BIOLOGICAL CONTROL OF GRASSHOPPERS (ORTHOPTERA: ACRIDIDAE) IN MANITOBA WITH EMPHASIS ON PREDATORS AND PARASITOIDS OF THE EGGS

A Thesis

Submitted to the Faculty

of

Graduate Studies

The University of Manitoba

by

Josephine M. Songa

In Partial Fulfilment of the

Requirements for the Degree

of

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JOSEPHINE M. SONGA

A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements for the degree of

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Dedicated to my husband,

Wilson A. Songa

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ABSTRACT

Songa, Josephine M. M.Sc., The University of Manitoba, October, 1994.

Biological control of grasshoppers (Orthoptera: Acrididae) in Manitoba with emphasis on predators and parasitoids of the eggs.

Major Professor: N. J. Holliday.

Studies were conducted to examine the occurrence of potential predators of grasshopper eggs, and their relationship with egg density in the field, at Aubigny Manitoba, in spring and fall of 1992 and 1993. Assessment of potential predators was done by pitfall trapping and soil sampling. Three sites were established in preliminary surveys of egg densities in farmers' fields. Egg densities in each site were assessed by quadrat sampling.

Grasshopper egg densities were higher in the spring and fall of 1992 than 1993; this was attributed to the cool wet weather that prevailed in 1993. The most commonly caught groups of potential predators in the spring of 1992 and 1993, were staphylinids, arachnids and carabid beetles. Carabids were the most abundant group in the spring, and *Pterostichus corvus* Lec. was the most prevalent species. The common potential predators caught in fall of 1992 and 1993, were staphylinids, arachnids, crickets and carabid beetles. Crickets were the most prevalent group in the fall.

Catches of *Pterostichus femoralis* Kirby and arachnids, had a significant relationship with egg densities in fall of 1992. Catches of *P. corvus* and

P. lucublandus Say, had a significant relationship with sites, which also represented relative densities of grasshopper eggs, in spring of 1992. Because spring has higher temperatures, and offers a longer period for predation of grasshopper eggs, than the fall, the most prevalent taxon in the spring, *P. corvus*, which also had a significant relationship with relative densities of eggs, had the greatest potential for predation of grasshopper eggs.

The influence of vegetative cover, soil moisture and soil compaction, on the density of grasshopper eggs was examined at the field, in fall of 1992. None of these factors had a significant relationship with egg density; this was attributed to the low egg densities that season.

In a two-choice feeding test of grasshopper eggs and cat food (Tender Vittles®) in the laboratory, both *P. corvus* and *P. femoralis* preferred grasshopper eggs to cat food. Of the two species *P. corvus* ate more eggs. A study on the preferred depth of feeding of *P. corvus* on grasshopper eggs in soil in terraria showed that, *P. corvus* preferred to feed below the soil surface to depths up to 5 cm. The predation of grasshopper eggs by *P. corvus* was studied under three types of ground cover: *Nicotiana*, barley and bare ground, in the laboratory. A significantly higher percentage of eggs was eaten under the *Nicotiana* ground cover than in the other types of ground cover. The higher predation in the *Nicotiana* treatment was attributed to the more favourable environment provided in terms of shelter.

A one-choice feeding test of harvestmen on grasshopper eggs, in the

laboratory, showed that harvestmen feed little on grasshopper eggs. A laboratory study on the parasitism of grasshopper eggs collected from the field in the spring of 1992 and 1993, showed that scelionid wasps were the only parasitoids of the eggs, and the percentage parasitism was low. The scelionids, *Scelio opacus* (= *calopteni*) Provancher and *S. striativentris* Kieffer were found to occur in the field site.

INTRODUCTION

Grasshoppers are important insect pests of crops and pastures in various parts of North America (Spawn 1945, Pickford 1963, Wellso et al. 1991). Though several species are recognized as pests, only six are considered to be of economic importance in the Great Plains of North America (Vickery and Kevan 1985).

Grasshoppers are mixed feeders; they feed on broad leaved plants, grasses, and even trees and shrubs (Philip and Mengersen 1989). Grasshoppers attack all stages of plant growth; they feed on the leaves, stems, flowers, fruits and seeds (Philip and Mengersen 1989). However, damage on annual plants is most severe in the spring when nymphs feed on young plants (Edwards 1964). Grasshoppers also encourage soil erosion, especially in outbreak years when grasshopper invasion results in bare fields that are exposed to wind (Spawn 1945).

The value of losses due to grasshopper feeding can be quite high. In South Dakota, grasshoppers caused more than 21% loss in value of cereal, forage and truck crops in 1937 - 1941. In Saskatchewan, losses were estimated at $18 million in 1933, $26 million in 1948, and more than $160 million in 1938-1958 (Beirne 1972). However, the extent of loss due to grasshopper damage varies with the prevailing environmental conditions. Losses are highest in hot dry weather, which favours grasshopper population growth (Philip and Mengersen 1989), and is unfavourable for plant growth and development (Beirne 1972).

Biological control of insect pests involves the use of predators, parasites, parasitoids and pathogens for the regulation of insect pest populations (DeBach 1974). Biological control is a desirable method of controlling grasshoppers; this is because, unlike insecticides, it is safe, cost-effective, and once established, is in certain cases self-perpetuating (Doutt 1967; Webster 1982). Use of indigenous predators and parasitoids of grasshopper eggs is a rational management strategy. Indigenous natural enemies are already established in the field; they may only require suitable conservation measures to enhance their populations to effective levels.

However, there is very limited information on the predators and parasitoids of grasshopper eggs in North America. Some of the common predators of grasshopper eggs in North America are the bee-fly, *Systoechus vulgaris* Loew., carabid beetles and some species of blister beetles (Greathead 1992).

Systoechus vulgaris, a larval predator of grasshopper eggs, is prevalent in some areas in Manitoba (Criddle 1921) and S.W. Saskatchewan (Paul and Putnam 1960). The blister beetles, *Epicauta murina* Lec. and *Linsleya sphoericollis* Say, which are also larval predators of grasshopper eggs, were common in crop fields during the grasshopper outbreak of 1920 (Criddle 1921). Surveys on predators of grasshopper eggs in Saskatchewan (Brown and Paul 1943) and southwestern Manitoba (Allen 1943c) showed that larvae of bee-flies, blister beetles and carabid beetles are the common predators in the field. Smith (1965) concluded that carabid beetle larvae feed on grasshopper eggs; this is because he found carabid

larvae in close association with grasshopper eggs in the field, in Saskatchewan.

However, there is still very limited information on the predators of grasshopper eggs; most of the available information is based on surveys conducted during the years when grasshopper outbreaks were very common. Such outbreaks have been very rare in recent years. A study on the predators of grasshopper eggs and their relationship with the eggs may provide updated basic information that can be used in the development of a biological control programme for grasshoppers in Manitoba.

Moore (1945) and Putnam (1953) assessed the parasitism of eggs of major grasshopper species in various parts of western Canada. Mukerji (1987) studied the parasitism of the eggs of *M. sanguinipes* Fabr. in Saskatchewan. Assessment of parasitism of grasshopper eggs in the Red River Valley may provide updated information on the parasitism of grasshopper eggs in this area.

The general objectives of this study were (i) to examine the occurrence of potential predators and parasitoids of grasshopper eggs, and the relationship with egg density in the field and (ii) to investigate the predation of grasshopper eggs in the laboratory. The specific objectives were:

1. to determine the occurrence of potential predators of grasshopper eggs and their relationship with egg density,
2. to determine the feeding preference of *P. corvus* and *P. femoralis* on grasshopper eggs,
3. to determine the preferred depth of feeding of *P. corvus* on

grasshopper eggs in the soil,

4. to determine the influence of ground cover on the density of grasshopper eggs, and on predation of the eggs,
5. to determine the effect of some soil characteristics on the density of grasshopper eggs at the field,
6. to determine whether harvestmen feed on grasshopper eggs, and
7. to study the parasitism of grasshopper eggs.

This thesis is divided into six major parts: Introduction, Literature Review, Methods, Results, Discussion and Conclusions. Information on the biology and ecology of grasshoppers and also on the naturally occurring predators and parasitoids of grasshopper eggs in the Great Plains of North America is presented in the literature review. The thesis research is dealt with in the Methods, Results, Discussion and Conclusions sections.

LITERATURE REVIEW

Grasshopper species

Several species of grasshoppers are recognized as pests in North America (Vickery and Kevan 1985). In Canada alone, 48 species have been recorded as attacking crops (Beirne 1972). However, only six species are considered to be of economic importance to agriculture in the Great Plains of North America (Vickery and Kevan 1985). These are the two-striped grasshopper, *Melanoplus bivittatus* Say, the migratory grasshopper, *M. sanguinipes* Fabr., the clear winged grasshopper, *Camnula pellucida* Scudd. (Vickery and Kevan 1985; Philip and Mengersen 1989), Packard's grasshopper, *M. packardii* Scudd. (Ewen and Mukerji 1984; Vickery and Kevan 1985), the differential grasshopper, *M. differentialis* Thomas (Spawn 1945; Vickery and Kevan 1985) and the red-legged grasshopper, *Melanoplus femur-rubrum* DeG. (Beirne 1972; Vickery and Kevan 1985).

The distribution of the various grasshopper species is influenced by the prevailing environmental conditions (Vickery and Kevan 1985), and the food plants (Beirne 1972). For example, *M. bivittatus* prefers moist habitats, and is rarely found in dry areas (Vickery and Kevan 1985). *Melanoplus bivittatus* is primarily a forb feeder (Brooks 1958), but it also eats grasses in areas where forbs occur. However, it is rarely found in areas where only grasses are available (Vickery and Kevan 1985). This species occurs from British Columbia to Newfoundland, south

to California and Georgia (Vickery and Kevan 1985). Because it prefers clay soils (Spawn 1945), *M. bivittatus* is the predominant grasshopper species in the Red River Valley of Manitoba (Putnam 1953; Vickery and Kevan 1985).

Melanoplus packardii feeds mainly on forbs, but it also feeds on grasses in proportion to their abundance (Mulkern et al. 1969). It prefers sandy, gravelly or drift soils (Brooks 1958). *Melanoplus femur-rubrum* feeds mainly on forbs; however, it also attacks grasses, especially *Poa pratensis* L. (Mulkern et al. 1969). It is generally found on all types of soils, mainly in wetter areas (Vickery and Kevan 1985). *Melanoplus differentialis* is mainly a forb feeder, though it also feeds on grassy plants when present. It is most commonly found in areas with disturbed soils (Vickery and Kevan 1985).

Melanoplus sanguinipes adults are primarily grass feeders, but the nymphs prefer forbs (Mulkern et al. 1969). *Melanoplus sanguinipes* prefers moist sandy soils (Philip and Mengersen 1989). *Camnula pellucida* is mainly a grass-feeder which rarely eats forbs (Philip and Mengersen 1989). It is most commonly found in undisturbed soils such as those at roadsides (Vickery and Kevan 1985).

Grasshopper life cycles

Most of the major grasshopper species in the Great Plains of North America are univoltine and have a similar life cycle (Edwards 1964; Vickery and Kevan 1985). Oviposition usually occurs during the summer, and extends into the fall

(Edwards 1964). Most grasshopper species oviposit in the soil; they deposit a batch of eggs which is protected by secretions from the accessory glands, together forming the 'egg pod' (Philip and Mengersen 1989; Greathead 1992).

Most of the major grasshopper species in the Great Plains of North America overwinter in the egg stage (Spawn 1945; Philip and Mengersen 1989). The overwintered eggs hatch in the spring; the nymphs usually moult four times, though they may occasionally moult five times (Philip and Mengersen 1989). Adults start appearing from late June and continue until September or October, when the fall frosts kill the adults (Vickery and Kevan 1985). Oviposition commences about one week after emergence of the adults (Philip and Mengersen 1989).

Population dynamics

Patterns of distribution of grasshopper life stages

The egg pods of most of the major grasshopper species in North America have an aggregated distribution in the field; this has been shown for *C. pellucida* (Putnam and Shklov 1956), and *M. sanguinipes* (Davis and Wadley 1949). *Melanoplus bivittatus* oviposits in very restricted sites (Spawn 1945; Philip and Mengersen 1989), thus its egg pods also have an aggregated distribution in the field. Putnam and Shklov (1956) noted that microhabitat variations may affect the

local distribution of breeding adults and thus may be responsible for the nature of the distribution of the eggs. For example adult *M. bivittatus* are mainly found, and prefer to oviposit in moist, vegetated habitats along field margins, roadsides, ditch banks and fence rows, but not in freshly cultivated fields (Spawn 1945; Philip and Mengersen 1989). *Melanoplus bivittatus* especially prefers to oviposit on clay soils (Beirne 1972; Philip and Mengersen 1989).

Grasshopper nymphs and adults are quite active, and they move in and out of a given field (Edwards 1964); therefore the pattern of distribution of these mobile stages usually keeps changing. A dense crop left standing in the field until late fall, coupled with cool weather, can make it difficult for adults to move far into the field from the edge. Consequently such conditions can limit adult grasshoppers to the margins of crop fields (Putnam and Shklov 1956). In such a case, the adults would be concentrated at the field margins, and would therefore have an aggregated distribution in the field.

Factors that influence grasshopper populations

Abiotic factors. Weather plays an important role in the population dynamics of grasshoppers (Dempster 1963; Gage et al. 1976). Edwards (1964) noted that weather can have a direct influence on the grasshopper physiology and behaviour, or have an indirect effect by influencing its food plants and natural enemies.

