



# Interactions between predatory ground beetles, the winter moth and an introduced parasitoid on the Lower Mainland of British Columbia

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Predation

## Summary

This study describes assemblages of predatory ground beetles in native birch forest and derived blueberry farms on the Lower Mainland of British Columbia and investigates their role in the successful biological control of winter moth (*Operopthera brumata* L.) by the parasitoid *Cyzenis albicans* Fallén. Pitfall traps at four sites in 1991 and 1992 indicated that natural birch forest was dominated by native carabid species, while open blueberry was dominated by introduced species and some native xerophilous species. Predation by generalist invertebrates was an important mortality factor for both winter moth and *C. albicans* at all sites and was greatest in the first 2 weeks after pupation. Ground beetles including *Harpalus affinus* (Schrank) and *Pterostichus* spp. consumed winter moth pupae in arenas but adult beetles rarely consumed *C. albicans* pupae. Much of the overall predation was due to smaller invertebrates including beetle larvae. Predators actively searched for buried pupae and selected among pupal types based on condition (dead, parasitised or healthy) and size. Prey-selection differed among sites but *C. albicans* pupae were preferred at three of the four sites. At the remaining site, an organic blueberry farm, over 90% of both parasitised and healthy pupae were consumed. High levels of predation did not affect the levels of parasitism by *C. albicans* at the sites. This herbivore–parasitoid–predator system demonstrates the importance of naturally occurring predatory invertebrates for successful integrated pest management, even where they prey upon a biological control agent.

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## Introduction

Farmers' decisions at landscape and plot levels directly influence the diversity of natural enemies associated with their crops (Vandermeer et al., 1998). Much of this associated diversity has its source in the native species pool and finds temporary refuge in wild areas amidst cultivated lands. Agricultural intensification and habitat-change often negatively affect the diversity or functioning of the associated fauna and potentially decrease the effectiveness of integrated pest management strategies or cause a heavier reliance on agrochemicals (Vandermeer et al., 1998). However, there may also be cases where the associated fauna negatively affects some planned biological component of the system. For example, when parasitoids are introduced into new regions for biological control purposes, natural enemies in the new environment may reduce their effectiveness or constrain their efficiency in regulating the host (Rosenheim, 1998). The functions of associated faunas and their interactions with biological control agents are important concepts in determining efficient farming landscapes and pest management strategies.

In the early 1980s, winter moth (*Operopthera brumata* [L.]) was detected in Richmond, on the Lower Mainland of British Columbia where it became an important pest of blueberry (*Vaccinium corymbosum* [L.]), and birch (*Betula* spp.) (Fitzpatrick et al., 1991). The tachinid parasitoid *Cyzenis albicans* Fallén was also present in the 1980s and probably arrived with the accidental introduction of moth larvae. This European species had been successfully introduced to control winter moth in Nova Scotia (1969) and on Vancouver Island (1982) (Roland and Embree, 1995). However, it did not prevent winter moth outbreaks from occurring between 1988 and 1991 on the Lower Mainland, although it was an important source of mortality for the populations. Levels of parasitism were already high by 1989 (25–40%) when data were first collected in the area. However, it was predation of winter moth pupae by unidentified generalist predators that was the most important mortality factor throughout the outbreak (Horgan et al., 1999). It is now apparent from this and a number of other Canadian sites that the successful control and sustained regulation of winter moth populations has depended on both the introduced parasitoid and naturally occurring ground predators (Roland, 1988, 1990; Roland and Embree, 1995). Furthermore, winter moth in commercial apple orchards in Nova Scotia continued to be a problem even after biological control introductions

possibly due to the use of pesticides and depletion of the naturally occurring predatory fauna (McPhee et al., 1988; Pearsall and Walde, 1994). The soil-dwelling nature of the moth and *C. albicans* pupae and the especially long pupal-stage of the parasitoid suggest that complex interactions occur between both species and their predators.

In this study, we describe carabid assemblages in stands of native birch and in blueberry plots on the Lower Mainland of British Columbia. We determine which species are likely predators of the moth pupae and investigate the timing of predation and prey selection by these and other epigeal invertebrates in the final year of high moth density, 1991 and in the following year in which pupal densities were approximately 10 times lower. We examine the impact of ground predators on parasitoid populations and discuss whether high levels of predation on *C. albicans* pupae might be expected to bring about a decrease in the levels of parasitism or the regulatory efficiency of the parasitoid at North American sites.

## Materials and methods

### Winter moth and parasitoid

Winter moth larvae are polyphagous, they feed mainly on deciduous trees, but also on some coniferous trees in Britain (Wint, 1983). Adult females emerge in early November in British Columbia to mate and oviposit from 70 to 200 eggs in cracks in bark and under lichens and mosses on tree trunks (Embree, 1970). The eggs over-winter and in British Columbia, larval eclosion is usually from mid-March until early April. There are five larval instars. Larvae feed from March until May when they drop to the ground to pupate. The pupa has a hibernaculum and is found 1–2 cm below the soil surface from May until late November.

Adult female *C. albicans* emerge in early April and feed for several weeks on nectar to develop 1000–2000 eggs (Hassell, 1980). The microtype eggs are laid on leaves near feeding damage and if ingested by a host larva, the egg hatches and the larva lodges in the host's salivary gland. After pupation of the host larva the parasitoid completes development and pupates inside the empty host pupa. *C. albicans* over-winters as a diapausing pupa and adults emerge the following spring. Only one individual emerges from each winter moth pupa (Hassell, 1980).

