INTERACTIONS AMONG ASSEMBLAGES OF GROUND BEETLES (COLEOPTERA: CARABIDAE) IN NATURAL AND AGROECOSYSTEMS

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CHAPTER I

INTRODUCTION

The Great Plains formerly was a vast area of grasslands stretching from Canada to Texas and from the Rocky Mountains to the eastern deciduous forests. The grasslands of the Great Plains changed longitudinally from the eastern tall grass prairies to the central mixed grass prairies to the western short grass prairies (Kaul 1986). The original boundaries of these grasslands were determined by edaphic and environmental factors. Intermingled with the grasslands of the Great Plains are rivers and their associated riparian habitats. These riparian habitats also provided natural boundaries among the grasslands.

Species of Carabidae that occurred in the Great Plains before European settlement could perhaps disperse for many kilometers before confronting a barrier such as a river. However, due to intensification of agriculture, the region is now a mosaic of agricultural crops, pastures, riparian zones, and relict grasslands in which insects may disperse only several meters before confronting a barrier such as a radical change in habitat. By fragmenting the Great Plains into a mosaic of agricultural and other ecosystems, European settlers significantly increased the ratio of habitat borders to habitat patch size. Populations of Carabidae could respond to this decrease in size of ecosystems and increase in habitat borders in three ways: 1) no effect; ground beetles easily traverse borders to colonize suitable habitat patches, 2) positive effect; population levels increase, perhaps due to their ability to exploit a range of available habitats and borders, 3) or negative effect; numbers decrease due to isolation of small populations by borders acting as barriers to dispersal.

Little is known about the effects of habitat borders on dispersal of Carabidae in the Southern Great Plains. This study is designed to determine which species of ground beetles are affected by borders of contiguous wheat fields and grasslands and contiguous wheat fields and riparian habitats. Because ground beetles are economically important predators of agricultural pests, knowledge of how they are affected by landscape structure may provide insight into future farm management practices.

Because ground beetles are polyphagous predators of many agricultural pests, it is critical that we understand the effects of farming practices on their species abundance and diversity. Little is known about the effects of farming practices on assemblages of Carabidae in the Southern Great Plains. In addition, farmland removed from agricultural production and enrolled in the Conservation Reserve Program will inevitably revert back to agricultural production. It is important to understand the effects on ground beetle assemblages of returning farmland to agricultural production. This study is designed to determine which species of ground beetles are affected by farm management practices in the Southern Great Plains. Because highly erodible crop lands may lose considerable top soil to conventional farming practices, knowledge of how ground beetles are affected by farming practices will provide insight into future farm management procedures.

Conventional farming practices often have detrimental effects on beneficial insects while creating favorable conditions for pest species. A means of improving pest regulation by beneficial organisms is to provide the natural enemies suitable habitat through farm management practices. Native habitat managed properly with agricultural ecosystems may encourage sufficient numbers of natural enemies to control pest outbreaks. Ground beetles, for example, are polyphagous predators and are found worldwide, but improperly managed habitats often keep their numbers low, and consequently limit their ability to control outbreaks of agricultural pests. By providing dispersal corridors for ground beetles and other polyphagous predators into arable fields, farmers may reduce the risk of pest outbreaks. These predators have been studied extensively in Europe to assess their ability to control aphid populations in wheat and other cereals. In North America, ground beetles have been studied in the midwest and Northern Great Plains, but little research has focused on their assemblages in the Southern Great Plains.

My overall goal is to determine effects of native habitat and farm management practices on ground beetle assemblages and dispersal among ecosystems. There are three objectives of my research: 1) determine the temporal and spatial dynamics of ground beetle assemblages in wheat fields bordered by grasslands and riparian habitats. 2) describe the interactions among species of ground beetles in grassland and riparian ecosystems and adjacent wheat fields. 3) assess the effects of farm management practices on ground beetle assemblages.

CHAPTER II

REVIEW OF THE LITERATURE

Ground Beetles in Agricultural Landscapes

Ground beetles are polyphagous predators that prey on a variety of agricultural pests. At high population densities aphids (e.g., *Schizaphis graminum* Rondoni) inflict serious damage to crops and can significantly reduce yield (Nemec and Stary 1984, Stary and Gonzalez 1991). Aphids become economic pests when introduced into areas where their host is abundant (e.g., agricultural crops) and natural enemies are rare or absent. Ground beetles include aphids in their diets (Thiele 1977, Edwards et al. 1979, Scheller 1984, Griffiths et al. 1985, Chiverton 1987, Winder 1990), and aggregate where aphid population densities are high (Sunderland and Vickerman 1980, Bryan and Wratten 1984). Because ground beetles aggregate at high aphid population densities, they assist in keeping aphid numbers below economically damaging levels (Potts and Vickerman 1974, Winder 1990, Ekbom et al., 1992, Holopainen and Helenius 1992).

Ground beetles vary in their ability to traverse habitats and habitat borders. Borders separating ecosystems may serve as corridors to enhance dispersal or as barriers to dispersal. In agroecosystems, several studies have focused on the ability of ground beetles to disperse through or along hedgerows (Burel 1989), windbreaks (Sustek 1992), forests (Wallin 1985, 1987), pastures or grasslands (Esau and Peters 1975, Gravesen and Toft 1987, Duelli et al. 1990), and grassy strips placed within crop fields (Desender and Alderweireldt 1988, Dennis and Fry 1992, Thomas et al. 1992a, 1992b, Frampton et al. 1995).

Wheat fields, grasslands or pastures, and riparian zones are prominent features in northcentral Oklahoma agricultural landscapes. These ecosystems, along with their borders, form landscape elements that potentially accommodate a variety of ground beetle species. In Sweden, species and numbers of ground beetles vary spatially and temporally in relation to cereal fields (Wallin 1985). The spatial and temporal relationships among ground beetle species in agricultural landscapes in the Southern Great Plains have not been investigated and represent one focus of this study.

Cropping Systems and Ground Beetles

The loss of topsoil due to water and wind erosion is of major concern worldwide (Pimentel et al. 1995). Arid regions are the most susceptible to soil erosion due to low levels of annual precipitation and high wind velocities. In the United States, the Conservation Reserve Program (CRP) of the 1985 Food Security Act was employed in an attempt to reduce the amount of topsoil lost from these lands. This program takes land out of agricultural production for 10 years while it is seeded to native and imported grasses. In Oklahoma, 0.5 million ha (1.2 million acres) are enrolled in CRP, most of which was formerly cropped annually with winter wheat. Anticipated changes in federal farm programs will significantly reduce the acreage in the CRP and bring this land back into agricultural production.

Conventional tillage practices increase erosion and can have significant effects on the way species occupy various habitats. The frequent plowing of the soil removes all vegetative residue from the ground, and consequently disrupts the life cycles of many species. Conservation tillage practices consist of leaving some residue on the soil, so-called reduced or minimum tillage. Another conservation practice is to leave all the crop residue in place and to sow the following year's crop into the residue. Stinner and House

(1990) review the effects of conservation tillage practices on various groups of arthropods and other invertebrates.

Farm management practices range from systems involving extensive use of chemical fertilizers and pesticides to “organic” where only organic fertilizers and biological controls are used. Pesticide use has been demonstrated to reduce populations of ground beetles (Barney et al. 1984, Purvis and Curry 1984, Hokkanen and Holopainen 1986, Kromp 1989, Carcamo et al. 1995). For example, Kromp (1989) found that abundances or numbers of ground beetles were higher in organically treated wheat fields than in conventionally treated wheat fields. Carcamo et al. (1995) also found that species abundance and species richness were higher in organically treated agroecosystems than in conventionally treated agroecosystems.

The effects of conventional (plowing) and conservation (minimum tillage or no tillage) tillage practices on species diversity and abundances of ground beetles have been widely studied (Tyler and Ellis 1979, Dritschilo and Wanner 1980, Barney and Pass 1986, Wiess et al. 1990, Laub and Luna 1992, Tonhasca 1993, Carcamo et al. 1995). Ground beetle diversity often increases with decreased tillage (Stinner and House 1990). In contrast, no change in ground beetle diversity or abundance may occur with decreased tillage (Barney and Pass 1986). In the Northern Great Plains, ground beetle diversity and abundance were reduced more by crop rotations than by tillage practices (Wiess et al., 1990). The goal of my project is to determine the effects of farming practices on ground beetle assemblages in the Southern Great Plains.

Natural History of Ground Beetles

Carabidae is a diverse family of Coleoptera comprising approximately 40,000 species worldwide (Lövei and Sunderland 1996). Ground beetles complete one or two generations each year, and are often classified as spring breeders or fall breeders. As adults, these insects are primarily ground dwellers (epigeal), however some species are subterranean (hypogeal) and others are arboreal. They are found in many types of ecosystems including grasslands, temperate forests, tropical forests, riparian zones, agricultural, and urban (Lenski 1982, Cockfield and Potter 1985, Wallin 1986, Gravesen and Toft 1987, Nilsson et al. 1988, Spence and Spence 1988, Epstein and Kulman 1990, Villalobos and Lavelle 1990, Andersen and Skorping 1991, Holliday 1991, Morrill 1992, Niemela et al. 1992, Braman and Pendley 1993, Sparks et al. 1995). Ground beetles are classified as either habitat generalists or specialists (Thiele 1977). Habitat generalists are found in different types of ecosystems and are not as restricted in their dispersal among differing landscape elements as habitat specialists, but still may prefer certain habitats over others. For example, in Belgium, *Clivina fossor* L. and *Pterostichus vernalis* Panzer vary seasonally in the amount of time spent in pasture borders and pastures (Maelfait et al. 1988). Their population levels change among habitats usually through dispersal, which ground beetles generally accomplish by walking. However, Matalin (1994) showed that sexually immature *Stenolophus* spp. made dispersal flights up to 200 meters.

Factors Affecting Ground Beetle Dispersal

Morphology of Carabidae

Ground beetle dispersal may be dictated by hind wing anatomy (den Boer 1971, 1977, Carter 1976). Brachypterous ground beetles (short or vestigial hind wings) are limited to walking. Other ground beetles are macropterous, possessing hind wings that are functional for flight, and can disperse by walking or flying. These characteristics are not always consistent within species in that a single species may be dimorphic or polymorphic for hind wing development. In addition, hind wing length may vary between males and females. In *Agonum retractum* LeConte for example, males collected in Alberta, Canada were brachypterous and females were both brachypterous and macropterous (Carter 1976).

Landscape Structure

Borders may serve as corridors or barriers for ground beetle dispersal into contiguous habitats. Thus, depending on the species of ground beetle, borders allow complete movement, partial movement, or no movement along them or across them. For example, paved and gravel roads serve as barriers to the movement of several species of ground beetles (Duelli et al. 1990). Mader et al. 1990, however found that grassy field roads did not deter movement of ground beetles. Similarly, Mader (1988) showed that paved roads served as barriers to the movement of wolf spiders, *Lycosa amentata* Clerck. Vermeulen (1994) found that the movements of *Pterostichus lepidus* Leske, *Harpalus servus* Duftschmid, and *Cymindis macularis* Say were restricted by forests and paved roads and that these species preferred open sandy areas. Duelli et al. (1990) described six functions of borders with respect to many species of ground beetles, rove beetles, and spiders. They listed the borders between the preferred habitat (natural or agricultural) and the immigration habitat as hard edge, negative influence, positive influence, mutual influence, ecotone, and no edge or very soft edge. Hard edge borders restrict or inhibit the movement of species across them. Soft edge borders do not restrict the movement of species across them. Borders that species avoid entirely have a negative influence, whereas borders that species seek have a positive influence. Some species of Carabidae prefer to inhabit the border areas between two adjacent habitats.

The density of vegetation within landscape elements can influence the dispersal rate of ground beetles (Honek 1988). They usually move swiftly through coarse grain habitats (e.g., sparse vegetation such as agricultural ecosystems) and more slowly through fine grain habitats (e.g., dense vegetation such as grasslands). For example, Frampton et al. (1995) found that grassy banks bordering a field of barley, *Hordeum vulgare* L., reduced recapture rates of *Pterostichus melanarius* Illiger, *P. niger* Schaller and *Harpalus rufipes* DeGeer. Similarly, the rate at which *H. rufipes*, *Pterostichus madidus* F. and *P. melanarius* traversed hedgerows was much slower than the rate moving through a barley field (Mauremooto et al. 1995).

Thomas et al. (1992b) created grassy borders within cereal fields and studied the species composition within fields and borders. They found that species composition of ground beetles in wheat fields changed from pioneer species (e.g., *Bembidion obtusum* Serville, *Notiophilus bigutattus* F., and *Trechus quadristriatus* Schrank) to edge species (e.g., *Agonum dorsale* Pontoppidan, *Bembidion lampros* Herbst, *Demetrias atricapillus*

L., and *Amara* spp.). In The Netherlands, de Vries (1994) showed that for ground beetles with limited powers of dispersal (e.g., *Agonum ericeti* Panzer), *Pterostichus lepidus*, and *Carabus arcensis* Herbst), the area of the habitat correlated strongly with the number of species.

Predatory Nature of Carabidae

Many ground beetles are polyphagous predators of arthropods and other animals. By preying on a variety of organisms and occupying a variety of habitats, ground beetles are believed by many researchers to help prevent pest outbreaks in agricultural ecosystems (Potts and Vickerman 1974, Winder 1990, Ekbom et al. 1992, Holopainen and Helenius 1992). For example, ground beetles are known to eat larvae and pupae of the gypsy moth, *Lymantria dispar* L., in temperate hardwood forests (Johnson and Reeves 1995); larvae and pupae of the beech moth, *Quadricalcarifera punctatella* Motschulsky (Kamata and Igarashi 1995); wheat midge larvae, *Sitodiplosis mosellana* Gehin, (Floate et al. 1990), potato aphids, *Macrosiphum euphorbiae* Thomas (Dixon and McKinley 1992); and cereal aphids, *Rhopalosiphum padi* L. and *Sitobion avenae* F. (Edwards et al. 1979, Scheller 1984, Griffiths et al. 1985, Chiverton 1987, Winder 1990). In New Zealand, Sunderland et al. (1995) found that aphids and larvae of Diptera were the predominant prey for *Harpalus affinis* Schrank while *Clivina australasiae* Boheman primarily ate earthworms. Other types of prey included nematodes, mollusks, and other arthropods.

In agroecosystems, many polyphagous ground beetles inhabit various types of field margins and move into the crops to feed and reproduce. Chiverton and Sotherton (1991) showed that the numbers of *A. dorsale* and *Pterostichus melanarius* were not significantly different between wheat fields with weedy borders and wheat fields with herbicide treated borders. *Agonum dorsale* did, however consume proportionately more cereal aphids in untreated plots than in treated plots. Both treated and untreated plots were dominated by the grass *Poa annua* L., but the untreated plots contained higher numbers of broadleaf plants. In Europe, several species of ground beetles that feed on cereal aphids overwinter in grassy borders surrounding wheat fields (Sotherton 1984, 1985, Coombes and Sotherton 1986). In particular, *A. dorsale* and *Demetrias atricapillus* L. almost exclusively preferred to overwinter in the grassy field boundaries. These two species rank very high on Sunderland and Vickerman's (1980) cereal aphid predator index.

In the United States, cereal aphids historically have been important pests of wheat and other small grains. In particular, the greenbug, *Schizaphis graminum* Rondani, has been a persistent pest for many years. The cost of controlling this species totals millions of dollars annually (Anonymous 1995). More recently, the Russian wheat aphid, *Diuraphis noxia* Mordvilko, has become a major pest of wheat. The cost of controlling this species also totals millions of dollars annually (Anonymous 1994).

Many species of Carabidae are important polyphagous predators of cereal aphids. In Finland, the ground beetles *Bembidion guttula* F., *B. quadrimaculaum* L., *Clivina fossor* L., *Amara plebeja* Gyllenhal, *Harpalus rufipes* DeGeer, *Pterostichus vernalis, and P. melanarius* were trapped in spring barley fields, dissected and found to contain parts of the exoskeleton of the bird cherry-oat aphid (Holopainen and Helenius 1992). In Sweden, Chiverton (1987) showed that *Bembidion lampros* Herbst and *Pterostichus cupreus* L. fed on *R. padi* during its establishment phase of population growth in wheat fields, while *P. melanarius* and *Harpalus rufipes* fed on it during the exponential phase of population growth. Chiverton also found cuticular parts of *R. padi* in the guts of *Synuchus nivalis* Panzer, *A. dorsale* and *Calathus melanocephalus* L. In England, Edwards *et al.* (1979) and Sunderland and Vickerman (1980) list *A. dorsale*, *D. atricapillus*, *S. nivalis*, *Harpalus affinis* Schrk, *H. rufipes*, *Nebria brevicollis*F., *Amara* spp., *C. fossor*, and *B. lampros* as predators of cereal aphids. They suggest that *A. dorsale* may be the most important species because it is common during all population growth phases of aphid populations. *Agonum dorsale* preys on the cereal aphids *S. avenae* (Griffiths et al. 1985, Winder 1990) and *R. padi* (Scheller 1984), which are serious pests of wheat and barley. Given the high species diversity, abundance, and predatory nature of ground beetles, the above authors suggest that ground beetles may play a significant role in the control of cereal aphid populations and consequently help keep their numbers below economic threshold levels.

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CHAPTER III

REVERTING CONSERVATION RESERVE PROGRAM LANDS TO WHEAT AND LIVESTOCK PRODUCTION: EFFECTS ON GROUND BEETLE (COLEOPTERA: CARABIDAE) ASSEMBLAGES

Abstract

Highly erodible lands enrolled in the Conservation Reserve Program (CRP) soon will revert to agricultural production. Ground beetles are generalist predators that feed on a variety of agricultural pests. This study began in spring, 1995, and was designed to determine the effects of reversion of CRP lands to wheat and livestock production on ground beetle assemblages. Reversion strategies included no reversion of CRP grass (OWBUM), simulated grazing of CRP grass (OWBM), no-tillage practices for wheat production (WNT), and minimum-tillage practices for wheat production (WMT). A randomized block experimental design was established with 4 replicates. Ground beetles were captured with pitfall traps and grouped by treatment. More ground beetles were captured in 1995 than in 1996, and abundances within years differed among reversion strategies. Of 73 ground beetle species collected, 9 species accounted for 61.7% of total abundance. Abundances of these 9 species differed with respect to reversion strategy. None of the community parameters (species richness, species diversity, and species evenness) differed among the reversion strategies. Canonical correspondence analysis (CCA) showed that annual and monthly variation were the predominant factors in separating ground beetle assemblages. Lack of rainfall may have accounted for a large portion of differences in abundances between years. A partial CCA showed that OWBM and WNT were the predominant reversion strategies in separating ground beetle assemblages. OWBM and WNT are intermediate disturbance levels between OWBUM and WMT.

Key Words: Carabidae, insect predators, biological control, CRP, tillage, wheat, pasture.

Introduction

The loss of topsoil due to water and wind erosion is a major concern worldwide (Pimentel et al. 1995). The U.S. government established the Conservation Reserve Program (CRP) in the 1985 Food Security Act to reduce the amount of topsoil lost from highly erodible lands. Farmers were compensated monetarily for enrolling their lands in this program. In Oklahoma, 0.5 million ha are enrolled as CRP lands. Anticipated changes in federal farm programs may significantly reduce the acreage in the CRP and bring this sensitive land back into agricultural production. Much of this land in Oklahoma will revert to wheat, *Triticum aestivum* L., and pasture for livestock production. With this reversion to agricultural production, farmers may employ strategies that maximize wheat and livestock production, yet minimize loss of topsoil.

Ground beetles are generalist predators of agricultural pests and play an important role in controlling pests in many agroecosystems (Sunderland and Vickerman 1980, Scheller 1984, Floate et al. 1990, Winder 1990, Ekbom et al. 1992, Holopainen and Helenius 1992, Sunderland et al. 1995). If CRP lands revert to pasture for grazing livestock, an increased level of disturbance to the vegetation and soil may occur and may significantly alter assemblages of ground beetles. If CRP lands revert to wheat production, complete and abrupt changes in the vegetation and ground cover will occur, and this too may alter assemblages of ground beetles.

Deep tillage of the soil, as is done with conventional methods, removes $\geq 70\%$ of all vegetative residue from the ground surface, and consequently disrupts the life cycles of many species. Conservation tillage practices leave $\geq 30\%$ plant residue on the soil surface after planting (Gebhardt et al. 1985). One conservation practice is no-tillage, which leaves ≥ 60% of plant residue on the soil surface after planting. Stinner and House (1990) reviewed the effects of conservation tillage practices on various groups of arthropods and other invertebrates.

The effects of conventional and conservation tillage practices on species diversity and relative abundances of ground beetle species have been studied widely (Tyler and Ellis 1979, Dritschilo and Wanner 1980, Barney and Pass 1986, Wiess et al. 1990, Laub and Luna 1992, Tonhasca 1993, Carcamo et al. 1995). Although ground beetle diversity sometimes increases with decreased tillage (Stinner and House 1990), other indications are that diversity and abundance are not changed (Barney and Pass 1986). In the northern Great Plains, ground beetle diversity and abundance were altered more by some crop rotations than by tillage practices (Wiess et al. 1990).

Farmers may encounter new pest problems with reversion of CRP lands to crop and livestock production. As generalist predators, ground beetles may play an important role in reducing pest problems (Potts and Vickerman 1974), and they could be especially important with respect to CRP land reversion. The effect that reversion from CRP to agricultural production will have on ground beetle species assemblages is currently unknown. My objectives were to determine: (1) the temporal structure of spring assemblages of ground beetles, (2) the effects on ground beetle assemblages of converting CRP lands to wheat production using minimum and no-tillage practices, and (3) the effects on ground beetle assemblages of converting CRP lands to grazing lands for livestock production.

Materials and Methods

Study Area and Pitfall Trap Design

This study was conducted in 1995 and 1996 in Beaver County of western Oklahoma on 18 ha of CRP land. This land entered CRP in 1989 and was planted with Old World Bluestem (OWB), *Bothriochloa bladhii* Retzius. This is an imported bunch grass that is commonly planted in the region for erosion control. The land will revert to agricultural production in 1999. Before enrollment in CRP, this land was routinely planted with winter wheat. Beaver County is part of the short grass prairie region of the southern Great Plains (Kaul 1986). The soil type at the study site is Dalhart fine sandy loam (Taxonomic Class: Fine-loamy, mixed, mesic Aridic Haplustalfs) (Anonymous 1962). The study was to represent the first year of reversion from CRP to wheat or pasture.

A randomized complete block experimental design was used having four replications of four treatments: 1) unmanaged Old World Bluestem (OWBUM), 2) managed Old World Bluestem (OWBM), 3) minimum-tillage wheat (WMT), and 4) no-tillage wheat (WNT) (Fig. 1). Dimensions of each plot were 92 by 46 m. Because this was only a two-year study, the three-year wheat-fallow-sorghum treatment planned for this experiment was not implemented. During the first year of reversion (1994 – 1995), the OWB was burned in May 1994 to remove previous growth. In July 1994, tillage was accomplished by undercutting the OWB with a 91-cm V-blade sweep. This reduced-tillage method contrasts with the no-tillage strategy where no disturbance to the soil occurred except for planting the wheat. Herbicide (1.1 kg^{-1} (AI)/ha glyphosate) was sprayed to kill the OWB in the WNT and WMT plots in August 1994 and June 1995. Wheat was planted, using a no-till drill, in the WNT and WMT plots in September 1994. For the 1995-1996 season, sweep tillage was performed on WMT in June, August, and October. The repeated tillage was used to reduce regrowth of OWB and weeds. Wheat was planted in the WNT and WMT plots in October 1995. Along with drilling of wheat, 110.7 kg^{-1} (AI)/ha of 18-46-0 fertilizer was placed in the seed rows. In addition, 66.3 kg^{-1} (AI)/ha of urea-N was applied to all plots in March. The OWBM plots were periodically mowed to simulate grazing effects by cattle. The mowed grass was not manually removed from the plots. In contrast, the OWBUM plots acted as controls and were not mowed.

Eight pitfall traps with guides were established in each plot to capture ground beetles (Fig. 2). These traps were placed in the center of each plot at equal distances from each other with the guides positioned in alternating directions to facilitate the capture of ground beetles walking in different directions. The trap design was after that of Morrill (1975). A trap consisted of a 455-ml plastic Solo (Concept Communications Company, Burr Ridge, IL) cup with a 145-mm inside diameter. This cup was buried in the soil with the lip slightly beneath the soil surface. A 148-ml Solo cup partially filled with ethylene glycol as a preservative was placed inside the larger cup to hold the beetles. A Solo Cozy Cup funnel was placed on the larger cup and set flush with the soil surface. Galvanized sheet metal strips (24 gauge, 14 by 122 cm) were used as guides to facilitate the capture of the beetles by channeling their movement into the traps. Traps were placed at both ends of the guides. Pitfall traps were established on 9 March 1995 and 27 March 1996 and checked weekly through 24 June 1995 and 14 June 1996, respectively. Simpson's diversity index (D) and Simpson's equitability index (E) were used to evaluate species diversity and species evenness (Begon et al. 1990).

Data Analysis

The number of ground beetles captured in each plot and relative abundances of species were calculated and analyzed with canonical correspondence analysis (CCA) of CANOCO (ter Braak 1987) to compare ground beetle species assemblages among treatments. Canonical correspondence analysis is a preferred method for ordinating data obtained from pitfall traps (Palmer 1993), and is commonly used for direct gradient analysis to relate abundances of species to environmental variables. The data were grouped by month in order to account for temporal changes in abundances of species. Species are separated and associated along these environmental gradients using trap capture data totaled for 10 variables: 1) 1995 season, 2) 1996 season, 3) March, 4) April, 5) May, 6) June, 7) OWBUM, 8) OWBM, 9) WNT, and 10) WMT. These environmental variables were used as dummy variables; i.e., they were not measured directly, instead each environmental variable was coded by its order of occurrence with respect to sampling date. With CANOCO only occurrences need to be input since non-occurrences are implied in the analysis. In a CCA, species that are strongly associated with a particular year, a particular month, or a particular treatment will ordinate along the respective environmental axis.

I used a partial CCA to focus on the effects of the 4 treatments on ground beetle assemblages (transformed to square-root of relative abundance) by factoring out the covariables years and months. Analysis of variance for a randomized complete block design was used to determine differences in mean ground beetle abundance, species richness, species diversity, and species evenness among treatments.

Results

Species Data

Nearly 3,000 ground beetles, representing 73 species, were captured over all treatments in 1995 and 1996 (Table 1). The total number of ground beetles captured differed significantly between years ($t = 4.217$; $df = 30$; $P < 0.001$), so years were analyzed separately. In both years, capture of ground beetles peaked in May (Fig. 3). In 1995, total abundance of all species differed significantly among treatments ($F = 10.91$; $df = 3, 12$; $P < 0.01$). Significantly more beetles were captured in OWBM plots than in OWBUM and WMT plots, and more in WNT plots than in OWBUM plots (Table 2). Five species including *Amara cupreolata* Putzeys, *Anisodactylus dulcicollis* LaFerté, *A. rusticus* Say, *Galerita janus* F., and *Pasimachus elongatus* LeConte accounted for 63% of all individuals captured in 1995 (Table 1). Significant differences among the treatments in numbers captured were found for three of the five species: *A. dulcicollis* ($F = 17.22$; $df = 3, 12$; $P < 0.01$), *G. janus* ($F = 10.79$; $df = 3, 12$; $P < 0.01$), and *P. elongatus* ($F = 6.66$; $df = 3, 12$; $P < 0.01$). Significantly more *A. dulcicollis* were captured in OWBM. *Galerita janus* were captured in greater numbers in the WNT. *Pasimachus elongatus* were captured in greater numbers in OWBM and WNT (Table 2). For *A. cupreolata* and *A. rusticus,* there were no significant differences in numbers captured among treatments;

however, numbers captured for *A. cupreolata* were close to significant (F = 3.31; df = 3, 12; P = 0.0572).

In 1996, total abundance of all species differed significantly among treatments (F = 3.52; df = 3, 12; $P < 0.05$). This difference was due to the low numbers captured in OWBUM (Table 2). Of 52 species captured in 1996, six species including *A. rusticus*, *Cratacanthus dubius* Palisot de Beauvois, *Cymindis laticollis* Say, *Harpalus desertus* LeConte, *P. elongatus*, and *Selenophorus planipennis* LeConte, accounted for 59% of all individuals (Table 1). Of these six species, significant differences among the treatments in numbers captured were found for three species: *A. rusticus* (F = 8.47; df = 3, 12; P < 0.01), *C. dubius* (F = 9.39; df = 3, 12; P < 0.01), and *H. desertus* (F = 3.72; df = 3, 12; P < 0.05). For *A. rusticus* and *H. desertus*, the difference was due to the low numbers captured in OWBUM (Table 2). *Cratacanthus dubius* was captured significantly more often in WMT (Table 2).