In general, hot dry weather favours grasshopper populations. Most

grasshopper outbreaks in western Canada, coincide with extended periods of hot dry weather (Edwards 1964). Grasshopper outbreaks at six localities in the United States between 1915-1933, were preceded by 2-4 years of either below normal rainfall in May-June or above normal temperatures in July-September (Parker 1933).

Hot dry weather is associated with more rapid development (Begon 1983) and fecundity (Beirne 1972) of grasshoppers. This weather is also unfavourable for the fungal pathogens of grasshoppers (Pickford and Riegert 1964; Beirne 1972). A drastic reduction in infestation by grasshoppers in Saskatchewan in 1963, and British Columbia in 1943 and 1944, was attributed to epizootics of a fungal disease of grasshoppers (Beirne 1972). Hewitt (1979) found that under conditions of prolonged cold wet weather, nymphal feeding was inhibited and many nymphs died from starvation.

Host plant. Plant nutritional quality influences host plant choice and the performance of grasshoppers (Bernays and Chapman 1973). For example, nitrogen content is important in the growth (McGinnis and Kasting 1966), and survival (Smith and Northcott 1951) of nymphs of *M. bivittatus*. *Melanoplus sanguinipes* lays fewer eggs when it feeds on wheat plants with a lower nitrogen content (Khrishna and Thorsteinson (1972). Plant sugar stimulates feeding in *C. pellucida* (Thorsteinson 1960) and *M. sanguinipes* (Mulkern et al. 1978); plant sugar therefore influences the performance of these grasshoppers.

Weather may influence host plant quality, and thus influence arthropod populations (White 1978). Chapman et al. (1979) found that poor-quality host plants associated with extreme drought, result in poor reproductive performance of grasshoppers, and hence a reduction in grasshopper populations.

Secondary plant metabolites also influence the performance of grasshoppers (Bernays and Chapman 1973). Harley and Thorsteinson (1967), found that the addition of six types of secondary plant metabolites (norticotine, dipricrate, solanine, tomatine, digitonin and saponin) to artificial diet of *M. bivittatus*, resulted in high nymphal mortalities. Mulkern and Toczek (1972) found that incorporation of extracts of selected plant species into artificial diet of *M. differentialis* and *M. sanguinipes*, resulted in significant effects on the survival and rate of development of these grasshoppers.

Physical properties of the plant may also influence host plant selection and performance of grasshoppers. For example, in the laboratory, the level of feeding and the survival of *M. bivittatus* and *M. sanguinipes* is higher when they are fed on leaves of *Artemisia ludoviciana* Nutt. where trichomes have been removed, than on those with trichomes (Knuston 1982).

The nutritional requirements of most phytophagous insects change through the various stages of development (Bernays and Simpson 1990). In grasshoppers, the required protein/carbohydrate ratios fall with the various stages of nymphal development. This is partly attributed to the slower growth rate of the later instars, and thus a decreased proportional need for protein (Peters 1983). Populations of

polyphagous insects like grasshoppers in the field, select a variety of plant species in the course of their development (Mulkern 1972).

A mixed diet is important to polyphagous species. For example MacFarlane and Thorsteinson (1980) showed that *M. bivittatus* has a higher growth and survival rate when allowed to feed on several plant species rather than on just one. This has also been demonstrated in other grasshopper species (Kaufmann 1965). The need for a mixed diet in grasshopper populations implies the requirement for grasshoppers to move in out of crop fields, in order to meet their nutritional requirements. This is because most crop fields in North America are kept weed-free.

Competition. There can be both intraspecific and interspecific competition in grasshopper populations; however, competition mainly occurs when essential resources (e.g. food) are in limited supply in relation to the population size. In the laboratory, Wall and Begon (1986) found that intraspecific competition among populations of the grasshopper, *Chorthippus brunneus* Thunberg, increased with an increase in the density, cohort age and size of individuals. However, they also found that density dependent mortality due to intraspecific competition did not have a significant influence on populations of *C. brunneus*.

Interspecific competition among four species of grasshoppers, i.e. *M. sanguinipes, M. femur-rubrum, Arphia pseudonietana pseudonietana* Thomas and *Dissosteira carolina* L., in cages in a grassland in Montana, had a significant

influence on the populations of each species (Belovsky 1986). However, the influence of interspecific competition on grasshopper populations is only minimal compared to that of other factors, e.g environment (Belovsky 1986).

Field cage studies by Evans (1989) showed that increasing the density of the grasshopper *Phoetaliotes nebrascensis* Thomas, even to four times its normal levels in field cage studies in Kansas, did not cause any significant responses in the densities of the other co-existing grasshopper species. A possible reason for the absence of interspecific competition, may be that the requirements of *P. nebrascensis* in terms of food and other resources were different from those of the other co-existing species.

Natural enemies. Grasshoppers are attacked by various types of predators, parasites, parasitoids and pathogens (Rees 1973; Greathead 1992). According to Dempster (1963), natural enemies have no significant influence on grasshopper populations. He suggested that this could be either because the response of the natural enemies is too slow, or their numbers are too low relative to the grasshopper populations. However, under certain conditions, some natural enemies, e.g. fungal pathogens (in cool moist conditions), are capable of having a significant influence on grasshopper populations (Hewitt 1979; Greathead 1992). Though natural enemies are not able to prevent grasshopper outbreaks, they help to hasten the rate of decline of grasshopper populations (Greathead 1966).

Naturally occurring parasitoids of the eggs

Scelionid wasps (Hymenoptera: Scelionidae)

Wasps of the genus *Scelio* are the most important parasitoids of grasshopper eggs in North America (Greathead 1992). *Scelio opacus* (= *calopteni*) Provancher attacks eggs of some of the major grasshopper species in various parts of western Canada (Criddle 1921; Moore 1945; Putnam 1953; Muesbeck 1972). Muesebeck and Walkley (1951) found *S. opacus* (= *calopteni*) parasitizing *Melanoplus* spp. in states adjacent to the prairie provinces of Canada. There are also records of six species of *Scelio* from the U.S.A. (Rees 1973).

Scelio spp. are univoltine, and adults emerge around the time of oviposition by the host grasshoppers (Criddle 1921). *Scelio opacus* (= *calopteni*) prefers to parasitize newly laid eggs of *M. bivittatus* in the laboratory (Pickford 1964). Other *Scelio* spp. in Australia (Noble 1938), and in Pakistan (Irshad et al. 1978) also prefer to parasitize newly laid eggs in the laboratory. Researchers from various parts of the world have shown that a female scelionid parasitoid may attend the ovipositing grasshopper closely and proceed to parasitize the grasshopper eggs immediately after, or even before completion of oviposition by the host (Clausen 1940).

Murai (1959) suggested that the frothy material that surrounds grasshopper eggs attracts the scelionids. A *Scelio fulgidus* Crwf. adult can bury itself to a depth

of up to 1 inch (2.5 cm) in the soil in the laboratory (Noble 1935); it can therefore reach many grasshopper eggs, which are laid less than 2 inches (5 cm) deep in the soil (Spawn 1945).

Lanham and Evans (1958) observed *S. bisulcus* Ashmead adults clinging to the underside of the abdomen of some melanopline species in Michigan. This phoretic behaviour may enable *S. bisulcus* to locate the site of oviposition of the hosts. Though phoresy has been reported among *Scelio* spp. in various parts of the world, it has not been observed in western Canada (Putnam 1953).

The scelionid egg hatches into a larva, which feeds and develops within the host egg. Pupation follows, and the adult wasp emerges from the host egg (Pickford 1964). Scelionid adults feed on dew on grasses and nectar from flowers (Rao 1952).

In the laboratory, Putnam (1953) observed that if one egg in a pod is parasitized, most or all eggs in that pod are also parasitized. When multiple oviposition on the host egg occurs, only one parasitoid larva survives; the survivor destroys the rest of the parasitoids (Noble 1935).

Parasitism of *M. bivittatus* and *M. sanguinipes* by *Scelio* spp. in western Canada is usually lower than 5%, but is sometimes 10-15%, and only rarely 20-30% (Moore 1945). However, parasitism is higher in *M. bivittatus* than in *M. sanguinipes*, and lowest in *C. pellucida* (Moore 1945; Putnam 1953). Putnam (1953) suggested that the apparent immunity of *C. pellucida*, is due to its early oviposition, which enables it to escape parasitism by the late-maturing scelionids.

Mukerji (1987) concluded that *S. opacus* (= *calopteni*) does not play a significant role in the population dynamics of *M. bivittatus* and *M. sanguinipes* in Saskatchewan because there was no numerical response of the parasitoid density to that of the grasshopper density. Mukerji (1987) attributed the absence of a relationship between *S. opacus* (= *calopteni*) and *M. sanguinipes* and *M. bivittatus* to poor synchrony between emergence of the parasitoids and oviposition by the grasshoppers, and possibly due to destruction of parasitized eggs by other factors e.g. predators. Irshad et al. (1978) suggested that one of the reasons for the lack of effective control of grasshopper populations by *Scelio* spp., may be the aggregated distribution of the host eggs which make it more difficult for the parasitoids to encounter a large proportion of the host eggs, and hence increase to high levels. They also noted that parasitism by *Scelio* spp. increased with host population density.

In the laboratory, Noble (1935) found that application of water to soil containing parasitized grasshopper eggs induced the emergence of large numbers of adult scelionid wasps. There is a significant relationship between parasitism of grasshopper eggs by *Scelio* sp. and rainfall in August, in Saskatchewan (Mukerji 1987). Mukerji (1987) concluded that soil moisture plays a critical role in the emergence of adult scelionids. Putnam (1953) found that warm local climates enhance the rate of parasitism in western Canada. He suggested that cooler climates possibly result in parasitoids maturing too late to have a significant effect on grasshopper populations.

Naturally occurring predators of the eggs

Blister beetles (Coleoptera: Meloidae)

Larvae of several species of blister beetles in the genera *Epicauta, Linsleya, Mylabris* and *Coryna* are common predators of grasshopper eggs in North America (Rees 1973; Greathead 1992). The predator eggs are laid in the soil, they hatch into triungulin larvae which then seek and feed on grasshopper eggs. The predator larvae develop within the egg pod, they moult six times. The first three instars are 'caraboid' larvae, the following two 'scaraboid' and the sixth a 'coarctate' which is a resting stage; development to the last stage, the 'scolytoid' larvae requires specific favourable weather conditions, and pupation follows. The adults feed on flowers and some species are important pests of crops, especially legumes (Greathead 1992).

During the grasshopper outbreak of 1920, several species of blister beetles were prevalent in Manitoba. The two most important ones were, *Epicauta murina* and *Linsleya sphoericollis* in crop fields. Other species of lesser importance were *Lytta nuttalli* Say and *Epicauta sericans* Lec. (Criddle 1921). However, Criddle (1921) noted that the abundance of each species was governed by the abundance of food plants of the adults. For example, adults of *E. murina* and *L. nuttalli* mainly feed on members of the pea family, whereas *C. sphoericollis* adults mainly feed on the prairie strawberry, and adults of *E. sericans* on *Anemone* sp. (Criddle

1921).

Blister beetle larvae have a greater preference for eggs of *Melanoplus* spp. than for those of *C. pellucida* (Criddle 1921). Allen (1943b) found that the five feeding instars of *E. subglabra* Lec. that precede the coarctate instar, consumed a total of 24 eggs of *M. bivittatus* and 20 eggs of *C. pellucida*. Not all predator species in the genus *Epicauta* feed on grasshopper eggs. For example, Selander (1981) found that larvae of *E. atrata* Fab. could not develop successfully on eggs of *M. differentialis* and *M. femur- rubrum*. This predator only developed successfully on eggs of *E. pennsylvanica* DeG..

Carabid beetles (Coleoptera: Carabidae)

Carabid beetles are common polyphagous predators in cultivated fields (Sunderland 1975). Carabid larvae occur in close association with grasshopper eggs in the field, and it is believed that they feed on the eggs (Smith 1965; Greathead 1992). In field surveys, Brown and Paul (1943) found that carabid beetles were one of the common predators of grasshopper eggs in stubble fields in south east Saskatchewan.

There are generally higher numbers of carabid beetles along field margins (Thiele 1977); these are also the preferred sites for oviposition by some grasshopper species e.g. *M. bivittatus* (Philip and Mengersen 1989).

Bee-flies (Diptera: Bombyliidae)

The bee-fly, *Systoechus vulgaris* Loew., which is an obligate larval predator of grasshopper eggs, is common in grasshopper egg beds in North America (Greathead 1992). *Systoechus vulgaris* oviposits in the soil; the eggs hatch into larvae which then search for grasshopper eggs on which they feed. After feeding, the larvae become dormant until pupation is triggered by favourable weather conditions (Greathead 1992). Adults of *Systoechus* spp. feed on flowers (Hynes 1947). During the grasshopper outbreak of 1920 in Manitoba, *S. vulgaris* was prevalent in most fields, and local infestations of eggs of *M. sanguinipes* and *C. pellucida* were as high as 90% in some districts in Manitoba (Criddle 1921). However, Criddle (1921) found that bee-fly larvae were more prevalent in egg pods of *C. pellucida*, than in those of *Melanoplus* spp.

Allen (1943c) found that bee-flies were the dominant predators responsible for a 69% egg pod mortality in the field in southwestern Manitoba in 1938. Allen (1943a) also found that third instar larvae of *S. vulgaris* consumed an average of 14 *M. bivittatus eggs*, in the laboratory.