## Study sites

Studies were carried out at four sites in Richmond, British Columbia (Table 1). Winter moth populations had reached high densities at the sites in 1989 and 1990, and declined in 1991 and 1992 (see Horgan et al., 1999). The blueberry plots were a mix of cultivated blueberry varieties (*V. corymbosum*) on the Watanabe and Schultz farms, each with an area of 50 × 20 m. A dense stand of young white birch (*Betula papyrifera* var. *communata* Marshall) with an area of 125 × 50 m was studied at Edwards farm. This stand was surrounded by agricultural land devoted to cranberry, *V. macrocarpon* Aiton, and blueberry production. A second birch site (100 × 100 m) was located at the western section of Richmond Nature Park, an area of 43 ha of native birch and bog habitat. Both birch sites had small numbers of hemlock (*Tsuga heterophylla* (Rafinesque-Schmaltz) Sargent) and extensive undergrowth vegetation mainly of blueberry and salal (*Gaultheria shallon* Pursh) (Table 1).

## The pupal complex

Pupal densities were estimated using the pupal drop tray method (Varley et al., 1973). Twenty plastic bedding trays containing peat moss were placed at each site between April and June of 1991 and 1992. At the end of winter moth pupation, the trays were collected and the peat moss sieved. Cocoons were counted, opened and the condition and weight of the pupae recorded. In 1992, parasitism at the blueberry sites was estimated by rearing prepupae collected by tree-beating.

## Ground beetle assemblages

Pitfall trapping was carried out in 1991 and 1992. In 1991, traps were set out from June until September. In 1992, traps were set out from May until March 1993. Each site had 20 traps spaced at ca. 15 m intervals and laid out in two transects of 10. Traps were 0.5 l plastic cups, with slits for water drainage and placed in the ground without any killing agent. Trap catches were removed every two weeks in 1991 and every week in 1992 until October after which they were removed at irregular intervals. Wire grids (1 cm) were placed over the traps in 1992 to prevent the capture of small mammals.

In 1991, 10 traps at each site were set out to identify possible small predators that live in the soil layer and may be responding to olfactory stimuli emitted from the moth pupae. Traps consisted of a 2 mm mesh over a metal frame that was tightly secured to a Petri dish lid with holes for drainage. A circular sheet of plastic coated with Tanglefoot<sup>®</sup> was placed in the Petri dish. Baited traps had four pupae suspended by flower wire between the mesh and the plastic sheet. A set of 10 unbaited control traps was also set out at each site. The traps were interspersed in two transects of 10 (five baited and five unbaited) buried 2 cm below the soil surface. Attached wooden skewers with coloured flagging indicated the locations of the traps. The plastic sheets were collected from the traps and replaced with fresh sheets every 2 weeks between July and September.

Studies were carried out to identify which of the abundant beetle species were capable of eating winter moth and *C. albicans* pupae. Beetles of undetermined sex were starved for 2 days before

**Table 1.** Habitat characteristics and management at four sites in Richmond

Site	Tree and bush density (50 m <sup>-2</sup> ) ± SEM				Hemlock	Ground cover (%) ± SEM			Management
	Blueberry	Birch <sup>a</sup>				Salal	Blueberry <sup>b</sup>		
		Small	Medium	Large					
Watanabe	10.2 ± 0.6	3.1 ± 0.8	0	0	0	13.0 ± 2.5	0	Largely abandoned Periodically mowed No pesticides since 1988	
Schultz	7.08 ± 0.1	1.2 ± 0.3	0	0	0	5.7 ± 3.8	0	Abandoned No pesticides since 1988	
Richmond N.P.	0	2.7 ± 1.0	10.1 ± 1.6	7.0 ± 1.3	0.3 ± 0.3	59.0 ± 9.7	8.5 ± 3.0	Public nature park	
Edwards	0	11.6 ± 2.8	15.7 ± 1.0	3.4 ± 3.3	0.1 ± 0.1	76.3 ± 8.0	6.7 ± 3.9	Wild area surrounded by farmland	

<sup>a</sup>Birch trees were categorised as small (diameter < 10 cm), medium (10–40 cm) and large (> 40 cm).

<sup>b</sup>Percentage cover by blueberry is presented where blueberry formed part of the undergrowth at the sites.

being placed in 5 l plastic containers covered with a mesh lid and containing 4 cm of moistened peat with dry leaves for beetle cover. Pupae were placed in the containers either without cocoons on top of the peat, or cocooned and buried beneath the soil. Groups of four pupae were used in each trial and trials were replicated five times. Two beetles were placed in each container. All trials lasted 1 week.

### Predation levels and prey selection

To estimate levels of predation, tethered pupae were deployed at the sites each year from June, generally about 1–2 weeks after pupation was complete, until October before adult winter moth emergence. In 1991, tethers consisted of groups of four pupae attached by flower wire to a central wooden skewer. Pupae were spaced at ca. 10 cm intervals along the wire. Skewers were placed along transects at intervals of 5 m, and cocoons were covered with a layer of humus ca. 2 cm deep. Twenty skewers were placed at each site in 1991. Pupae used in tethers at all the sites were collected at Edwards birch so that ca. 60% were parasitized. In 1992, pupae were weighed before tethering. A hole was made at one end of the cocoon and the pupa taken out with a fine forceps. All pupae were weighed and categorised, then placed back inside the cocoons. The cocoon has an elastic consistency and closes around the pupa leaving only a small perforation where the pupa was removed. Ten skewers with each of four types of live pupae (large moth pupae (20–30 mg), small moth pupae (10–20 mg), large *C. albicans* pupae (10–20 mg) and small *C. albicans* pupae (<10 mg)) were set out at the sites. Because of a shortage of pupae in 1992, small moth pupae (10–20 mg) and large *C. albicans* pupae (10–20 mg) were set out only at the birch sites. About 50% of winter moth pupae at the birch and blueberry sites were large, whereas small moth pupae represented ca. 20% of available pupae at the birch sites and 15% at the blueberry sites. About 65% of available *C. albicans* pupae at birch and blueberry sites were large, whereas ca. 30% at the birch sites and only 10% at the blueberry sites were small. Where possible estimates of overall predation on *C. albicans* or moth pupae are based on these percentages. At each birch site, a set of 20 skewers with dead pupae (death due to unknown causes) were also deployed. The tethers, marked with coloured flagging, were set out interspersing the different pupal types. Pupae were examined each week to record the timing of predation.