Community Parameters

Species richness is the number of species collected, with no consideration of the relative numbers captured, thus rare and common species are rated equally. There were no significant differences in species richness between years or treatments (Table 3). Species diversity considers relative species abundance in addition to the number of species, and therefore accounts for differences in species abundance. There were no significant differences in Simpson's species diversity indices between years or treatments. The evenness index accounts for variation in relative abundances, with values ranging from 0 (high variability in numbers among species) to 1 (no variability in numbers among species). There were no significant differences in Simpson's species evenness index between years or treatments.

Multivariate Analysis

Because species abundances differed significantly between 1995 and 1996, year was included in the CCA as an environmental dummy variable. The eigenvalues for CCA axes 1 through 4 were 0.321, 0.247, 0.111, and 0.094. These values represent the amount of variation in species scores explained by their respective axis, and therefore by the environmental variables (ter Braak 1987). The cumulative percentage variance of species--environment relationship explained by the 4 axes was 78.6. When the environmental variables year and month are plotted, axis 1 and axis 2 were seen to represent temporal gradients (Fig. 4). Axis 1 separated ground beetle assemblages by year, and axis 2 separated ground beetle assemblages by month. Ground beetles associated with 1995 had negative scores on axis 1, while ground beetles associated with 1996 had positive scores on this axis (Fig. 5). Note that the dominant ground beetles for 1995 and 1996 separated along axis 1. Ground beetles associated with early spring (March and April) had positive scores on axis 2, while those associated with late spring (May and June) had negative scores on this axis. Ground beetles scores positioned near the origin were not strongly associated with either of these temporal gradients. To determine the robustness of the CCA ordination of ground beetle assemblages, a Monte Carlo randomization test was performed (ter Braak 1987). Based on this test, the observed patterns of ground beetle abundances and environmental variables differed significantly from random (Monte Carlo test statistic = 1.67; $P < 0.01$), indicating that the ordination was a valid representation of patterns in the ground beetle assemblages.

To describe the effects of type of treatments on species composition, the 2 years and 4 months were factored out as covariables. The eigenvalues for axes 1 through 3 were 0.100, 0.079, and 0.069. Again, these values measured the amount of variation in species scores explained by their respective axes, with axis 1 explaining more variation in species scores than the other axes (Fig. 6). These eigenvalues were much smaller than the previous eigenvalues because of the strong annual and monthly influences on ground beetle assemblages. Together, these 3 axes explained 100% of the variation in species scores remaining after partialling out year and seasonal effects. The distribution of ground beetle species associated with OWBUM, OWBM, WNT, and WMT separated along axes 1 and 2 (Fig. 7). The 1st axis separated species trapped most often in wheat and Old World Bluestem. Species plotted near the origin were equally distributed among treatments, while those occurring near the ends of the axes preferred a particular treatment. Ground beetles preferring wheat appear in the positive space of axis 1, whereas ground beetles preferring Old World Bluestem appear in the negative space of axis 1. Ground beetles associated with OWBUM and OWBM were separated along axis 2. Ground beetles preferring OWBUM appear in the positive space of axis 2, whereas ground beetles preferring OWBM appear in the negative space of axis 2. Additionally, axis 2 partially separated ground beetles with respect to wheat management. WMT ordinated in negative space of axis 2, whereas WNT slightly ordinated in positive space of axis 2. When plotted on axis 1 and axis 3, however WMT and its associated ground beetles separated strongly along the positive space of axis 3 (Fig. 7).

Discussion

It is typical for a few ground beetle species to dominate an assemblage in terms of relative abundance (Thiele 1977). In this study, 9 of the 73 species captured (12.3%) accounted for 61.7% of the total captured. Other studies also have found that a few species dominate the ground beetle fauna in agroecosystems (Kirk 1971, Barney and Pass 1986, Laub and Luna 1992, Tonhasca 1993, Carcamo 1995). The number of ground beetles captured in 1995 more than doubled the number captured in 1996. This difference may be because of the variation in rainfall amount between the two years. Total rainfall during the 1994 – 1995 wheat-growing season was 80 mm above the 30 year average (Fig. 8). In contrast, total rainfall during 1995 – 1996 wheat-growing season was 65 mm below the 30 year average (Fig. 8). Even though this is a relatively dry region of the Great Plains and ground beetles probably are adapted to the average precipitation levels, their eggs and larvae are highly susceptible to desiccation (Allen 1979, Lövei and Sunderland 1996). The desiccation of eggs could certainly keep population numbers low. It is also possible that they crawled into crevices in the ground and simply became inactive. In any event, the drought possibly affected *A. dulcicollis* population numbers quite drastically. In 1995, 480 individuals were captured, while only 3 individuals were captured in 1996. I found similar differences for *G. janus* (301 and 4), but less extreme differences for some other species.

In addition to variation in annual rainfall, differences in abundances could be accounted for by other factors, such as predation, parasitism, intraspecific and interspecific competition, differential reproductive potential, differential powers of dispersal, and other life history traits. Variation in numbers of ground beetles captured among years and habitats is common and seems to be the rule rather than the exception (den Boer 1986). However, determining the important factors affecting the variation in population numbers must be elucidated through empirical tests (Loreau 1986). Predation and cannibalism occur among ground beetles (Currie et al. 1996), as does competition for food (Lenski 1982, Loreau 1986), but these factors have not been shown to cause a 160 or 75 multiple decrease in population numbers, as was observed in the present study for *A. dulcicollis* and *G. janus*, respectively.

In the Southern Great Plains, spring months (March – June) are active periods for many species of ground beetles. Because most ground beetles are nocturnal predators and their activity is influenced by temperature (Thiele 1977), an increase in nightly temperatures may partly explain a peak in numbers captured. Activity peaked in May and June of both years, which corresponds to the period where nightly temperatures are higher relative to nightly temperatures in March and April (Fig. 9). In the Northern Great Plains, where nightly temperatures remain cold throughout spring, activity periods for ground beetles peaked in August and September over a sampling period from June to November (Kirk 1971). Although Kirk did not present any temperature data, presumably nightly temperatures correlated with ground beetle activity. Many of the same species captured by Kirk were captured in this study. For example, *P. elongatus* was one of the most abundant species in Kirk's study and in this study.

Ground beetles differed in their response to tillage practices of converting CRP lands to wheat production. Overall, more ground beetles were captured in no-tillage wheat (862) than in minimum-tillage wheat (572). This trend was evident in both 1995 and 1996, although it was not statistically significant in either year. Among the most abundant species captured, only *G. janus* showed a strong preference for no-tillage wheat over minimum-tillage wheat. This species is common in many habitats in Oklahoma (B.W.F. and N.C.E., unpublished data). Other species that preferred no-tillage wheat over included *A. cupreolata*, *A. dulcicollis*, *C. laticollis*, and *P. elongatus*. In contrast, *A. rusticus*, *C. dubius*, and *S. planipennis* preferred minimum-tillage wheat. Although there were differences in species abundances among the tillage regimes, species richness, species diversity, and species evenness did not differ significantly.

Other studies have shown mixed preferences by ground beetles in agricultural crops for reduced tillage vs. conventional tillage (Carcamo 1995, Barney and Pass 1986, Dritschilo and Wanner 1980). Carcamo (1995) found higher abundance of ground beetles with conventional tillage vs. reduced-tillage in barley that was attributable to an unusually high number of a single species. Conversely, species diversity was higher with reduced-tillage barley. In alfalfa, ground beetle abundances were higher in reduced tillage than in conventional tillage, yet there were no differences in species diversity (Barney and Pass 1986). This is similar to my findings with ground beetle assemblages, except that here both no-tillage and minimum-tillage regimes are conservation practices. As indicated by the differences in abundance, but not by community parameters, no-tillage wheat tended to support higher populations of ground beetles. This may be related to the level of disturbance each treatment received. The soil in no-tillage wheat is less disturbed than in minimum-tillage wheat.

Ground beetles differed in their response to converting CRP lands to livestock production. Overall, more ground beetles were captured in managed Old World Bluestem (1,061) than in unmanaged Old World Bluestem (367). This trend was evident in 1995 and 1996, but significantly so only in 1995. Similar to the wheat plots, there were no significant differences in species richness, species diversity, and species evenness between the unmanaged and managed Old World Bluestem plots. Other studies have shown mixed preferences by ground beetles to managed and unmanaged grasslands (Luff and Rushton 1988, Morrill 1992, Dennis et al. 1997). In direct contrast to my study, Luff and Rushton (1988) showed that ground beetle diversity was higher in undisturbed grassland and decreased with increasing levels of disturbance. In their study, however increasing disturbance included conventional tillage methods with and without grazing. They also grazed sheep as opposed to the simulated grazing effects used in my study. At a moderate level of disturbance, artificially applied farmyard manure was shown to increase ground beetle abundance and diversity in sugar beet plots (Purvis and Curry 1984). Dennis et al. (1997) showed that most of the dominant ground beetle species were captured in grasslands grazed only by sheep as opposed to ungrazed grasslands and grasslands grazed by sheep and cattle. The ground beetles in my study may have responded to the disturbance level of the soil and vegetation in relation to the reversion of CRP lands to pastures.

Highly erodible lands may be the most difficult lands to manage (Pimentel et al. 1995). These lands are sensitive to natural and human-induced levels of disturbance to the soil and vegetation. For CRP lands being converted to wheat production, no-tillage practice appears to support higher levels of ground beetles. These beetles are known to contribute significantly to the control of agricultural pests, which can reduce applications of pesticides and increase profit for wheat farmers. Converting CRP lands to livestock production may enhance ground beetle abundance. Although this study did not use livestock, the simulated grazing effects showed relatively higher numbers of ground beetles in the managed Old World Bluestem. Again, the increased numbers of ground beetles may benefit farmers.

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Table 3. Community parameters for ground beetles captured in unmanaged Old World bluestem (OWBUM), managed Old World bluestem (OWBM), no-tillage wheat (WNT), and minimum-tillage wheat (WMT) plots. These values are combined across years. Depicted are means ± 1 SE. All parameters are not significant among treatments.

Community parameter	OWBUM	OWBM	WNT	WMT
Species Richness	38.00 ± 1.00	39.00 ± 4.00	41.50 ± 0.50	35.00 ± 2.00
Simpson's Diversity Index	14.66 ± 0.88	9.27 ± 2.93	9.58 ± 3.82	10.14 ± 0.36
Simpson's Evenness Index	0.38 ± 0.04	0.25 ± 0.10	0.23 ± 0.09	0.29 ± 0.03

Table 1. Numbers captured and % of total capture for ground beetle species in unmanaged Old World bluestem (OWBUM), managed Old World bluestem (OWBM), no-tillage wheat (WNT), and minimum-tillage wheat (WMT) in 1995 and 1996.

Species	OWBUM	OWBM	WNT	WMT	Total	%
1995						
Anisodactylus dulcicollis	27	284	51	43	405	20.3
Galerita janus	25	16	238	22	301	15.1
Pasimachus elongatus	27	123	70	50	270	13.5
Anisodactylus rusticus	22	51	42	69	184	9.2
Amara cupreolata	15	66	14	10	105	5.3
Other Species	103	293	188	148	732	36.6
Total	219	833	603	342	1,997	100.0
1996						
Pasimachus elongatus	23	29	26	17	95	11.0
Cymindis laticollis	19	17	49	9	94	10.9
Anisodactylus rusticus	5	20	29	32	86	9.9
Cratacanthus dubius	2	14	19	49	84	9.7
Selenophorus planipennis	4	41	17	21	83	9.6
Harpalus desertus	4	22	17	21	64	7.4
Other Species	91	85	102	81	359	41.5
Total	148	228	259	230	865	100.0

Table 2. Mean numbers captured (± 1 SE) and Fisher's Protected LSD tests for total capture and dominant ground beetle species in unmanaged Old World bluestem (OWBUM), managed Old World bluestem (OWBM), no-tillage wheat (WNT), and minimum-tillage wheat (WMT) plots in 1995 and 1996. Means were calculated by monthly captures.

Year/Species	OWBUM	OWBM	WNT	WMT
1995 - Total	55.25 ± 5.27a	207.75 ± 37.76b	145.75 ± 27.83bc	85.50 ± 14.06c
Anisodactylus dulcicollis	6.75 ± 1.80a	71.00 ± 19.16b	12.75 ± 3.35a	10.75 ± 2.53a
Galerita janus	6.25 ± 3.97a	4.00 ± 1.58a	54.25 ± 10.99b	5.50 ± 1.66a
Pasimachus elongatus	6.75 ± 2.87a	30.75 ± 6.56b	17.50 ± 3.50bc	12.50 ± 2.40ac
1996 - Total	36.75 ± 5.02a	53.75 ± 7.70ab	67.50 ± 11.35b	57.00 ± 2.12b
Anisodactylus rusticus	1.25 ± 0.63a	4.75 ± 0.75b	7.25 ± 1.75b	8.00 ± 1.08b
Cratacanthus dubius	0.50 ± 0.29a	3.50 ± 1.66b	4.75 ± 2.50b	12.00 ± 1.22c
Harpalus desertus	1.00 ± 0.58a	5.50 ± 1.85b	4.75 ± 1.31b	5.25 ± 1.31b

Values within rows with different letters are significantly different.

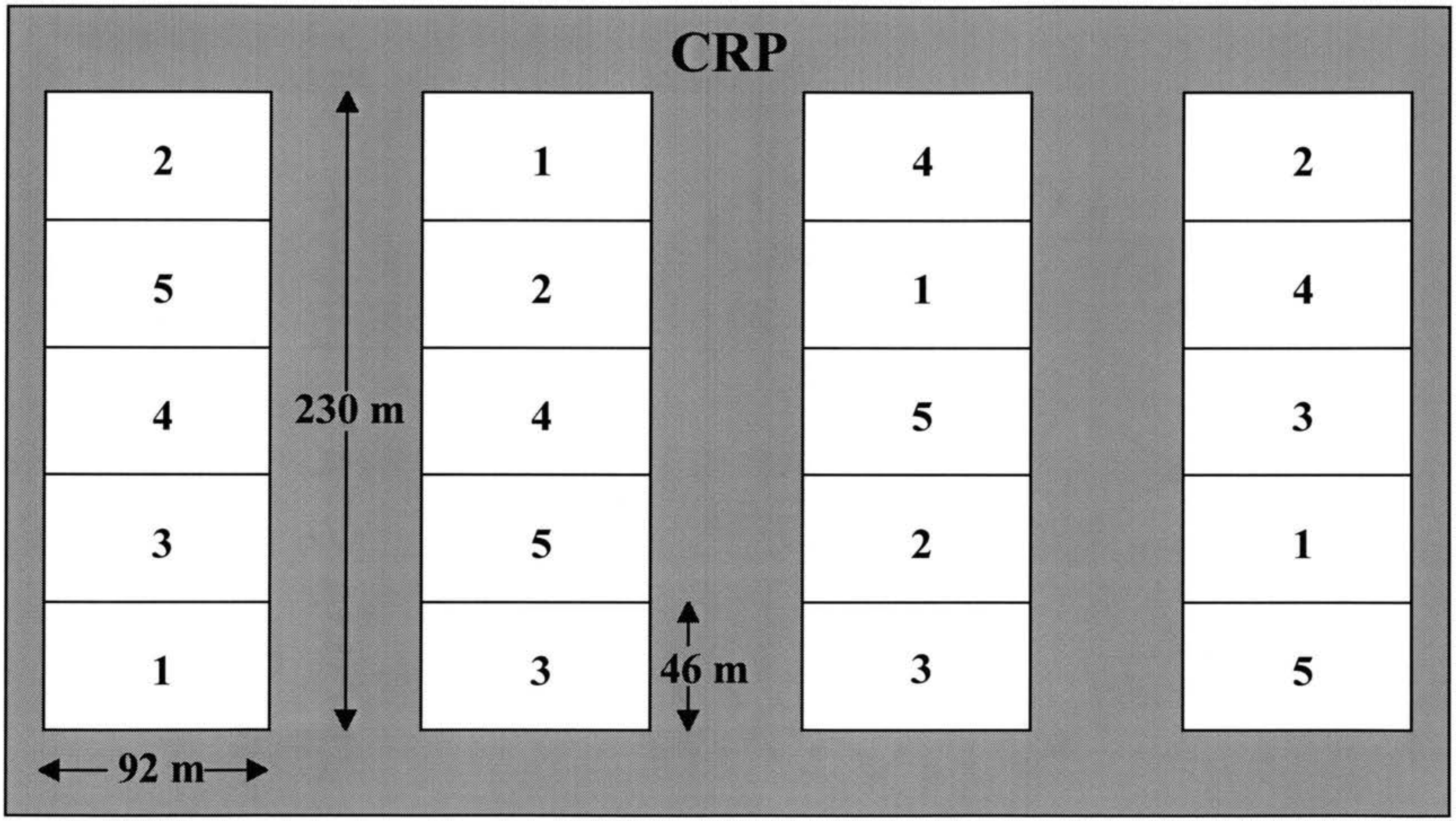

Figure 1. The randomized arrangement of plots set on 18 ha of CRP in Beaver County, OK. The dimension of each plot was 46 x 92 m. Plots representing reversion strategies are numbered 1) managed Old World bluestem (OWBM), 2) unmanaged Old World bluestem (OWBUM), 3) no-tillage wheat (WNT), and 4) minimum-tillage wheat (WMT). A fifth plot, wheat-fallow-sorghum (WFS), was also established, but was not included in this study.

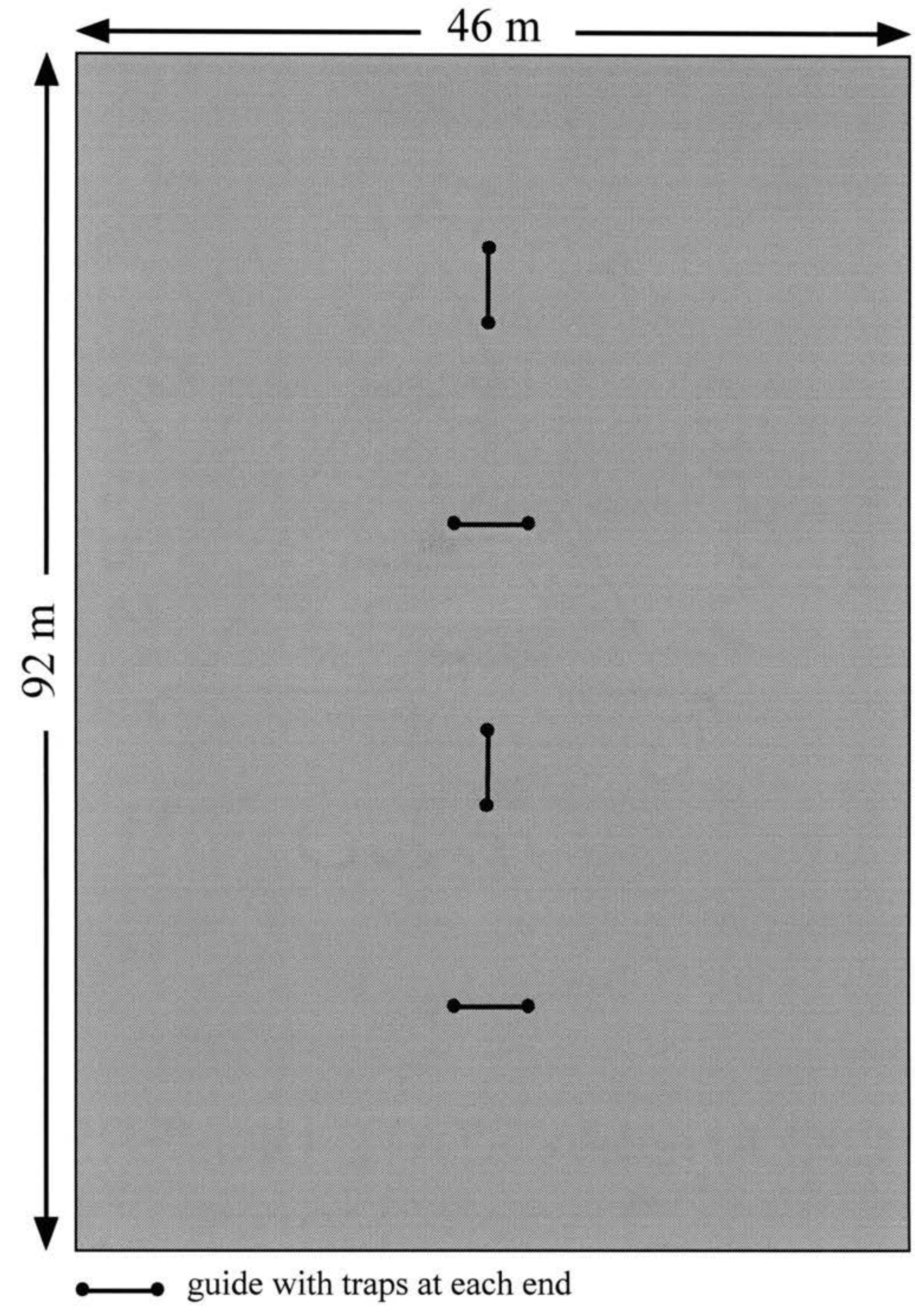

Figure 2. The arrangement of pitfall traps and guides within each plot. Traps were placed on both ends of the guides and positioned in the center of each plot at equal distances from one another. The guides were placed in alternate directions to facilitate the capture of ground beetles walking in different directions.

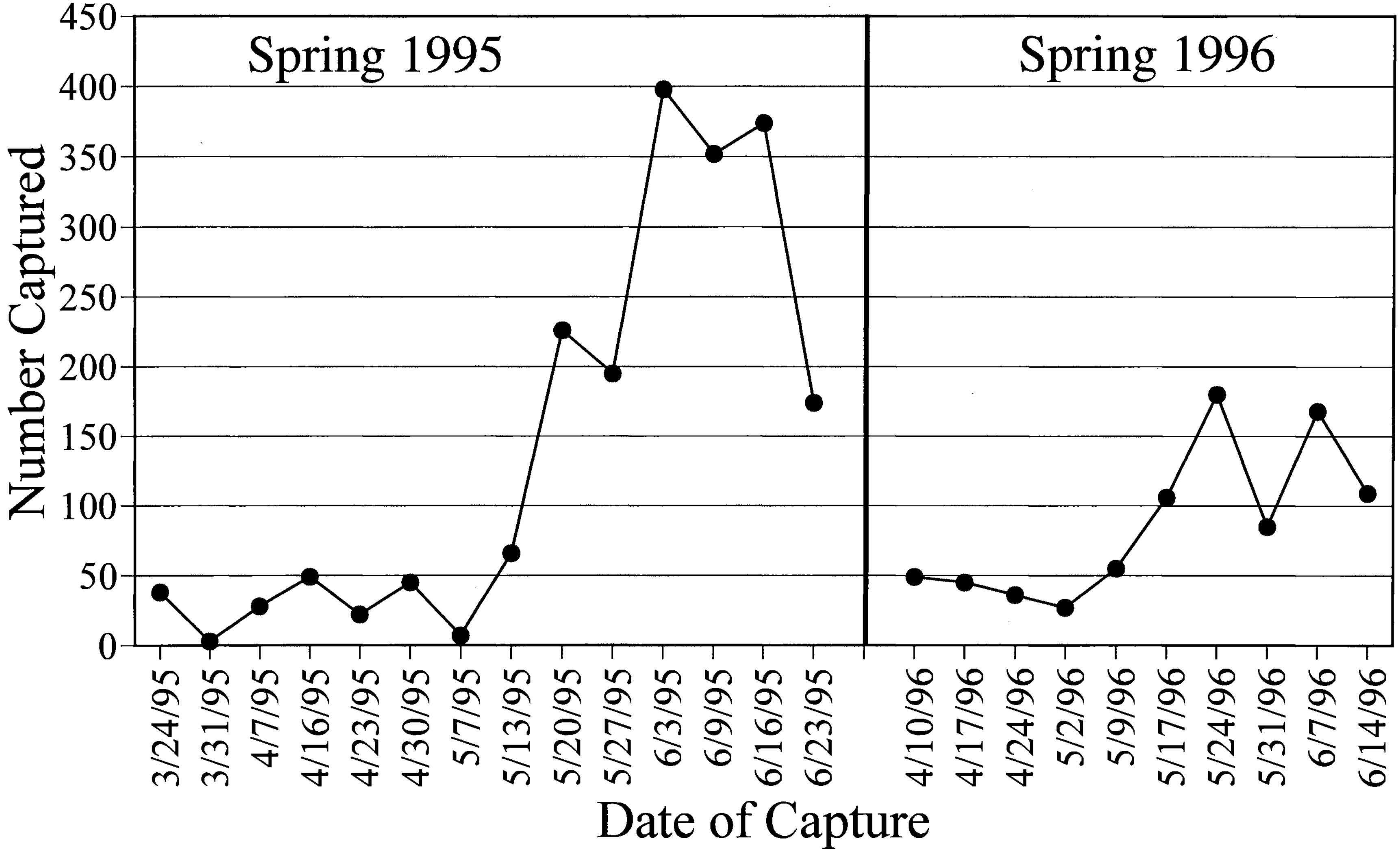

Figure 3. The total number of ground beetles captured in the springs of 1995 and 1996 by sampling date.

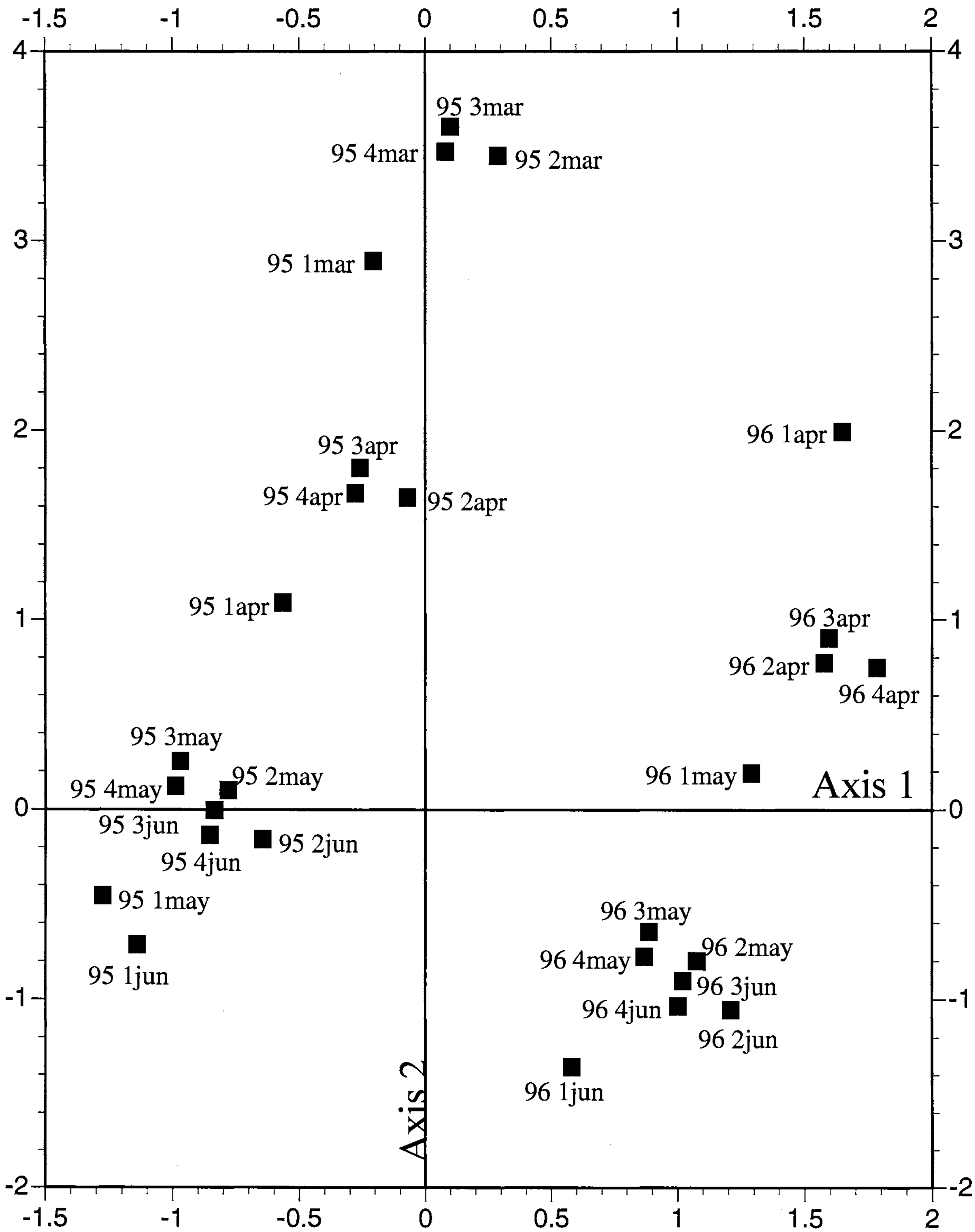

Figure 4. Scatterplot of site scores classified by year and month obtained from canonical correspondence analysis. Axis 1 (x) and axis 2 (y) are shown.

