, Monteith E. 1954. *Trybliographa rapae* (Westw.) (Hymenoptera: Cynipidae), a parasite of *Hylemya* spp. (Diptera: Anthomyiidae). The Canadian Entomologist 86:145–154.

Withers T, Browne LB. 2004. Behavioural and physiological processes affecting outcomes of host range testing. In: Van Driesche RG, Reardon R, editors. Assessing host ranges for parasitoids and predators used for classical biological control: a guide to best practice. Morgantown: USDA Forest Service. p 40–55.

Withers T, Mansfield S. Choice or no-choice tests? effects of experimental design on the expression of host range. In: Hoddle M, editor; 2005; Davos, Switzerland. USDA Forest Service. p 620–633.

Wright DW, Geering QA, Ashby DG. 1946. The insect parasites of the carrot fly, *Psila rosae* Fab. Bulletin of Entomological Research 37:507–529.

Wright DW, Hughes RD, Worrall J. 1960. The effect of certain predators on the numbers of cabbage root fly (*Erioschia brassicae* (Bouche)) and on the subsequent damage caused by the pest. Annals of Applied Biology 48:756–763.

Wright EJ, Muller P. 1989. Laboratory studies of host finding, acceptance and suitability of the dung-breeding fly, *Haematobia thirouxi potans* (Dipt.: Muscidae), by *Aleochara* sp. (Col.: Staphylinidae). Entomophaga 34:61–71.

Wright EJ, Muller P, Kerr JD. 1989. Agents for biological control of novel hosts: assessing an aleocharine parasitoid of dung-breeding flies. Journal of Applied Ecology 26:453–461.

Wylie HG, Bucher GE. 1977. The bertha armyworm, *Mamestra configurata* (Lepidoptera: Noctuidae). Mortality of immature stages on the rape crop, 1972–1975. The Canadian Entomologist 109:823–837.

Wyman JA, Libby JL, Chapman RK. 1976. The role of seed-corn beetles in predation of cabbage maggot immature stages. Environmental Entomology 5:259–263.

Wyman JA, Libby JL, Chapman RK. 1977. Cabbage maggot management aided by predictions of adult emergence. Journal of Economic Entomology 70:327–331.

Yong T-H, Hoffmann MP. 2006. Habitat selection by the introduced biological control agent *Trichogramma ostriniae* (Hymenoptera: Trichogrammatidae) and implications for nontarget effects. Environmental Entomology 35:725–732.

Zabirov SM. 1961. Factors governing the seasonal development cycles of the spinach leaf miner (*Pegomyia hyosciami* Panz) and the cabbage maggot (*Hylemyia brassicae* Bouche) (Diptera, Anthomyiidae). Entomological Review 40:148–151.

Zatjamina VV. 1971. Staphylinids (Coleoptera) on pea sowings. Zoologicheskii Zhurnal 50:138–141.

Zentner RP, Brandt SA, Campbell CA. 1996. Economics of monoculture cereal and mixed oilseed-cereal rotations in west-central Saskatchewan. Canadian Journal of Plant Science 76:393–400.