Pupae were also deployed in beetle enclosures to estimate the levels of pupal predation due to small, soil-dwelling invertebrates other than adult ground beetles. In 1991, 10 enclosures were set out at each site. In 1992, enclosures were set out only at the birch sites. The enclosures were similar to the traps used for soil-layer predators and consisted of two metal frames covered with 2 mm mesh, with four pupae suspended between them by flower wire. Enclosures were set out at the same time as the tethered pupae and were covered with ca. 2 cm of humus. The pupae were examined in early October.

### Data analyses

Pupal weights were compared at the birch sites and in two years using two-way ANOVA on log-transformed data. Parasitism and “death due to unknown causes” were arcsine-transformed and analysed with a two-way ANOVA. Data on captures in soil-layer traps were analysed using paired t-tests on log-transformed data. Data residuals were plotted to test for normality and homogeneity after all analyses. Differences in the levels of predation on different pupal types in the field were compared using an extension of the Kruskal–Wallis test as a non-parametric two-way ANOVA (Zar, 1984).

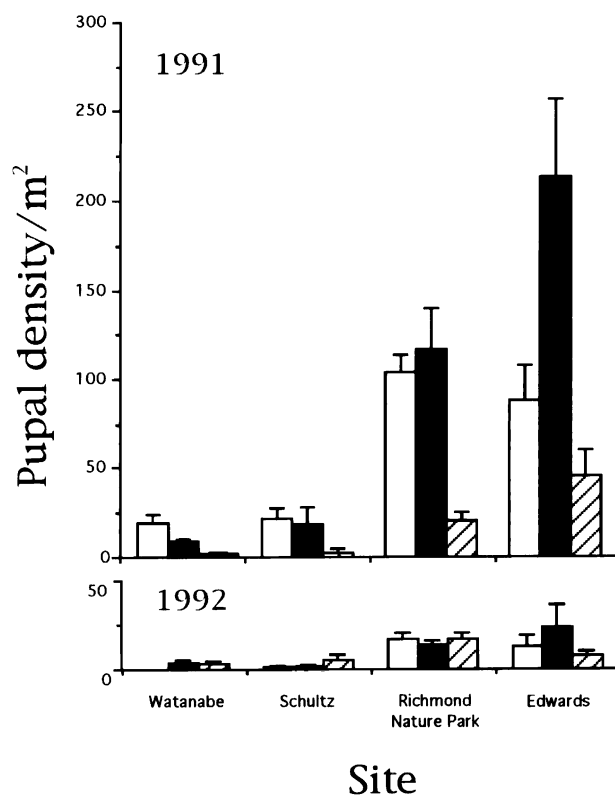
Regression analysis was used to determine the relationship between the mean winter moth pupal weight per tray and the mean *C. albicans* pupal weight per tray. Data residuals were plotted to test for normality and homogeneity.

We used a multidimensional scaling technique (MDS) (Everitt and Dunn, 1991) based on mean proximities to indicate assemblage similarity of carabid beetles captured between June and September (the time of winter moth availability in the soil) at four sites in 1991 and 1992.

## Results

### Pupal densities and sizes

In late May and early June, winter moth prepupae had dropped to the soil at blueberry and birch sites. By early June, developing *C. albicans* larvae entirely consumed their hosts so that there were two separate and abundant species of pupae in the soil at the sites (Fig. 1). The proportions of parasitised prepupae did not differ between sites or between the 2 years of study (Table 2) (two-way ANOVA (sites):  $F_{2,114} = 1.90$ ,  $P = 0.14$ ; (year):  $F_{1,114} = 2.00$ ,  $P = 0.16$ ; interaction ns). The proportions of dead and deformed pupae were similar



**Figure 1.** Densities of healthy (open), parasitised (solid) and dead (shaded) winter moth pupae at four sites in Richmond in 1991 and 1992. Bars indicate standard errors ( $n=20$ ).

across sites each year but increased significantly between 1991 and 1992 (Table 2) (two-way ANOVA (sites):  $F_{1,90}=0.60$ ,  $P=0.67$ ; (year):  $F_{1,90}=24$ ,  $P<0.001$ ; interaction ns).

*Cyzenis albicans* pupae are smaller than winter moth pupae. In 1991, the smallest sized pupae of both species occurred at the same sites with significant differences in pupal weights across the sites (Table 2) (two-way ANOVA (species):  $F_{1,105}=199.0$ ,  $P=0.003$ ; (sites):  $F_{3,105}=2$ ,  $P=0.001$ ; interaction ns). Pupae from Edwards were smaller than those from Richmond Nature Park, but weights did not change between 1991 and 1992 (Table 2) (two-way ANOVA (sites):  $F_{1,67}=9.11$ ,  $P=0.004$ ; (years):  $F_{1,67}=0.916$ ,  $P=0.341$ ; interaction ns). The mean weights of winter moth and parasitoid pupae for individual trays were significantly related at the birch sites in 1991 (Richmond Nature park:  $Y=0.99+0.20X$ ,  $R^2=0.46$ ,  $P=0.002$ ; Edwards birch stand:  $Y=7.80+0.20X$ ,  $R^2=0.46$ ,  $P=0.002$ ) and at Schultz farm in the same year ( $Y=2.84+0.48X$ ,  $R^2=0.68$ ,  $P=0.022$ ). There were too few trays containing both winter moth and parasitoid pupae for analysis at Watanabe farm in 1991 and at all the sites in 1992.