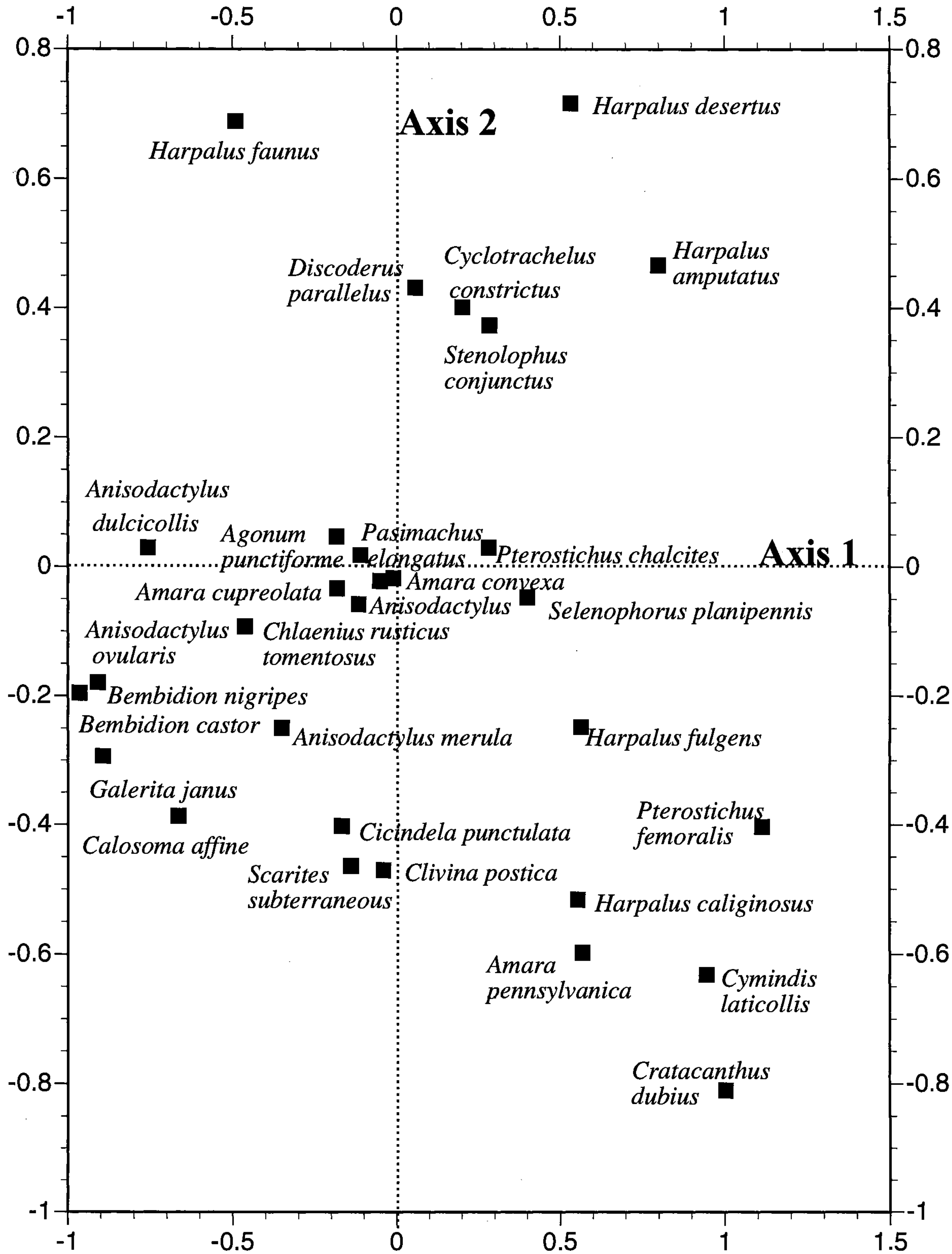

Figure 5. Scatterplot of species scores obtained from canonical correspondence analysis. Axis 1 (x) and axis 2 (y) are shown.

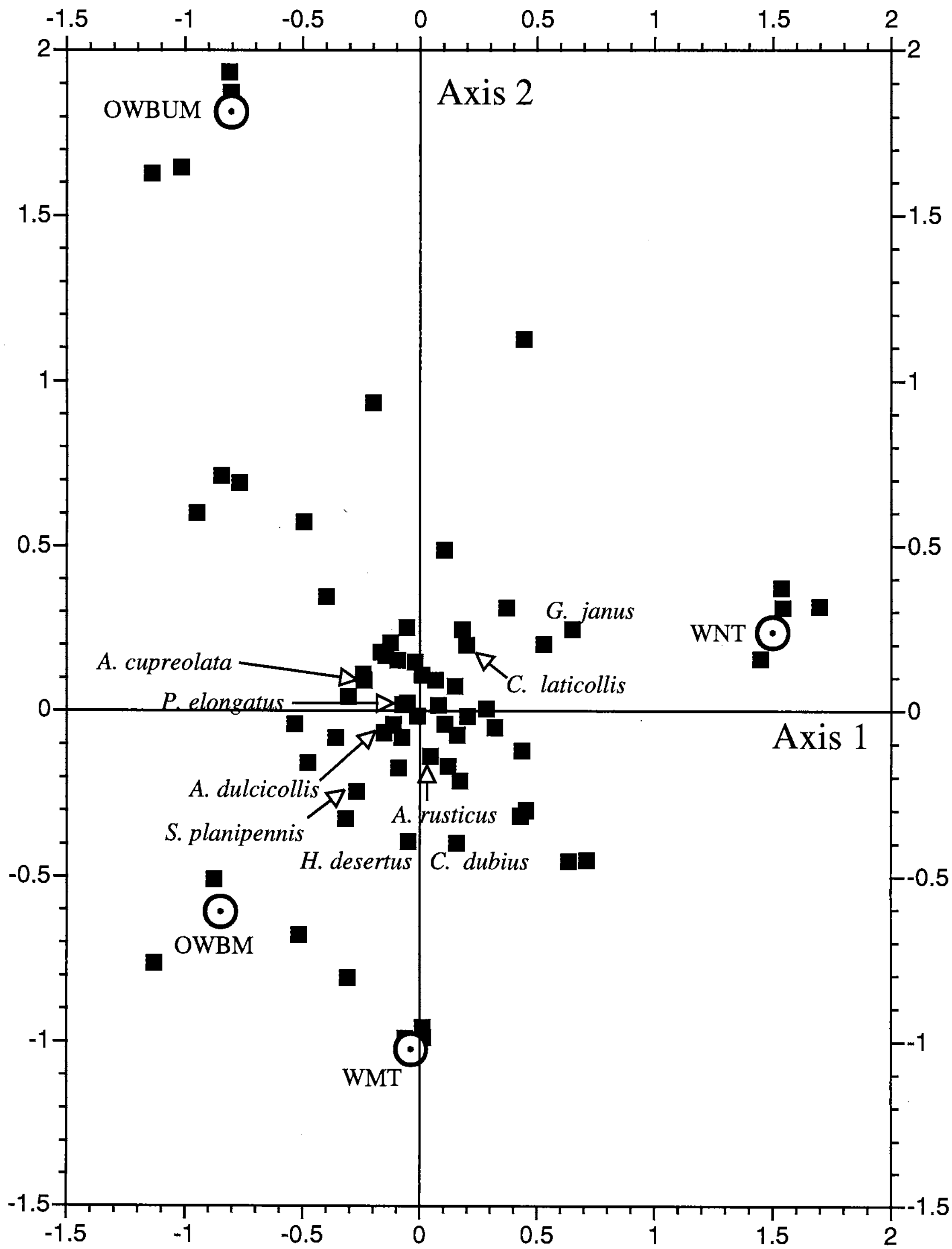

Figure 6. Biplot of species scores and CRP reversion strategies (depicted as centroids) obtained from a partial canonical correspondence analysis. Year and month were treated as covariables. Axis 1 (x) and axis 2 (y) are shown.

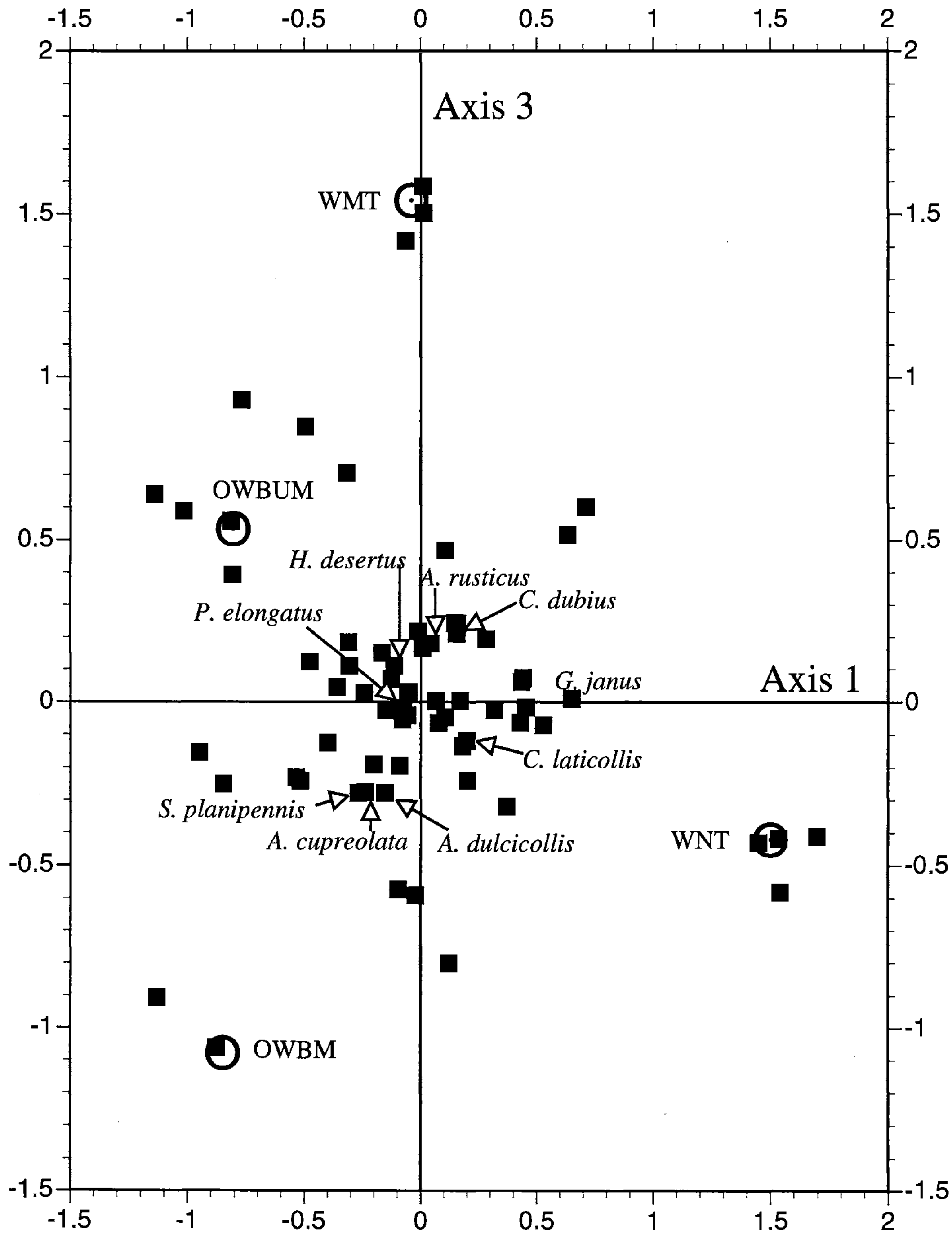

Figure 7. Biplot of species scores and CRP reversion strategies (depicted as centroids) obtained from a partial canonical correspondence analysis. Year and month were treated as covariables. Axis 1 (x) and axis 3 (y) are shown.

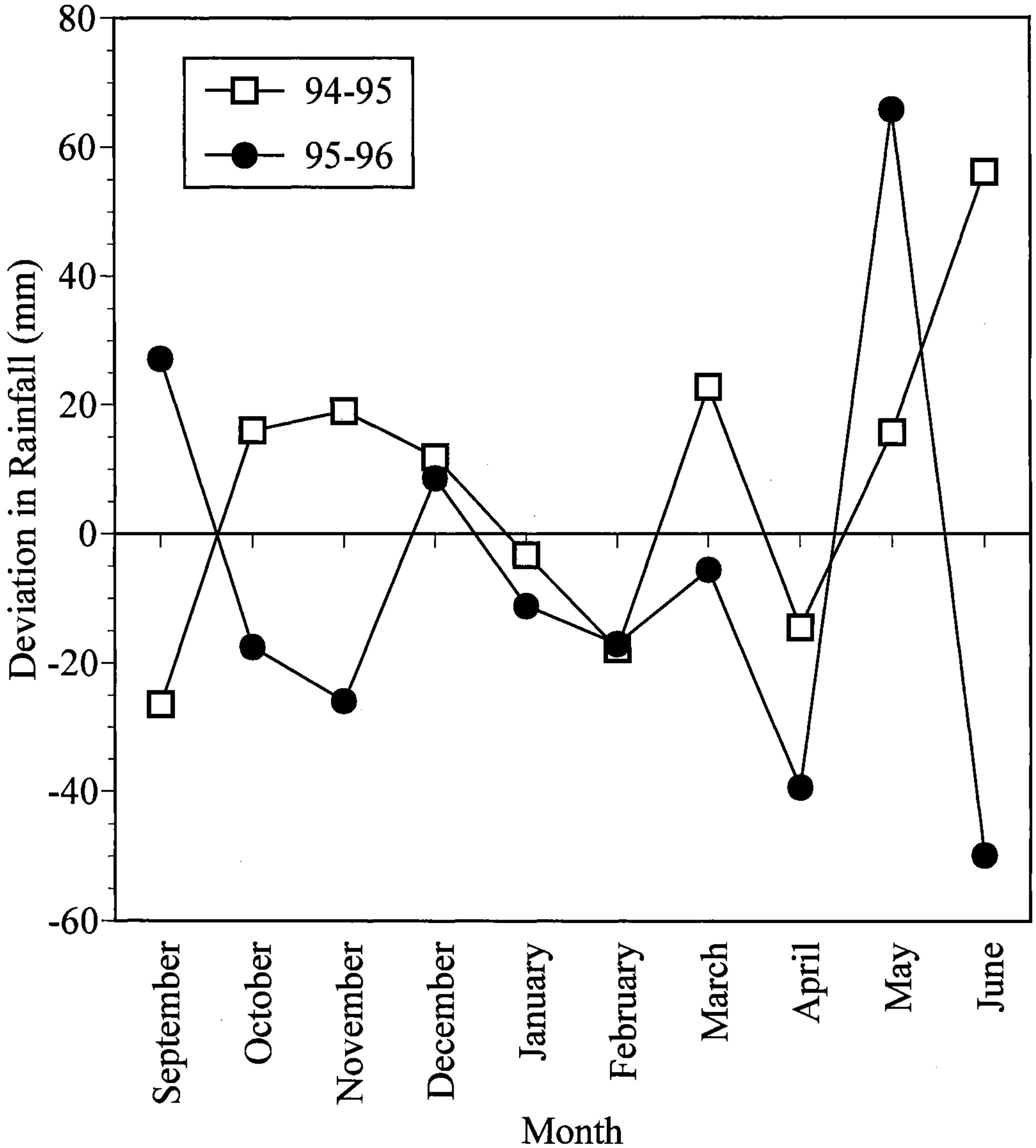

Figure 8. Monthly deviation of rainfall (mm) from 30 year averages (1961 – 1990). Data obtained from the National Oceanic and Atmospheric Administration (NOAA) for the city of Beaver, OK, approximately 10 km from the study site.

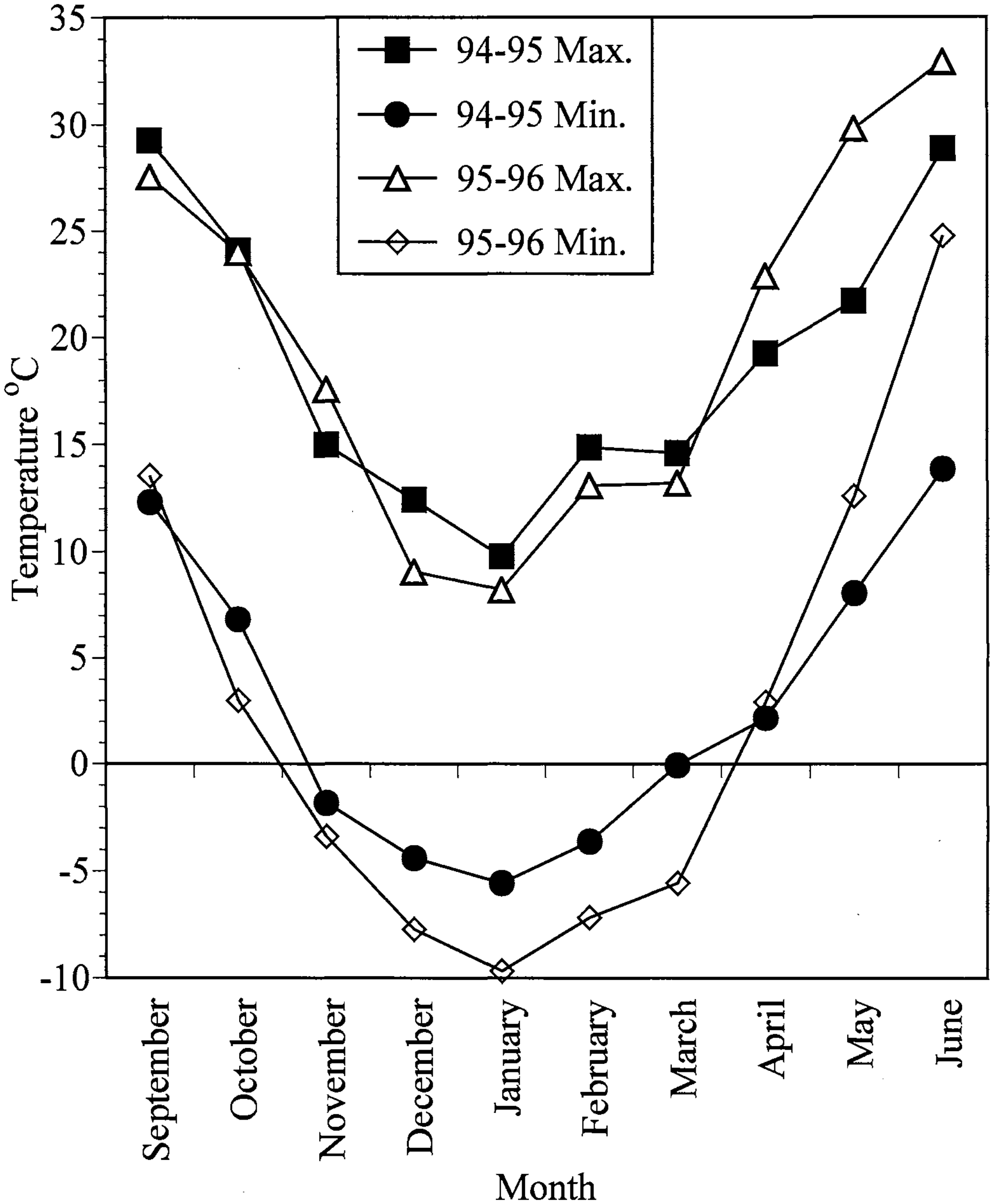

Figure 9. Monthly averages for maximum and minimum temperatures (°C). Data obtained from the NOAA for the city of Beaver, OK.

CHAPTER IV

GROUND BEETLE (COLEOPTERA: CARABIDAE) ASSEMBLAGES IN GRASSLANDS AND ADJACENT WHEAT FIELDS

Abstract

Ground beetles are polyphagous predators of cereal crop pests and are capable of regulating pest populations below economically damaging levels. Ground beetles generally reproduce either in fall or spring and may be habitat generalists or specialists. Ground beetles were captured in 1993 – 1994 at four sites and in 1996 – 1997 at two sites using pitfall traps positioned in grasslands, wheat fields, and along grassland-wheat field edges. Of 69 species collected, six species accounted for 75.5 % of the total number of beetles captured. The numbers of these species captured varied among years, seasons, and habitats. Species composition was most strongly influenced by season, followed by year, and then habitat (wheat vs. grassland). Ground beetles that reproduce in spring were separated from those producing young in autumn along the first axis of a canonical correspondence analysis (CCA). With the effects of season and year removed, ground beetles were classified with respect to habitat preference along axes one and two of a partial CCA. Based on the ordination by partial CCA, ground beetles were classified as either habitat generalists, wheat specialists, grassland specialists, or boundary specialists. Landscape structure was an important component in determining the spatial distribution of ground beetles.

Key Words: Insecta, predator, canonical correspondence analysis, community structure, *Triticum aestivum*, ecotone.

Introduction

Many species of ground beetles overwinter in grasses growing along borders adjacent to cereal grains and disperse into the fields in the spring (Sotherton 1984, 1985). Several studies have focused on the effects of grassy areas as winter reservoirs and points of dispersal for ground beetles into cereal fields (Gravesen and Toft 1987, Morris and Webb 1987, Thomas 1990, Dennis and Fry 1992, Frampton et al. 1995). After dispersing into the field, some ground beetles prey upon cereal pests such as the bird-cherry oat aphid, *Rhopalosiphum padi* L. and English grain aphid, *Sitobion avenae* F. (Edwards et al. 1979, Griffiths et al. 1985, Chiverton 1987) to the extent that some aggregate in areas of high aphid population density within a field (Sunderland and Vickerman 1980, Bryan and Wratten 1984). These ground beetles may assist in regulating aphid numbers below economically damaging levels (Potts and Vickerman 1974, Winder 1990, Ekbom et al., 1992, Holopainen and Helenius 1992).

Most of the studies mentioned above occurred in spring cereals, a time when agriculturally important species of ground beetles are active. Those studies were also conducted at higher latitudes where primarily spring season small grains are grown. In Oklahoma, which is located at a much lower latitude, the most important cereal crop is winter wheat (*Triticum aestivum* L). Winter wheat is planted in autumn and harvested the following spring. From autumn through mid-March the wheat is decumbent with the leaf blades close to the soil surface. The leaf blades are locations on wheat plants where aphids (such as greenbugs, *Schizaphis graminum* Rondoni) often feed, and ground beetles generally search for prey at the soil surface (Winder 1990). Thus, in addition to spring active ground beetles, autumn and winter active ground beetles may also be important predators of winter wheat pests (Potts and Vickerman 1974). Ground beetles have not been studied in winter wheat in Oklahoma.

While many ground beetles disperse into cereal grains from field edges, other species may remain near edge areas. Still others remain in the interiors of adjacent habitats (Wallin 1985). Species that routinely cross habitat edges are classified as habitat generalists or soft edge species. In contrast, species that rarely cross habitat edges are classified as habitat specialists or hard edge species (Duelli 1990). Species that generally remain at the boundary of adjacent habitats are classified as edge species.

Wheat fields and grasslands are prominent features in northcentral Oklahoma agricultural landscapes. These habitats, along with their edges, form landscape elements that potentially accommodate a variety of ground beetle species. Little is known about the spatial and temporal patterns of abundance of ground beetles in grasslands and adjacent wheat fields in Oklahoma. The objectives of this study are 1) to describe the species assemblages of ground beetles that occupy wheat fields, grasslands, and edges of these habitat areas; 2) to determine the seasonal patterns of occurrence of ground beetles during the winter wheat growing season; and 3) to assess seasonal changes in ground beetle assemblages in wheat fields, grasslands, and edges of these habitats during the winter wheat growing season in Oklahoma.

Materials and Methods

Study Sites

I established four study sites (numbers 1 – 4) in the autumn of 1993 and two study sites (numbers 5 – 6) in the autumn of 1996 in fields of winter wheat and adjacent grass pastures located in Noble County, Oklahoma. These sites were in northcentral Oklahoma, and within the tall grass prairie region of the southern Great Plains (Kaul 1986). The grasslands ranged in size from 8 ha to 61 ha, whereas the wheat fields ranged in size from 15 ha to 40 ha (Table 1). The grasslands at site 1 and site 2 abutted the same wheat field on opposite sides, however study sites were separated by at least 0.5 km.

Sampling with Pitfall Traps

Ground beetles were captured in grasslands, wheat fields, and grassland-wheat field boundaries using pitfall traps. These traps were selected for the study because they are easy to install, effective for capturing Carabidae, and work continuously (Halsall and Wratten 1988). These traps alone do not provide estimates of absolute density, rather they provide estimates of activity density (Greenslade 1964). Activity density may be more important than absolute density in relation to biological control of pests because active predators may be more likely to encounter prey than sedentary predators (Lenski 1982). In addition, sampling continuously over a period of weeks or months with pitfall traps effectively estimates relative abundance of species within a habitat and permits comparison of abundance among years or seasons in that habitat (Baars 1979).

Trap design was similar to that used by Morrill et al. (1990). In constructing the traps, I used Nalgene® polypropylene funnels (14.5 cm inside diameter) with 125 ml

Nalgene® plastic containers beneath to confine the ground beetles. To provide for easy exchange of containers, the screw top caps of the plastic containers were glued to the base of the funnels. I cut out the bottoms of the containers and replaced them with screen mesh (12.6 strands per cm) to permit water to pass through the container while retaining the ground beetles, and placed Deckem™ insecticide cattle ear tags (Active ingredient = permethrin) in the cups to kill the insects that were trapped. A preliminary study using traps with and without eartags indicated they had no effect on numbers of ground beetle captured (see Appendix A). For each trap, a PVC plastic pipe (13 cm inside diameter) was buried in the soil such that the top of the pipe was approximately 2 cm below the soil surface, which allowed setting the funnels at the soil surface. The PVC pipes supported the traps and prevented soil from collapsing around them. To increase the efficiency of capture of ground beetles, galvanized sheet metal strips (14 cm x 122 cm) were used as guides (Durkis and Reeves 1982). The guides were angled forward slightly and driven into the soil a few centimeters. The traps were positioned at the center of the guides.

In 1993 – 1994, barbed wire fences separated the grasslands and wheat fields. The landowners used the fences to confine cattle to the grasslands and wheat fields. I put steel-meshed panels (each panel was 1.5 m long x 1.2 m high) in a triangular pattern around all traps to prevent cattle from stepping into the traps. During the 1993 – 1994 study, it was determined that cattle avoided the traps and in 1996 – 1997 no fences were placed around the traps.

The arrangement of the pitfall trap network in grasslands, winter wheat fields, and grassland and wheat field edges is illustrated in Fig. 1. Traps were placed in wheat field interiors at 10 m, 25 m, and 50 m from the border. At the wheat field edge, traps were set at 60 cm, 120 cm, and 180 cm from the border. At the grassland edge, traps were placed at 30 cm, 60 cm, and 90 cm from the border. In the grassland interiors, traps were set at 10 m and 25 m from the border. Traps were checked weekly soon after wheat emerged from the soil in autumn until shortly before harvest the following spring.

Data Analysis

I used ANOVA to test for differences in the mean abundance of ground beetles and mean abundances of predominant ground beetle species. I focused the analysis on differences in seasonal occurrences and habitat choices. Ground beetles were classified as actively reproducing in spring, autumn, or at other times. Autumn active beetles included species captured from the beginning of trapping through December 21, winter active beetles included those captured from December 22 through March 21, and spring active beetles included those captured from March 22 through the end of trapping. If season changed from autumn to winter or from winter to spring during a sampling period, beetles captured during that week were applied to the season at the beginning of the sampling period. Ground beetles were also classified as habitat generalists or habitat specialists. I considered the wheat field, wheat field edge, grassland, and grass edge as distinct habitats, and totaled the numbers of ground beetles captured from traps positioned in these habitats. ANOVA was also used to test for significant differences among years, sites, seasons, and habitats in species richness, Shannon-Wiener species diversity, and species evenness (Begon et al. 1994). Species abundance data were transformed to natural logarithms prior to ANOVA to homogenize variances of numbers captured.