Paul and Putnam (1960) in Saskachewan found that populations of *S. vulgaris* were lower in grasshopper outbreak areas (where the grasshopper populations build up) than in the invaded areas (areas to which grasshopper populations spread by dispersal from outbreak areas), in Saskatchewan. They concluded that *S. vulgaris* disperses with its prey *M. sanguinipes.* However, in my

opinion, assuming that the invaded areas had a higher grasshopper population (and hence grasshopper eggs) than the outbreak areas, this may have allowed a faster multiplication of the bee-fly populations in the invaded areas.

MATERIALS AND METHODS

Selection of sites

The field sites were at Aubigny, Manitoba in the Red River Valley. The sites were selected in spring 1992 based on preliminary surveys of densities of grasshopper eggs in farmers' fields. In these surveys, up to 40 soil samples were collected randomly along field margins. Each sample was taken to a depth of about 5 cm below the soil using a 0.07 m^2 shovel, and egg densities were assessed by visual observation. Three sites were established, the North (with > 5 egg pods/shovel), middle (with 2-5 egg pods/shovel) and the South (with < 2 egg pods/shovel) sites, and they were located at R2E T6 Section 2, R2E T6 Section 3 and R2W T5 Section 28, respectively. A total of seven transects were selected along field margins; three in the North, and two in the middle and South sites. A field margin is a strip of land about 1 m wide from the last row of crop plants. A transect is a sampling line along the field margin; each transect was 110 m long.

Preliminary surveys for egg densities were only conducted in the spring of 1992, however the sites selected were also used in the subsequent three study seasons.

Assessment of grasshopper egg densities

Assessment of egg densities was done in the spring and fall of 1992 and 1993. In the spring, assessment was done in early May before the eggs started

hatching; in the fall it was done at the end of October when oviposition was generally complete.

In the spring of 1992, five soil samples were taken in each transect, to a depth of about 6 cm, using a 0.1 m^2 quadrat. The sampling points were spaced 10 m apart. The eggs were sorted from the soil samples, and then taken to the laboratory for counting. Because five soil samples appeared to be insufficient (since the results they gave were not representative of the egg densities in the field), 10 samples per transect were taken in fall 1992, and in the spring and fall of 1993.

Occurrence of potential predators of grasshopper eggs

Two types of sampling methods were used: pitfall trapping and soil sampling.

Pitfall trapping

Sampling for predators was conducted in the spring and fall of 1992 and 1993. In the spring, sampling commenced before egg hatch began, and continued until most eggs had hatched. In the fall, sampling was done from early to the completion of grasshopper oviposition. In the spring of 1992 and 1993, sampling was conducted from 13 May to 24 June and from 11 May to 29 June, respectively. In fall of 1992 and 1993, sampling was done from 10 September to 29 October

and from 24 September to 29 October, respectively.

Ten pitfall traps were set 10 m apart along each transect (Fig. 1). Each trap consisted of a large cup of diameter 9.5 cm and depth 11.5 cm, and a smaller cup of diameter 9.0 cm and depth 10 cm. The small cup was fitted into the larger cup, which in turn was fitted into a hole in the ground, such that the lip of the inner cup was level with the ground surface. To preserve the catch, the inner cup contained 50 ml of an aqueous solution of 50% ethylene glycol mixed with quinine sulphate (at a rate of 4 g/l). A 15 x 15 cm wooden cover was supported above each trap to prevent the entry of rain water, reduce evaporation, and deter veterbrates from falling into the trap. The traps were emptied once a week on a regular basis. The arthropods caught in each trap were taken back to the laboratory for identification and counting.

Data for the most commonly caught potential predators were subjected to Barttlet's test for homogeneity of variance. The data were transformed to stabilize the variance, and Taylor's power law was used to determine the appropriate transformation (Southwood 1978). An analysis of variance was conducted to examine differences among transects for the various potential predators.

For the taxa in which catch varied significantly among transects, the variance was partitioned to examine the relationship between mean catch and grasshopper egg density (Wilkinson 1990).

Soil sampling

Soil sampling for potential predators was done using a 0.1 m^2 quadrat of depth 6 cm, and it was done at the same time as the assessment of grasshopper egg densities. The arthropods were sorted from the soil samples, and taken to the laboratory for identification and counting.

There were too many zeros for valid statistical analysis. Means for the commonly caught potential predators were calculated and used to assess the occurrence of the various taxa.

Feeding preferrence of *Pterostichus corvus* Lec. and *P. femoralis* Kirby

This study was conducted on a laboratory bench in the summer, and was maintained at a temperature of about 20°C and 16 hours of natural lighting from the window supplemented by lighting in the laboratory, and 8 hours of darkness. Four petri dishes, each of 9 cm diameter, and 1.5 cm depth, were filled to half their depth with moist potting soil. Twenty grasshopper eggs and 0.8 g of cat food (Tender Vittles®) (which was about the same amount by volume, with twenty grasshopper eggs), were put on separate pieces of filter paper in each petri dish. Cat food was used in this choice test because, *P. corvus* has been reared successfully in the laboratory, on only cat food for as long as 3 months.

Two petri dishes were allocated to each species, and two beetles were put in each dish (Fig. 2). The amount of each of the food items eaten was determined

after 4 days. The experiment was repeated four times.

The data were compared using an unpaired t-test (Wilkinson 1990).

Preferred depth of feeding of *P. corvus* on grasshopper eggs in the soil

This study was conducted in a temperature controlled room, maintained at 20°C with 16 h light and 8 h dark. Four terraria, each 30 × 30 × 60 cm (W × H × L cm), were filled with potting soil to a depth of about 8 cm (Fig. 3). Batches of 20 grasshopper eggs were put at the surface, 2.5 and 5 cm below the soil in each terrarium; the batches of eggs at each level were spaced 20 cm apart horizontally. Two *P. corvus* adults were put in each terrarium Some dry leaves were scattered evenly on the surface of each of the terraria to offer refuge for the insects. The number of eggs remaining at each depth was counted after 7 days. The experiment was repeated three times.

A control study was also conducted; it had exactly the same set up as the main study, explained above; the only difference was that no carabids were put in the terraria. The number of eggs recovered from the various depths after seven days was counted.

Data from the study with beetles and the control study, were subjected to a two-way analysis of variance. Following this, a one-way analysis of variance was conducted on the study with beetles alone, and orthogonal contrasts were used to identify differences in the number of grasshopper eggs eaten among the

various soil depths (Wilkinson 1990).

Influence of ground cover on predation of grasshopper eggs by *P. corvus*

This study was conducted on the laboratory bench at a temperature of 20°C with 16 h light and 8 h darkness. Soil-filled plastic trays, 27 × 6 × 54 cm (W × H × L cm, were each divided into three sections, 18 × 27 cm. Three types of ground cover were established in the three sections. *Nicotiana*, a plant with a rosette growth habit, and barley, a plant with a vertical growth habit, were planted in two sections (each at a plant spacing of 3.5 × 3.5 cm), and the third section was left bare (Fig. 4). The three treatments were assigned randomly within each tray; there was a total of 22 trays.

Barley was planted 5 weeks after the day of planting *Nicotiana* to ensure that each of the two types of plants had attained the required stage (*Nicotiana* a good ground cover, and the barley plants, a height of about 13 cm), before proceeding to the next stage of the study. Batches of 15 grasshopper eggs were put about 2.5 cm below the soil surface at the center of each of the sections. Two adult *P. corvus* beetles were introduced into each of the trays.

Each tray was covered with a transparent cover of a height of 17 cm, to prevent escape of the beetles. The covers had perforations to prevent the build up of humidity and heat within the trays. The number of eggs eaten from each of the treatments was determined 7 days after the eggs were introduced into the

trays.

The data were analysed using chi-square tests of contingency tables (Wilkinson 1990).

Influence of vegetation and some soil characteristics on the density of grasshopper eggs

This study was done in the fall of 1992 at the same time as the assessment of egg densities, and the same 0.1 m^2 quadrat samples were used on each transect. Before removal of the soil in the quadrat to assess its contents, the percentage vegetative cover of each plant species within each quadrat was assessed. Soil compaction was determined by taking one measurement within each quadrat with a soil penetrometer.

One soil sample was taken on the outer corner of each quadrat with a soil corer of 5 cm diameter and 5 cm depth. Each soil sample was stored in a sealed plastic pot, to prevent the escape of moisture. The soil samples were taken to the laboratory for determination of soil moisture content.

In the laboratory, the weight of each soil sample plus the pot, without the lid was taken. The samples were then dried in an oven at 60°C, for 4 days. After 4 days, each sample was reweighed, and then returned to the oven. From then on, the samples were weighed daily until three constant readings for each soil sample was obtained, indicating that all the moisture had been driven off. The final

weight of the pot and the dry sample was recorded. The weight of moisture in each pot was calculated by subtraction, and the percentage soil moisture was calculated for each sample.

The data were first transformed to stabilize the variance; they were then analysed by step-up multiple regression analysis (Wilkinson 1990).

Determination of whether harvestmen feed on grasshopper eggs

A box 9 × 7 × 20 cm (W × H × L cm), was filled with moist potting soil to a depth of about 4.0 cm. Twenty grasshopper eggs were put at the surface and another 20 at 2.5 cm below the soil surface. Five harvestmen were introduced into the box. The number of eggs and harvestmen remaining was determined after 11 days.

Since this study had no replication, no analysis was conducted; means of the data were calculated.

Parasitism of grasshopper eggs

The eggs that were used in this study were obtained from the samples used to estimate densities of grasshopper eggs in the spring of 1992 and 1993. Petri dishes of 9 cm diameter, and 1.5 cm depth, were each filled with moist potting soil, to about half their depth. Batches of known numbers of eggs from the various transects were put in these petri dishes. Each petri dish was in turn put in a larger

petri dish of 14 cm diameter, and 2.5 cm depth, and lined with moist filter paper. The eggs were incubated for 30 days at 25°C. The filter paper was changed regularly to discourage the growth of mould.

The eggs were checked every 4 days, starting one week after incubation commenced and continued until the 30th day. During each observation period, the hatched parasitoids (Fig. 5) were identified to family level, counted and then removed from the petri dishes. A record was maintained of the number of hatched parasitoids throughout the sampling period. Identification of the parasitoids to species level was done by L. Masner (Centre for Land and Biological Resource Research in Ottawa).

After 30 days of incubation, eggs from which neither grasshoppers nor parasitoids had emerged, were bleached to render the vitelline membrane transparent. The eggs were soaked for 2-6 hours in 3% sodium hypochlorite solution (Pickford 1964), and the egg contents examined microscopically. The total number of parasitised eggs was the sum of the number of emerged parasitoids and the number of bleached eggs that contained parasitoids. The rate of parasitism was calculated from the total number of parasitized eggs and the total number of eggs at the beginning of incubation.

Figure 1. Photograph of one of the transects from which predators and grasshopper egg densities were assessed in the field site at Aubigny, Manitoba, in spring 1992.

Figure 2. Photograph of layout of the study on the feeding preferrence of *P. corvus* and *P. femoralis* on grasshopper eggs and cat food (Tender Vittles®).

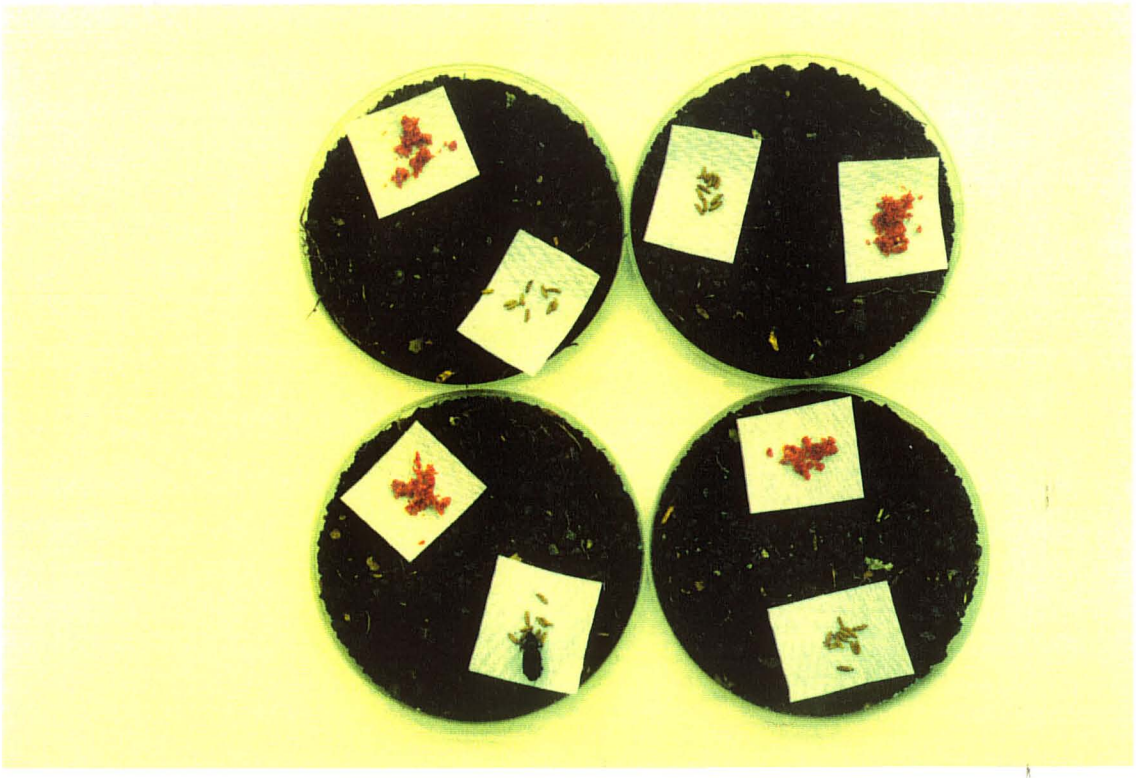


Figure 3. Terraria used in the study on the preferred depth of feeding of *Pterostichus corvus* on grasshopper eggs in the soil.