### Predator assemblages

A total of 523 predatory beetles were caught in pitfall traps in 1991, and 1737 in 1992. Higher catches in 1992 were due to a longer trapping period that included May and early June when *Bembidion* spp., *Dyschrius* spp., *Notiophilus* sp., epigeal beetle larvae and adult staphylinids were most active (Table 3). Birch sites were more species rich and were dominated by species of the genus *Pterostichus*. Species favoured by drier habitats (i.e. *Amara* spp. and *Harpalus* spp., see Lindroth, 1961) predominated at Watanabe farm, but were rare or absent at Schultz farm. Beetle larvae, including a number of Lampyridae and Elateridae were most abundant at Schultz farm (ANOVA:  $F_{3,79}=11.00$ ,  $P>0.001$ ).

Most beetle activity was in the early months of trapping with a decline in mid-August or early September through to winter (Fig. 2). The maximum activity of beetles at all sites coincided with the time of highest pupal densities in the soil. Differences in the abundances of beetle predators between sites were significant but there was no change in the annual abundance of beetles across

**Table 2.** Estimated winter moth and *C. albicans* population parameters (means  $\pm$  SEM) at four sites in Richmond in 1991 and 1992

Population parameters	Watanabe		Schultz		Richmond Nature Park		Edwards	
	1991	1992 <sup>a</sup>	1991	1992 <sup>a</sup>	1991	1992	1991	1992
<i>Pupal weight (mg)</i>								
Winter moth <sup>b</sup>	26 $\pm$ 1	—	22 $\pm$ 2	—	28 $\pm$ 1	29 $\pm$ 2	25 $\pm$ 1	24 $\pm$ 1
<i>C. albicans</i> <sup>b</sup>	14 $\pm$ 1	—	13 $\pm$ 1	—	14 $\pm$ 1	14 $\pm$ 1	13 $\pm$ 1	12 $\pm$ 1
<i>Mortality and predation (%)</i>								
Parasitism <sup>c</sup>	31.7 $\pm$ 10.4	36	38.9 $\pm$ 9.9	14	68.1 $\pm$ 4.9	54.6 $\pm$ 6.4	65.4 $\pm$ 5.0	61.5 $\pm$ 7.8
Death due to unknown causes <sup>c</sup>	0.0	50.0 $\pm$ 23.9	2.2 $\pm$ 1.2	40.0 $\pm$ 24.5	9.1 $\pm$ 2.5	37.7 $\pm$ 5.9	9.8 $\pm$ 1.9	24.4 $\pm$ 6.3
Predation of pupal complex <sup>d</sup>	92.5 $\pm$ 3.9	—	94.2 $\pm$ 2.8	—	92.1 $\pm$ 11.9	—	92.3 $\pm$ 15.5	—
Predation of winter moth <sup>e</sup>	$\approx$ 90.0	95.5 $\pm$ 5.3	$\approx$ 90.0	63.6 $\pm$ 10.2	$\approx$ 90.0	80.0 $\pm$ 10.0	$\approx$ 90.0	67.5 $\pm$ 12.1
Predation of <i>C. albicans</i> <sup>e</sup>	$\approx$ 90.0	95.0 $\pm$ 4.3	$\approx$ 90.0	98.2 $\pm$ 3.4	$\approx$ 90.0	90.0 $\pm$ 4.4	$\approx$ 90.0	77.5 $\pm$ 5.1
Dead pupae consumed <sup>e</sup>	—	—	—	—	—	100.0 $\pm$ 0.0	—	100.0 $\pm$ 0.0

<sup>a</sup>Insufficient pupae to estimate pupal weights, parasitism estimated from collected prepupae and predation of *C. albicans* estimated only for small pupae.

<sup>b</sup> $n \geq 50$  pupae.

<sup>c</sup> $n = 20$  pupal drop trays.

<sup>d</sup> $n = 20$  tethers.

<sup>e</sup> $n = 10$  tethers at blueberry sites in 1992 (small *C. albicans* and large moth pupae only),  $n = 20$  tethers at birch sites in 1992 (all *C. albicans* and moth pupae taking account of relative contributions to the overall pupal complex). Prey selection was not estimated in 1991, but predation is estimated at ca. 90% for both species given the high overall levels of predation detected in that year.

**Table 3.** Predatory epigeal invertebrates captured in pitfall traps in 1991 (July until September) and 1992 (May until March 1993) at four sites in Richmond ( $n=20$ )