Due to the unbalanced study design among years and treatments, significance levels of main effects are reported for ground beetles despite the presence of significant interactions of year with treatments. Significance levels for main effects are reported because, as previously stated, the emphasis was placed on differences in seasonal occurrences and habitat choices. In addition, even sampling over several years (only two years in this study) may not be representative of what occurs in future years (Steel and Torrie 1980), thus inferences regarding effects of years may be invalid. Furthermore, the interaction between year and treatment may have little meaning if its size is small relative to the average effect of treatments (Gomez and Gomez 1984).

The computer program CANOCO™ (ter Braak 1987) was used to perform canonical correspondence analysis (CCA) on species abundance data. Canonical correspondence analysis relates species abundances to environmental variables and is a robust method for analyzing data from pitfall traps (Palmer 1993). I included the following 15 independent variables, year 1 (1993 – 1994), year 2 (1996 – 1997), autumn, winter, spring, site 1, site 2, site 3, site 4, site 5, site 6, wheat field, wheat field edge, grassland, and grass edge in CCA analyses. I used a partial CCA to focus on the effects of the four habitats on species abundances by using seasons, years, and sites as covariables and removing their effects prior to conducting CCA. All abundance data were transformed to square-roots prior to CCA analysis.

Results

Nearly 6000 ground beetles representing 69 species were captured. For each year, the mean numbers of ground beetles captured were calculated for each site, habitat, and season. The mean numbers captured for 1993 – 1994 and 1996 – 1997 did not differ significantly (Table 2). However, more beetles were captured in spring (Table 3) than in autumn or winter ($F = 70.71$; $df = 2, 32$; $P < 0.001$), and in wheat field interiors (Table 4) than in other habitats ($F = 8.82$; $df = 3, 12$; $P < 0.01$). Six of the 69 species accounted for 75.5 % of the total collected. The six dominant species were *Agonum punctiforme* Say, *Anisodactylus dulcicollis* LaFerté, *Bembidion castor* Lindroth, *B. nigripes* Kirby, *Harpalus pensylvanicus* DeGeer, and *Pterostichus chalcites* Say. Significantly more *A. punctiforme* were captured in 1993 – 1994 than in 1996 – 1997 ($F = 35.91$, $df = 1, 4$, $P < 0.01$) (Table 2). In addition, significantly more *A. punctiforme* were captured in wheat field interiors ($F = 5.20$, $df = 3, 12$, $P < 0.05$) than in other habitats (Table 4). *Anisodactylus dulcicollis* was caught primarily in 1996 – 1997 ($F = 20.46$, $df = 1, 4$, $P < 0.05$) (Table 2) and during spring ($F = 156.03$; $df = 2, 32$; $P < 0.001$) (Table 3). *Bembidion castor* and *B. nigripes* were captured significantly more often in wheat ($F = 23.27$, $df = 3, 12$, $P < 0.001$; $F = 22.42$, $df = 3, 12$, $P < 0.001$) during winter and spring ($F = 25.04$, $df = 2, 32$, $P < 0.001$; $F = 7.30$, $df = 2, 32$, $P < 0.01$) (Tables 3 and 4). *Pterostichus chalcites* was captured significantly more often in wheat ($F = 54.22$, $df = 3, 12$, $P < 0.001$) during spring ($F = 117.63$, $df = 2, 32$, $P < 0.001$) (Tables 3 and 4). In contrast, *H. pensylvanicus* was captured significantly more often in the habitat edges and grassland interiors (F =

6.78, df = 3, 12, P < 0.01) during autumn (F = 51.96, df = 2, 32, P < 0.001) (Tables 3 and 4).

Ten other species of ground beetles accounted for an additional 12.9 % of those captured including *Anisodactylus rusticus* Say, *Calathus opaculus* LeConte, *Calosoma affine* Chaudoir, *Chlaenius tomentosus* Say, *Cyclotrachelus torvus* LeConte, *Galerita janus* F., *Harpalus fulgens* Csiki, *Pasimachus elongatus* LeConte, *Scarites subterraneous* F., and *Stenolophus conjunctus* Say. These were classified as common species.

Nine of the 16 most common species reproduce in spring, two in autumn, and five were considered opportunistic in that they were captured consistently during all seasons. (Table 5). Consistent with the times of greatest abundance for dominant and common species, both species richness (F = 225.95, df = 2, 158, P < 0.001) and species diversity (F = 166.23, df = 2, 158, P < 0.001) were highest in spring and lowest in winter (Table 6), however there was no difference among seasons for species evenness.

Among dominant and common species, four species were classified as grassland species, two as edge species, five as wheat field species, and five as habitat generalists (Table 5). The edge class was based on numbers captured in both grassland and wheat edges. Generalist species represent ground beetles captured consistently in all habitats. Shannon-Wiener diversity was greater in the habitat edges and grassland interiors than in wheat (F = 4.93, df = 3, 12, P < 0.05) (Table 6). Species richness and species evenness did not differ significantly among the habitats.

Multivariate Analysis

The eigenvalues of the CCA measure the proportion of total variation in ground beetle abundance explained by their respective axes (ter Braak 1986, 1987, 1995). The eigenvalues, based on species relative abundances, for CCA axes 1 through 4 were 0.376, 0.299, 0.160, and 0.114. Axis one explained 31.4 % of the species-environment relationship, and together with axis 2, explained 56.4 % of the species-environment relationship. Axes 1 through 4 explained 79.3 % of the total species-environment relationship. A biplot of the environmental variables and species scores (sites not shown) shows that axis 1 represents a seasonal gradient in abundance (Fig. 2). Species names and abbreviations are given in Table 7. A relatively long arrow positioned close to an axis indicates a strong relationship with that axis (ter Braak 1986, Palmer 1993). Species positioned close to the arrows have a strong association with that variable. Assemblages that predominate in autumn and winter ordinated on the right side of axis 1, whereas spring assemblages ordinated on the left side of axis 1. Axis 2 separated ground beetle assemblages with respect to years, and hence, with respect to sites 1 – 4 (1993 – 1994) and sites 5 – 6 (1996 – 1997). The observed patterns of species relative abundances with respect to the environmental variables differed from random (Monte Carlo test statistic = 5.35, $P < 0.01$) (ter Braak 1987).

Partial CCA was employed to depict the effect of habitats on patterns of species abundance. In this partial CCA, the effects of years, seasons, and sites on species relative abundances were factored out as covariables. Only three canonical axes were calculated because only four environmental variables were defined. The eigenvalues for axes 1 through 3 were 0.130, 0.037, and 0.024. These values measured the amount of variation in species scores explained by their respective axes, with axis 1 explaining more variation in species scores than axes two or three. Of the variation in species composition remaining after factoring out the covariables, axis 1 explained 68.1 % of the species-environment relationship, and together with axis 2, explained 87.5 % of the remaining variation in species-environment relationship. A biplot of the habitat and species scores (only the 16 dominant and common species are shown) shows that assemblages in grassland and wheat fields separated along axis 1 (Fig. 3). The second axis separated species occupying grassland and wheat field edges from those occupying wheat fields and grassland. Species occurring at the origin of the axes represent habitat generalists while species occurring far from the origin represent habitat specialists. Grassland specialists ordinated in the positive space of axis 1 and 2, whereas wheat field specialists appear in the negative space of axis 1 and positive space of axis 2. Edge species (ground beetles occurring in both grassland edge and wheat field edge) ordinated in the negative space of axis 2.

Discussion

Annual variation in the number of ground beetle species and their abundances may be expected in both temporary and permanent habitats (den Boer 1986, Luff 1990). However, in this study the overall capture rate of ground beetles did not differ among years. Nor did species richness, evenness, or Shannon-Wiener diversity differ among years. Yet, among the 16 dominant and common species captured, some species varied widely in abundance. For example, *A. punctiforme* was most abundant in 1993 – 1994, but was uncommon in 1996 – 1997. In contrast, *A. dulcicollis* was uncommon in 1993 – 1994, but was abundant in 1996 – 1997. In research conducted over several years in agricultural landscapes, both Luff (1990) and den Boer (1986) found marked differences in annual abundance of several dominant species of ground beetles. They related much of the variation in abundance to the extent of species dispersal. Den Boer (1986) suggested that the abundance of species with limited capability for dispersal (walking) should be more consistent over years as opposed to those that disperse by flying, which should show higher rates of local extinction and recolonization. Both *A. punctiforme* and *A. dulcicollis* are macropterous and capable of flight (Lindroth 1966), although the extent to which they disperse by flight has not been investigated. Conversely, *B. castor* and *B. nigripes* are capable of flying (Lindroth 1963), but their abundances did not vary significantly between years.

This was a two-year study and long-term inferences may not be reliable, however my results suggest that extent of dispersal alone may not determine population abundance of ground beetles in habitats. Other factors such as variation in soil properties, micro- and macroclimatic conditions, intra- and interspecific competition, predation and parasitism, and chemical and cultural treatment of the land (e.g., pesticide use and tillage practices) probably affect ground beetle populations over time.

A fundamental principle in community ecology is the competitive exclusion principle, which states that similar species compete for similar resources and consequently are separated in space and/or time (Begon et al. 1994). One way that competition is reduced among insect species is for them to evolve life cycles that reduce direct interactions. Species abundance, species richness and species diversity were highest in the spring than in either autumn or winter. In addition, time of year was the primary factor in separating ground beetle assemblages in this study. However, enough species were captured during autumn and winter to form separate assemblages. In fact, two of the most dominant species, *B. castor* and *B. nigripes,* were often captured during autumn and winter.

The mating and ovipositional period is when male and female ground beetles are generally most active. This probably represents the period when competition for resources is greatest among ground beetle species (Loreau 1986, 1990). Some species may have highly restricted activity periods, whereas others may extend their activity over several weeks or months (Thiele 1977, den Boer and den Boer-Daanje 1990). Of the 16 dominant and common species, nine reproduced primarily in spring, while only two reproduced in autumn. Five species appear to complete several generations/year. Similarly, in central Alberta, Niemela et al. (1992) found more species and greater abundances of beetles in spring than during summer and autumn. This contrasts with studies of Rivard (1964, 1966) in Ontario, in which there was a preponderance of adults reproducing in autumn. In my study, *H. pensylvanicus* was a dominant autumn species. *Harpalus pensylvanicus* is widely distributed in North America (Bousquet and Larochelle 1993), and throughout its range appears consistently to be most abundant in autumn (Rivard 1964, 1966, Best et al. 1981). Also in my study, *P. chalcites* was captured predominantly in the spring of both years. *Pterostichus chalcites* is also widely distributed in North America (Bousquet and Larochelle 1993), and throughout its range appears consistently to be most abundant in spring (Best et al. 1981). Of the beetles I captured, *A. punctiforme*, *B. castor*, and *B. nigripes* were collected regularly over all three seasons and they seem to reproduce at opportunistic times.

Competition in the past could have resulted in the temporal asynchrony of life cycles for species of ground beetles, however whether observed temporal asynchrony is due entirely to interspecific competition has been questioned (Niemela 1993), and other biotic and abiotic factors such as avoidance of predators and parasites may be important selective forces also affecting life history traits (Andersen and Skorping 1991, Currie et al. 1996). It is difficult or impossible to prove that previous competition among ground beetles has resulted in temporal shifts in life cycles. But, Loreau (1990) suggested that competition may be significant only among the dominant species. As previously indicated, the findings in my study among dominant and common species activity periods are consistent with this hypothesis.

Some studies examining species composition of ground beetles among adjacent habitats have indicated that certain species exhibit a preference for one type over another, while other species appear indifferent to the habitats and occupy them with equal frequencies (Esau and Peters 1975, Best et al. 1981). In my study, species of ground beetles were separated spatially among habitat types and classified by habitat preference. However, when comparing the ordering of species in Fig. 3 with classification of species in Table 5, we see some similarities and discrepancies. Based on CCA, the dominant species, with the exception of *P. chalcites*, ordinated closer to the axes origins indicating they are habitat generalists. Of these dominant species, only *A. punctiforme* was classified as a habitat generalist. Even though the dominant species ordinated near the axes origins, most showed mild preferences for particular habitats, which agreed with the generalized habitat classification. For example, both *B. castor*, and *B. nigripes* were classified as preferring wheat fields and both ordinated on the wheat side of axis 1. Similarly, *A. dulcicollis* was classified as an edge species and ordinated near the grassland edge. *Harpalus pensylvanicus* was classified as a grassland species, and apparently prefers grassy habitats over wheat habitats. However, *H. pensylvanicus* ordinated near the axes origins indicating it to be a habitat generalist.

A dominant species that apparently has benefited from farming within its distribution is *P. chalcites*. This species clearly prefers wheat field interiors over the other habitats. Esau and Peters (1975) captured *P. chalcites* much more often in cornfields than in fence rows and prairies. *Pterostichus chalcites* may be regarded as a North American synanthropic species in that it shares a close association with human activities (Spence and Spence 1988).

Farther from the axes origins, there appears to be an association or specialization of common species with particular habitats. For example, *C. tomentosus* was strongly associated with grassland interiors and was classified as a grassland interior species. In addition, *C. opaculus* was strongly associated with grassland edge and was classified as an edge species. *Cyclotrachelus torvus* was classified as a grassland species, but seems to show a slight preference for the grassland edge. In contrast, *P. elongatus* was classified as generalist, however this species appeared to have a strong preference for grassland habitats. Also showing a discrepancy, *H. fulgens* was classified as a grassland species, but ordinated near the axes origins indicating it to be a habitat generalist. A somewhat peculiar situation, *S. subterraneous* was classified as a habitat generalist, but ordinated between grassland and wheat field interiors, thus appearing to avoid the edge habitats.

In this study, ground beetle assemblages were found to be separated seasonally and spatially in relation to wheat fields and adjacent grasslands. A small number of species accounted for a large portion of all ground beetles captured in all seasons and habitats. Many of the dominant and common species preferred to inhabit wheat fields over grasslands. It is not clear whether these dominant and common species overwinter in the grassy edges and disperse into the wheat fields, however their continuous seasonal activity and predatory nature makes them potential candidates as biological control agents of wheat pests.

Wissinger (1997) described four criteria for biological control agents to be effective in annual crop systems such as wheat. First, natural enemies should have sufficient overwintering sites available near the crops. Second, the crop field size to edge ratio should not be too great as to inhibit or delay natural enemies from reaching field centers. Third, the benefits from boundaries (e.g., overwintering sites, refuge from pesticides, and shelter) should out-weigh their costs (e.g., reduced dispersal among habitats). Fourth, broad-spectrum pesticides should not eliminate natural enemies once they have established in the crop fields. The dominant and common species that preferred wheat habitats, *A. punctiforme*, *B. castor*, *B. nigripes*, *P. chalcites,* and *C. affine* are potential biological control agents of wheat pests. Because wheat fields vary considerably in size in the great plains, it is important to determine whether these ground beetles overwinter in adjacent grassland edges, and if they do, how far they will disperse into the wheat field interior (1 and 2 of Wissinger 1997). Equally important is to determine which species have evolved life cycles that are completed exclusively in crop fields. This aspect of effective biological control strategies was not covered by Wissinger (1997), and seems relevant for species such as *P. chalcites*. For these species, their survival and reproduction depends entirely on available prey in the wheat fields.

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Table 1. Sizes in hectares of wheat fields and grasslands at the six study sites.

Habitat	Site 1	Site 2*	Site 3	Site 4	Site 5	Site 6
Wheat Field	15	15	20	34	18	40
Grassland	24	40	44	61	8	16

*The wheat field at site 1 and site 2 was the same field.

Table 2. Least square mean abundances (± 1 SE) for ground beetles captured in 1993 – 1994 (N = 48) and 1996 – 1997 (N = 24). Means calculated per site per season per habitat.

	Year	
Species	1993 – 1994	1996 – 1997
All Species	27.33 ± 2.74 a	33.27 ± 3.87 a
A. punctiforme	9.28 ± 1.02 a	0.85 ± 1.45 b
A. dulcicollis	0.62 ± 0.56 a	4.64 ± 0.79 b
B. castor	5.55 ± 0.78 a	3.48 ± 1.11 a
B. nigripes	4.45 ± 1.03 a	6.24 ± 1.45 a
H. pensylvanicus	0.78 ± 0.29 a	2.60 ± 1.21 a
P. chalcites	2.04 ± 0.79 a	2.38 ± 1.44 a

Values within rows with different letters are significantly different.

Table 3. Mean (± 1 SE, N = 24) numbers captured per site per habitat for all species and dominant species by season. Ryan-Einot-Gabriel-Welsch multiple range test used to determine mean differences with respect to season.

	Season		
Species	Autumn	Winter	Spring
All Species	18.91 ± 2.57 a	20.75 ± 2.81 a	48.28 ± 6.59 b
A. punctiforme	5.46 ± 1.43 a	6.74 ± 2.08 a	7.21 ± 1.73 a
A. dulcicollis	0.07 ± 0.03 a	0.00 ± 0.00 a	5.81 ± 1.51 b
B. castor	1.45 ± 0.48 a	6.65 ± 1.38 b	6.48 ± 1.61 b
B. nigripes	3.26 ± 0.68 a	5.03 ± 0.76 b	6.85 ± 2.51 ab
H. pensylvanicus	3.99 ± 1.21 a	0.06 ± 0.03 b	0.12 ± 0.05 b
P. chalcites	0.07 ± 0.06 a	0.02 ± 0.02 a	6.37 ± 1.86 b

Values within rows with different letters are significantly different.

Table 4. Mean (± 1 SE, N = 18) numbers captured per site per season for all species and dominant species by habitat. Ryan-Einot-Gabriel-Welsch multiple range test used to determine mean differences with respect to habitat.

	Habitat			
Species	Grass	Grass Edge	Wheat Edge	Wheat Interior
All Species	19.25 ± 2.00 a	22.35 ± 3.64 a	29.15 ± 4.63 a	46.50 ± 9.05 b
A. punctiforme	4.42 ± 1.07 a	3.30 ± 0.61 a	6.44 ± 2.11 a	11.72 ± 2.93 b
A. dulcicollis	1.36 ± 0.67 a	2.50 ± 1.57 a	2.63 ± 1.53 a	1.35 ± 0.69 a
B. castor	2.00 ± 0.52 a	2.63 ± 0.60 a	5.22 ± 1.27 b	9.59 ± 2.37 c
B. nigripes	1.78 ± 0.56 a	2.89 ± 0.46 b	5.50 ± 0.87 c	10.02 ± 3.18 c
H. pensylvanicus	1.78 ± 0.94 a	2.43 ± 1.47 a	0.94 ± 0.47 ab	0.41 ± 0.19 b
P. chalcites	0.17 ± 0.08 a	0.31 ± 0.14 a	2.07 ± 0.92 b	6.05 ± 2.48 c

Values within rows with different letters are significantly different.

Table 5. The generalized reproductive seasons and habitat preferences for the 6 dominant and 10 common species of ground beetles.

Reproductive Season	Habitat Preference			
	Grassland	Edge	Wheat Field	Generalist
Autumn	*H. pensylvanicus*	*C. opaculus*		
Other	*C. torvus*		*B. castor*	*A. punctiforme*
			B. nigripes	*S. conjunctus*
Spring	*C. tomentosus*	*A. dulcicollis*	*P. chalcites*	*A. rusticus*
	H. fulgens		*C. affine*	*P. elongatus*
			G. janus	*S. subterraneous*

Table 6. Mean (± 1 SE) values for species richness, Shannon-Wiener's species diversity index, and species evenness index with respect to season and habitat. Ryan-Einot-Gabriel-Welsch multiple range test used to determine mean differences with respect to habitat.

		Community Parameter		
	N	Species Richness	Species Diversity	Species Evenness
Season				
Autumn	66	5.61 ± 0.31 a	1.54 ± 0.05 a	0.95 ± 0.003 a
Winter	66	4.00 ± 0.19 b	1.25 ± 0.04 b	0.94 ± 0.004 a
Spring	66	12.18 ± 0.59 c	2.30 ± 0.05 c	0.95 ± 0.002 a
Habitat				
Grassland	36	6.89 ± 0.59 a	1.72 ± 0.09 ab	0.95 ± 0.005 a
Grass Edge	54	7.72 ± 0.65 a	1.80 ± 0.07 a	0.95 ± 0.003 a
Wheat Edge	54	7.24 ± 0.67 a	1.67 ± 0.09 ab	0.95 ± 0.004 a
Wheat Fields	54	7.07 ± 0.74 a	1.60 ± 0.09 b	0.94 ± 0.004 a

Values within columns with different letters are significantly different.

Table 7. Species names of abbreviations (Abbr.) used in CCA and partial CCA biplots.

Species	Abbr.	Species	Abbr.
Abacidus permundus Say	Abp	*Clivina bipustulata* F.	Clb
Agonum nutans Say	Agn	*C. postica* LeConte	Clp
A. pallipes F.	Agp	*Colliuris pensylvanica* L.	Cop
A. punctiforme Say	Apu	*Cratacanthus dubius* Beauvois	Crd
Amara convexa LeConte	Amc	*Cyclotrachelus constrictus* Say	Cyc
A. cupreolata Putzeys	Acu	*C. torvus* LeConte	Cyt
A. impuncticollis Say	Ami	*Cymindis laticollis* Say	Cyl
A. musculis Say	Amm	*C. pilosa* Say	Cyp
A. obesa Say	Amo	*Dicaelus elongatus* Bon	Die
A. pennsylvanica Hayward	Amp	*Discoderus parallelus* Haldeman	Dip
A. rubrica Haldeman	Amr	*Dyschiriodes globulosus* Say	Dyg
Anisodactylus carbonarius Say	Anc	*Elaphropus dolosus* LeConte	Eld
A. dulcicollis LaFerté	And	*E. granarius* Dejean	Elg
A. harpaloides LaFerté	Anh	*Galerita atripes* LeConte	Gaa
A. merula Germar	Anm	*G. janus* F.	Gaj
A. ovularis Casey	Ano	*Harpalus amputatus* Say	Haa
A. rusticus Say	Anr	*H. caliginosus* F.	Hac
A. sanctaecruscis F.	Ans	*H. desertus* LeConte	Had
Apristus latens LeConte	Apl	*H. faunus* LeConte	Haf
Atranus pubescens Dejean	Atp	*H. fulgens* Csiki	Hfu
Bembidion castor Lindroth	Bec	*H. pensylvanicus* DeGeer	Hpe
B. nigripes Kirby	Ben	*Microlestes linearis* LeConte	Mil
Calathus opaculus LeConte	Cao	*Notiophilus novemstriatus* LeConte	Non
Calosoma affine Chaudoir	Caf	*Notiobia terminata* Say	Not
C. externum Say	Cae	*Olisthopus parmatus* Say	Olp
Chlaenius nemoralis Say	Chn	*Pasimachus elongatus* LeConte	Pae
C. pennsylvanicus Say	Chp	*Pterostichus chalcites*	Ptc
C. platyderus Chaudoir	Cpl	*P. femoralis* Kirby	Ptf
C. sericeus Forst	Chs	*Scaphinotus cavicollis* Say	Scc
C. tomentosus Say	Cht	*Scarites subterraneus* F.	Scs
C. vafer LeConte	Chv	*Semiardistomis viridis* Say	Sev
Cicindela denverensis Casey	Cid	*Stenolophus comma* F.	Stc
C. punctulata Olivier	Cip	*S. conjunctus* Say	Sco
C. scutellaris Say	Cis	*S. ochropezus* Say	Sto
		Stenomorphus rotundatus LeConte	Str

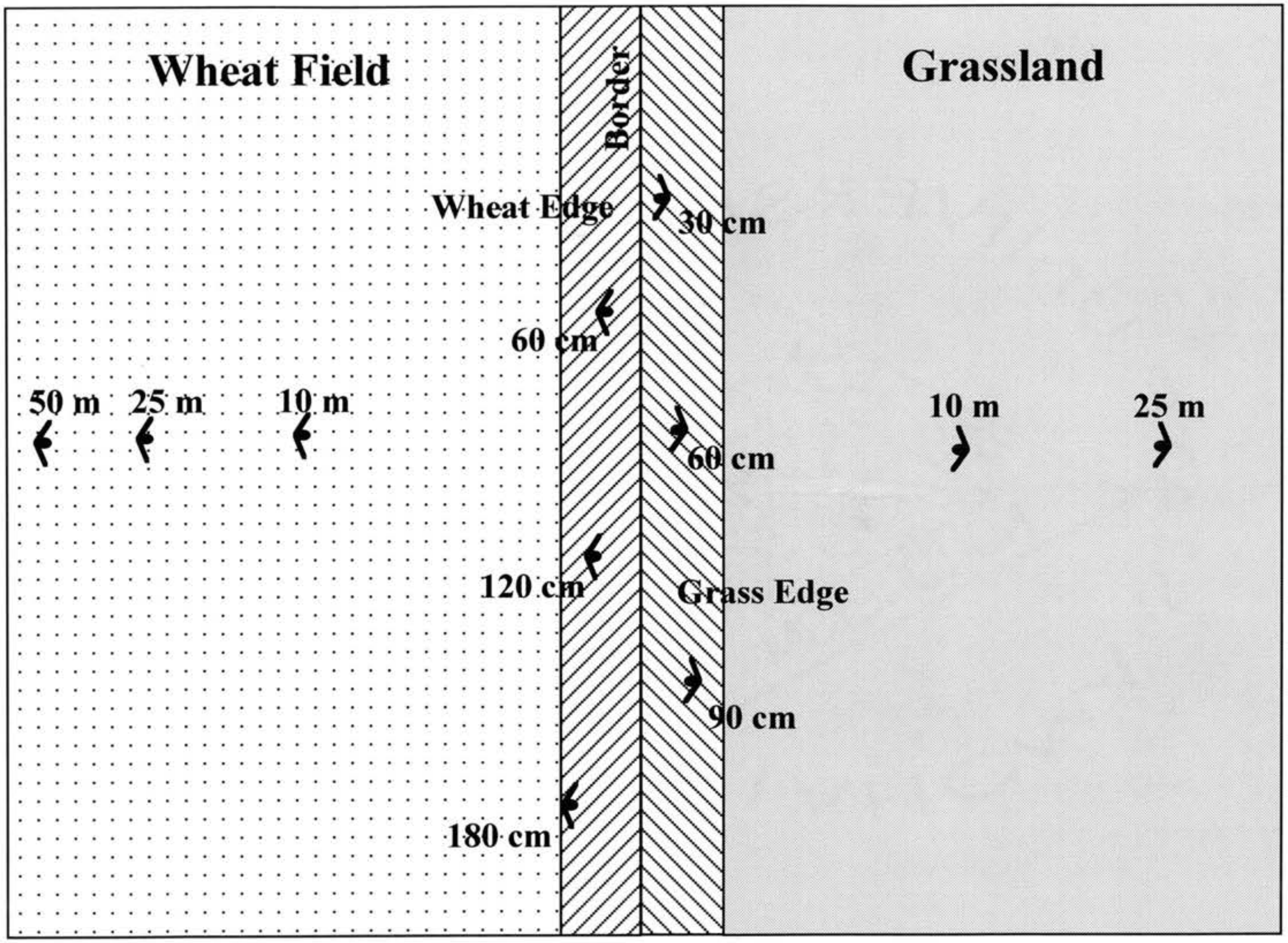

Figure 1. Arrangement of guided pitfall traps in wheat fields, grasslands, and their edges. Traps were placed at varying distances from the border and facing the border. The border represented an abrupt change in vegetation from wheat to grasses.