A
B
C

Figure 4. A tray with three types of ground cover in the study on the influence of vegetative ground cover on predation of *Pterostichus corvus* on grasshopper eggs.

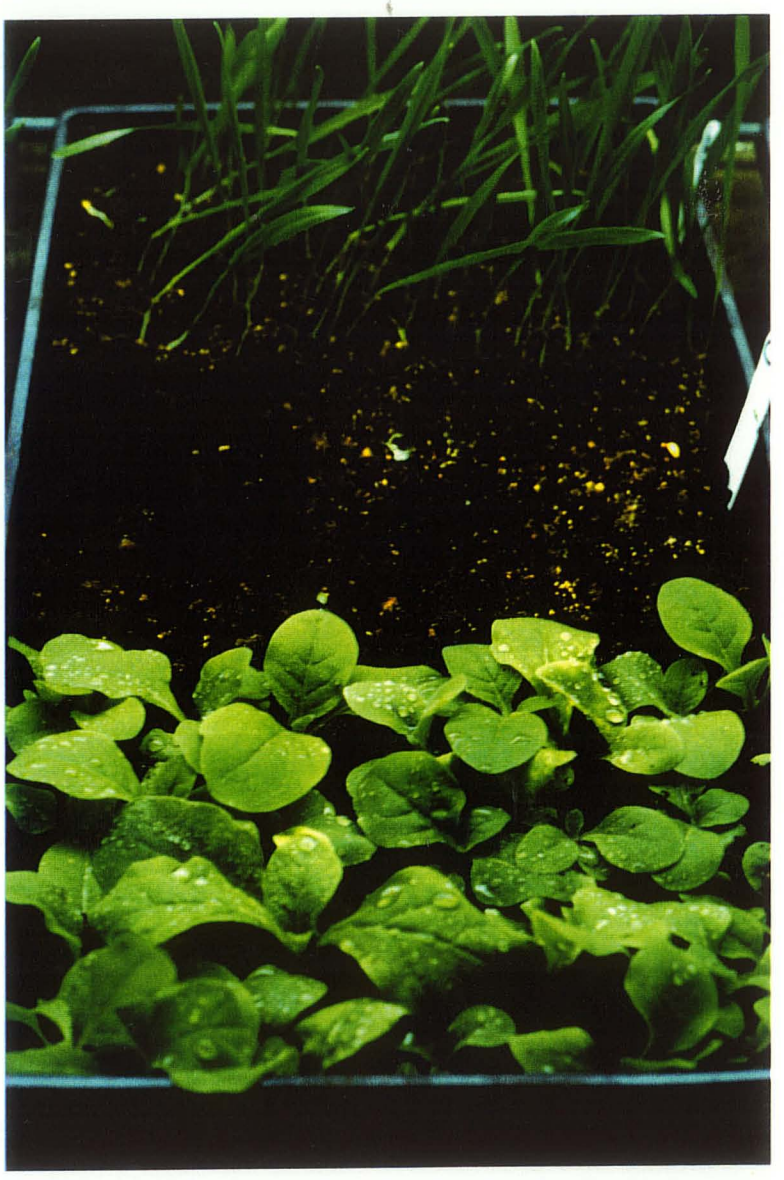
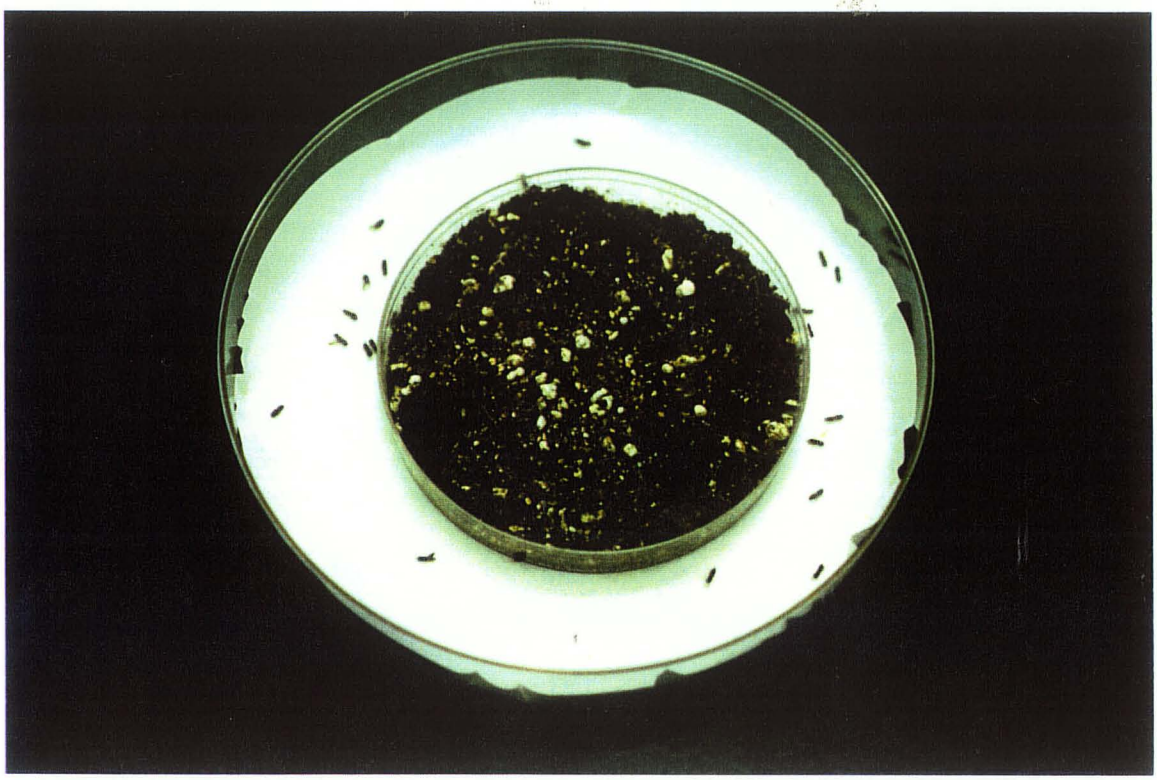


Figure 5. *Scelionid* wasps that have emerged from grasshopper eggs, in a petri dish.



RESULTS

Egg densities

The North site had the highest density of eggs in the spring of 1992 and 1993 (Table 1). In spring 1992, there was an underestimation of egg densities in the middle site; there were no eggs sampled in this site, but the preliminary survey had indicated the presence of eggs in the site. It was for this reason that more samples were taken in later sample periods. If the three sites are considered together, there was a higher density of eggs in spring 1992 than in spring 1993.

In fall 1992, the North site had the highest density of eggs, though it did not appear to be significantly different from that of the South site (Table 2). In fall 1993, no eggs were found in any of the three sites.

In spring 1992, the best estimate of grasshopper egg densities was from the preliminary surveys for egg density. This is because in spring 1992, the egg density estimates from the quadrat samples were not reliable due to the small sample size. However in the subsequent study periods, the best estimate of grasshopper egg densities was from the quadrat samples, this is because a larger sample size was taken, and no preliminary sampling for egg densities was conducted.

Table 1. Mean (± S.E.) grasshopper egg densities in samples from the field sites at Aubigny, Manitoba, in spring 1992 and 1993.

Year	Grasshopper eggs / m^2 in each site		
	North	Middle	South
1992[a]	2540.0 ± 1400.5	0.0	0.0
1993[b]	738.0 ± 168.3	145.0 ± 53.2	255.5 ± 83.1

[a]N = 35; [b]N = 70.

Table 2. Mean (± S.E.) (n = 70) grasshopper egg densities in samples from the field sites at Aubigny, Manitoba, in fall 1992 and 1993.

Year	Grasshopper eggs / m^2 in each site		
	North	Middle	South
1992	383.0 ± 84.9	30.0 ± 27.0	327.0 ± 120.9
1993	0.0	0.0	0.0

Pit-fall trap catches

Three groups of potential predators were caught in spring of 1992 and 1993, and these were staphylinids, arachnids and carabid beetles (Table 3). Carabids were the most commonly caught group of potential predators, when springs 1992 and 1993 were considered together. For this reason, most of the subsequent evaluations were concentrated on carabid beetles. Arachnids and staphylinids were the second and third most common groups respectively.

In fall 1992 and 1993, four groups of potential predators were captured. These were staphylinids, arachnids, crickets and carabid beetles (Table 4). Crickets were the most commonly caught group of potential predators, when both fall 1992 and 1993 were considered together. Arachnids, carabid beetles and staphylinids were the second, third and fourth most common groups respectively.

The total number of carabid beetles (all species) in both spring 1992 and 1993 (Table 3) were higher than in both fall 1992 and 1993 (Table 4). *Pterostichus corvus* was the most frequently captured carabid species, in springs of 1992 and 1993 combined and in falls of 1992 and 1993 combined (Tables 3 and 4).

The numbers of *P. corvus* caught in both spring 1992 and 1993 (Table 3), were higher than in both fall 1992 and 1993 (Tables 4). The numbers of *P. corvus* varied significantly among transects in spring 1992 and 1993 (Table 3). Grasshopper egg densities did not contribute significantly to the variation in numbers of *P. corvus* among transects in spring 1993 (Table 6). In spring 1992, sites (which

also represented relative densities of grasshopper eggs), contributed significantly to the variation in numbers of *P. corvus* among transects (Table 5).

In spring 1992, orthogonal contrasts were conducted to examine the differences in mean catches of *P. corvus* among sites. The contrasts were done by using the error term of the residual of the among transect variation alone; this is because the variation among transects was significantly greater than that within transects ($P < 0.05$). The South site, which had low relative densities of grasshopper eggs, had significantly fewer catches of *P. corvus* than the other sites ($F = 43.19$; d.f = 1,4; $P < 0.01$) (Fig. 6). However, there were no significant differences in the catch of *P. corvus* between the middle and North sites ($F = 0.67$; d.f = 1,4; $P > 0.05$), which had intermediate and high densities of grasshopper eggs respectively.

The catches of *P. corvus* varied significantly among transects in fall 1992 but not in 1993 (Table 4). Grasshopper egg density, did not contribute significantly to the variation of in numbers of *P. corvus* among transects in fall 1992 (Table 7).

The numbers of *Pterostichus lucublandus* caught in both spring 1992 and 1993 (Table 3) were higher than in both fall 1992 and 1993; numbers in the fall of 1992 (Appendix 4) and 1993 (Appendix 5) were too low to be included in the analysis. The catches of *P. lucublandus* varied significantly among transects in spring 1992 and 1993 (Table 3). Grasshopper egg densities did not contribute significantly to the variation in numbers of *P. lucublandus* among transects in spring 1993 (Table 6). However, in spring 1992, sites (which also represented relative

of *P. lucublandus* among transects (Table 5).

In spring 1992, orthogonal contrasts were conducted on the mean catches of *P. lucublandus* among sites. The contrasts were done by using the pooled error term of the residuals of the among and within transect variation. This is because the variation among transects was not significantly different from that within transects ($P > 0.05$). The South site which had low relative densities of grasshopper eggs, had significantly fewer catches of *P. lucublandus* than the other sites ($F = 12.63$; $d.f = 1,67$; $P < 0.01$) (Fig. 7). However, there were no significant differences in the catch of *P. lucublandus* between the middle and North sites ($F = 1.93$; $d.f = 1,67$; $P > 0.05$), which had intermediate and high densities of grasshopper eggs.

The numbers of *Chlaenius sericeus* Forst. caught in both spring 1992 and 1993, were higher than in the fall; numbers in the fall of 1992 (Appendix 4) and 1993 (Appendix 5), were too low to be included in the analysis. The catches of *C. sericeus* varied significantly among transects in spring 1992, but not in 1993 (Table 3). In spring 1992, sites (which also represented relative densities of grasshopper eggs) did not contribute significantly to the variation of in numbers of *C. sericeus* among transects (Table 5).

The numbers of *Agonum placidum* Say caught in both spring 1992 and 1993 (Table 3), were greater than in the fall; numbers in the fall of 1992 (Appendix 4) and 1993 (Appendix 5), were too low to be included in the analysis. The catches of *Agonum placidum* varied significantly among transects in spring 1992 and 1993 (Table 3). Grasshopper egg densities did not contribute significantly to the variation

of *A. placidum* among transects, in spring 1993 (Table 6). In spring 1992, sites (which also represented relative densities of grasshopper eggs), did not contribute significantly to the variation in numbers of *A. placidum* among transects (Table 5).

The numbers of *Calosoma calidum* Fabr. caught in both spring 1992 and 1993 (Table 3), were greater than in the fall; numbers in the fall of 1992 (Appendix 4) and 1993 (Appendix 5), were too low to be included in the analysis. The catches of *C. calidum* varied significantly among transects in spring 1992 but not in 1993 (Table 3). Sites (which also represented relative densities of grasshopper eggs), did not contribute significantly to the variation of *C. calidum* among transects in spring 1992 (Table 5).

The numbers of *Pterostichus femoralis* Kirby caught in both spring 1992 and 1993 (Table 3) were less than in the fall of 1992 and 1993 (Table 4). The catches of *P. femoralis* varied significantly among transects in spring 1993, but not in 1992 (Table 3). Grasshopper egg densities did not contribute significantly to the variation in numbers of *P. femoralis* among transects in spring 1993 (Table 6).