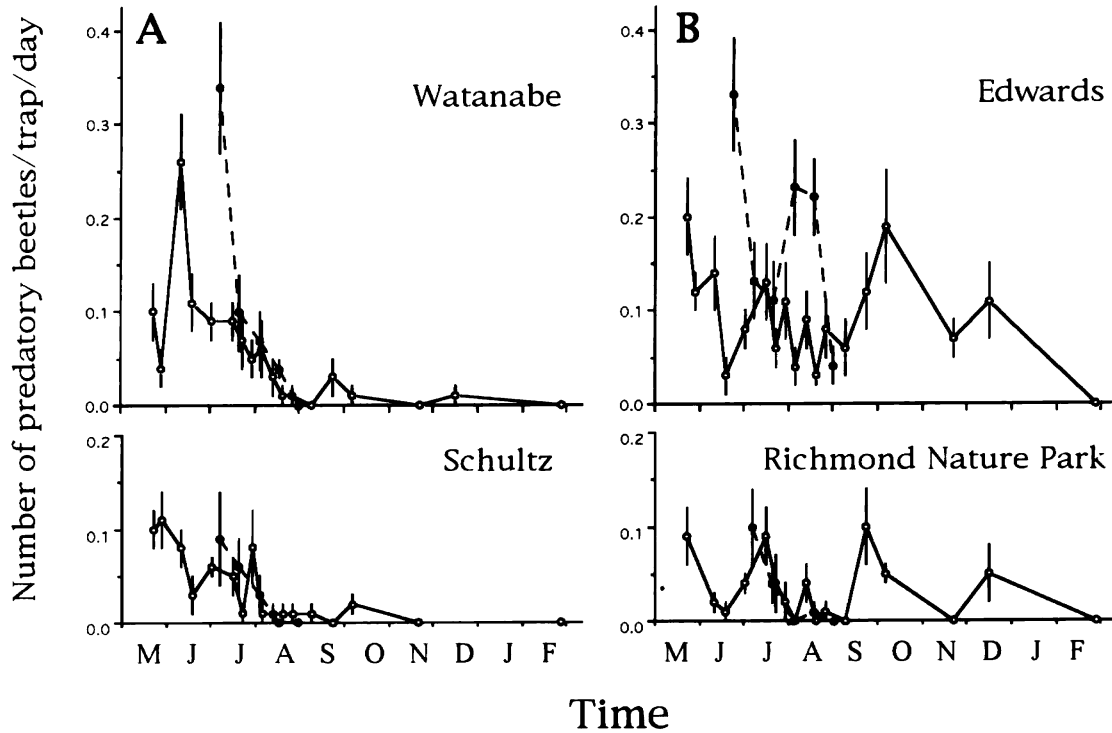
Taxa <sup>a</sup>	Watanabe		Schultz		Richmond N.P.		Edwards	
	1991	1992	1991	1992	1991	1992	1991	1992
<i>Carabidae</i>								
<i>Agonum</i> sp.	0	0	0	0	0	0	0	5
λ <i>Amara aurata</i> Dejean	45	81	0	0	0	0	2	6
λ <i>A. laevipennis</i> Kirby	0	3	0	0	0	0	0	0
λ <i>A. litteralis</i> Mannerheim	55	25	0	0	0	0	0	0
<i>Bembidion</i> sp.1	0	7	0	15	0	259	0	17
<i>Bembidion</i> sp.2	0	0	0	0	0	0	0	4
<i>Bembidion</i> sp.3	0	0	0	4	0	1	0	2
<i>Bembidion</i> sp.4	0	0	0	32	0	4	0	3
<i>Bembidion</i> sp.5	0	1	0	0	0	0	0	0
<i>Bembidion</i> sp.6	0	6	0	0	0	0	0	0
<i>Calathus fuscipes</i> (Goeze)	1	0	0	0	1	0	1	0
λ <i>Callisthenus wilkerii</i> LeConte	0	0	0	0	0	0	0	1
<i>Carabus granulatus</i> Linné	0	3	7	21	0	5	9	45
<i>C. nemoralis</i> Müller	0	11	15	5	0	0	0	7
<i>Dyschrius</i> sp.1	0	0	0	49	0	4	0	3
<i>Dyschrius</i> sp.2	0	0	0	0	0	1	0	1
<i>Harpalus affinus</i> (Schrank)	36	29	0	0	0	0	0	1
<i>H. rufipes</i> (DeGeer)	0	1	0	0	0	0	0	0
λ <i>Leistus ferruginosus</i> Mannerheim	0	0	0	0	0	0	0	2
λ <i>Loricera decempunctata</i> Eschscholtz	0	0	2	2	4	15	1	8
<i>Notiophilus</i> sp.	0	0	0	4	0	12	0	6
λ <i>Pterostichus algidus</i> LeConte	0	0	0	0	0	0	3	35
λ <i>P. herculeanus</i> Mannerheim	0	0	0	0	42	109	186	276
<i>P. melanarius</i> (Illiger)	2	9	13	33	0	0	4	11
λ <i>Scaphinotus marginatus</i> (Fischer)	0	0	8	60	1	88	25	91
<i>Carabus</i> spp. larvae	17	11	13	25	0	1	0	3
Other Carabidae larvae	0	4	3	3	0	0	1	7
<i>Elateridae</i>								
Elateridae larvae	0	0	0	2	0	0	0	0
<i>Lampyridae</i>								
Lampyridae larvae	0	0	0	5	0	0	0	0
<i>Staphylinidae</i>								
<i>Hesperlinus</i> sp.	0	0	0	0	0	2	0	0
<i>Philonthus</i> spp.	0	2	0	14	0	20	3	29
<i>Tachinus</i> spp.	0	0	0	1	0	104	1	39
<i>Quedius</i> sp.	0	0	0	0	0	0	18	0
Other Staphylinidae	0	1	0	4	0	3	0	4
Staphylinidae larvae	3	0	0	3	0	3	0	3
<i>Formicidae</i>								
<i>Myrmica</i> sp.	265	103	0	0	0	0	2	2
<i>Formica</i> sp.	57	60	5	0	0	0	0	0

<sup>a</sup>Early Spring invertebrates were not identified to species level. 'λ' indicates that the species is a known native.

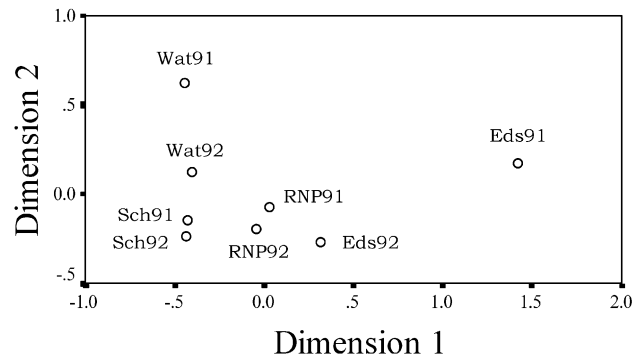
the sites (two-way ANOVA (sites):  $F_{3,79} = 58.6$ ,  $P > 0.001$ ; (years):  $F_{1,79} = 0.80$ ,  $P = 0.32$ ; interaction ns).