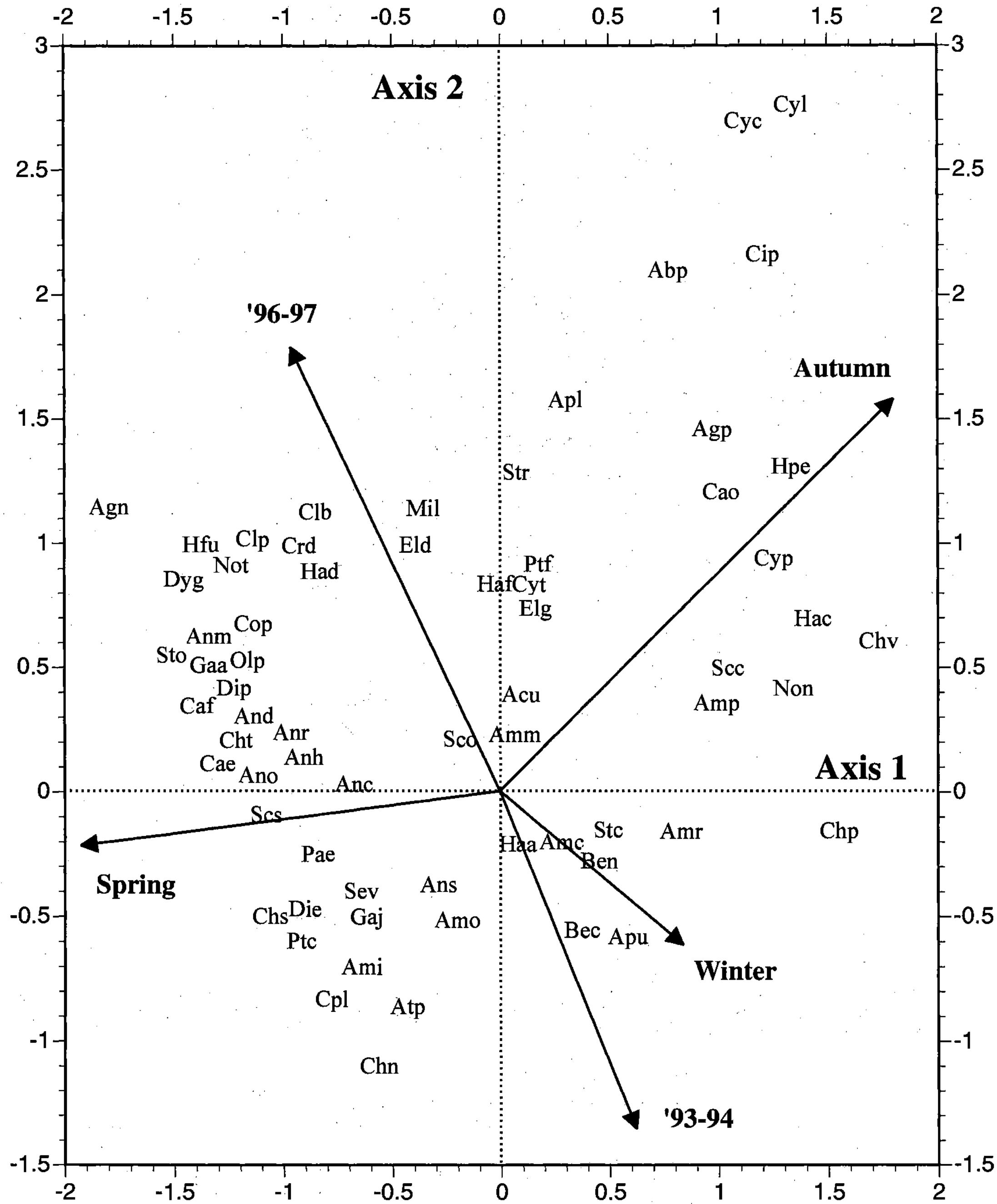

Figure 2. Biplot of ground beetle abundances and the most important environmental variables from CCA. The abbreviation of species names are plotted and complete names are listed in Table 7. Environmental variables are represented by arrows.

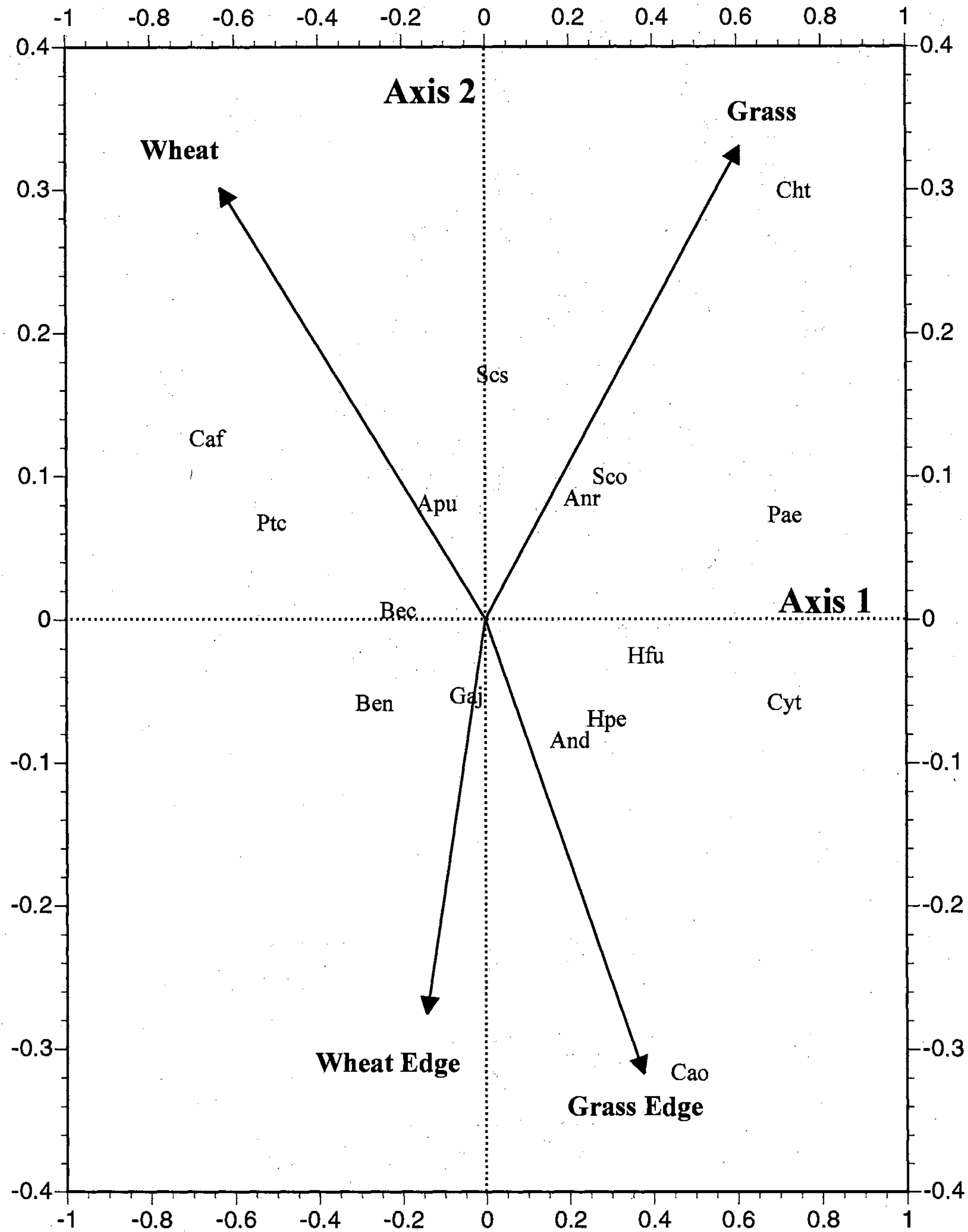

Figure 3. Biplot of 6 dominant and 10 common ground beetle abundances and environmental variables from a partial CCA. The abbreviation of species names are plotted and complete names are listed in Table 7. Environmental variables are represented by arrows.

CHAPTER V

GROUND BEETLE (COLEOPTERA: CARABIDAE) ASSEMBLAGES IN RIPARIAN STRIPS AND ADJACENT WHEAT FIELDS

Abstract

Ground beetles are polyphagous predators of cereal crop pests and are capable of regulating pest populations below economically damaging levels. Ground beetles generally reproduce either in fall or spring and may be habitat generalists or specialists. Ground beetles were captured in spring 1995 at four sites, autumn through spring 1995 – 1996 at four sites, and autumn through spring 1996 – 1997 at two sites using pitfall traps positioned in riparian strips, wheat fields, and along riparian-wheat field edges. Of 45 species collected in autumn, six species accounted for 64 % of the total abundance. Of 36 species collected in winter, six species accounted for 84 % of the total abundance. Of 101 species collected in spring, six species accounted for 56 % of the total abundance. The numbers of these ground beetles captured varied among years and habitats. Species composition was most strongly related to season, followed by year, and then habitat (wheat vs. riparian strip). Ground beetles that reproduce in spring were separated from those reproducing in autumn along the first axis of a canonical correspondence analysis (CCA). With the effects of season and year removed, ground beetles were classified with respect to habitat preference along axes one and two of a partial CCA. Based on the ordination by partial CCA, ground beetles were classified as either habitat generalists, wheat specialists, riparian specialists, or boundary specialists. Landscape structure was an important component in determining the spatial distribution of ground beetles.

Key Words: Insecta, predator, canonical correspondence analysis, community structure, *Triticum aestivum*, ecotone.

Introduction

Riparian strips, because of their sinuous patterns across a matrix of grass pastures and agricultural fields, are distinctive features of Oklahoma landscapes. They serve many important ecological functions, including dispersal corridors for forest inhabiting animals and plants (Forman and Godron 1986, Malanson 1993). Riparian strips may also serve as permanent habitats for animals (Spence 1979), and consequently as a source of individuals to disperse and colonize surrounding habitats (Malanson 1993). Ground beetles are polyphagous predators, and many species overwinter in grassy edges adjacent to cereal grains and disperse into the fields in the spring (Sotherton 1984, 1985). The edges of riparian strips are often composed of grasses, shrubs, and small trees and serve as overwintering sites and points of dispersal for ground beetles. While several studies have focused on the effects of natural and artificially maintained grassy areas as winter reservoirs and points of dispersal for ground beetles into cereal grains (Gravesen and Toft 1987, Morris and Webb 1987, Thomas 1990, Dennis and Fry 1992, Frampton et al. 1995), little is known about habitat use of ground beetles in naturally occurring riparian strips and adjacent cereal fields. It is known, however, that after dispersing into cereal fields, some ground beetles eat cereal pests such as the bird-cherry oat aphid, *Rhopalosiphum padi* L. and English grain aphid, *Sitobion avenae* F. (Edwards et al. 1979, Griffiths et al. 1985, Chiverton 1987). Some species are known to aggregate in areas of high aphid population density within fields and possibly exert spatially density dependent mortality on aphid population (Sunderland and Vickerman 1980, Bryan and Wratten 1984). These ground beetles may assist in maintaining aphid numbers below economically damaging levels (Potts and Vickerman 1974, Winder 1990, Ekbom et al., 1992, Holopainen and Helenius 1992).

Most of the studies mentioned above occurred in spring cereals, a time when agriculturally important species of ground beetles are active. Those studies were also conducted at higher latitudes where primarily spring season small grains are grown. In Oklahoma, which is located at a much lower latitude, the most important cereal crop is winter wheat (*Triticum aestivum* L). Winter wheat is planted in autumn and harvested the following spring. From autumn through mid-March the wheat is decumbent with the leaf blades close to the soil surface. The leaf blades are locations on wheat plants where aphids (e.g., *Schizaphis graminum* Rondoni) often feed, and ground beetles generally search for prey at the soil surface(Winder 1990). Thus, in addition to spring active ground beetles, autumn and winter active ground beetles may also be important predators of winter wheat pests (Potts and Vickerman 1974). Ground beetles have not been studied in winter wheat in Oklahoma.

Although many ground beetles disperse into cereal fields from field edges, other species may remain near field edges, or in the interiors of adjacent habitats (Wallin 1985). Species that routinely cross habitat edges are classified as habitat generalists or soft edge species. In contrast, species that rarely cross habitat edges are classified as habitat specialists or hard edge species (Duelli 1990). Species that generally remain at the boundary of adjacent habitats are classified as edge species.

Wheat fields and riparian strips are prominent features in northcentral Oklahoma agricultural landscapes. These ecosystems, along with their edges, form landscape elements that potentially accommodate a variety of ground beetle species. Little is known about the spatial and temporal patterns of abundance of ground beetles in riparian strips and adjacent wheat fields in Oklahoma. The objectives of this study were, 1) to determine the species composition of ground beetle assemblages in wheat fields and adjacent riparian strips, and 2) to determine the degree to which these species occupy wheat fields and riparian strips. Specifically, I trapped ground beetles throughout the growing season in each of these potential habitats. I used the data to determine the seasonal patterns of occurrence and abundance of ground beetles during the winter wheat growing season and to assess seasonal changes in ground beetle assemblages in wheat fields, wheat field edges, riparian edges, and riparian strips.

Materials and Methods

Study Sites

I established four study sites (numbers 1 – 4) in the spring of 1995 and again in the autumn of 1995 on winter wheat and adjacent riparian strips located in Payne County, Oklahoma. Wheat failed at sites 2 – 4 due to drought and heavy infestations of *S. graminum*. Three additional sites (numbers 5 – 7) were established in early March 1996. Sites 1 – 7 were situated along Stillwater Creek. Two study sites (numbers 8 and 9) were established in the autumn of 1996 on winter wheat and adjacent riparian strips located along unnamed creeks in Noble County, Oklahoma. The wheat fields ranged in size from 3.7 ha to 40 ha. Study sites 5 and 6 were located on opposite sides of Stillwater Creek while all other sites were separated by at least 0.5 km.

Sampling with Pitfall Traps

Ground beetles were captured in adjacent riparian strips, wheat fields, and their edges using pitfall traps. These traps were selected for the study because they are easy to install, effective for capturing Carabidae, and work continuously (Halsall and Wratten 1988). Numbers generated from pitfall trap catches alone do not provide estimates of absolute density, rather they provide estimates of activity densities (Greenslade 1964). Activity density may be more important than absolute density in relation to biological control of pests because active predators may be more likely to encounter prey than sedentary predators (Lenski 1982). In addition, sampling continuously over a period of weeks or months with pitfall traps provides data for effectively estimating relative abundance of species, and abundances of particular species within a habitat for comparison of abundance among years or seasons in that habitat (Baars 1979).

Trap design was similar to that used by Morrill et al. (1990). In constructing the traps, I used Nalgene® polypropylene funnels (14.5 cm inside diameter) with 125 ml Nalgene® plastic containers beneath to confine the ground beetles. To provide for easy exchange of containers, the screw top caps of the plastic containers were glued to the base of the funnels. I cut out the bottoms of the containers and replaced them with screen mesh (12.6 strands per cm) to permit water to pass through the container while retaining the ground beetles, and placed Deckem™ insecticide cattle ear tags (Active ingredient = permethrin) in the cups to kill the insects that were trapped. A preliminary study using traps with and without eartags indicated they had no effect on ground beetle catch (see Appendix A). For each trap, a PVC plastic pipe (13 cm inside diameter) was buried in the soil such that the top of the pipe was approximately 2 cm below the soil surface, which allowed setting the funnels at the soil surface. The PVC pipes supported the traps and prevented soil from collapsing around them. To increase the efficiency of capture of ground beetles, galvanized sheet metal strips (14 cm x 122 cm) were used as guides (Durkis and Reeves 1982). The guides were angled forward slightly and driven into the soil a few centimeters. The traps were positioned at the center of the guides.

The arrangement of the pitfall trap network in riparian strips, winter wheat fields, and riparian and wheat field edges is illustrated in Fig. 1. Traps were placed in the wheat fields at 10 m, 25 m, and 50 m from the border. At the wheat field edge, traps were set at 60 cm, 120 cm, and 180 cm from the border. At the riparian edge, traps were placed at 30 cm, 60 cm, and 90 cm from the border. In the riparian strips, traps were set at 3 m and 5.5 m from the border. Traps were checked weekly in the spring 1995 and soon after wheat emerged from the soil in autumn until shortly before harvest the following spring in 1995 – 1996 and 1996 – 1997.

Data Analysis

I used ANOVA to test for differences in mean abundance of all ground beetles and mean abundances of predominant ground beetle species. I separated the occurrence of ground beetles by season and focused the analysis on differences in habitat choice. Ground beetles were classified as reproducing in spring, autumn, or at other times. Autumn active beetles included those captured from the beginning of trapping in early October through December 21, winter active beetles included those captured from December 22 through March 21, and spring active beetles included those captured from

March 22 through the end of trapping in early June. If a change of season occurred during a sampling period, beetles captured during that week were applied to the season at the beginning of the sampling period. Ground beetles were also classified as habitat generalists or habitat specialists. I considered wheat, wheat edge, riparian edge, and riparian strips as distinct habitats, and pooled the numbers of ground beetles captured from traps positioned in these habitats. Species abundance data were transformed to natural logarithms to homogenize variances of numbers captured.

Due to the unbalanced study design among years and treatments, ground beetles collected in autumn, winter, and spring were analyzed separately. Also, significance levels of main effects are reported for ground beetles in addition to the presence of significant interaction of year with habitat. Significance levels for main effects are reported because, as previously stated, 1996 was an aberrant year in terms of precipitation, and consequently had adverse effects on wheat production as well as other flora and fauna in Oklahoma. In addition, even sampling over several years (only two years in this study) may not be representative of what occurs in future years (Steel and Torrie 1980), thus inferences regarding effects of years may be invalid. Furthermore, the interaction between year and treatment may have little meaning if its size is small relative to the average effect of treatments (Gomez and Gomez 1984).

The computer program CANOCO™ (ter Braak 1987) was used to perform canonical correspondence analysis (CCA) on species abundance data. Canonical correspondence analysis relates species abundances to environmental variables and is a robust method for analyzing data from pitfall traps (Palmer 1993). I included the following 19 independent variables, year 1 (spring 1995), year 2 (1995 – 1996), year 3 (1996 – 1997), autumn, winter, spring, site 1, site 2, site 3, site 4, site 5, site 6, site 7, site 8, site 9, wheat field, wheat field edge, riparian edge, and riparian strip in CCA analyses. I used a partial CCA to focus on the effects of the four habitats on species abundances by using seasons, years, and sites as covariables and removing their effects prior to conducting CCA. All abundance data were transformed to square-roots prior to CCA analysis.

Results

Nearly 9200 ground beetles representing 103 species were captured during the study (Table 1). For each season, the mean numbers of ground beetles captured were calculated for each year by site and habitat. During autumn in 1995 and 1996, a total of 599 ground beetles were captured, representing 45 species. The mean number of beetles captured per site over all sampling dates was 9.1 (1 SE = 1.4) (Table 1). The mean abundance of beetles captured per site per sampling date in autumn during 1995 and 1996 did not differ significantly (Table 2). More beetles were captured in riparian strips than in habitat edges and wheat interiors ($F = 12.44$, $df = 3, 12$, $P < 0.001$) (Table 3). There was a significant interaction of year with habitat ($F = 6.09$, $df = 3, 12$, $P < 0.01$), which appeared to be due to relative greater numbers captured in riparian strips in 1996 than in 1995 (Fig. 2).

Six of the 45 species collected in autumn accounted for 64 % of total collections. The six species, which I classify as dominant autumn species, were *Agonum pallipes* F., *Calathus opaculus* LeConte, *Galerita janus* F., *Harpalus caliginosus* F., *H. pensylvanicus* DeGeer, and *Notiophilus novemstriatus* LeConte. The mean abundances per site per sampling date for these species by year are in Table 2, and by habitat in Table 3. *Calathus opaculus* was captured significantly more often in riparian habitats (F = 8.18, df = 3, 12, P < 0.01) than in wheat habitats, and *G. janus* was captured significantly more frequently in riparian and wheat edge habitats (F = 3.91, df = 3, 12, P < 0.05) than in riparian edge and wheat interior (Table 3). There was a significant interaction of year with habitat (F = 4.27, df = 3, 12, P < 0.05) for *H. pensylvanicus* and appears due to relative greater numbers captured in riparian strips in 1996 (Fig. 3). For *N. novemstriatus*, mean abundance was greater in 1996 than in 1995 (F = 45.58, df = 3, 4, P < 0.01) (Table 2), and significantly more were captured in riparian interior and wheat edge habitats (F = 5.24, df = 3, 12, P < 0.05) than in riparian edge and wheat interior habitats (Table 3). These relative differences resulted in a significant interaction of year with habitat (F = 5.55, df = 3, 12, P < 0.05).

During the winters of 1996 and 1997, a total of 713 ground beetles were captured, representing 36 species. The mean number captured per site per sampling date for both years was 8.1 (1 SE = 1.2) (Table 1). Significantly more beetles were captured in the winter of 1997 than in 1996 (F = 19.67, df = 1, 6, P < 0.01) (Table 4). There were no significant differences in mean abundances of ground beetles captured among habitats (Table 5). Six of the 36 species collected in winter accounted for 84 % of total abundance. The six species, which I classify as dominant winter species, were *Agonum pallipes*, *A. punctiforme* Say, *Bembidion castor* Lindroth, *B. nigripes* Kirby, *N. novemstriatus*, and

Stenolophus conjunctus Say. The mean abundances per site per sampling date for these species by year are in Table 4, and by habitat in Table 5. The mean abundances for *B. castor* and *B. nigripes* were greater in 1997 than in 1996 (F = 45.81, df = 1, 6, P < 0.001; F = 1002.17, df = 1, 6, P < 0.001) (Table 4). There were no differences in mean abundances among habitats for *B. castor*, however for *B. nigripes,* mean abundances were significantly greater in the wheat edge habitat (F = 12.76, df = 3, 18, P < 0.001) followed by wheat field interior and riparian edge, and then riparian habitats (Table 5). For *B. nigripes*, there was also a significant interaction of year with habitat (F = 8.40, df = 3, 18, P < 0.01). For *N. novemstriatus*, significantly more beetles were captured in riparian and edge habitats (F = 4.88, df = 3, 18, P < 0.05) than in wheat field interiors (Tables 5). The mean abundance for *S. conjunctus* was significantly greater in 1997 than in 1996 (F = 33.89, df = 1, 6, P < 0.001) (Table 4). Additionally, mean abundances were greater in riparian interiors and wheat field edges (F = 21.76, df = 3, 18, P < 0.001) than in riparian edges and wheat field interiors (Table 5), which may have resulted in the significant interaction of year with habitat (F = 18.51, df = 3, 18, P < 0.001).

During spring in 1995, 1996, and 1997, a total of 7869 ground beetles were captured, representing 101 species. The mean number captured per site per sampling date for the three years was 65.0 (1 SE = 5.0) (Table 1). There were no significant differences in mean abundances of ground beetles captured among years (Table 6). More beetles were captured in wheat habitats than in riparian habitats (F = 7.79, df = 3, 24, P < 0.001) (Table 7). There was a significant interaction of year with habitat (F = 3.34, df = 6, 24, P < 0.001) that appears due to relative greater numbers captured in wheat habitats and riparian strips in 1997 (Fig. 4). Six of 101 species collected in winter accounted for 56 % of total abundance. The six species, which I classify as dominant spring species, were *Anisodactylus dulcicollis* LaFerté, *B. castor*, *B. nigripes*, *Clivina bipustulata* F., *G. janus*, and *Pterostichus chalcites* Say. The mean abundances per site per sampling date for these species by year are in Table 6, and by habitat in Table 7. Significantly more *A. dulcicollis* were captured in 1997 ($F = 46.29$, $df = 2, 8$, $P < 0.001$), than in 1995 and 1996 (Table 6). For *A. dulcicollis,* there was a significant interaction of year with habitat ($F = 2.70$, $df = 6, 24$, $P < 0.05$), and appears due to relative greater numbers captured in wheat fields and riparian strips in 1997 (Fig. 5). The mean abundances for *B. castor* and *B. nigripes* were significantly greater in 1997 than in 1995 and 1996 ($F = 13.90$, $df = 2, 8$, $P < 0.01$; $F = 30.83$, $df = 2, 8$, $P < 0.001$) (Table 6). These two species were also significantly more abundant in wheat habitats ($F = 12.05$, $df = 3, 24$, $P < 0.001$; $F = 17.42$, $df = 3, 24$, $P < 0.001$) than in riparian habitats (Table 7). For *B. nigripes*, the relative differences in mean abundances among years and habitats may have resulted in the significant interaction of year with habitat ($F = 4.13$, $df = 6, 24$, $P < 0.01$). The mean abundances for *C. bipustulata* were significantly greater in 1995 and 1997 than in 1996 ($F = 13.94$, $df = 2, 8$, $P < 0.01$) (Table 6). *Clivina bipustulata* was also captured significantly more frequently in habitat edges than in habitat interiors ($F = 5.60$, $df = 3, 24$, $P < 0.01$) (Table 7), and the relative differences in mean abundances among years and habitats may have resulted in the significant interaction of year with habitat ($F = 6.78$, $df = 6, 24$, $P < 0.001$). For *P. chalcites*, significantly more were captured in wheat field interiors ($F = 13.29$, $df = 3, 24$, $P < 0.01$) than in other habitats (Table 7).

In addition to dominant ground beetle species captured in autumn, winter, and spring, several other species were captured in sufficient numbers to classify by habitat preference. During autumn, 3 other species of ground beetles accounted for an additional 10 % of captures. These 3 species are *A. punctiforme*, *Cicindela punctulata* Olivier, and *Cyclotrachelus torvus* LeConte. During winter, 3 other species of ground beetles accounted for an additional 7 % of captures. These 3 species are *Elaphropus granarius* Dejean, *G. janus*, and *Stenolophus comma* F. During spring, 12 other species of ground beetles accounted for an additional 26 % of captures. These 12 species are *A. punctiforme*, *Anisodactylus merula* Germar, *A. rusticus* Say, *Calathus opaculus* LeConte, *Calosoma affine* Chaudoir, *C. externum* Say, *Clivina postica* LeConte, *Elaphropus dolosus* LeConte, *Galerita atripes* F., *Harpalus fulgens* Csiki, *Scarites subterraneous* F., and *Stenolophus conjunctus* Say. The generalized habitat preferences for these common and dominant species are given in Table 8. With respect to autumn species, four were classified as riparian species, one as an edge species, and four as generalist species. Edge species are based on numbers captured in the riparian edge and wheat edge. Generalist species represent ground beetles captured consistently in all habitats. Although many species were captured in wheat, none seemingly preferred it over other habitats. With respect to winter species, one was classified as a riparian species, none as edge species, six as generalist species, and two as wheat species. With respect to spring species, four were classified as riparian species, one as an edge species, seven as generalist species, and six as wheat species.

Multivariate Analysis

The eigenvalues of the CCA measure the proportion of total variation in ground beetle abundance explained by their respective axis (ter Braak 1986, 1987, 1995). The eigenvalues, based on species relative abundances, for CCA axes 1 through 4 were 0.371, 0.242, 0.179, and 0.155. Axis one explained 24.9 % of the species-environment relationship, and together with axis 2, explained 41.2 % of the species-environment relationship. Axes 1 through 4 explained 63.6 % of the total species-environment relationship. A biplot of the environmental variables (sites not shown) and species scores (sites not shown) illustrates that axis 1 represents a seasonal gradient (Fig. 6). Species names and abbreviations are given in Table 9. Environmental variables are represented by arrows, and a relatively long arrow positioned close to an axis indicates a strong relationship with that axis (ter Braak 1986, Palmer 1993). Ground beetles positioned close to the arrows have a strong association with that variable. Beetle assemblages that predominate in autumn ordinated on the right side of axis 1, whereas spring and winter assemblages ordinated on the left side of axis 1. The winter assemblage also ordinated on the lower side of axis 2. Axis 2 mainly separated ground beetle assemblages among years. Ground beetles predominating in 1995 – 1996 ordinated along the upper portion of axis 2, whereas those species predominating in spring 1995 and in 1996 – 1997 ordinated along the lower portion of axis 2. The observed patterns for ground beetles with environmental variables were significantly different from random (Monte Carlo test statistic = 4.37, $P < 0.01$) (ter Braak 1987).

Partial CCA was used to depict the effects of habitats on patterns of species abundance. In this partial CCA, the effects on species composition of years, seasons, and sites were factored out as covariables. With four environmental variables, only three canonical axes were calculated. The eigenvalues for axes 1 through 3 were 0.124, 0.044, and 0.026. Again, these values measure the amount of variation in species scores explained by their respective axis, with axis 1 explaining more variation in species scores than axes 2 or 3. Of the variation in species composition remaining after factoring out the covariables, axis 1 explained 64.1 % of the species-environment relationship, and together with axis 2, explained 86.6 % of the species-environment relationship. A biplot of the habitat and species scores (only the 26 dominant and common species are shown) reveal that assemblages in riparian habitats and wheat fields separated along axis 1 (Fig. 7). The second axis separated ground beetle species occupying riparian and wheat field edges from those occupying wheat fields and riparian strips. Ground beetles occurring at the origin of the axes may represent habitat generalists, while species occurring far from the origin represent habitat specialists. Riparian specialists ordinated in the positive space of axis 1 and 2, whereas wheat field specialists appear in the negative space of axis 1 and positive space of axis 2. Edge species (ground beetles occurring in both riparian edge and wheat field edge) ordinated in the negative space of axis 2.