The numbers of *P. femoralis* varied significantly among transects in the fall of 1993, but not in 1992 (Table 4). The contribution of grasshopper egg densities to the variation in numbers of *P. femoralis* among transects in fall 1993 was not examined because there were no eggs in the quadrat samples.

The numbers of *Amara obesa* Say caught in both fall 1992 and 1993 (Table 4), were greater than in the spring; numbers in the spring of 1992 (Appendix 2) and 1993 (Appendix 3), were too low to be included in the analysis. The catches of *A.*

obesa varied significantly among transects in fall 1992 but not in 1993 (Table 4). Grasshopper egg densities did not contribute significantly to the variation in numbers of *A. obesa* among transects in fall 1992 (Table 7).

The numbers of *Amara carinata* Lec. caught in both fall 1992 and 1993 (Table 4) were higher than in the spring; numbers in the spring of 1992 (Appendix 2) and 1993 (Appendix 3), were too low to be included in the analysis. The catches of *A. carinata* varied significantly among transects in fall 1992, but not in 1993 (Table 4). Grasshopper egg densities did not contribute significantly to the variation in numbers of *A. carinata* among transects in fall 1992 (Table 7).

The numbers of arachnids caught in both spring 1992 and 1993 (Table 3) was greater than in both fall 1992 and 1993 (Table 4). The catches of arachnids varied significantly among transects in spring 1993 but not in 1992 (Table 3). Grasshopper egg densities did not contribute significantly to the variation in numbers of arachnids among transects in spring 1993 (Table 6).

The catches of arachnids varied significantly among transects in fall 1992 and 1993 (Table 4). Grasshopper egg densities contributed significantly to the variation in numbers of arachnids among transects in fall 1992 (Table 5). The contribution of egg densities to the variation in numbers of arachnids among transects in fall 1993 was not examined, because there were no eggs in the quadrat soil samples.

The numbers of staphylinids caught in both spring 1992 and 1993 (Table 3), were greater than in both fall 1992 and 1993 (Table 4). The numbers of staphylinids varied significantly among transects in spring 1993 but not in spring 1992 (Table 3).

Grasshopper egg densities did not contribute significantly to the variation in numbers of staphylinids among transects in spring 1993 (Table 6). The catches of staphylinids did not vary significantly among transects in fall 1992 and 1993 (Table 4).

The catches of crickets in both fall 1992 and 1993 (Table 4) were greater than in the spring; the number in spring 1992 was too low to be included in the analysis (Appendix 2), and no crickets were trapped in spring 1993 (Appendix 3). The number of crickets varied significantly among transects in fall 1992 but not in 1993 (Table 4). Grasshopper egg densities did not contribute significantly to the variation in numbers of crickets among transects in fall 1992 (Table 7).

Table 3. Mean (± S.E.) catch per trap of each of the potential predators in the field sites at Aubigny, Manitoba in spring 1992 and 1993.

Taxon	1992[1]	1993[2]
Pterostichus corvus Lec.	70.7 ± 5.6***	44.8 ± 2.3**
P. femoralis Kirby	0.8 ± 0.1	2.0 ± 0.2**
P. lucublandus Say	1.5 ± 0.2*	2.7 ± 0.4***
Chlaenius sericeus Forst.	9.7 ± 1.3***	3.2 ± 0.3
Agonum placidum Say	0.9 ± 0.1*	2.3 ± 0.5***
Calosoma calidum Fabr.	1.9 ± 0.1**	1.0 ± 0.1
Total carabid beetles	86.6 ± 6.5***	59.6 ± 3.1***
Arachnids[3]	5.5 ± 0.4	101.2 ± 7.2***
Staphylinid adults and larvae	1.6 ± 0.2	1.5 ± 0.2***

[1]Mean catch per trap, of 70 traps in 7 transects, over 6 weeks, in spring 1992.
[2]Mean catch per trap, of 70 traps in 7 transects, over 8 weeks, in spring 1993.
[3]Arachnids = Harvstmen and spiders.
*, **, *** - Significant variation among transects, at the 0.05, 0.01, and 0.001 probability levels, respectively.

Table 4. Mean (± S.E) catch per trap of each of the potential predators in the field sites at Aubigny, Manitoba in fall 1992 and 1993.

Taxon	1992[1]	1993[2]
Pterostichus corvus Lec.	4.1 ± 0.5***	2.1 ± 0.4
P. femoralis Kirby	0.5 ± 0.2	3.2 ± 0.9***
Amara obesa Say	1.6 ± 0.3***	0.5 ± 0.2
A. carinata Lec.	2.0 ± 0.3**	0.1 ± 0.1
Total carabid beetles	10.2 ± 0.9***	8.5 ± 1.7***
Crickets[3] adults and nymphs	62.8 ± 8.8***	0.4 ± 0.3
Arachnids[4]	24.9 ± 1.9***	2.5 ± 0.6**
Staphylinid adults and larvae	0.5 ± 0.1	0.4 ± 0.2

[1]Mean catch per trap, of 70 traps over 7 transects, in 7 weeks, in fall 1992.
[2]Mean catch per trap, of 70 traps over 7 transects, in 5 weeks, in fall 1993.
[3]Crickets were predominantly *Gryllus pennsylvanicus* Burm. adults.
[4]Arachnids = Harvestmen and spiders.
*, **, *** - Significant variation among transects, at the 0.05, 0.01, and 0.001 probability levels, respectively.

Table 5. Relationship of potential predators with sites[1] at Aubigny, Manitoba in spring 1992.

Taxon	F-value (d.f = 2,4)	P-value
Pterostichus corvus Lec.	21.60	< 0.01
P. lucublandus Say	10.13	< 0.05
Chlaenius sericeus Forst.	6.51	> 0.05
Agonum placidum Say	0.83	> 0.05
Calosoma calidum Fabr.	6.09	> 0.05

[1]sites also represented relative densities of grasshopper eggs.

Table 6. Relationship of potential predators with grasshopper egg densities at Aubigny, Manitoba in Spring 1993.

Taxon	F-value (d.f = 2,4)	P-value
Pterostichus corvus Lec.	0.78	> 0.05
P. lucublandus Say	0.91	> 0.05
P. femoralis Kirby	0.45	> 0.05
Agonum placidum Say	4.87	> 0.05
Arachnids[1]	1.79	> 0.05
Staphylinid adults and larvae	0.49	> 0.05

[1]Arachnids = Harvestmen and spiders.

Table 7. Relationship of potential predators with grasshopper egg densities at Aubigny, Manitoba in fall 1992.

Taxon	F-value (d.f = 2,4)	P-value
Pterostichus corvus	1.38	> 0.05
Amara obesa Say	2.64	> 0.05
Amara carinata Lec.	0.00	> 0.05
Crickets[1] adults and nymphs	4.79	> 0.05
Arachnids[2]	8.50	< 0.05

[1]Crickets were predominatly *G. pennsylvanicus* adults.
[2]Arachnids = Harvestmen and spiders.

Figure 6. Mean numbers (± S.E) of *Pterostichus corvus* caught per trap, over six weeks in spring 1992, in three sites at Aubigny, Manitoba.

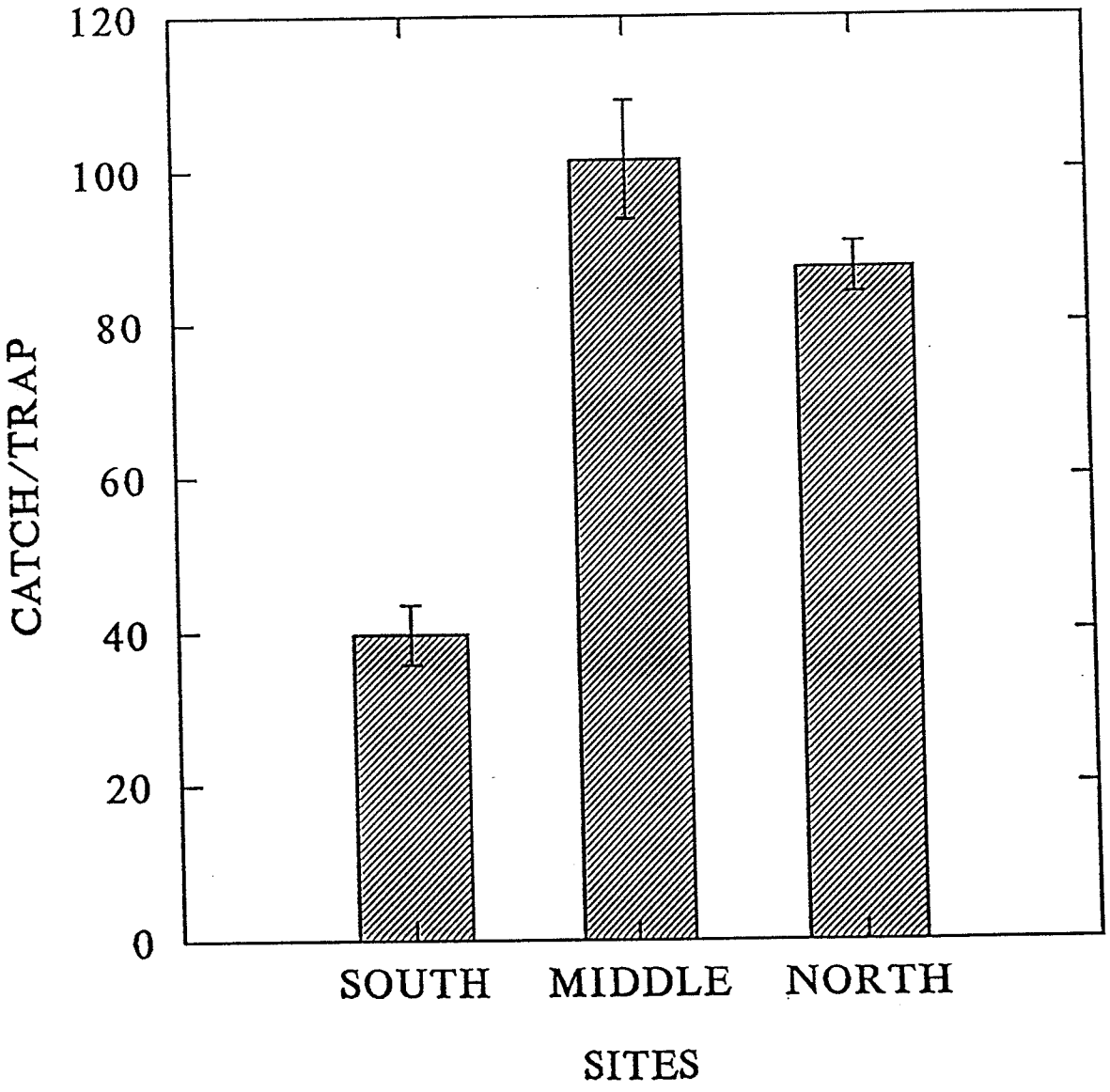
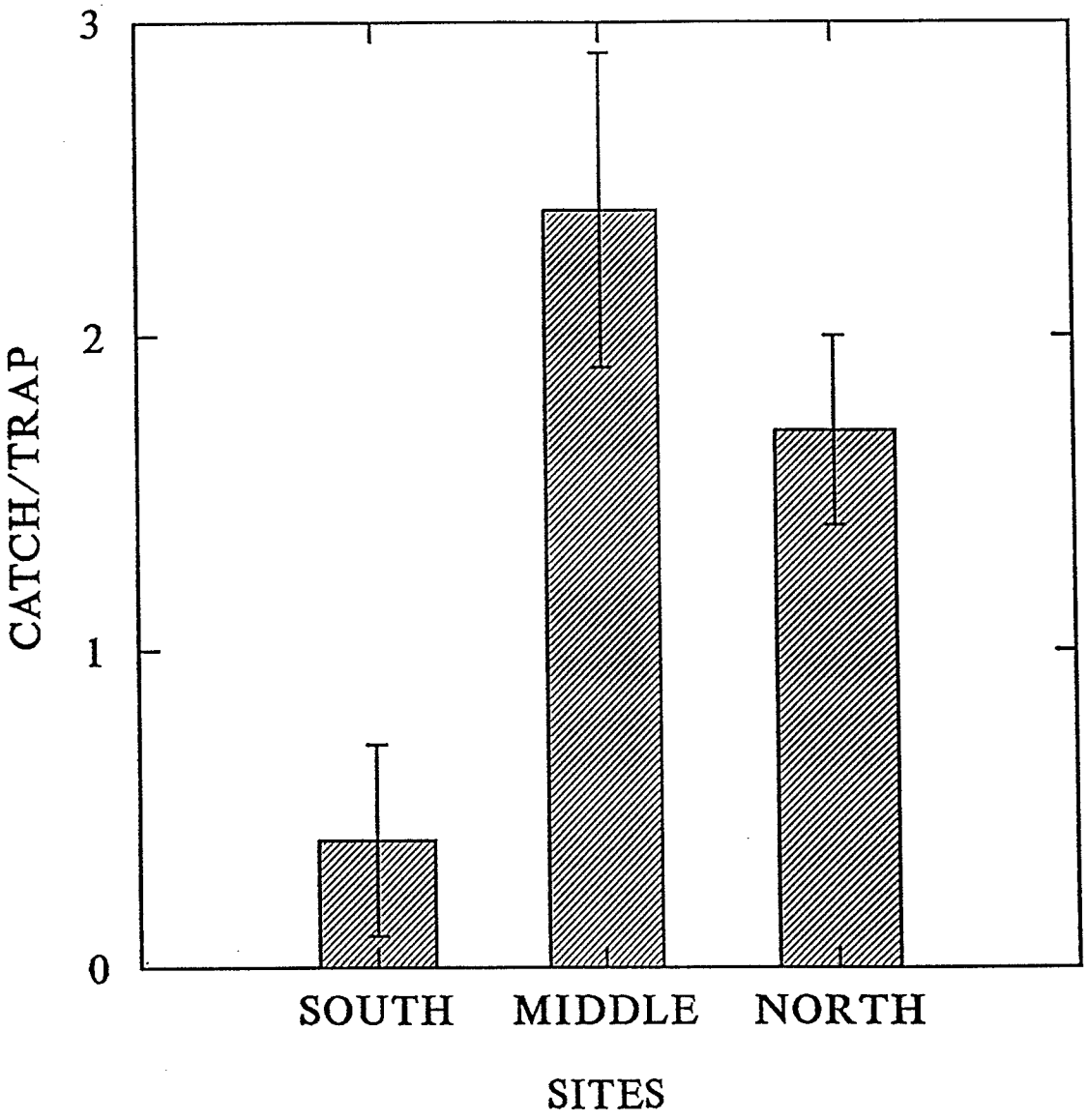

120
100
80
60
40
20
0
CATCH/TRAP
SOUTH
MIDDLE
NORTH
SITES

Figure 7. Mean numbers (± S.E) of *Pterostichus lucublandus* caught per trap, over six weeks in spring 1992, in three sites at Aubigny, Manitoba.