Fig. 3 indicates the overall similarity among the four sites over 2 years based on June to September

carabid species composition and abundance. Dimension 1 is related to the overall abundance of beetles, while dimension 2 roughly corresponds to species shared between the sites and years and their relative abundances. Assemblages at



**Figure 2.** Activity of predatory beetles at four sites in Richmond during 1991 (solid points) and 1992 (open points). Bars indicate standard errors ( $n = 20$ ).



**Figure 3.** Multidimensional scaling (MDS) plot indicating the similarity between adult carabid beetle assemblages sampled between June and September of 1991 and 1992 at four field sites in Richmond. Eds, Edwards; RNP, Richmond Nature Park; Sch, Schultz; Wat, Watanabe.

Watanabe farm and Edwards birch stand during 1991 were clearly different from the other sites due to a high overall abundance of beetles at Edwards (dimension 1) and the high abundances of certain species unique to Watanabe farm (dimension 2).

### Pupal predation

*Harpalus affinis* (Schrank) and *Pterostichus herculeanus* Mannerheim were facile at consuming buried pupae in arena studies (Table 4). *Cyzenis*

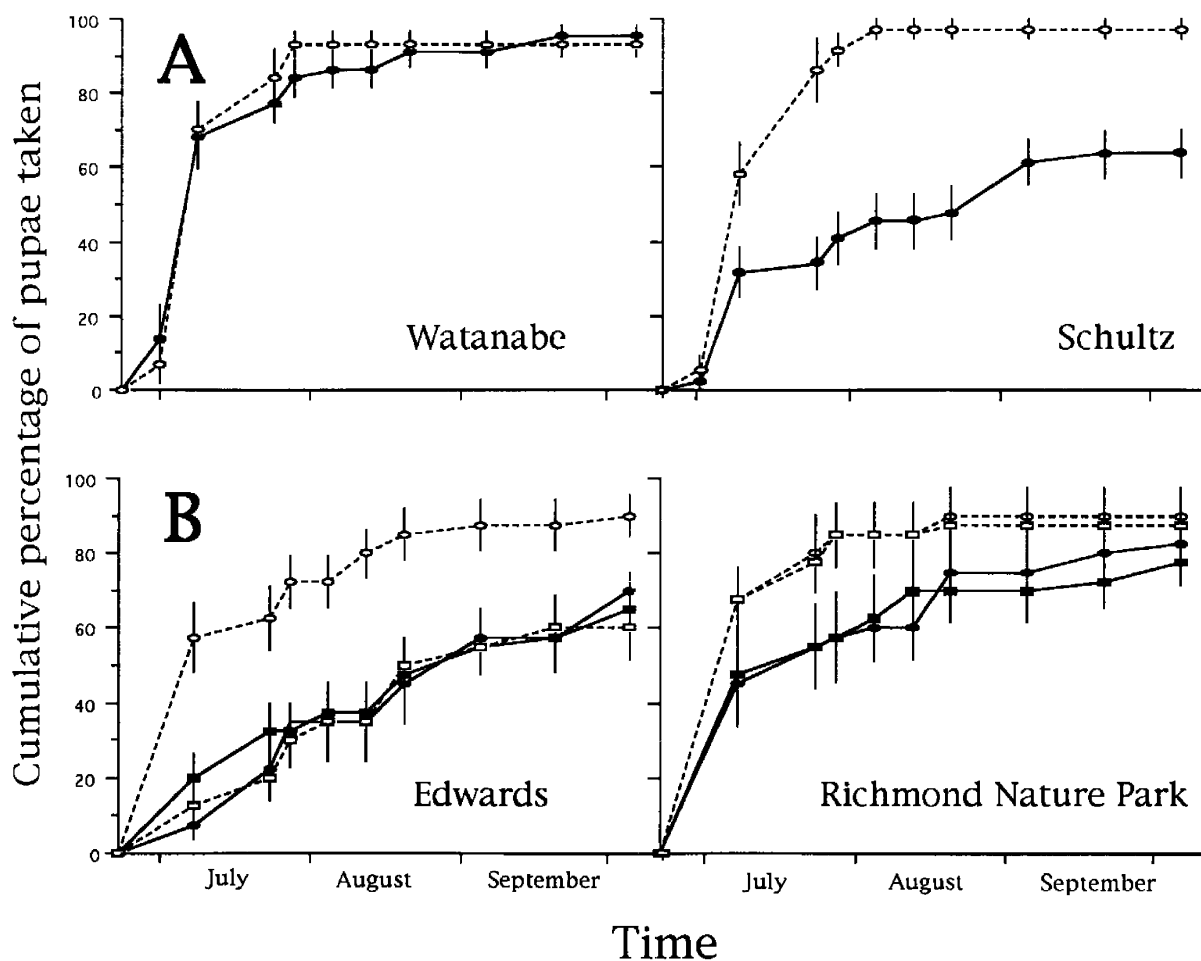
*albicans* pupae were consumed less often than winter moth pupae. In general, the other species tested consumed few buried pupae. Burial of the pupae and the presence of a hibernaculum protected pupae from predation by most adult epigeal beetles but had little effect on predation by adult *H. affinis* (Table 4). In 1991, over 90% of tethered pupae were consumed by generalist predators at all the sites. Predation levels generally declined in 1992, but predation of *C. albicans* pupae remained high (Table 2). Most of the predation occurred in June and early July (Fig. 4).