Discussion

Annual variation in the number of ground beetle species and relative abundances may be expected in both temporary and permanent habitats (den Boer 1986, Luff 1990).

In this study the overall capture rate of ground beetles did not differ among years for autumn and spring species. However, more beetles were captured in winter 1997 than in winter 1996, due to the much larger numbers of *B. castor* and *B. nigripes* captured in winter 1997. The abundance of *S. conjunctus* also differed between years during winter, however this difference contributed little to the overall difference in numbers captured. During autumn, only *N. novemstriatus* was captured more frequently in 1996 than in 1995. No other dominant autumn species differed in abundance between years.

In spring, however four of the six dominant species differed in abundance among years. Three species, *A. dulcicollis*, *B. castor*, and *B. nigripes* were captured predominantly in 1997, whereas *C. bipustulata* was captured predominantly in 1995. In research conducted over several years in agricultural landscapes, both Luff (1990) and den Boer (1986) found marked annual differences in abundances of several dominant species of ground beetles. They related much of the variation in species abundance to the relative dispersal powers. Den Boer (1986) suggested that the abundance of species with limited capability for dispersal (walking) should be more consistent over years in comparison to those that are strong flyers, which tend to exhibit higher rates of local extinction and recolonization. Consistent with suggestion of den Boer (1986) *A. dulcicollis, B. castor,* and *B. nigripes*, are macropterous (Lindroth 1963, 1968), but the extent to which they disperse by flying was not investigated in this study. Conversely, *S. conjunctus* and others are capable of flying (Lindroth 1968), but their abundances did not vary significantly between years. This was a short-term study and long-term inferences may not be reliable, however my results suggest that the extent of dispersal alone could not account for relative species abundances in the various habitats. Other factors such as variation in soil properties, micro- and macroclimatic conditions, intra- and interspecific competition, predation and parasitism, and chemical and cultural treatment of the land (e.g., pesticide use and tillage practices) probably affect ground beetle populations over time.

Some studies have shown that certain species of ground beetles prefer to occupy natural habitats over nearby agricultural habitats. In this study, ground beetles were separated spatially. For example, *H. pensylvanicus* preferred the riparian habitat over wheat fields. This contrasts with Esau and Peter's (1975) findings where *H. pensylvanicus* was found predominantly in cornfields and fencerows as opposed to grassy prairies. But, when considering the partial CCA, *H. pensylvanicus* ordinated between the riparian interior and riparian edge, which concurs with Best et al. (1981) findings. *Anisodactylus dulcicollis* was classified as a habitat generalist, but the partial CCA indicated this species had a preference for wheat field interiors. No other data on habitat preference could be found for *A. dulcicollis*, however other *Anisodactylus* spp. seem to prefer habitat edges over habitat interiors (Esau and Peters 1975). *Agonum punctiforme* was classified as an edge species in autumn and a habitat generalist in winter and spring, however the partial CCA indicated a preference for wheat field interior. The two most abundant species, *B. castor* and *B. nigripes*, were captured in all habitats, but their numbers were considerably greater in wheat habitats than in riparian habitats, and their classification is supported by the partial CCA. A species that apparently has benefited from farming within its distribution is *P. chalcites*. This species clearly prefers wheat field interiors over other habitats. Esau and Peters (1975) captured *P chalcites* most often in cornfields as opposed to fencerows and prairies, while I found *P. chalcites* most often in wheat fields as opposed to grasslands (see Chapter IV). *Pterostichus chalcites* may be regarded as a North American synanthropic species, meaning it shares a close association with human activities (Spence and Spence 1988).

In this study, ground beetle assemblages were found to be separated seasonally and spatially in relation to wheat fields and adjacent riparian habitats. A small number of species accounted for a large portion of all ground beetles captured in all seasons and habitats. Many of the dominant and common species preferred wheat fields over riparian habitats. It is not clear whether these abundant species overwinter in the riparian edges and disperse into the wheat fields, however their continuous seasonal activity and predatory nature makes them good candidates for biological control of wheat pests.

Wissinger (1997) suggested that natural enemies of annual crop pests are most effective as "cyclic colonizers" of the ephemeral crop system. He described cyclic colonizers as insects that respond to disturbance by dispersing to permanent habitats, delay reproduction, overwinter, and then recolonize the crop the following year. Before fragmenting the landscape for agricultural purposes, cyclic colonizers would probably be species or subpopulation of species that inhabited natural boundaries of riparian strips and grasslands or between forests and grasslands. As opposed to habitat interiors, it is at these boundaries where disturbances and the flux of materials and organisms may be greatest (Wiens et. al. 1985). Wissinger (1997) suggested that insects occupying these boundaries were preadapted for survival and reproduction in agricultural landscapes.

These insects had already evolved life history traits to a cyclic, predictable environment and possessed enough additive genetic variation underlying the traits to evolve in response to additional human disturbances to the landscape. The life history traits important for cyclic colonizers include dispersal from permanent or overwintering habitats to ephemeral habitats, ability to efficiently locate hosts or prey, efficient reproduction resulting in multiple generations, dispersal back to permanent or overwintering habitat, and survival in overwintering habitat.

Based on the important life history traits of cyclic colonizers, Wissinger (1997) described four criteria for biological control agents to be effective in annual crop systems such as wheat. First, natural enemies should have sufficient overwintering sites available near the crops. Second, the crop field size to edge ratio should not be too great as to inhibit or delay natural enemies from reaching field centers. Third, the benefits from boundaries (e.g., overwintering sites, refuge from pesticides, and shelter) should out-weigh their costs (e.g., reduced dispersal among habitats). Fourth, broad-spectrum pesticides should not eliminate natural enemies once they have established in the crop fields. In reference to ground beetles, habitat generalists may have been the beneficiaries of modern agriculture and resulted in a shift from habitat generalists to habitat specialists. In this study, the abundant species that preferred wheat habitats, *B. castor*, *B. nigripes*, *P. chalcites,* and *C. affine,* may have once dominated landscape boundaries and now exploit the wheat ecosystem for reproductive purposes. These species are potential biological control agents of wheat pests. Because wheat fields vary considerably in size in the great plains, it is important to determine whether these ground beetles overwinter in adjacent riparian edges, and if they do, how far they will disperse into the wheat field interior (criteria 1 and 2 of Wissinger 1997). Equally important is to determine which species have evolved life cycles that are completed exclusively in crop fields. This aspect of effective biological control strategies was not covered by Wissinger (1997), but seems relevant for species such as *P. chalcites*. For such species, survival and reproduction depends entirely on availability of prey in the wheat fields.

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Table 1. Number of species, total abundance, and mean ± 1 SE abundance of ground beetles captured in each season. Means were calculated per site per sampling date (N).

Season	Species	Abundance	Mean ± 1 SE	N
Autumn	45	599	9.1 ± 1.4	66
Winter	36	713	8.1 ± 1.2	88
Spring	101	7869	65.0 ± 5.0	121
Total	103	9181	33.4 ± 2.8	275

Table 2. Least square mean abundances (± 1 SE) for all species and dominant species of ground beetles captured in autumn 1995 (N = 16) and 1996 (N = 8). Means calculated per site per habitat for each year.

	Year	
Species	1995	1996
All Species	8.26 ± 1.62 a	13.56 ± 2.29 a
A. pallipes	0.69 ± 0.14 a	0.06 ± 0.20 a
C. opaculus	2.07 ± 0.52 a	0.92 ± 0.73 a
G. janus	0.27 ± 0.18 a	0.92 ± 0.25 a
H. caliginosus	0.68 ± 0.16 a	0.00 ± 0.23 a
H. pensylvanicus	1.27 ± 1.36 a	4.96 ± 1.92 a
N. novemstriatus	0.28 ± 0.37 a	2.31 ± 0.52 b

Values within rows with different letters are significantly different.

Table 3. Least square mean abundances (± 1 SE) for all species and dominant species of ground beetles captured in riparian strips, riparian edges, wheat edges, and wheat interiors during autumn 1995 and 1996 (N = 6 for all habitats). Means calculated per site.

	Habitat			
Species	Riparian	Riparian Edge	Wheat Edge	Wheat Interior
All Species	25.81 ± 2.81 a	8.96 ± 2.81 b	4.63 ± 2.81 bc	4.25 ± 2.81 c
A. pallipes	0.38 ± 0.24 a	0.38 ± 0.24 a	0.13 ± 0.24 a	0.63 ± 0.24 a
C. opaculus	3.69 ± 0.90 a	1.79 ± 0.90 a	0.17 ± 0.90 b	0.33 ± 0.90 b
G. janus	1.50 ± 0.31 a	0.33 ± 0.31 b	0.46 ± 0.31 ab	0.08 ± 0.31 b
H. caliginosus	0.31 ± 0.28 a	0.83 ± 0.28 a	0.21 ± 0.28 a	0.00 ± 0.28 a
H. pensylvanicus	9.50 ± 2.35 a	1.33 ± 2.35 a	0.92 ± 2.35 a	0.71 ± 2.35 a
N. novemstriatus	3.44 ± 0.63 a	0.75 ± 0.63 b	0.83 ± 0.63 ab	0.17 ± 0.63 b

Values within rows with different letters are significantly different.

Table 4. Least square mean abundances (± 1 SE) for all species and dominant species of ground beetles captured in winter 1996 (N = 24) and 1997 (N = 8). Means calculated per site per habitat for each year.

	Year	
Species	1996	1997
All Species	3.05 ± 0.70 a	22.56 ± 1.22 b
A. pallipes	0.72 ± 0.32 a	0.00 ± 0.55 a
A. punctiforme	0.63 ± 0.16 a	0.35 ± 0.28 a
B. castor	0.83 ± 0.46 a	7.25 ± 0.80 b
B. nigripes	0.04 ± 0.20 a	8.69 ± 0.35 b
N. novemstriatus	0.19 ± 0.12 a	1.25 ± 0.20 a
S. conjunctus	0.06 ± 0.04 a	1.42 ± 0.07 b

Values within rows with different letters are significantly different.

Table 5. Least square mean abundances (± 1 SE) for all species and dominant species of ground beetles captured in riparian strips, riparian edges, wheat edges, and wheat interiors during winter 1996 and 1997 (N = 8 for all habitats). Means calculated per site.

	Habitat			
Species	Riparian	Riparian Edge	Wheat Edge	Wheat Interior
All Species	10.58 ± 1.40 a	10.89 ± 1.40 a	17.72 ± 1.40 a	12.03 ± 1.40 a
A. pallipes	0.08 ± 0.64 a	0.22 ± 0.64 a	0.11 ± 0.64 a	1.02 ± 0.64 a
A. punctiforme	0.21 ± 0.33 a	0.50 ± 0.33 a	0.42 ± 0.33 a	0.83 ± 0.33 a
B. castor	1.83 ± 0.92 a	3.50 ± 0.92 a	5.56 ± 0.92 a	5.28 ± 0.92 a
B. nigripes	2.63 ± 0.40 a	3.92 ± 0.40 b	6.89 ± 0.40 c	4.03 ± 0.40 b
N. novemstriatus	0.88 ± 0.48 a	0.46 ± 0.24 a	0.46 ± 0.41 a	0.04 ± 0.04 b
S. conjunctus	1.25 ± 0.08 a	0.59 ± 0.08 b	0.95 ± 0.08 a	0.17 ± 0.08 c

Values within rows with different letters are significantly different.

Table 6. Least square mean abundances (± 1 SE) for all species and dominant species of ground beetles captured in spring 1995 (N=16), 1996 (N = 20), and 1997 (N = 8). Means calculated per site per habitat for each year.

	Year		
Species	1995	1996	1997
All Species	69.95 ± 6.88 a	33.02 ± 6.15 a	128.08 ± 9.73 a
A. dulcicollis	2.99 ± 0.68 a	0.18 ± 0.62 b	14.71 ± 0.97 c
B. castor	5.65 ± 1.32 a	1.22 ± 1.18 b	15.06 ± 1.87 c
B. nigripes	14.53 ± 3.03 a	0.47 ± 2.71 b	39.71 ± 4.28 c
C. bipustulata	5.17 ± 0.84 a	0.42 ± 0.75 b	3.98 ± 1.19 a
G. janus	5.93 ± 0.67 a	2.19 ± 0.60 a	3.13 ± 0.94 a
P. chalcites	0.92 ± 2.86 a	11.52 ± 2.56 a	4.85 ± 4.05 a

Values within rows with different letters are significantly different.

Table 7. Least square mean abundances (± 1 SE) for all species and dominant species of ground beetles captured in riparian strips, riparian edges, wheat edges, and wheat interiors during spring 1995, 1996, and 1997 (N = 11 for all habitats). Means calculated per site.

	Habitat			
Species	Riparian	Riparian Edge	Wheat Edge	Wheat Interior
All Species	67.34 ± 8.94 a	57.33 ± 8.94 a	82.56 ± 8.94 b	100.84 ± 8.94 b
A. dulcicollis	8.96 ± 0.89 a	3.23 ± 0.89 a	4.07 ± 0.89 a	7.57 ± 0.89 a
B. castor	1.75 ± 1.71 a	3.19 ± 1.71 a	9.84 ± 1.71 b	14.46 ± 1.71 b
B. nigripes	6.21 ± 3.93 a	10.40 ± 3.93 b	25.66 ± 3.93 c	30.67 ± 3.93 c
C. bipustulata	2.50 ± 1.09 a	2.98 ± 1.09 abc	5.52 ± 1.09 b	1.75 ± 1.09 ac
G. janus	4.38 ± 0.87 a	4.47 ± 0.87 a	2.97 ± 0.87 a	3.18 ± 0.87 a
P. chalcites	0.48 ± 3.72 a	0.87 ± 3.72 a	4.16 ± 3.72 a	17.54 ± 3.72 b

Values within rows with different letters are significantly different.

Table 8. Generalized habitat preferences for the most abundant species of ground beetles captured during autumn, winter, and spring.

	Habitat Preference			
Season	Riparian	Edge	Wheat	Generalist
Autumn	*C. opaculus*	*A. punctiforme*		*A. pallipes*
	C. torvus			*C. punctulata*
	H. pensylvanicus			*G. janus*
	N. novemstriatus			*H. caliginosus*
Winter	*N. novemstriatus*		*B. castor*	*A. pallipes*
			B. nigripes	*A. punctiforme*
				E. granarius
				G. janus
				S. conjunctus
				S. comma
Spring	*A. merula*	*C. bipustulata*	*B. castor*	*A. punctiforme*
	C. opaculus		*B. nigripes*	*A. dulcicollis*
	G. atripes		*C. affine*	*A. rusticus*
	H. fulgens		*C. externum*	*C. postica*
			P. chalcites	*E. dolosus*
			S. subterraneous	*G. janus*
				S. conjunctus

Table 9. Species names of abbreviations (Abbr.) used in CCA and partial CCA biplots.

Species	Abbr.	Species	Abbr.
Abacidus permundus Say	Abp	*Dicaelus elongatus* Bonelli	Die
Acupalpus testaceus Dejean	Act	*Discoderus parallelus* Haldeman	Dip
Agonum pallipes F.	Agp	*Dyschiriodes globulosus* Say	Dyg
A. punctiforme Say	Apu	*D. pilosus* Say	Dyp
Amara convexa LeConte	Amc	*Elaphropus dolosus* LeConte	Eld
A. cupreolata Putzeys	Acu	*E. granarius* Dejean	Elg
A. exarata Dejean	Ame	*Euryderus grossus* Say	Eug
A. musculis Say	Amm	*Galerita atripes* LeConte	Gaa
A. obesa Say	Amo	*G. janus* F.	Gaj
A. pennsylvanica Hayward	Amp	*Harpalus amputatus* Say	Haa
A. rubrica Haldeman	Amr	*H. caliginosus* F.	Hac
Amphasia interstitialis Say	Ain	*H. desertus* LeConte	Had
Anisodactylus carbonarius Say	Anc	*H. faunus* LeConte	Haf
A. dulcicollis LaFerté	And	*H. fulgens* Csiki	Hfu
A. harpaloides LaFerté	Anh	*H. paratus* Say	Hap
A. merula Germar	Anm	*H. pensylvanicus* DeGeer	Hpe
A. ovularis Casey	Ano	*Helluomorphoides praeustus* Harris	Hep
A. rusticus Say	Anr	*Lebia atriventris* Say	Lat
A. sanctaecruscis F.	Ans	*L. tricolor* Say	Let
Apenes sinuata Say	Aps	*Microlestes linearis* LeConte	Mil
Apristus latens LeConte	Apl	*Notiobia terminata* Say	Not
Bembidion castor Lindroth	Bec	*Notiophilus novemstriatus* LeConte	Non
B. nigripes Kirby	Ben	*Olisthopus parmatus* Say	Olp
Brachinus fumans F.	Brf	*Panagueus fasciatus* Say	Paf
Calathus opaculus LeConte	Cao	*Pasimachus elongatus* LeConte	Pae
Calosoma affine Chaudoir	Caf	*Pterostichus chalcites*	Ptc
C. externum Say	Cae	*P. lucublandus* Say	Ptl
Chlaenius tomentosus Say	Cht	*Scaphinotus cavicollis* Say	Scc
Cicindela denverensis Casey	Cid	*Scarites subterraneus* F.	Scs
C. punctulata Olivier	Cip	*Semiardistomis viridis* Say	Sev
C. scutellaris Say	Cis	*Stenolophus comma* F.	Stc
Clivina bipustulata F.	Clb	*S. conjunctus* Say	Sco
C. postica LeConte	Clp	*S. lineola* F.	Stl
Colliuris pensylvanica L.	Cop	*S. ochropezus* LeConte	Sto
Cratacanthus dubius Beauvois	Crd	*Stenomorphus rotundatus* LeConte	Str
Cyclotrachelus torvus LeConte	Cyt	*Tetragonoderus fasciatus* Halderman	Tef

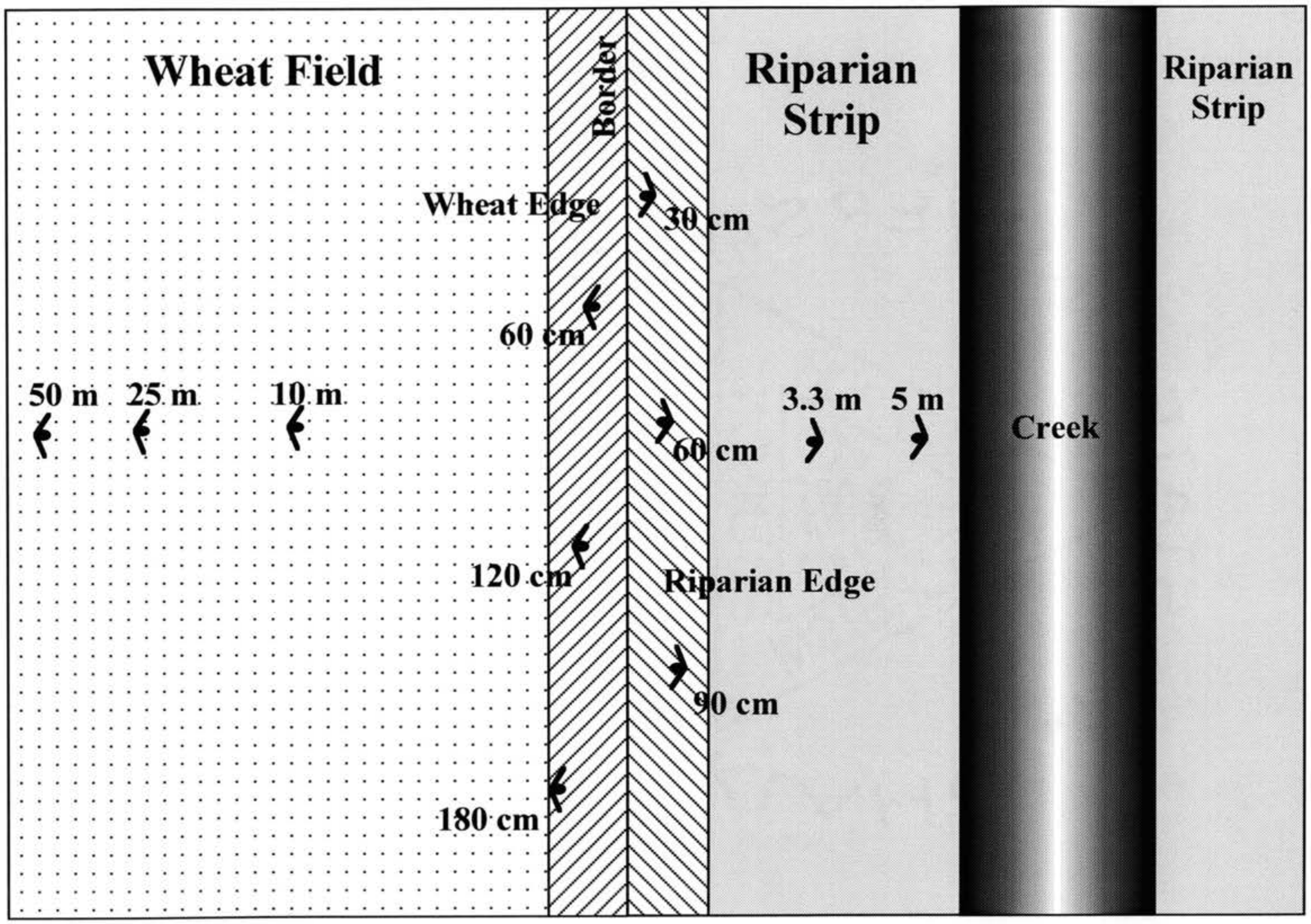

Figure 1. Arrangement of guided pitfall traps in wheat fields, riparian strips, and their edges. Traps were placed at varying distances from the border and facing the border. The border represented an abrupt change in vegetation from wheat to riparian strip.

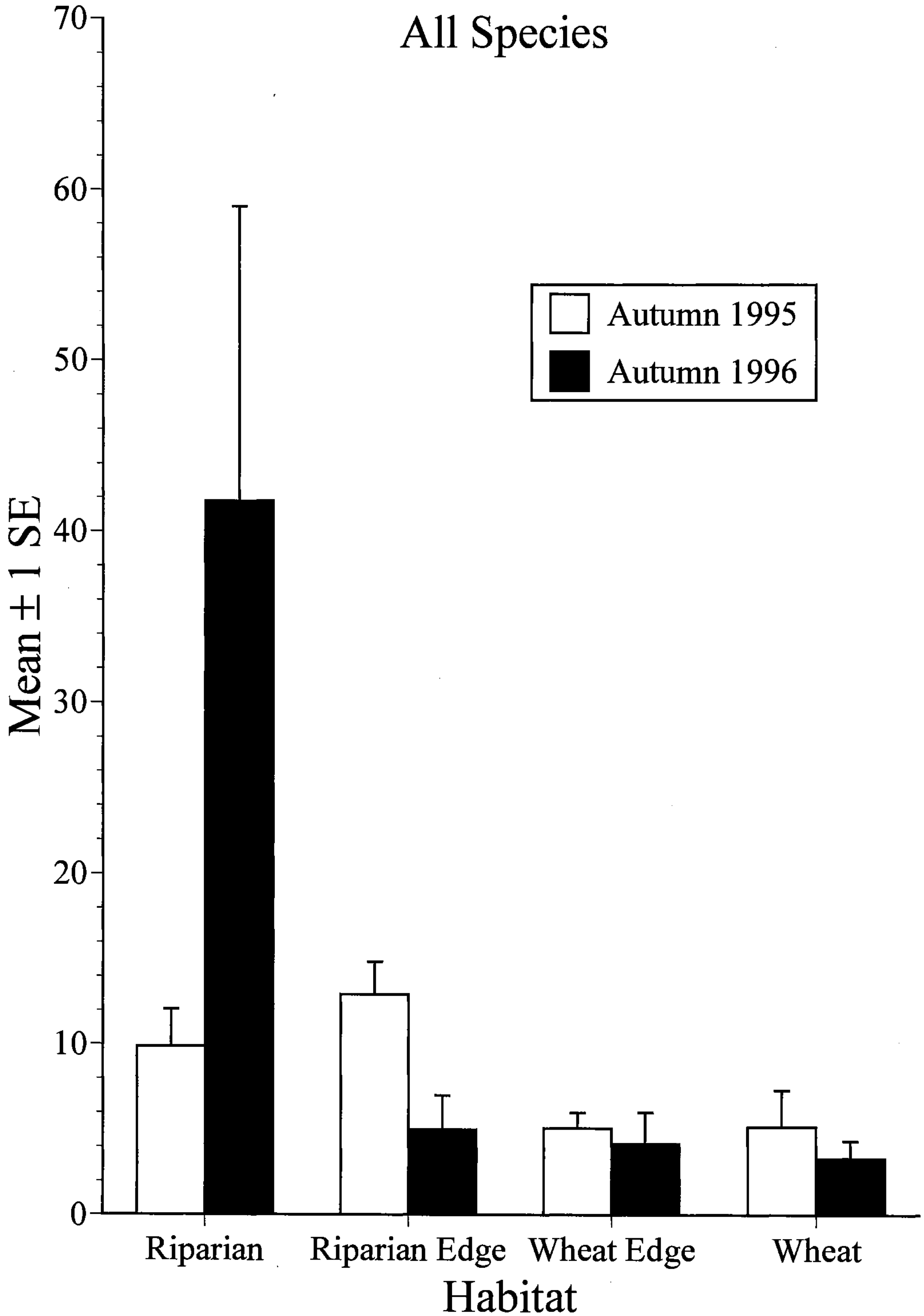

Figure 2. Mean (± 1 SE) number per site per sampling date of all ground beetles captured in autumn by year and habitat.

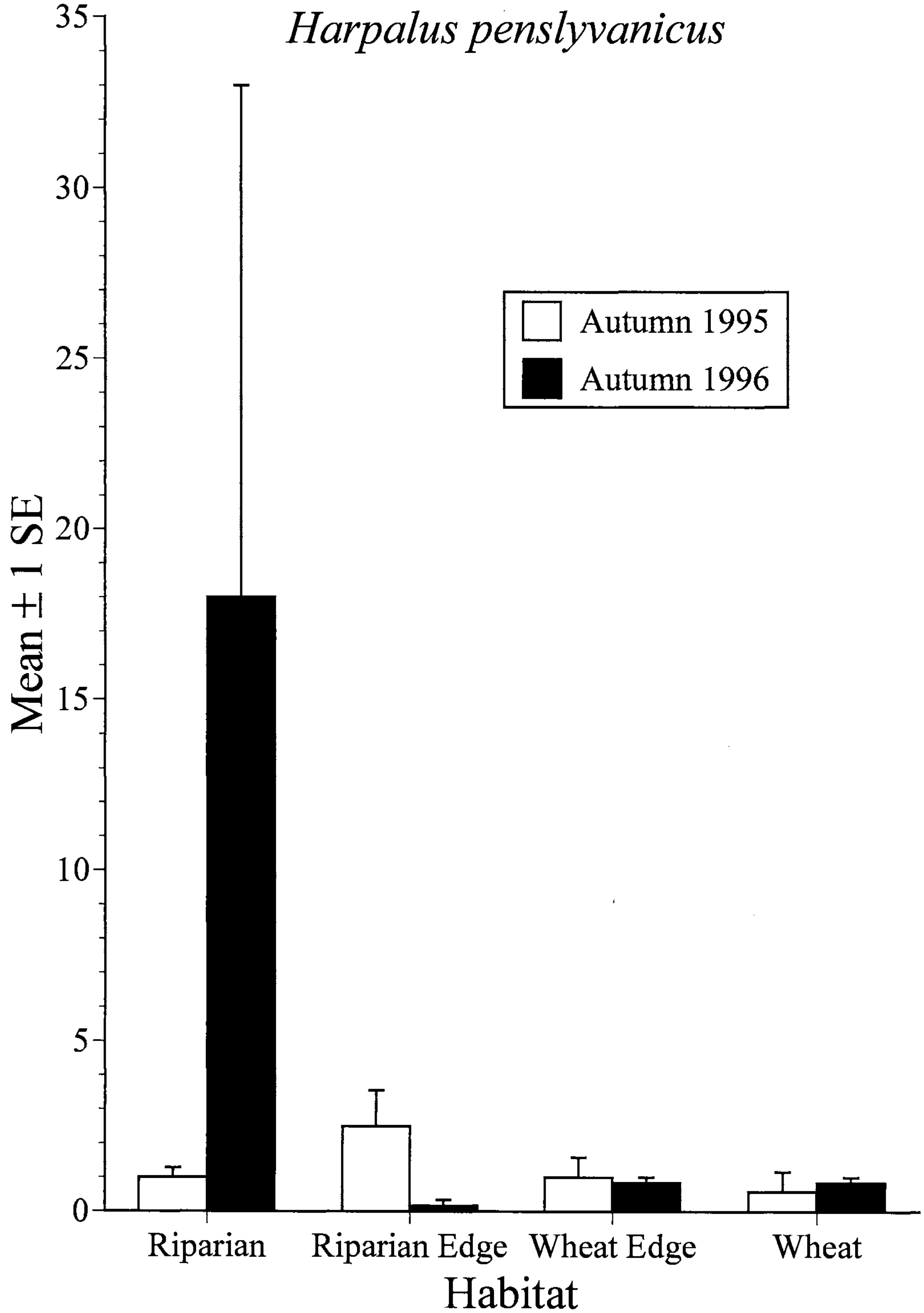

Figure 3. Mean (± 1 SE) number per site per sampling date of *H. pensylvanicus* captured in autumn by year and habitat.