3
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CATCH/TRAP
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Potential predators in soil samples

The numbers of potential predators recovered from the soil samples in spring 1992 and 1993 (Table 8) and fall 1992 and 1993 (Table 9) were too few to permit statistical analysis. There were only small differences in the number of potential predators between the two seasons and years. The most prevalent group of potential predators in the spring and fall of 1992 and 1993, was carabid beetles. Other groups of potential predators recovered from the soil samples in the spring and fall were centipedes, larvae of soft-winged flower beetles (*Cóllops* sp.), staphylinid beetles and arachnids.

Table 8. Mean (± S.E.) numbers of potential predators in soil samples from the field site at Aubigny, Manitoba, in the spring of 1992 and 1993.

Taxon	Number/0.1 m^2	
	1992[a]	1993[b]
Pterostichus corvus Lec.	0.06 ± 0.06	0.07 ± 0.05
P. femoralis Kirby	0.03 ± 0.03	0.04 ± 0.03
Amara obesa Say larvae	0.06 ± 0.04	0.00
A. carinata Lec. larvae	0.03 ± 0.03	0.04 ± 0.04
Total carabids	0.17 ± 0.07	0.16 ± 0.07
Centipedes	0.14 ± 0.10	0.20 ± 0.07
Cóllops sp. larvae	0.14 ± 0.07	0.04 ± 0.03
[1]Arachnids	0.06 ± 0.04	0.07 ± 0.04
Staphylinid adults and larvae	0.06 ± 0.05	0.09 ± 0.05

[a]N = 35; [b]N = 70.
[1]Arachnids = Harvestmen and spiders.

Table 9. Mean (± S.E.) (n = 70) numbers of potential predators in soil samples from the field site at Aubigny, Manitoba, in the fall of 1992 and 1993.

	Number/0.1 m^2	
Taxon	1992	1993
Pterostichus corvus Lec.	0.04 ± 0.02	0.10 ± 0.05
Amara carinata Lec. larvae	0.11 ± 0.06	0.21 ± 0.10
A. obesa Say Larvae	0.30 ± 0.13	0.36 ± 0.13
unidentified carabid larvae	0.03 ± 0.03	0.03 ± 0.03
Total carabids	0.49 ± 0.15	0.70 ± 0.16
Cóllops sp. larvae	0.10 ± 0.07	0.10 ± 0.06
Centipedes	0.06 ± 0.04	0.13 ± 0.06
[1]Arachnids	0.09 ± 0.04	0.07 ± 0.04

[1]Arachnids = Harvestmen and spiders.

Feeding preference of *P. corvus* and *P. femoralis*

Both *P. corvus* and *P. femoralis* consumed a higher percentage of grasshopper eggs than of cat food (Table 10). *Pterostichus corvus* ate a significantly higher number of grasshopper eggs than *P. femoralis* in four days ($t = 8.598$; d.f. = 14; $P < 0.001$).

Table 10. Mean (± S.E) % of the original[1] number of grasshopper eggs and amount of cat food (Tender vittles®) eaten, and the mean (± S.E) number of eggs eaten in 4 days, in the laboratory.

Taxon	% of original amount eaten[2]		Number of eggs eaten[3]
	Grasshopper eggs	Cat food	
Pterostichus corvus	96.3 ± 2.6	6.0 ± 4.2	19.3 ± 0.5
P. femoralis	57.5 ± 3.7	0.0	11.5 ± 0.7

[2]N = 8; [3]N = 8.

[1]original number of grasshopper eggs was 20, and the amount of cat food was 0.8 g.

[2]Mean % of original amount of each food eaten by two beetles of each species in 4 days.

[3]Mean number of eggs eaten by two beetles of each species in 4 days.

Preferred depth of feeding of *P. corvus* on grasshopper eggs in the soil

In the two-way analysis of data from the treatment study (with beetles) and control study (without beetles), there was a significant effect of beetles ($F = 124.22$; $d.f = 1,48$; $P < 0.001$); this implies that the presence or absence of beetles had a significant effect on the number of eggs recovered. There was also a significant interaction between the presence of the beetles and depth ($F = 6.41$; $d.f = 2,48$; $P < 0.01$); examination of the data indicates that efficiency of recovery of eggs in controls was unaffected by depth (Table 11), so the interaction implies that the beetles fed at different intensities in the various soil depths.

In the one-way analysis of data from the terraria with beetles, there was a significant difference among the three soil depths, in the number of eggs eaten ($F = 13.81$; $d.f = 2,33$; $P < 0.001$) (Table 11). A significantly lower number of eggs was eaten at the surface as compared to the 2.5 and 5 cm depths ($F = 28.67$; $d.f = 1,33$; $P < 0.001$). However, there was no significant difference in the numbers eaten at the 2.5 and 5 cm depths ($F = 0.73$; $d.f = 1,33$; $P > 0.05$).

Table 11. Mean (± S.E) (n = 12) % of grasshopper eggs recovered, and number of eggs eaten from an original number of 20 at each soil depth, in terraria maintained at 16 : 8 h L : D, 20° C.

Depth (cm)	% of eggs recovered from terraria		No. of eggs eaten[1]
	With beetles	Without beetles	
0.0	77.0	100.0	4.6 ± 1.1
2.5	45.0	98.5	11.0 ± 0.4
5.0	50.5	99.0	9.9 ± 0.6

[1]Mean number of eggs eaten by two *P. corvus* adults.

Influence of ground cover on predation of grasshopper eggs by *P. corvus*.

There were significant effects of the three types of ground cover on the predation of grasshopper eggs (χ^2 = 82.4; d.f = 2; $P < 0.001$) (Table 12). A significantly greater number of eggs was eaten from the *Nicotiana* treatment than from the barley and bare treatments (χ^2 = 79.6; d.f = 1; $P < 0.001$). However, there was no significant difference in the number of eggs eaten between the barley and bare treatments, (χ^2 = 2.8; d.f = 1; $P > 0.05$)

Table 12. Mean (± S.E.) (n = 22) percentage of grasshopper eggs eaten by two *P. corvus* adults, from an original number of 15, in each of three types of ground cover, in the laboratory.

Ground cover	% of eggs
Nicotiana	40.3 ± 6.9
Barley	16.7 ± 4.2
Bare	12.2 ± 4.4

Influence of vegetation and some soil characteristics on the density of grasshopper eggs

None of the plant species contributed significantly to the variation in numbers of grasshopper eggs, among or within transects (Table 13). Also, none of the summary variables, crop, weed, broadleaf or grasses contributed significantly to the variation in numbers of grasshopper eggs among or within transects. Neither soil compaction, nor soil moisture contributed significantly to the variation in numbers of grasshopper eggs among or within transects (Table 14). Neither main vegetation effects, soil effects nor interactions contributed significantly to the variation in numbers of grasshopper eggs within transects (Table 15).

Table 13. Mean (± S.E.) (n = 70) % vegetative cover, and relationship with egg density[1], in the field site at Aubigny, Manitoba, in fall 1992.

Factor	% cover[2]	Relationship with egg density[1]	
		Among trans.[3]	Within trans.[4]
Wheat *Triticum aestivum* L.	16.0 ± 3.6	0.264	0.782
Canola *Brassica campestris* L.	6.1 ± 2.2	0.615	0.349
Flax *Linum utilatissimus* L.	2.8 ± 1.2	0.195	0.797
Curled dock *Rumex crispus* L.	14.6 ± 3.0	0.372	0.784
Yellow foxtail *Setaria glauca* L.	14.3 ± 3.7	0.944	0.810
Wild oats *Avena fatua* L.	4.5 ± 1.8	0.965	0.763
Smooth brome *Bromus inermis* L.	0.1 ± 0.1	0.313	0.809
Redroot pigweed *Amaranthus retroflexus* L.	0.2 ± 0.1	0.313	0.671
Crop[5]	24.8 ± 3.8	0.219	0.467
Weeds[6]	33.7 ± 4.7	0.581	0.794
Grasses[7]	34.9 ± 5.3	0.470	0.800
Broadleaf[8]	23.6 ± 3.4	0.470	0.439
Total cover[9]	58.5 ± 4.7	0.690	0.392

[1]Number of grasshopper eggs /0.1 m^2.
[2]Mean % vegetative cover in a an area of 0.1m^2.
[3] P-value, of relationship of each factor with grasshopper egg density, among transects.
[4]P-value, of relationship of each factor with grasshopper egg density, within transects.
([5]Crop = Wheat + canola + flax; [6]Weeds = Yellow foxtail + wild oats + smooth brome + redroot pigweed + curled dock; [7]Grasses = Wheat + yellow foxtail + wild oats + smooth brome; [8]Broadleaf = Canola + flax + redroot pigweed + curled dock; [9]Total cover = Grasses + broadleaf).

Table 14. Mean (± S.E.) (n = 70) of soil compaction and % soil moisture, and relationship with egg density[1], in the field site at Aubigny, Manitoba, in fall 1992.

Factor	Mean	Relationship with egg density[1]	
		Among transects[2]	Within transects[3]
Compaction (kg/cm^2)	1.2 ± 0.1	0.540	0.911
% moisture	32.5 ± 0.4	0.591	0.789

[1]Number of grasshopper eggs /0.1 m^2.
[2]P-value, of relationship of the soil factors, with egg density, among transects.
[3]P-value, of relationship of the soil factors, with egg density, within transects.

Table 15. Relationship of plant and soil factors with grasshopper egg density[1] in the field site at Aubigny, Manitoba, in fall 1992.

Factor	Relationship with egg density[1] within transects[2]
Weeds	0.884
Weeds * transect	0.947
Total cover	0.318
Total cover * transect	0.927
Compaction	0.970
Compaction * transect	0.997
% moisture * transect	1.000

[1]Number of grasshopper eggs / 0.1 m^2.
[2] P-value of relationship of each factor with egg density, within transects.

Determination of whether harvestmen feed on grasshopper eggs

There were 38 grasshopper eggs remaining, out of the original 40 eggs that were put in the box at the start of the experiment. Of the original five harvestmen, there was only one remaining at the end of the experiment, but it was dead.

Parasitism of grasshopper eggs

Scelionid wasps were the only parasitoids that were reared from the grasshopper eggs. Samples sent for identification were a mixture of *Scelio striativentris* Kieffer and *S. opacus* Provancher (Masner, personal communication). The percentage parasitism of the scelionid wasps, in 1992 and 1993 was 5.7% and 11.9% respectively.

DISCUSSION

Egg densities

The apparent underestimation of egg densities in the middle site in spring 1992 (Table 1), may be partly because grasshopper eggs have an aggregated distribution at the field (Spawn 1945; Davis and Wadley 1949; Putnam and Shklov 1956). For this reason, and especially under conditions of low grasshopper egg densities, soil sampling for eggs may sometimes give unreliable results on the density of eggs at the field. Edwards (1964) found that egg surveys did not give a reliable measure of the grasshopper population; he said that this was due to the aggregated nature of distribution of grasshopper eggs. Mukerji (!987) also had difficulty estimating grasshopper egg densities, due to the aggregated distribution of grasshopper eggs. The accuracy of results could be improved by taking large numbers of samples e.g. 40/transect. However, this could destroy the habitat of the predators to a great extent. Large sample sizes are also labour intensive, and very costly financially. This is the reason why a sample size of 10 per transect was used in the subsequent sampling periods.

A possible explanation for the higher egg densities in the spring of 1992 than in 1993 (Table 1), was due to the higher temperatures in the summer of 1991 as compared to that of 1992 (Appendix 1.). Low temperatures reduce the survival and fecundity of grasshoppers (Beirne 1972), resulting in low numbers of eggs the

following year. In 1992, oviposition did not start until late September, because of delayed development caused by low temperatures. As a result, the duration of oviposition before the fall frosts set in, was shorter than usual; this further contributed to the low egg densities in spring 1993. Paul et al. (1943) found that the development of grasshopper eggs and commencement of oviposition were greatly delayed by the cool wet environmental conditions that prevailed in 1942.

The wet conditions in the summer of 1992, accompanied by the low air temperatures (Appendix 1), may have reduced the soil temperatures considerably, making them unfavourable for oviposition. Soil temperatures must be above 20°C for oviposition in *M. bivittatus* to occur (Philip and Mengersen 1989).