**Table 4.** Predation of winter moth and *C. albicans* pupae (mean percentage  $\pm$  SEM) by beetles in arenas ( $n = 5$ )

Taxa	Uncocooned/surface <sup>a</sup>		Cocooned/buried	
	Winter moth	<i>C. albicans</i>	Winter moth	<i>C. albicans</i>
<i>A. aurata</i>	nt	nt	5.0 $\pm$ 5.0	0
<i>A. littoralis</i>	nt	nt	10.0 $\pm$ 6.1	0
<i>Agonum</i> sp.	nt	nt	0	0
<i>Bembidion</i> sp.	nt	nt	0	0
<i>C. granulatus</i>	20.0 $\pm$ 9.3	20.0 $\pm$ 20.0	0	0
<i>C. nemoralis</i>	100	100	0	0
<i>C. sp. larvae</i>	0	0	5.0 $\pm$ 5.0	0
<i>H. affinis</i>	50.0 $\pm$ 28.9	33.3 $\pm$ 23.6	55.0 $\pm$ 14.6	30.0 $\pm$ 9.3
<i>L. decampunctata</i>	0	0	0	0
<i>P. algidus</i>	55.0 $\pm$ 22.9	30.0 $\pm$ 14.6	12.5 $\pm$ 7.2	0
<i>P. herculeanus</i>	100	100	41.7 $\pm$ 5.4	4.16 $\pm$ 4.0
<i>P. melanarius</i>	100	100	10.0 $\pm$ 6.1	5.0 $\pm$ 5.0
<i>S. marginatus</i>	5.0 $\pm$ 5.0	0	0	0

<sup>a</sup>nt: no trials carried out.



**Figure 4.** Percentage predation of pupae from the winter moth–*C. albicans* complex in 1992 at (A) blueberry and (B) birch sites. Pupae include: Large winter moth pupae (solid squares), small winter moth pupae (solid circles), large *C. albicans* pupae (open squares) and small *C. albicans* pupae (open circles). Bars indicate standard errors ( $n = 20$ ).

**Table 5.** Invertebrates captured in subterranean traps (10 baited with winter moth pupae, 10 unbaited controls) at four sites in Richmond during the summer of 1991 with corresponding estimates of predation by small invertebrates at the same sites in 1991 and 1992 (10 beetle exclusion cages)

Predators	Site							
	Watanabe <sup>a</sup>		Schultz <sup>a</sup>		Richmond NP		Edwards	
	Control	Baited	Control	Baited	Control	Baited	Control	Baited
Coleoptera larvae	0	1	4	20	0	8	0	7
Staphylinidae	0	2	0	1	2	5	0	3
Formicidae	0	2	0	7	0	0	2	0
Areneae	0	1	0	0	0	0	1	4
Diptera larvae	12	0	0	0	0	5	2	1
Predation %								
1991	40.0 ± 12.7		25.0 ± 7.9		33.0 ± 22.5		15.0 ± 9.9	
1992	—		—		15.0 ± 10.0		20.0 ± 12.5	

<sup>a</sup>Predation in exclusion cages was not estimated at blueberry sites in 1992.

The levels of predation on four different pupal types (two sizes of moth and *C. albicans* pupae) differed at the birch sites (Fig. 4B). In general, predation was lower at the Edwards site. However, this was dependent on the type and size of pupae (Kruskal–Wallis (pupal type):  $H=16$ ,  $df=3$ ,  $P<0.001$ ; (site):  $H=12$ ,  $df=1$ ,  $P<0.001$ ; (interaction):  $H=51$ ,  $df=3$ ,  $P<0.001$ ). Predation of moth and parasitoid pupae was similar at Richmond Nature Park, but at Edwards predation of small parasitoid pupae was greater than that of the moth pupae and the large parasitoid pupae. At all four sites over 90% of small parasitoid pupae were consumed (Fig. 4). At Watanabe farm, moth pupae also suffered over 90% predation, while only 64% of moth pupae were taken at Schultz farm. Deployed dead pupae were all consumed within two weeks (Table 2).

Insects that can fit through a 2 mm mesh consumed large numbers of winter moth pupae. However, the exclusion of larger invertebrates reduced predation. Predation of pupae in exclusion cages was highest at birch sites in 1991 and the level dropped in 1992 (Table 5). Predation by small-sized invertebrates at blueberry sites was lower than at birch sites in 1991 but was not measured in 1992 (Table 5).

The larvae of a number of beetles (including both Carabidae and Staphylinidae), adult Staphylinidae and ants were caught in soil-layer traps (Table 5). The beetle larvae were not identified to species level. However, *Pterostichus* spp. larvae were frequently captured and were observed feeding on pupae in exclusion cages. Larvae were mainly captured in the baited traps ( $t_3=4.552$ ,  $P=0.02$ ).

All species that were caught in the traps were brevimandibular suggesting a polyphagous habit (Thiele, 1977). The number of adult Staphylinidae caught in subterranean baited traps was also higher than those trapped in the unbaited traps ( $t_3=4.357$ ,  $P=0.022$ ). More ants were caught in subterranean traps but this was not significant.

## Discussion

### Predator assemblages

Richmond, on the Lower Mainland of British Columbia, is a mosaic of native birch, bog land, and fruit crops including blueberry, raspberry and cranberry. Like much of North America, the epigeal invertebrate fauna in the area is a mix of native and introduced species. Introduced species are generally of European origin and tend to do well in agricultural areas possibly due to a pre-adaptation to farming habitat (see Cárcamo et al., 1995). Watanabe farm, which was similar to commercial blueberry plots, was dominated by introduced species and two common native species that probably invaded from natural dry habitat. An adjacent commercial blueberry farm was sampled in June 1990 and like Watanabe farm, the most abundant species included *Amara* spp. and *H. affinis* with small numbers of *P. melanarius* (R. van Meel, personal communication). Richmond Nature Park, which includes a large area of older birch trees with a closed canopy had few European invaders. This site is a remnant of the native

habitat of the region. A small birch stand was also dominated by native beetles.