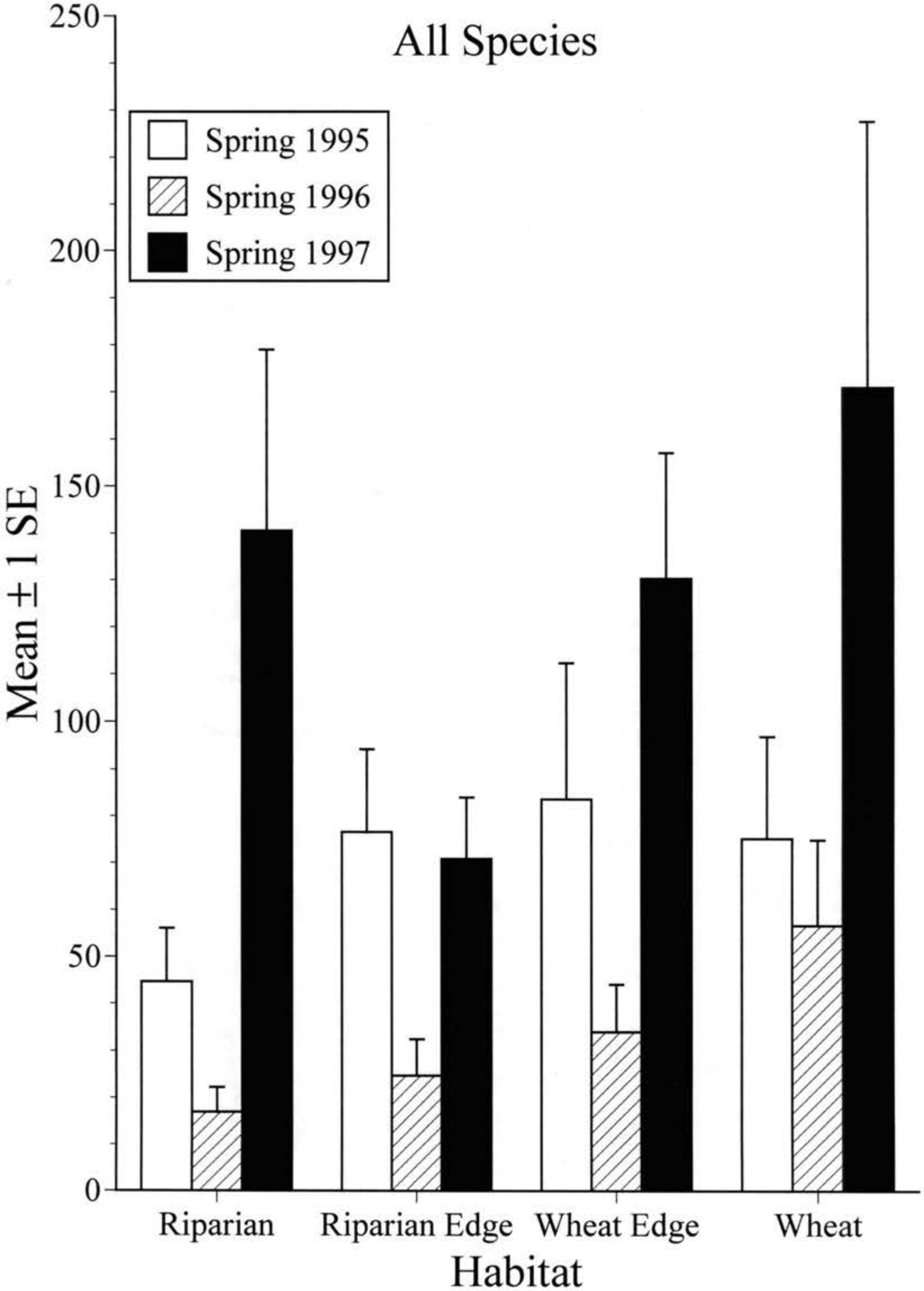

Figure 4. Mean (± 1 SE) number per site per sampling date of all ground beetles captured in spring by year and habitat.

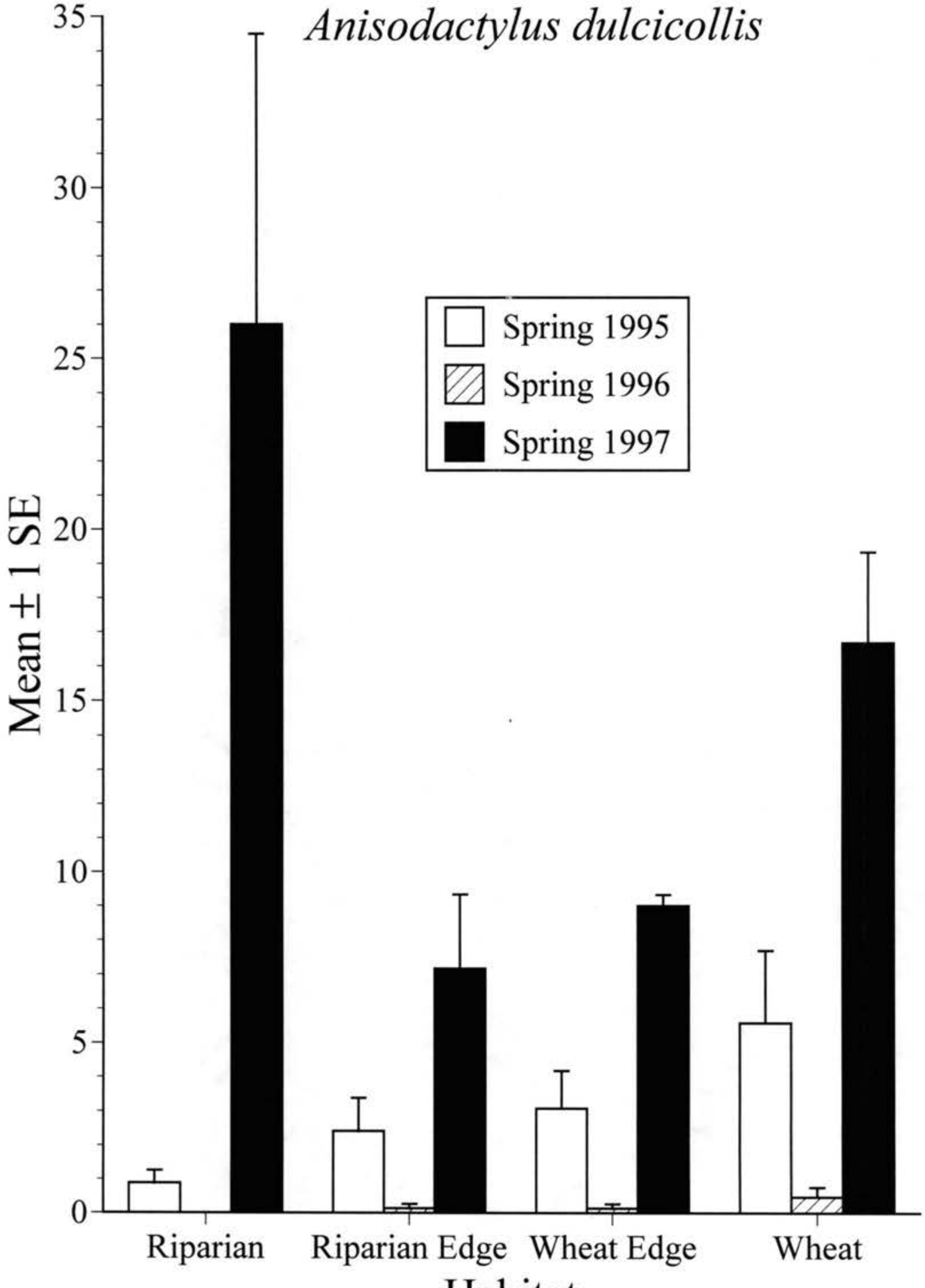

Figure 5. Mean (± 1 SE) number per site per sampling date of *A. dulcicollis* captured in spring by year and habitat.

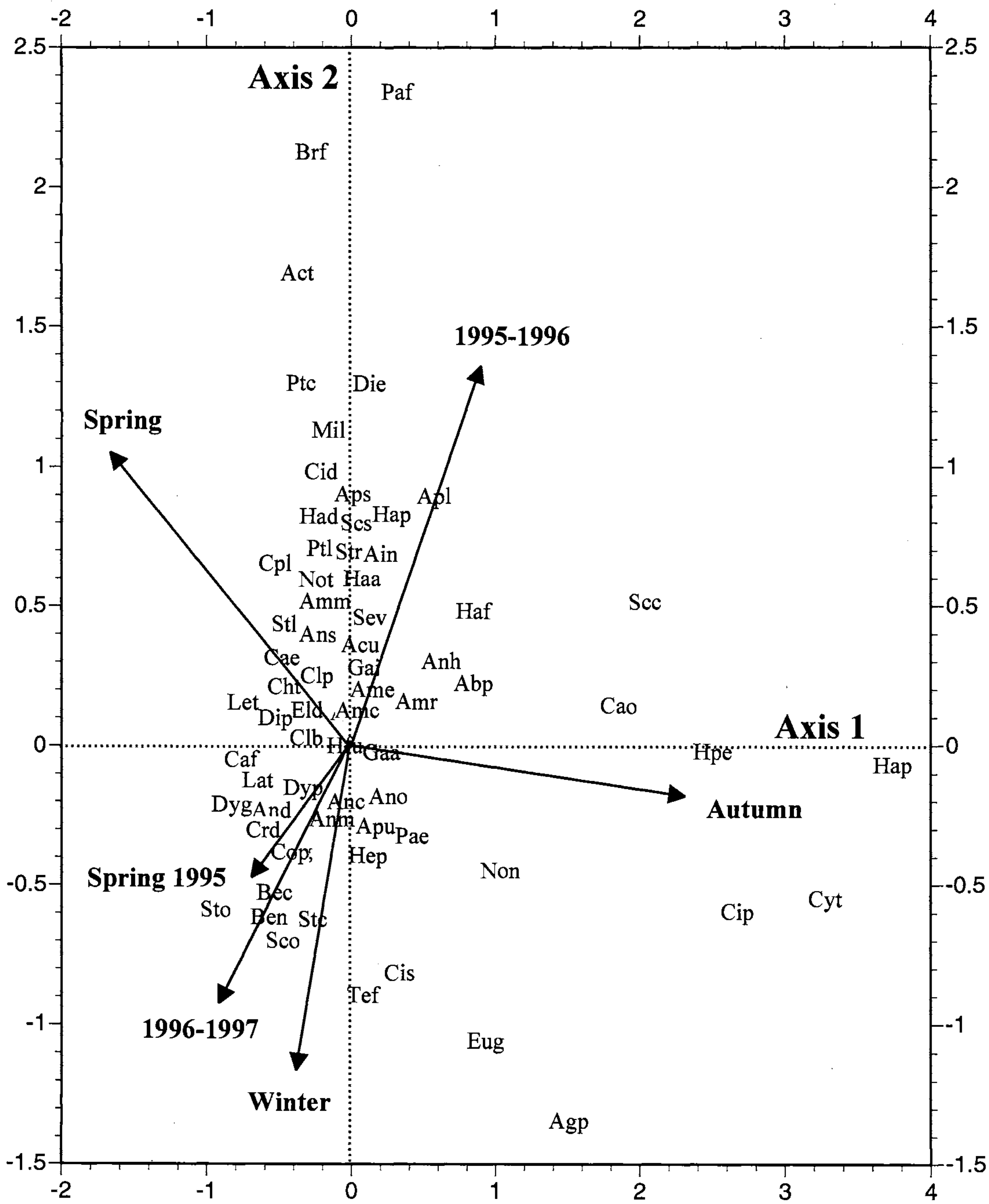

Figure 6. Biplot of ground beetle abundances and most important independent variables from CCA. Only 70 of 103 species are plotted. The abbreviation of species names are plotted and complete names are listed in Table 9. Independent variables are represented by arrows.

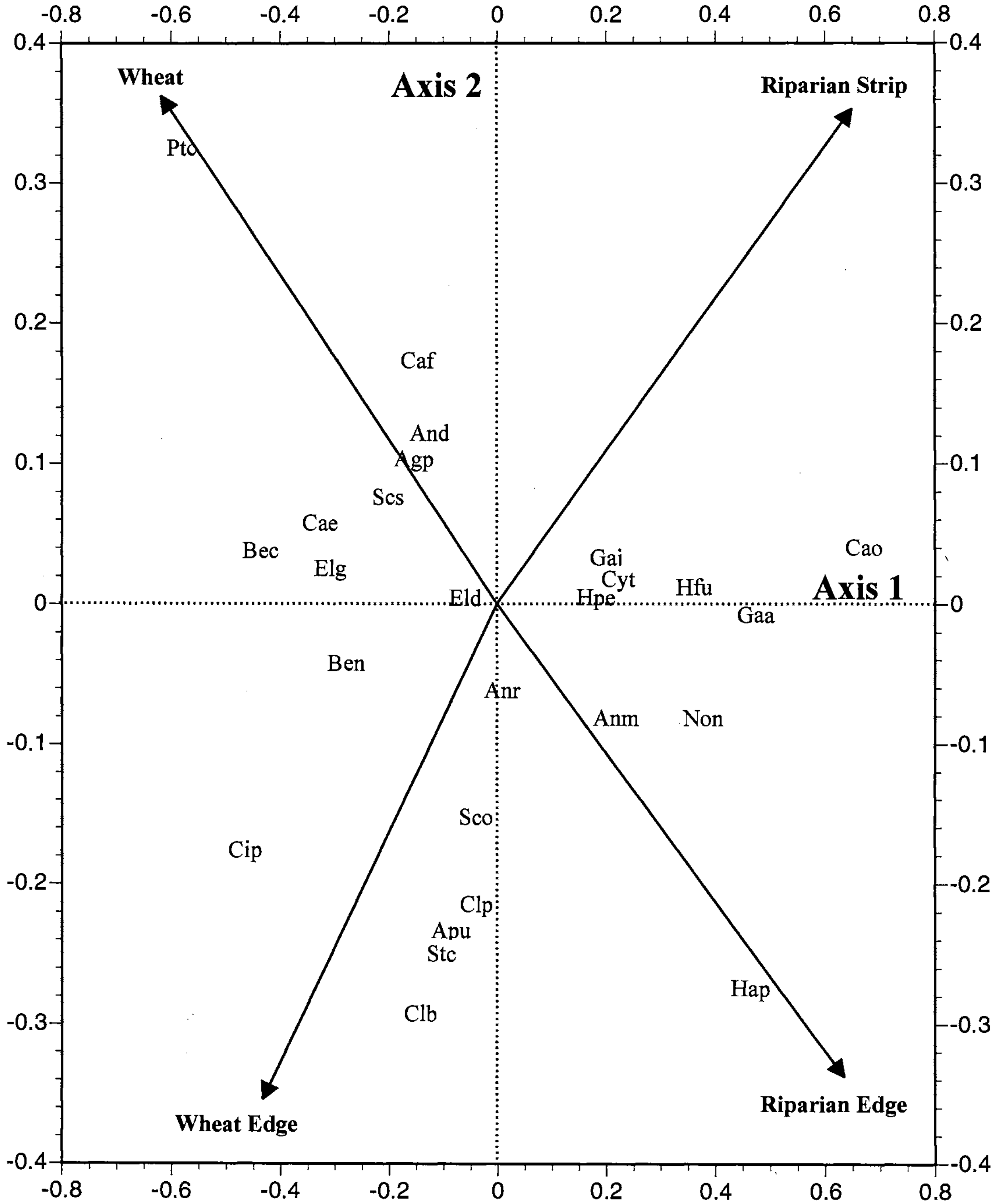

Figure 7. Biplot of ground beetle abundances and independent variables from a partial CCA. Only the 26 dominant and common species are plotted. The abbreviation of species names are plotted and complete names are listed in Table 9. Independent variables are represented by arrows.

CHAPTER VI

ADJACENCY EFFECTS OF RIPARIAN ZONES AND GRASSLANDS ON GROUND BEETLE (COLEOPTERA: CARABIDAE) ASSEMBLAGES IN WINTER WHEAT FIELDS

Abstract

The boundaries among landscape elements filters the dispersal of organisms across them, resulting in differential community structures within the landscape elements. Ground beetles are numerous, beneficial predators, and generally disperse by walking. These qualities make them excellent organisms to study boundary dynamics in agricultural landscapes. Ground beetles were captured in autumn through spring 1996 – 1997 at two sites using pitfall traps placed in wheat fields and adjacent grasslands and riparian zones. Ground beetle abundance showed two activity peaks; one in autumn and the other in spring. Species composition was most strongly related to these seasons. Ground beetles reproducing in spring were separated from those reproducing in autumn along the first and second axes of a canonical correspondence analysis (CCA). Winter assemblages were separated along the second axis. With the effects of season and sites removed, ground beetles were classified with respect to habitat preference along axes one and two of a partial CCA. Based on this ordination, ground beetles were separated into wheat assemblages and natural habitat assemblages along axis 1. Ground beetle assemblages were further separated along axis 2 by wheat adjacent to grasslands and wheat adjacent to riparian zones. Grassland, grassland edge, and riparian edge assemblages were similar, while riparian assemblages were unique. Net dispersal of beetles across the boundaries showed no consistent dispersal patterns during autumn, winter, or spring. However, mark-recapture studies showed that several species routinely cross the boundaries, which probably resulted in the increase in abundance of ground beetles in the wheat interiors during spring.

Key Words: Insecta, predators, communities, boundaries, agroecosystems, dispersal.

Introduction

In agricultural landscapes, the land is fragmented into a mosaic of natural and anthropogenic habitat patches. In northcentral Oklahoma, this mosaic is composed of a patchwork of grasslands, riparian zones, and crop lands. Ground beetles are important predators of agricultural pests and many disperse only by walking (Thiele 1977, Allen 1979, Luff 1987). Local populations of ground beetles may be linked by dispersal among patches in this mosaic (Duelli et al. 1990). Dispersal of beetles may differ at the boundaries between patches compared to patch interiors due to the filtering effect of boundaries (Wiens et al. 1985, Pickett and Cadenasso 1995, Wiens 1997). This has obvious consequences for colonization of ephemeral habitats such as wheat fields (Wissinger 1997). The species composition and abundance of ground beetles in a wheat field may be considerably affected by the composition of surrounding patches (Forman and Godron 1981).

Some studies have shown that many ground beetle species overwinter in grassy and wooded habitats surrounding cereal fields and disperse into the fields during spring (Wallin 1985, Coombes and Sotherton 1986). Wissinger (1997) suggested that natural enemies inhabiting ephemeral crop systems such as wheat fields colonize the crops under favorable conditions and retreat to surrounding natural habitats under adverse conditions. This results in a cyclic colonization process. To the best of my knowledge, ground beetle dispersal among grasslands and riparian zones adjacent to wheat fields has not been investigated in winter wheat fields. My objectives are (1) to determine the seasonal patterns of ground beetle abundance in winter wheat surrounded by both grasslands and riparian zones; (2) ascertain the effects of surrounding grasslands and riparian zones on ground beetle assemblages in winter wheat; and (3) describe the movement of ground beetles across boundaries between these landscape elements during the winter wheat growing season in Oklahoma.

Materials and Methods

I established two study sites in the autumn of 1996 in fields of winter wheat (*Triticum aestivum* L.) and adjacent grass pastures (numbers 1g and 2g) and riparian zones (numbers 1r and 2r) located in Noble County, Oklahoma. These study sites were separated by approximately 10 km. The grass pastures and riparian zones abutted the same wheat fields on different sides. These sites are in northcentral Oklahoma and are within the tall grass prairie region of the southern Great Plains (Kaul 1986). The size of the grassland at site 1 was 8 ha and at site 2 was 16 ha. The size of the wheat field at site 1 was 18 ha and at site 2 was 40 ha. The riparian zones were situated along unnamed creeks.

Sampling with Pitfall Traps

Ground beetles were captured in grasslands and riparian zones adjacent to wheat fields using pitfall traps. Pitfall trap design was similar to that used by Morrill et al. (1990). In constructing the traps, I used Nalgene® polypropylene funnels (14.5 cm inside diameter) with 125 ml Nalgene® plastic containers beneath to confine the ground beetles. To provide for easy exchange of containers, the screw top caps of the plastic containers were glued to the base of the funnels. I cut out the bottoms of the containers and replaced them with screen mesh (12.6 strands per cm) to permit water to pass through the container while retaining the ground beetles, and placed Ectrin® insecticide cattle ear tags (Active ingredient = Cyanomethyl-4-chloro-alpha-benzeneacetate) in the cups to kill the insects that were trapped. A preliminary study using another brand of eartags placed in traps indicated they had no effect on ground beetle catch (see Appendix A). The study was not repeated with the current eartags. For each trap, a PVC plastic pipe (13 cm inside diameter) was buried in the soil such that the top of the pipe was approximately 2 cm below the soil surface, which allowed setting the funnels at the soil surface. The PVC pipes supported the traps and prevented soil from collapsing around them. To increase the efficiency of capture of ground beetles, galvanized sheet metal strips (14 cm x 122 cm) were used as guides (Durkis and Reeves 1982). The guides were angled forward slightly and driven into the soil a few centimeters. The traps were positioned at the center of the guides.

Six traps were placed in each of the wheat fields on 21 September 1996 and sampled through 5 October 1996. This sampling period was approximately two weeks prior to drilling of wheat. Two traps were placed in the fallow fields 50 m from the grassland border and two traps 50 m from the riparian border. Two additional traps were set near the center of the fallow fields. Nineteen traps were established in the grasslands and riparian zones (see below) on 1 October 1996 and sampled through 15 October 1996. All traps were set on 15 October 1996 and checked weekly through 9 June 1997, shortly before wheat harvest. The arrangement of the pitfall trap network in grasslands, riparian zones, winter wheat fields, and grassland, riparian zone, and wheat field edges is illustrated in Fig. 1. Traps were placed in the wheat fields at 10 m, 25 m, and 50 m from the border. At the wheat field edge, pairs of traps were set at 60 cm, 120 cm, and 180 cm from the border. At the riparian edge, pairs of traps were placed at 30 cm, 60 cm, and 90 cm from the border. The paired traps were set facing opposite directions in order to estimate net dispersal of the ground beetles across the boundaries. In the riparian zones I set traps at 3 m and 5.5 m from the border, whereas, in the grasslands traps were set at 10 m and 25 m from the border.

Data Analysis

The computer program CANOCO™ (ter Braak 1987) was used to perform canonical correspondence analysis (CCA) on species abundance data. Canonical correspondence analysis relates species abundances to environmental variables and is a robust method for analyzing data from pitfall traps (Palmer 1993). I included the following 15 independent variables, autumn, winter, spring, site 1g, site 2g, site 1r, site 2r, grassland, grassland edge, grassland-wheat edge, grassland-wheat interior, riparian zone, riparian edge, riparian-wheat edge, and riparian-wheat interior in CCA analyses. I used a partial CCA to focus on the effects of the eight habitats on species abundances by using seasons and sites as covariables and removing their effects prior to conducting CCA. In order to relate species assemblages to dispersal, only beetles captured on more than five occasions were used in the CCA analyses. All abundance data were transformed to square-roots prior to CCA analysis.

Mark-Recapture

The mark-recapture method was employed to verify ground beetle dispersal across the boundaries. A 10 m x 11 m plot was established at site 1 at the grassland-wheat field boundary on 21 March 1997 (Fig. 2). Eight pitfall traps with metal guides were established in each subplot to capture ground beetles. I placed four traps 0.5 m from the grassland-wheat field border and four traps 0.5 m from the edge of each subplot in their respective habitat. Trap design followed that of Morrill (1975). These traps consisted of a 455 ml Solo® cup with a 145 mm inside diameter, a Solo Cozy Cup® funnel, and an inner 148 ml Solo® cup partially filled with ethylene glycol as a preservative. Galvanized sheet metal strips (14 cm x 122 cm) were used as guides to facilitate the capture of the beetles by channeling their movement into the traps. The beetles were marked with Testors enamel paint on the pronotum and elytra (Southwood 1978). Previous marking on *Pasimachus elongatus* LeConte, a species with a smooth exoskeleton and inclination to burrow, were maintained in terraria in the laboratory indicated the mark was durable over several weeks to several months. One mark was applied each day to either the pronotum, upper left elytra, lower left elytra, upper right elytra, or lower right elytra. In order to distinguish beetles captured in grassland from those captured in wheat fields, I used two sets of five different colors. This allowed 25 days of marking before reusing a specific color at a specific location on a beetle. Beetles were captured, returned to the laboratory, processed, held overnight, and then released into the center of the subplot in which they were captured (Fig. 2). An identical plot was established on the riparian zone-wheat field boundary at site 1 on 22 April 1997. Traps were checked daily through 4 June 1997.

Results

Temporal Distribution of Ground Beetle Assemblages

A total of 9,148 ground beetles were captured representing 91 species. Overall, there were two peaks in activity; the first, smaller peak occurred in autumn followed by a decrease in activity during winter, and then a second, larger peak occurred in spring (Fig. 3). These trends in activity were observed in both the grassland-wheat field and riparian zone-wheat field sites.

The eigenvalues of the CCA measure the proportion of total variation in ground beetle abundance explained by their respective axis (ter Braak 1986, 1987, 1995). The eigenvalues, based on species relative abundances, for CCA axes 1 through 4 were 0.455, 0.235, 0.171, and 0.107. Axis one explained 38.3 % of the species-environment relationship, and together with axis 2, explained 58.1 % of the species-environment relationship. Axes 1 through 4 explained 81.5 % of the total species-environment relationship. A biplot of the environmental variables and species scores (sites not shown) illustrates that axes 1 and 2 represent seasonal gradients (Fig. 4). Species names and abbreviations are given in Table 1. Environmental variables are represented by arrows, and a relatively long arrow positioned close to an axis indicates a strong relationship with that axis (ter Braak 1986, Palmer 1993). Ground beetles positioned close to the arrows have a strong association with that variable. Beetle assemblages that predominate in autumn ordinated on the right side of axis 1, whereas spring assemblages ordinated on the left side of axis 1 and lower portion of axis 2. The winter assemblage ordinated on the upper line of axis 2. The observed patterns for ground beetle abundance with environmental variables were significantly different from random (F-ratio = 7.38, $P < 0.01$), based on a Monte-Carlo randomization test (ter Braak 1987).

Partial CCA was used to determine the effects of habitats on patterns of species abundance. In this partial CCA, the effects on species composition of seasons and sites were factored out as covariables. The eigenvalues for axes 1 through 4 were 0.121, 0.053, 0.35 and 0.020. Again, these values measure the amount of variation in species scores explained by their respective axis, with axis 1 explaining more variation in species scores than axes 2, 3, and 4. Of the variation in species composition remaining after factoring out the covariables, axis 1 explained 47.6 % of the species-environment relationship, and together with axes 2 – 4, explained 90.0 % of the species-environment relationship. Axis 1 separated wheat field assemblages and natural habitat assemblages (Fig. 5). Assemblages associated with wheat fields ordinated on the right side of axis 1, whereas assemblages associated with natural vegetation ordinated on the left side of axis 1. Beetle assemblages were further separated along axis 2. Riparian species were distinct and ordinated along the upper portion of axis 2. Beetle assemblages were very similar in riparian zone edges, grassland edges, and grassland interiors, where they ordinated along the lower portion of axis 2. The ordering of beetle species in wheat interiors and wheat edges occurred in the upper portion of axis 2 for wheat fields adjacent to grasslands. In contrast, the ordering of beetle species in wheat interiors and wheat edges occurred in the lower portion of axis 2 for wheat fields adjacent to riparian zones. There was a clear distinction between assemblages in wheat interiors adjacent to grasslands from wheat interiors adjacent to riparian zones (Fig. 5). Assemblages in grassland-wheat edge and riparian-wheat edge were more similar to the assemblages in the wheat field interior they were adjacent to. This pattern was significantly different from random (Monte Carlo test statistic = 2.91, $P < 0.01$) indicating that it reflected a meaningful ecological pattern.