Cool wet conditions, such as those in spring and summer of 1992 and 1993, favour fungal pathogens of grasshoppers (Pickford and Riegert 1964). In the summer of 1992, there were heavy grasshopper mortalities due to high infection rates by the fungal pathogen *Entomophthora* spp. (Personal observation). This further contributed to the reduction of egg densities in the spring of 1993. *Entomophthora* spp. were responsible for the reduction in abundance of *M. bivittatus*, in Saskatchewan, in 1950, 1951, 1954 and 1966 (Riegert 1968).

Grasshoppers generally prefer ovipositing on bare ground with sparse vegetation (Dempster 1963). The prolonged wet conditions in the spring and summer of 1993 enhanced the growth of dense vegetation along the field margins. This reduced the availability of suitable sites for oviposition along the field margins, hence resulting in even lower egg densities in fall 1993. Paul et al. (1943) found

that there was a much greater proportion of oviposition toward the field margin in 1942 than usual. They attributed this to the cool wet weather and the very dense crop growth that year.

Potential predators

Of the two methods used to determine the occurrence of potential predators of grasshopper eggs, quadrat sampling was unsatisfactory. This was due to the small numbers of potential predators recovered (Table 8 and 9), and to the destruction of the habitat of the potential predators that necessarily occurred. The small numbers in the soil samples may have been due to escape of the surface active arthropods from the sampling area in the process of sampling. It is also possible that some species may have been deeper than the depth that the quadrat could reach (i.e 6 cm). Richardson and Holliday (1982) were unsuccessful in assessing carabid beetle populations by soil sampling.

Pitfall trap catches depend on the population size and locomotor activity (Mitchell 1963; Greenslade 1964) of the arthropods. Baars (1979) showed that there were higher captures in areas with unfavourable habitats; he suggested that this was due to the increased activity of the beetles in such habitats. Dense vegetation reduces the actvity of carabid beetles by offering resistance to their movement, as a result it reduces the number of captures of the carabids (Greenslade 1964). Temperature (Luff 1982) and humidity (Rivard 1966; Kirk

1974) influence the number of carabids captured in pitfall traps.

The occurrence of an arthropod in a given area is also influenced by availability of its food. For this reason, polyphagous arthropods may have a wider distribution than monophagous ones. Although polyphagous predators feed on many types of prey, they usually prefer feeding on the most prevalent type of prey, in a given site (Luff 1983). For this reason, the frequent occurrence of a polyphagous predator in a given site, may give an indication of the abundance of a particular known prey in that site.

Greater total numbers of carabid beetles were caught in the springs of 1992 and 1993 (Table 3), than in the fall of 1992 and 1993 (Table 4). This may be due to the higher temperatures in the spring than in the fall of the two years (Appendix 1.). High temperatures are associated with increased activity of carabid beetles (Mitchell 1963), resulting in more being trapped. Luff (1982) found that there was a significant positive correlation between temperature and activity of the carabid *Harpalus rufipes* De Geer.

Another possible explanation for the smaller total number of carabids in the fall of 1992 and 1993, is that rainfall was high in the summer of the two years, especially in 1993 (Appendix 1). The prolonged heavy rainfall enhanced the growth of dense vegetation along the field margins. This vegetation may have reduced the activity of the carabids, hence reducing the total number captured. Dense vegetation offers more resistance to the movement of carabid beetles than bare ground; this results in fewer beetles being caught in areas with dense

vegetation (Rivard 1965; Greenslade 1964; Baars 1979).

Another possible reason for the greater total number of carabids in the spring of 1992 and 1993, is the life cycle of the predominant carabid species, *P. corvus*. *Pterostichus corvus* is most probably a spring breeder; spring breeders oviposit in the spring, and overwinter as adults (Larsson 1939). The presence of *P. corvus* adults in soil samples taken in the spring and fall of 1992 and 1993 (Tables 8 and 9) accords with the hypothesis that *P. corvus* is a spring breeder. Spring breeders are most active in the spring and early summer, while searching for mates, hence greater numbers are caught during this period than in the fall. As in my study, Richardson (1982), at Glenlea, Manitoba, caught more *P. corvus* adults in the spring than later in the year. The numbers of *P. lucublandus* in springs of 1992 and 1993 were higher than in the fall. This is because *P. lucublandus* is a spring breeder (Lindroth 1966).

In spring 1992, sites (which also represented relative densities of grasshopper eggs) contributed significantly to the variation in catches of *P. corvus* and *P. lucublandus* among transects (Table 5). This may be because spring 1992 had higher grasshopper egg densities than the other seasons (Table 1 and 2).

In the spring of 1992, there were significantly smaller numbers of *P. corvus* and *P. lucublandus* in the South site (with low egg densities), than in the middle and North sites (with intermediate and high egg densities respectively) (Figs. 6 and 7). A possible reason is that these species prefer similar sites as ovipositing grasshoppers. It is also possible that *P. corvus* and *P. lucublandus* feed on

grasshopper eggs, and their populations are influenced by grasshopper egg populations.

Because carabid beetles are polyphagous (Sunderland 1975), there may be a threshold population of grasshopper eggs below which the carabids lose interest in grasshopper eggs and switch to other more prevalent prey. If this hypothesis is correct, then the low number of *P. corvus* and *P. lucublandus* adults caught at the South site may be because the egg populations were below the threshold population for carabid feeding on grasshopper eggs. The lack of a significant difference in the numbers of *P. corvus* and *P. lucublandus* between the middle and North sites may be because, as long as the grasshopper egg populations are above a certain threshold, any further increase in egg populations, does not make much difference to the feeding behaviour of carabid beetles. In a field study in southeast Saskatchewan, Brown and Paul (1943) found that populations of *M. sanguinipes* egg pods have a greater influence on the predators than does weather. In a survey, Brown and Paul (1943) suggested that, above an egg pod density of 0.3-0.4 / ft^2 (0.03-0.04 / m^2) in stubble, numbers of blister beetle, bee-fly and carabid larvae, are low, while above this level, the predator numbers are high.

The absence of a significant contribution of grasshopper egg densities to the variation in catches of *P. corvus* and *P. lucublandus* among transects in spring 1993 (Table 6), may be due to the low egg densities in that season (Table 1). The egg numbers in all the transects may have been below the threshold population for carabid feeding on grasshopper eggs, resulting in a general low level of carabid

actvity in all the transects. Lack of a relationship between catches of these two carabid species and grasshopper eggs may also be due to variation of microhabitat factors such as vegetation. Microhabitat conditions influence the populations of various species of carabids, to different extents (Thiele 1977).

Catches of *P. femoralis* were higher in the fall of both 1992 and 1993 (Table 4), than in the spring (Table 3). However, the differences in catches between the spring of 1992 and 1993, and fall were very small. The presence of *P. femoralis* adults in soil samples in the spring implies it is probably a spring breeder. Grasshopper egg densities did not contribute significantly to the variation in catches of *P. femoralis* among transects in spring 1993 (Table 6), possibly due to the low egg densities in that season. It is also possible that *P. femoralis* occurence is not influenced by grasshopper eggs. If it were, a relationship would have been detected in the spring of 1992, when egg densities were higher.

The numbers of *Amara obesa* and *Amara carinata* were higher in the fall of both 1992 and 1993 (Table 4), than in the spring (Table 3). This is because these two species are autumn breeders (Lindroth 1968). Autumn breeders oviposit in the fall, and overwinter as larvae (Larsson 1939). This explains the presence of larvae of *A. obesa* and *A. carinata* in samples taken in fall of 1992 and 1993.

Grasshopper egg densities did not contribute significantly to the variation of catches of *A. obesa* and *A. carinata* among transects in fall of 1992 (Table 7). This may be due to the low grasshopper egg densities (Table 2), or the low numbers of these carabid species trapped in the fall of 1992 (Table 4). It is also

possible that these two species are not important predators of grasshopper eggs. This is because even though adults of *Amara* species are polyphagous like other carabids, they are more phytophagous than carnivorous (Thiele 1977).

Numbers of the carabid beetles *Chlaenius sericeus, Calosoma calidum* and *Agonum placidum*, were higher in the spring of both 1992 and 1993 (Table 3) than in the fall (Table 4). This is because *C. calidum* (Lindroth 1961), *A. placidum* (Lindroth 1966) and *C. sericeus* (Lindroth 1969) are all spring breeders. In spring of 1992, sites (which also represented relative densities of grasshopper eggs) did not contribute significantly to the variation in catches among transects of any of these three carabid species (Table 5). It is possible that these carabid species are not important predators of grasshopper eggs. This is because, when grasshopper egg populations were high in spring 1992, I would have expected a relationship.

The same soil samples were used in the assessment of grasshopper egg densities and occurrence of potential predators of the eggs. The presence of carabid larvae and adults in the soil samples (Table 8 and 9) is evidence that carabids occur in similar sites as grasshopper eggs. Smith (1965) found carabid larvae in close association with grasshopper eggs in grasshopper egg beds in the field. He suggested that the carabids were feeding on the grasshopper eggs. The carabid *A. obesa* was reared from grasshopper eggs from several places in Manitoba (Bird pers. comm. in Lindroth 1968). Clearly carabid larvae occur in close association with grasshopper eggs; there is however need for studies to provide information on the predation of carabid larvae on grasshopper eggs.

The numbers of arachnids were higher in the spring of 1992 and 1993 (Table 3) than in the fall (Table 4). The arachnids which consisted of two groups of arthropods: harvestmen and spiders, were not identified to species level. However, it is possible that the predominant species of harvestmen (which comprised a large proportion of the arachnids), breeds and is most active in the spring. In spring of 1993, egg densities contributed significantly to the variation in catches of arachnids among transects (Table 6), and a high proportion of the arachnids were harvestmen. At present, there is no information about whether harvestmen feed on grasshopper eggs. Therefore, there is no certainty as to whether the observed relationship is real, or just a consequence of the effect of other factors such as the microhabitat conditions. Most harvestmen feed mainly on plant juices and dead insects; but a few also feed on live insects (Borror et al. 1977).

The numbers of staphylinids were higher in the spring of 1992 and 1993 (Table 3) than in the fall (Table 4). The staphylinids were not identified to species level; however, it is possible that the predominant staphylinid species among the ones trapped, breeds and is most active in the spring. In spring of 1993, grasshopper egg densities did not contribute significantly to the variation in catches of staphylinids among transects (Table 6). This implies that grasshopper egg populations do not influence the occurence of staphylinids in the field. Even though staphylinids are one of the important polyphagous predators of insect pests at the field (Sunderland 1975), there is no information on whether they feed on

grasshopper eggs. It may be useful to conduct studies on predation of staphylinids on grasshopper eggs.

The number of crickets in the fall of 1992 and 1993 (Table 4) was greater than in the spring (Table 3). This is because the predominant species, *Gryllus pennsylvanicus* matures in late summer, and the adults are most abundant and active in the fall, which is their breeding season. Grasshopper egg densities did not contribute significantly to the variation in catches of crickets in the fall of 1992, despite the high abundance of crickets that season (Table 7). Although crickets feed on grasshopper eggs (Beirne 1972), I do not expect them to be important mortality factors of grasshopper eggs. This is because, though they are omnivorous, they mainly feed on plant material e.g flax bolls (Beirne 1972).

I think predators in the spring have a higher potential for predation of grasshopper eggs than in the fall. This is because temperatures in the spring are higher than in the fall; high temperatures increase the rate of feeding in most arthropods (Mitchell 1963). In the laboratory, adults of the carabid *Abax ater* Vill., do not feed at temperatures below 6°C; they feed at temperatures above 7°C, and feeding increases with temperature between 7°C and 15°C (Khalid et al. 1993).

Spring also offers a longer period for predation of grasshopper eggs than the fall. This was especially so during the period of this study. The cool summer temperatures in 1992 and 1993, retarded the rate of development of grasshoppers, resulting in late commencement of oviposition. This reduced the period for predation of grasshopper eggs in fall of 1992 and 1993. Because of the foregoing

reasons, the most prevalent potential predator species in the spring, *P. corvus*, had the greatest potential of influencing grasshopper populations in the field.

Feeding preference of *P. corvus* and *P. femoralis*

Both *P. corvus* and *P. femoralis* ate a higher percentage of grasshopper eggs than cat food, implying that these two species preferred grasshopper eggs to cat food. Clearly, *P. corvus* prefers grasshopper eggs to cat food, because it has been previously maintained successfully on cat food alone for as long as 3 months. *Pterostichus corvus* appears to be an avid consumer of grasshopper eggs, as it ate 96.3% of the original number of eggs in 4 days (Table 10).

Pterostichus corvus appears to be a voracious predator; for example, Floate et al. (1990) found that, of four species of carabids studied, *P. corvus* consumed the highest number of wheat midge larvae per day in the laboratory. A follow up study on the predation of grasshopper eggs, in the presence of a wider prey choice including e.g aphids (which are a common prey of carabid beetles at the field (Sunderland and Vickerman 1980)), may provide additional information on the potential of *P. corvus* as a predator of grasshopper eggs at the field.

Preferred depth of feeding of *P. corvus* on grasshopper eggs in the soil

There was a significant effect of beetles, and also a significant interaction between beetles and the soil depths at which the eggs were found. This confirms

that it is the beetles rather than variable recovery efficiency that caused variation in number of eggs recovered at different depths in the study with beetles.