These results indicate that birch habitat acts as an important refuge for native species and there is little overlap in composition with commercial blueberry possibly due to the open dry nature of the latter. Native birch does not act as a refuge for the introduced species that are such important natural enemies in agricultural land and cannot be expected to function as a source for re-colonisation by adults of agriculture-tolerant species after predator depletion due to heavy pesticide use.

### Predators and prey selection

In spite of differences in predator assemblages and abundances at the four sites, the relative importance of winter moth mortality due to pupal predation largely followed the same trends at all the sites between 1989 and 1992 (Horgan et al., 1999). Significant differences in prey selection at the sites did not cause site-specific deviations from the gross patterns of winter moth outbreak or the role and levels of mortality caused by the introduced parasitoid (see Horgan et al., 1999). However, sites with low abundances of winter moth predators could act as focal points for future outbreaks in the region (see Raymond et al., 2002).

Both native and introduced beetles consumed pupae in arenas. However, in general, *C. albicans* pupae were rarely eaten. These results contrast with our field experiments using tethered pupae and suggest that some other component of the predator assemblage actively consumed parasitoid pupae. Parasitoid pupae in the field were preferred over winter moth pupae and the smaller parasitoid pupae were preferred over larger pupae. This combined with the observation that small predators may contribute as much as 40% to the overall predation, and field observations of *Pterostichus* spp. larvae feeding on pupae in enclosures, suggests that beetle larvae are important predators and that these may select for the smaller parasitoid pupae. However, our results differ from those of Roland (1990) on Vancouver Island where healthy moth pupae suffered greater predation, and also from Hassell's (1969) observations in England that pupal predators showed no preference for either moth or parasitoid pupae. It could be that the sizes of pupae vary among years and sites in ways that influence predation levels. In 1992, when our tests of predator preferences were made, moth larvae and leaf development appeared to be poorly synchronised and many moth pupae were malformed (Horgan et al., 1999). Predators appeared

to be particularly attracted to dead as well as to smaller pupae.

The attraction of ground predators to baited traps indicates that predation is not the result of random encounters, but that beetle larvae actively search for pupae buried in the soil. Because *C. albicans* pupae remain in the soil from early June until late April or early May of the next year while winter moth are only in the soil from June until late November, it is assumed that parasitoid pupae might be subjected to higher predation (Hassell, 1969). However, our results indicate that most of the predation in Richmond occurs in the first several weeks following pupation. At birch sites, small numbers of generalist predators are active throughout November and December. However, during the winter, parasitoid pupal densities are considerably lower than previous summer densities, and beetle larvae in particular are largely inactive, so that predation of the parasitoid is probably very low.

### Predation and the levels of parasitism

Pupal predation was an important source of mortality for *C. albicans* in 1991 when over 90% of all tethered pupae (including a combination of winter moth and *C. albicans* pupae) were consumed. In 1992 at the blueberry sites and at Richmond Nature Park, estimates of *C. albicans* predation were similar to those for all pupae in 1991, though only small parasitoid pupae were offered at the blueberry sites. However at Edwards birch, predation of *C. albicans* pupae decreased. In spite of these different trends at the birch sites, parasitism remained high at both sites in 1993 (53%, see Horgan et al., 1999).

In Richmond and at other Canadian sites following winter moth population collapse (Nova Scotia and Vancouver Island), parasitism was not density dependent (McPhee et al., 1988; Pearsall and Walde, 1994; Roland and Embree, 1995; Horgan et al., 1999). However, egg laying by the parasitoid is density dependent (Embree, 1965; Roland, 1986). Predation of *C. albicans* pupae by the same generalist predators as winter moth pupae could constrain its ability to regulate the moth. Since both the predators and the parasitoid respond to winter moth densities (Roland, 1986, 1988; Pearsall and Walde, 1994) and given the possibilities for active selection of pupae by predators, then it is possible that any density-dependent response by the parasitoid is hidden by subsequent predation. The levels of parasitism by *C. albicans* in Canada have remained significantly higher (ca. 50%) than

those reported from Britain (ca. 4%) (Roland and Embree, 1995). However, our estimates of *C. albicans* mortality due to predation of pupae are within the range of values estimated by Hassell (1969) in Britain. Therefore, other factors are likely responsible for the high levels of parasitism in North America.

Hassell (1969) found that synchrony of the parasitoid with the winter moth host was an important determinant of *C. albicans* egg survival in England. In Richmond, mortality of *C. albicans* at the above soil stages (adults, eggs and first instars) should have increased between 1991 and 1992 due to reductions in winter moth larval densities at the sites and thus the failure of large numbers of parasitoid eggs to be ingested. Furthermore, winter moth larval mortality was particularly high in 1992 possibly due to poor synchronisation between the moth and its host plants (Horgan et al., 1999). This suggests that large numbers of first instar *C. albicans* larvae may have died within their hosts. In spite of high egg and larval mortality in 1992, the levels of parasitism estimated from prepupae did not change significantly at the sites between 1991 and 1992, indicating that some strong compensatory factor operates among *C. albicans* populations at the above soil stages. Such a factor might include the high fecundity of the parasitoid or efficient host infection by *C. albicans* in the absence of competing parasitoids. Similar mechanisms might also explain why high levels of *C. albicans* pupal predation at Richmond do not appear to diminish winter moth mortality caused by this introduced parasitoid.

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