Pterostichus corvus preferred to feed below the soil, to depths up to 5 cm (Table 11). Most of the major grasshopper species in North America lay their eggs no deeper than 5 cm in the soil (Spawn 1945; Philip and Mengersen 1989). *Pterostichus corvus* may be able to locate grasshopper eggs at the depths they occur in the field. A possible reason why *P. corvus* preferred to feed below the soil surface, may be that the soil provided better shelter than the surface of the soil. Also, carabid beetles are positively thigmotactic (Thiele 1977).

Influence of ground cover on predation of grasshopper eggs by *P. corvus*

A significantly higher percentage of grasshopper eggs was eaten from the *Nicotiana*, than from the barley and bare sections (Table 12). The higher predation in the *Nicotiana* section may have been because it offered a more favourable environment for the beetles in terms of shelter. This may have resulted in the beetles spending more time in the *Nicotiana* section than in the other sections. Undersowing Brassicas with clover increases predation of larvae of the butterfly *Pieris rapae* L.. This is possibly due to the additional cover provided for the carabid *H. rufipes* and the harvestman *Phalangium* spp. (Dempster and Coaker 1974). There is a higher number of predatory ground beetles, and a significantly greater predation of *Drosophila* pupae in areas where the ground covering grassy

weed *Poa annua* L. is abundant, than where it is scarce (Speight and Lawton 1976). This is possibly because the areas of high densities of *P. annua* offer a more suitable environment for the beetles (Speight and Lawton 1976).

Another possible explanation for the lower predation in the bare section, is that it was unfavourable for the beetles; as a result the beetles spent more time searching for a more favourable environment, and hence had less time to settle down and feed in the bare section. Baars (1979) showed that carabid beetles are more active in unfavourable habitats. Open areas are unfavourable to carabids, due to the lower humidity as compared to vegetated areas (Rivard 1966; Kirk 1974; Speight and Lawton 1976). Greenslade (1964) found that carabid beetles are more active in areas that offer least resistance to their travel, e.g bare ground.

Influence of vegetation and some soil characteristics on the density of grasshopper eggs

Lack of a significant contribution of any of the plant species, plant types, soil compaction and soil moisture, to the variation of grasshopper egg densities (Table 13, 14 and 15), could be largely due to the prolonged cool wet conditions of 1992 (Appendix 1). Cool wet conditions are unfavourable for grasshopper survival and fecundity, consequently leading to low egg populations (Beirne 1972; Philip and Mengersen 1989). The resulting low grasshopper egg populations increase the difficulty of detecting any existing relationships.

There was no relationship between vegetative ground cover by any plant species, and grasshopper egg densities (Table 13), and hence grasshopper oviposition. This is contrary to what I had expected. I would have expected to see a decrease in density of eggs, with an increase in percentage vegetative cover. Most grasshopper species prefer to oviposit on bare ground within sparse vegetation (Dempster 1963).

Assessment of the various parameters in this study was conducted in October (because this is around the time when oviposition terminated). By this time, most of the weeds along the field margins had dried and lost their leaves. The vegetative cover in late August and September was much denser than at the end of October when the assessment was done. For this reason, there may have been an underestimation of the vegetative ground cover; this error may have increased the difficulty of detecting any existing relationships with grasshopper egg populations. However in warm years, oviposition begins much earlier, when plants would have many leaves.

Soil compaction also had no relationship with grasshopper egg densities (Table 14), and hence grasshopper oviposition. I had expected to see a decrease in egg densities as the soil compaction decreased. This is because the major grasshopper species in the Red River Valley, *M. bivittatus*, prefers to oviposit in compacted soil; it does not prefer soils that have been recently loosened through e.g cultivation (Spawn 1945).

Melanoplus bivittatus, which is the predominant grasshopper species in the

Red River Valley of Manitoba (Putnam 1953), prefers to oviposit in moist conditions (Beirne 1972; Vickery and Kevan 1985). This species requires a minimum soil moisture of 10-20% for egg laying to occur (Philip and Mengersen 1989). Since the average soil moisture of the soil samples in this study was 32.5% (Table 14), it is likely that all the sites had adequate soil moisture for oviposition. Above the minimum required soil moisture, I would not expect a significant increase in oviposition with increase in soil moisture. This may explain the absence of a relationship between grasshopper egg densities and soil moisture at the sites. A relationship may have been detected if the soil moisture in some of the sites was less than the required minimum soil moisture of 10-20%.

Determination of whether harvestmen feed on grasshopper eggs

Harvestmen do not appear to prefer feeding on grasshopper eggs; this is because, of the original 40 eggs put in the box, 38 were recovered after 11 days. Therefore the harvestmen only ate 2 grasshopper eggs. The absence of four of the original five harvestmen, may have been due to cannibalism. Most harvestmen feed on plant juices and dead insects (Borror et al. 1977); it is possible that the harvestmen preferred cannibalising on each other, instead of feeding on grasshopper eggs.

Parasitism of grasshopper eggs

Scelionid wasps were the only parasitoids that were reared out of the grasshopper eggs, and the scelionids *Scelio opacus* (= *calopteni*) and *S. striativentris* occurred at the study site. The percentage parasitism was generally low in the two years. These results are similar to the ones obtained by Moore (1945) and Putnam (1953). They found that the percentage parasitism of grasshopper eggs by scelionids was generally low in various parts of western Canada; it was usually less than 5% and occasionally 10-15%.

A possible reason for the low parasitism may be that *Scelio* sp. is univoltine (Criddle 1921) and has only one generation to that of its host; as a result, the parasitoids have a delayed effect on the population of grasshopper eggs. This delayed density dependence of the parasitoids may be the reason why the rate of parasitism was higher in 1993, when the density of grasshopper eggs was lower. Another possible explanation for the low parasitism in spring 1992 and 1993, may be poor synchrony between emergence of the parasitoids, and oviposition by the host grasshoppers (Mukerji 1987).

Application in pest management

There is a limited information in the literature on the indigenous predators and parasitoids of grasshoppers eggs in North America. Additional information is required; this would provide basic information for the development of a biological

control programme for grasshoppers in North America.

The study demonstrated that *Pterostichus corvus* was the most prevalent indigenous potential predator of grasshopper eggs in the field sites at Aubigny, Manitoba. *Pterostichus corvus* could also eat and locate grasshopper eggs at the depths they occur at the field. Therefore *P. corvus* is a promising predator of grasshopper eggs. Future studies on predators of grasshopper eggs, should therefore be focused on the extent of predation of grasshopper eggs by *P. corvus* in the field.

This study showed that *Pterostichus corvus* fed on a higher number of grasshopper eggs in areas with dense vegetative cover in the laboratory. This may have been partly because the dense vegetative cover provided better shelter for the beetles. The effectiveness of most native natural enemies could be improved through conservation of their populations (Greathead 1992), which involves the utilisation of management practices to enhance the existing natural enemies (Bernays 1984). An example is through provision of shelter (Desender et al. 1981).

Since there is a higher potential for predation of grasshopper eggs in the spring, predation of grasshopper eggs by *P. corvus* could be improved by sowing a fast establishing, broad leaf plant species, along crop field margins, very early in the spring. Since eggs of *M. bivittatus* are concentrated along the field margins (Spawn 1945; Vickery and Kevan 1985; Philip and Mengersen 1989), establishment of a dense vegetative cover along field margins, would enhance

activity of *P. corvus* in the sites of highest concentration of grasshopper eggs.

The study showed that scelionid wasps were the only parasitoids of grasshopper eggs, at the study site at Aubigny, Manitoba. However the percentage parasitism was quite low. The effect of these parasitoids, though small when considered singly, is still important because it contributes to the various factors that help to suppress grasshopper populations. The percentage parasitism by scelionids may possibly be improved by enhancing populations of this parasitoid in areas of highest concentration of grasshopper eggs. *Scelio* spp. prefer moist habitats with short vegetation, partly because these habitats provide protection from extreme temperatures (Irshad et. al. 1978). Establishing vegetation along crop field margins may enhance populations of *Scelio* spp., in sites where grasshopper eggs are concentrated.

Vegetative ground cover, soil moisture and soil compaction had no relationship with egg densities. The absence of any relationships may be partly due to the very low egg densities in the fall of 1992. A similar long term study during years of high grasshopper populations may provide more useful information that can be used in the management of grasshoppers.

CONCLUSIONS

1. *Pterostichus corvus* appears to be a promising predator of grasshopper eggs because it was prevalent in the spring, and it had a significant relationship with relative densities of grasshopper eggs in the spring of 1992. It also ate and located grasshopper eggs at the depths at which they occur in the field.
2. Increased ground cover resulted in, increased predation of grasshopper eggs by *P.corvus* in the laboratory.
3. Harvestmen fed little on grasshopper eggs in the laboratory.
4. The percentage parasitism of grasshopper eggs by scelionid wasps at Aubigny, Manitoba was low.
5. Percentage ground cover, soil moisture and soil compaction, did not appear to influence grasshopper egg populations. The absence of any relationship was largely attributed to the particulary low egg populations in the fall of 1992, when the sampling was done.

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Appendix 1. Mean temperatures (°C ± S.E), and total precipitation at the University of Manitoba Field Station at Glenlea[1].

Year	Season	Temperature (°C)	Total precipitation (mm)
1991	Summer	18.6 ± 0.4	229.6
	Fall	3.0 ± 0.9	123.0
1992	Spring	8.5 ± 0.9	146.7
	Summer	14.8 ± 0.4	258.6
	Fall	5.7 ± 1.0	7.0
1993	Spring	8.2 ± 0.8	104.8
	Summer	16.0 ± 0.4	463.8
	Fall	4.7 ± 0.7	45.6
1961-1990	Spring	7.6 ± 2.0	158.1
	Summer	17.5 ± 0.6	204.3
	Fall	6.1 ± 1.1	59.8

Spring = March 21 - June 20.
Summer = June 21 - September 20.
Fall = September 21 - October 31.
[1]Glenlea is about 20.8 Km north of Aubigny.

Appendix 2. Total numbers of arthropods caught in pitfall traps, in the field site at Aubigny, Manitoba, in Spring 1992.

Taxon	Number
Pterostichus corvus Leconte	4949
Pterostichus lucublandus Say	107
Pterostichus femoralis Kirby	54
Chlaenius sericeus Forster	677
Chlaenius tomentosus Say	1
Chlaenius purpuricollis Randall	2
Calosoma calidum Fabricius	131
Calosoma lepidum Leconte	2
Harpalus herbivagus Say	7
Harpalus amputatus Say	4
Harpalus paratus Casey	1
Harpalus fulvilabris Mannerheim	2
Agonum placidum Say	60
Agonum cupreum Dejean	4
Platynus decentis Say	3
Amara obesa Say	10
Agonum corvus Leconte	10
Amara farcta Leconte	12
Amara carinata Leconte	20
Anisodactylus sanctaecrusis Fabricius	3
Brachinus fulminatus Erwin	2
Total carabids	6061

Appendix 2 Continued.

Taxon	Number
Staphylinids	42
Arachnids	384
Crickets	19
Cóllops sp. larvae	3
Millipedes	85
Noctuid larvae	125

Appendix 3. Total numbers of arthropods caught in pitfall traps in the field site at Aubigny, Manitoba, in Spring 1993.

Taxon	Number
Pterostichus corvus Leconte	3137
Pterostichus lucublandus Say	188
Pterostichus femoralis Kirby	138
Pterostichus melanarius Illiger	38
Chlaenius sericeus Forster	223
Calosoma calidum Fabricius	71
Harpalus herbivagus Say	14
Harpalus amputatus Say	1
Harpalus pensylvanicus De Geer	11
Agonum placidum Say	160
Agonum cupreum Dejean	58
Platynus decentis Say	4
Amara obesa Say	81
Agonum corvus Leconte	2
Amara farcta Leconte	2
Amara carinata Leconte	22
Amara littoralis Mannerheim	8
Anisodactylus sanctaecrusis Fabricius	10
Total carabids	4168
Staphylinids	103
Arachnids	7083
Centipedes	12
Millipedes	137
Noctuid larvae	20

Appendix 4. Total numbers of arthropods caught in pitfall traps in the field site at Aubigny, Manitoba, in Fall 1992.

Taxon	Number
Pterostichus corvus Leconte	289
Pterostichus lucublandus Say	18
Pterostichus femoralis Horn	32
Chlaenius sericeus Forster	2
Pterostichus melanarius Illiger	19
Calosoma calidum Fabricius	6
Harpalus pensylvanicus De Geer	8
Agonum placidum Say	11
Agonum cupreum Dejean	13
Amara obesa Say	113
Agonum corvus Leconte	7
Amara farcta Leconte	1
Amara carinata Leconte	138
Amara littoralis Mannerheim	1
Amara apricaria Paykull	3
Anisodactylus sanctaecrusis Fabricius	4
Total carabids	666
Staphylinids	38
Arachnids	1740
Crickets	4359
Centipedes	2
Millipedes	19
Noctuid larvae	6
Click beetles	3

Appendix 5. Total numbers of arthropods caught in pitfall traps in the field site at Aubigny, Manitoba, in fall 1993.

Taxon	Number
Pterostichus corvus Leconte	156
Pterostichus lucublandus Say	11
Pterostichus femoralis Horn	225
Pterostichus melanarius Illiger	8
Chlaenius sericeus Forster	2
Harpalus herbivagus Say	4
Agonum placidum Say	45
Agonum cupreum Dejean	31
Amara obesa Say	35
Agonum corvus Leconte	76
Amara farcta Leconte	2
Amara carinata Leconte	5
Total carabids	600
Staphylinids	30
Arachnids	172
Crickets	28
Centipedes	8
Millipedes	74
Noctuid larvae	11