Ground Beetle Dynamics at Boundaries

It is presumed that natural enemies of agricultural pests cannot survive the tillage and other treatments applied to most agricultural lands and that they disperse into the fields from surrounding natural habitats (Wissinger 1997). Furthermore, several studies from temperate regions have shown that ground beetles move from fields into field boundaries to overwinter (Wallin 1985, Coombes and Sotherton 1986, Duelli 1990, Wratten and Thomas 1990). The CCA results indicated three distinct ground beetle assemblages occurring in autumn, winter, and spring. If these patterns of movement occur in Oklahoma, we should observe a steady increase in numbers of ground beetles captured in wheat fields in autumn, dispersal back into natural habitats during winter, and then another net increase in wheat fields in spring. During the first week of trapping in autumn, immediately after planting, there was a net increase in number of beetles captured from the border to 180 cm into the wheat field at the grassland-wheat field boundary, but not at the riparian-wheat field boundary (Figs. 6 and 7). During the second week, this trend extended only 60 cm into the wheat field from the grassland. No clear trend in net movement into the wheat field from the grassland edge was observed following the second week. However, in late autumn there was a perceptible trend of movement into the area between 30 and 60 cm into the grassland edge, whereas in the riparian-wheat field boundary dispersal seemed to continue beyond 90 cm into the riparian edge. During winter, the number of beetles captured was low and net dispersal into the natural habitats was not detectable. Except for beetles collected at the grassland-wheat field border, net movement from the natural habitats into the wheat fields was not obvious during late winter and early spring. Even as the population of ground beetles increased during spring, no trend in net displacement was observed.

Although the trends in ground beetle dispersal into wheat fields from the natural habitats edges were difficult to detect, there were several species that crossed the grassland-wheat field and riparian zone-wheat field boundaries based on mark-recapture studies (Tables 2 and 3). The dispersal of these beetles apparently resulted in differences in numbers captured with respect to trap location and sampling date. Based on traps facing the border, which allowed direct comparisons of edge traps with interior traps, I found that during autumn more beetles were captured in grassland, riparian zones, and boundary habitats than in wheat field interiors (Fig. 8 and 9). The numbers captured dropped during late autumn through mid-winter, however beetles were still captured predominantly in grassland and riparian habitats. A shift in capture rates among the traps occurred in late winter through spring, with more beetles being captured in wheat field interiors than in the other habitats (Figs. 10 – 13). This shift in location of captures coincides with the overall increase in numbers captured during late-winter and spring, indicating dispersal into wheat field interiors (Fig. 3). Lending further support to my contention that beetles crossed the boundaries from natural habitats to wheat field interiors is the observation that only 14 species were captured in the fallow wheat field just before planting, and most of these were caught in very low numbers, while 22 and 24 species were captured in the grasslands and riparian zones in much higher numbers at this time (Table 4).

Discussion

Season had the most profound effect on the structure of ground beetle assemblages. Species composition in autumn, winter, and spring represented unique assemblages of ground beetles. The spring and autumn assemblages correspond to the peaks in activity observed in my study. The spring peak was much greater than the autumn peak. Activity of ground beetles in autumn and spring is related to their life cycles, where species active in the spring generally overwinter as adults, and species active in autumn generally overwinter as larvae (Allen 1979, Luff 1987). For most insects, activity is driven by temperature (Southwood 1978). Thus, the spring peak observed in my study may be related to the time when temperatures are increasing, and autumn peak may be related to the time when temperatures are decreasing. In a study conducted at a similar latitude to my study, Allen and Thompson (1977) found spring and autumn peaks for many species of ground beetles in hardwood and pine forests in northwestern Arkansas. In their study spring peaks in activity were also much greater than autumn peaks. At these lower latitudes, some species may not be restricted to a single period of activity, and these species may be bivoltine or multivoltine under favorable conditions (Luff 1987). These bivoltine or multivoltine species may represent the winter ground beetle assemblage in my study.

Patches in a landscape interact through their boundaries (Wiens et al. 1985). A boundary consists of an edge from each adjacent patch and a border separating the edges (Duelli et al. 1990, Forman and Godron 1986). Boundaries are characterized by steep ecological gradients in factors such as temperature, relative humidity, wind speed, and vegetation structure. As a result, boundaries filter organisms as they disperse across them. This filtering process influences the species composition in boundaries and the habitats they connect. For example, Duelli et al. (1990) noted differences in ground beetle species dispersing across boundaries in a mosaic of cultivated and natural habitats, and this resulted in different species assemblages among the habitats. Differences in beetle assemblages among habitat types were also found in my study. Ground beetle assemblages were associated with wheat habitats and natural habitats. Grassland, grassland edge, and riparian edge assemblages were similar, whereas the riparian interior assemblage was unique. The ground beetle assemblages associated with wheat fields adjacent to grasslands differed from assemblages associated with wheat fields adjacent to riparian zones. Because grassland, grassland edge, and riparian edge were similar in community structure, it seems reasonable to conclude that the riparian interior beetle assemblage contributed some species to the assemblage in the adjacent wheat field, otherwise the wheat field interior and edge assemblage adjacent to riparian zones would not have differed from the wheat field interior and edge assemblage adjacent to grasslands.

In this study, boundaries filtered species of ground beetles as they dispersed from grasslands and riparian zones into adjacent wheat fields. Although not conclusive from my measurements of net dispersal of beetles, the mark-recapture studies showed that several species readily crossed the boundaries from grasslands and riparian zones that served as reservoirs for ground beetles that colonize agricultural fields. Additional evidence is provided from trap captures the few weeks before and during planting of wheat. Initially only 14 species were captured in the fallow wheat fields in very low numbers, while 22 species were captured in the grasslands and 24 in the riparian zones. Therefore, it is reasonable to conclude that, since ground beetles generally disperse by walking, the additional species observed in the wheat fields originated from the adjacent grassland and riparian habitats.

In this study, ground beetle assemblages differed with respect to seasons and habitats. I could not clearly demonstrate dispersal of ground beetles from grassland and riparian habitats into wheat fields. However, I did demonstrate that many species dispersed from the grassland and riparian habitats into the wheat fields and that their dispersal resulted in different structure of wheat field interior assemblages adjacent to different habitats. Because of their continuous seasonal activity and predatory nature, ground beetles are good candidates for biological control of wheat pests.

Wissinger (1997) suggested that natural enemies of annual crop pests are most effective as "cyclic colonizers" of the ephemeral crop system. He described cyclic colonizers as insects that respond to disturbance by dispersing to permanent habitats, delay reproduction, overwinter, and then recolonize the crop the following year. Prior to fragmenting the landscape for agricultural purposes, cyclic colonizers would probably be species or subpopulations of species that inhabited natural boundaries between riparian zones and grasslands or between forests and grasslands. As opposed to habitat interiors, it is at these boundaries where disturbance and the flux of materials and organisms may be greatest (Wiens et. al. 1985, Wiens 1997). Wissinger (1997) suggested that insects occupying these boundaries were preadapted for survival and reproduction in agricultural landscapes. In other words, these insects had already evolved life history traits adapted to a changing, but predictable environment, and possessed enough additive genetic variation underlying these traits to evolve in response to additional human disturbances to the landscape. The life history traits important for cyclic colonizers include dispersal from permanent or overwintering habitats to ephemeral habitats, ability to efficiently locate hosts or prey, efficient reproduction resulting in multiple generations, dispersal back to permanent or overwintering habitat, and survival in overwintering habitat.

Based on the important life history traits of cyclic colonizers, Wissinger (1997) described four criteria for biological control agents to be effective in annual crop systems such as wheat. First, natural enemies should have sufficient overwintering sites available near the crops. Second, the crop field size to edge ratio should not be too great as to inhibit or delay natural enemies from reaching field centers. Third, the benefits from boundaries (e.g., overwintering sites, refuge from pesticides, and shelter) should out-weigh their costs (e.g., reduced dispersal among habitats). Fourth, broad-spectrum pesticides should not eliminate natural enemies once they have established in the crop fields. In reference to ground beetles, habitat generalists may have been the beneficiaries of modern agriculture and resulted in a shift from habitat generalists to habitat specialists. From this study, several species are potential biological control agents of wheat pests. Because wheat fields vary considerably in size in the Great Plains, it is important to determine whether ground beetles overwinter in adjacent grassland and riparian edges, and if they do, how far they will disperse into the wheat field interior (criteria 1 and 2 of Wissinger 1997). Equally important is to determine which species have evolved life cycles that are completed exclusively in crop fields. This aspect of effective biological control strategies was not covered by Wissinger (1997), but seems relevant for wheat specialists. For such species, survival and reproduction depends entirely on availability of prey in the wheat fields.

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Table 1. Species names of abbreviations (Abbr.) used in CCA and partial CCA biplots.

Species	Abbr.	Species	Abbr.
Abacidus permundus Say	Abp	*Cymindis pilosa Say*	Cyp
Agonum pallipes F.	Agp	*Dicaelus elongatus* Bonelli	Die
A. punctiforme Say	Apu	*Discoderus parallelus* Haldeman	Dip
Amara convexa LeConte	Amc	*Dyschiriodes globulosus* Say	Dyg
A. cupreolata Putzeys	Acu	*D. pilosus* Say	Dyp
A. musculis Say	Amm	*Elaphropus dolosus* LeConte	Eld
A. rubrica Haldeman	Amr	*E. granarius* Dejean	Elg
Anisodactylus carbonarius Say	Anc	*Galerita atripes* LeConte	Gaa
A. dulcicollis LaFerté	And	*G. janus* F.	Gaj
A. harpaloides LaFerté	Anh	*Harpalus amputatus* Say	Haa
A. merula Germar	Anm	*H. desertus* LeConte	Had
A. ovularis Casey	Ano	*H. faunus* LeConte	Haf
A. rusticus Say	Anr	*H. fulgens* Csiki	Hfu
A. sanctaecruscis F.	Ans	*H. paratus* Say	Hap
Apristus latens LeConte	Apl	*H. pensylvanicus* DeGeer	Hpe
Bembidion castor Lindroth	Bec	*Helluomorphoides praeustus* Harris	Hep
B. nigripes Kirby	Ben	*Lebia tricolor* Say	Let
Calathus opaculus LeConte	Cao	*Microlestes linearis* LeConte	Mil
Calosoma affine Chaudoir	Caf	*Notiophilus novemstriatus* LeConte	Non
C. externum Say	Cae	*Pasimachus elongatus* LeConte	Pae
Chlaenius platyderus Chaudoir	Cpl	*Pterostichus chalcites*	Ptc
C. tomentosus Say	Cht	*P. femoralis* Kirby	Ptf
Cicindela denverensis Casey	Cid	*Scarites subterraneus* F.	Scs
C. punctulata Olivier	Cip	*Stenolophus comma* F.	Stc
Clivina bipustulata F.	Clb	*S. conjunctus* Say	Sco
C. postica LeConte	Clp	*S. lineola* F.	Stl
Colliuris pensylvanica L.	Cop	*S. ochropezus* LeConte	Sto
Cratacanthus dubius Beauvois	Crd	*Stenomorphus rotundatus* LeConte	Str
Cyclotrachelus torvus LeConte	Cyt		

Table 2. Species of ground beetles determined to cross the grassland-wheat field boundary. Also listed are species collected in both grassland and wheat field, but due to low numbers captured was unable to verify crossing of borders. The *Bembidion* spp. were *B. nigripes* and *B. castor* and the *Elaphropus* spp. were *E. granarius* and *E. dolosus*.

Grassland – Wheat	Wheat – Grassland	Grassland and Wheat
Amara cupreolata	*A. convexa*	*Abacidus permundus*
A. convexa	*A. carbonarius*	*Agonum punctiforme*
Anisodactylus carbonarius	*A. merula*	*Amara musculis*
A. dulcicollis	*A. ovularis*	*A. pennsylvanica*
A. harpaloides	*C. affine*	*Anisodactylus opaculus*
A. merula	*Clivina bipustulata*	*A. rusticus*
A. ovularis	*C. torvus*	*A. dulcicollis*
Calathus opaculus	*P. elongatus*	*Apristus latens*
Calosoma affine	*S. subterraneus*	*Bembidion* spp.
C. externum		*Clivina postica*
Chlaenius tomentosus		*Colliuris pensylvanica*
Cyclotrachelus torvus		*Cratacanthus dubius*
Harpalus fulgens		*Cyclotrachelus seximpressus*
Pasimachus elongatus		*Elaphropus* spp.
Scarites subterraneus		*Galerita janus*
		Olisthopus parmatus
		Panagueus fasciatus
		Pterostichus chalcites
		P. femoralis
		Stenolophus conjunctus

Table 3. Listed are species of ground beetles determined to cross the riparian strip-wheat field boundary. Also listed are species collected in both riparian strip and wheat field, but due to low numbers captured was unable to verify crossing of borders. The *Bembidion* spp. were *B. nigripes* and *B. castor*, the *Elaphropus* spp. were *E. dolosus* and *E. granarius*, and the *Dyschiroides* spp. were *D. globulosus* and *D. pilosus*.

Riparian – Wheat	Wheat – Riparian	Riparian and Wheat
A. convexa	*A. carbonarius*	*Amara pennsylvanica*
Anisodactylus carbonarius	*A. merula*	*Anisodactylus harpaloides*
A. dulcicollis	*A. ovularis*	*A. opaculus*
A. merula	*Bembidion* spp.	*A. rusticus*
A. ovularis	*Calosoma affine*	*C. externum*
Bembidion spp.	*Clivina bipustulata*	*Clivina postica*
Chlaenius tomentosus	*H. praeustus*	*A. harpaloides*
Galerita janus	*G. janus*	*Apristus latens*
Harpalus desertus		*Bembidion* spp.
Helluomorphoides praeustus		*Cratacanthus dubius*
		Diacaelus elongatus
		Dyschiroides spp.
		Elaphropus spp.
		Galerita atripes
		Harpalus fulgens
		Notiophilus novemstriatus
		Olisthopus parmatus
		Panagueus fasciatus
		Pasimachus elongatus
		Pterostichus chalcites
		Scarites subterraneus
		Selenophorus planipennis

Table 4. Mean numbers per trap (total) of ground beetles captured in fallow fields prior to drilling of wheat, and in grasslands and riparian zones while wheat was being drilled.

	9/21 – 10/5	10/1 – 10/15	
Species	Fallow	Grassland	Riparian
Abacidus permundus Say	0.00	0.82 (31)	0.24 (9)
Agonum pallipes F.	0.00	0.05 (2)	0.08 (3)
Amara impuncticollis Say	0.00	0.00	0.03 (1)
Amara rubrica Haldeman	0.08 (1)	0.05 (2)	0.03 (1)
Anisodactylus rusticus Say	0.17 (2)	0.18 (7)	0.16 (6)
A. harpaloides LaFerté	0.08 (1)	0.00	0.03(1)
A. dulcicollis LaF.	0.00	0.03 (1)	0.00
Apenes sinuata Say	0.00	0.00	0.03 (1)
Apristus latens LeConte	0.17 (2)	0.05 (2)	0.24 (9)
Bembidion nigripes Kirby	0.00	0.03 (1)	0.00
Calathus opaculus LeConte	0.00	0.37 (14)	0.26 (10)
Calosoma affine Chaudoir	0.00	0.00	0.03 (1)
Chlaenius tomentosus Say	0.08 (1)	0.05 (2)	0.03 (1)
Cicindela punctulata Olivier	1.17 (14)	0.53 (20)	0.58 (22)
Clivina bipustulata F.	0.00	0.05 (2)	0.08 (3)
C. postica LeConte	0.00	0.03 (1)	0.00
Cratacanthus dubius Beauvois	0.17 (2)	0.03 (1)	0.00
Cyclotrachelus torvus LeConte	0.08 (1)	0.18 (7)	0.34 (13)
Elaphropus dolosus LeConte	0.00	0.03 (1)	0.03 (1)
Galerita atripes LeConte	0.00	0.00	0.08 (3)
Galerita janus F.	0.00	0.05 (2)	0.63 (24)
Harpalus caliginosus F.	0.08 (1)	0.00	0.00
H. faunus LeConte	0.25 (3)	0.39 (15)	0.29 (11)
H. fulgens Csiki	0.00	0.03 (1)	0.00
H. pensylvanicus DeGeer	1.25 (15)	3.24 (123)	2.53 (96)
Notiophilus novemstriatus LeConte	0.00	0.00	0.32 (12)
Pasimachus elongatus LeConte	0.17 (2)	0.00	0.03 (1)
Pterostichus chalcites Say	0.08 (1)	0.05 (2)	0.13 (5)
Scarites subterraneous F.	0.92 (11)	0.05 (2)	0.03 (1)
Stenolophus rotundatus LeConte	0.00	0.00	0.03 (1)
Stenomorphus californicus LeConte	0.00	0.03 (1)	0.00
Grand Total	4.75 (57)	6.29 (239)	6.21 (236)

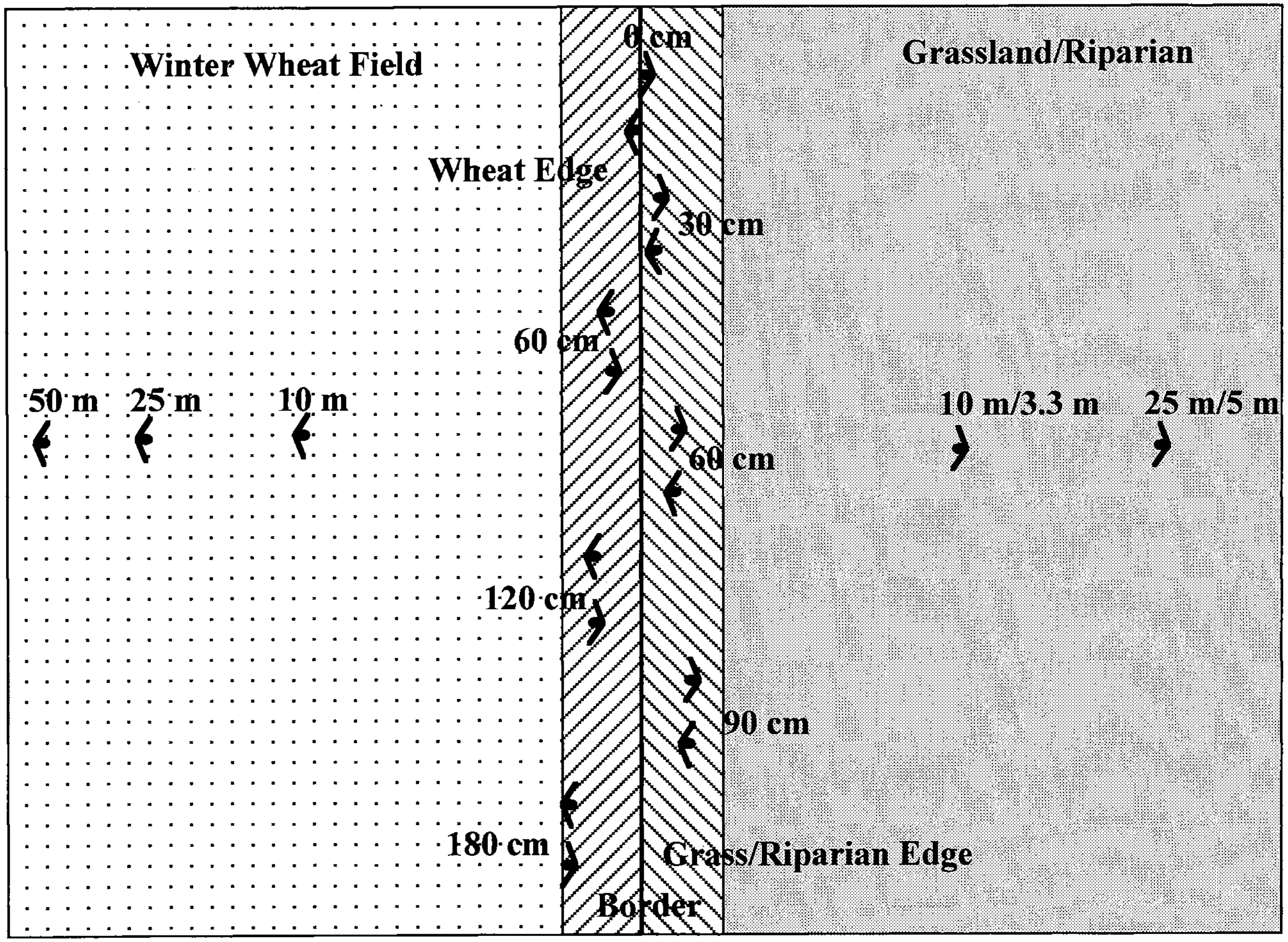

Figure 1. Arrangement of guided pitfall traps in wheat fields, grasslands, riparian zones, and their edges. Traps were placed at varying distances from the border and facing the border. The border represented an abrupt change in vegetation from wheat to natural vegetation.

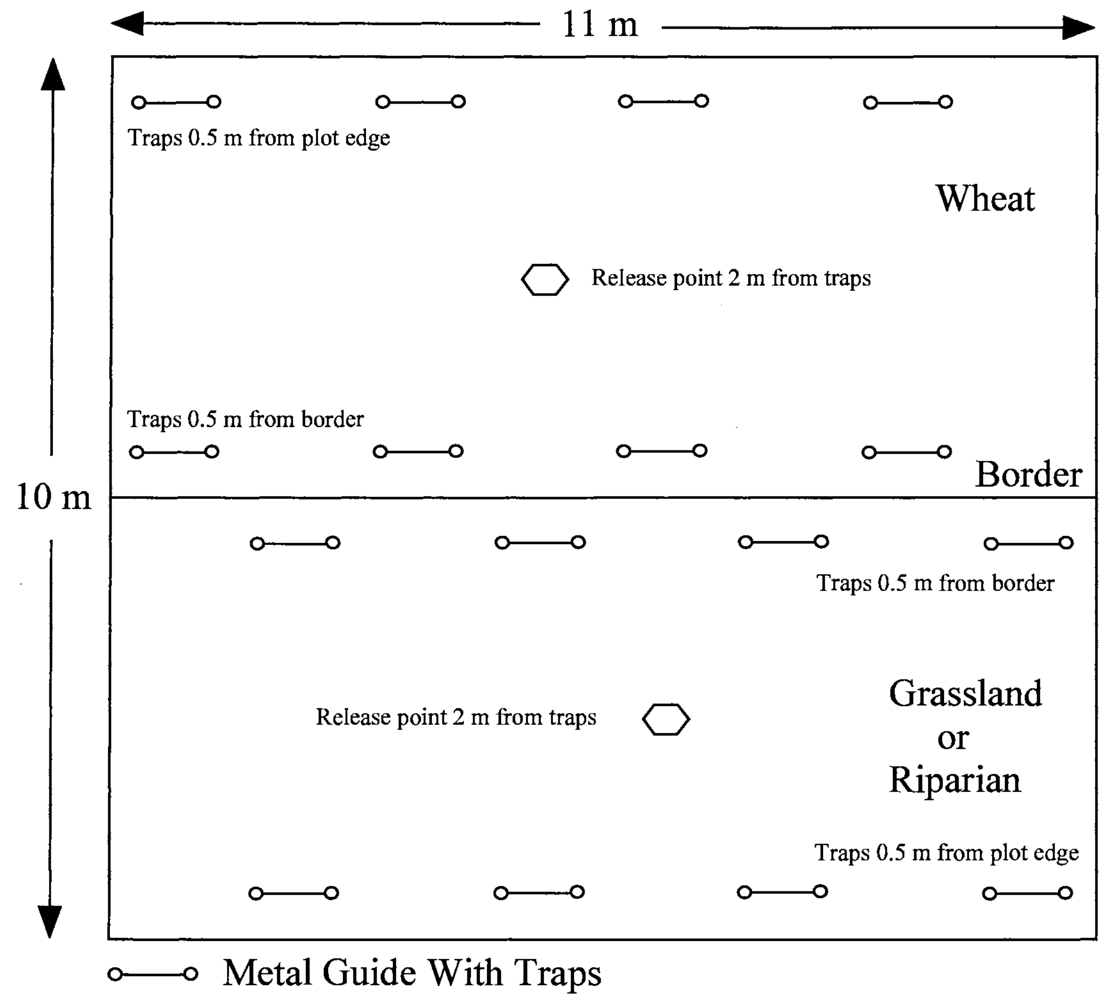

Figure 2. Arrangement of guided pitfall traps in the mark-recapture study. The border represented an abrupt change in vegetation from wheat to natural vegetation.

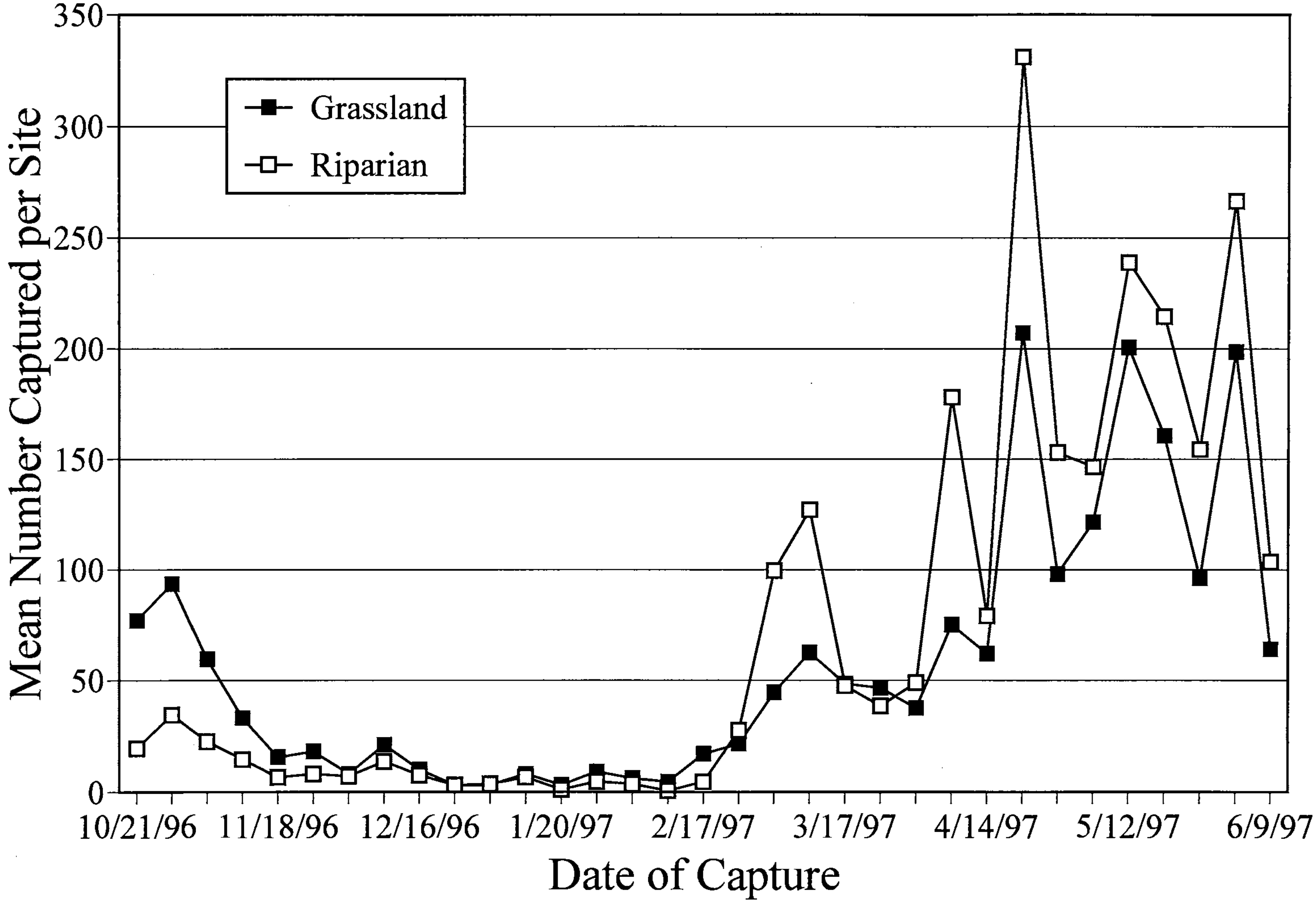

Figure 3. Temporal distribution of mean number of ground beetles captured by date from the grassland-wheat field and riparian-wheat field sites.

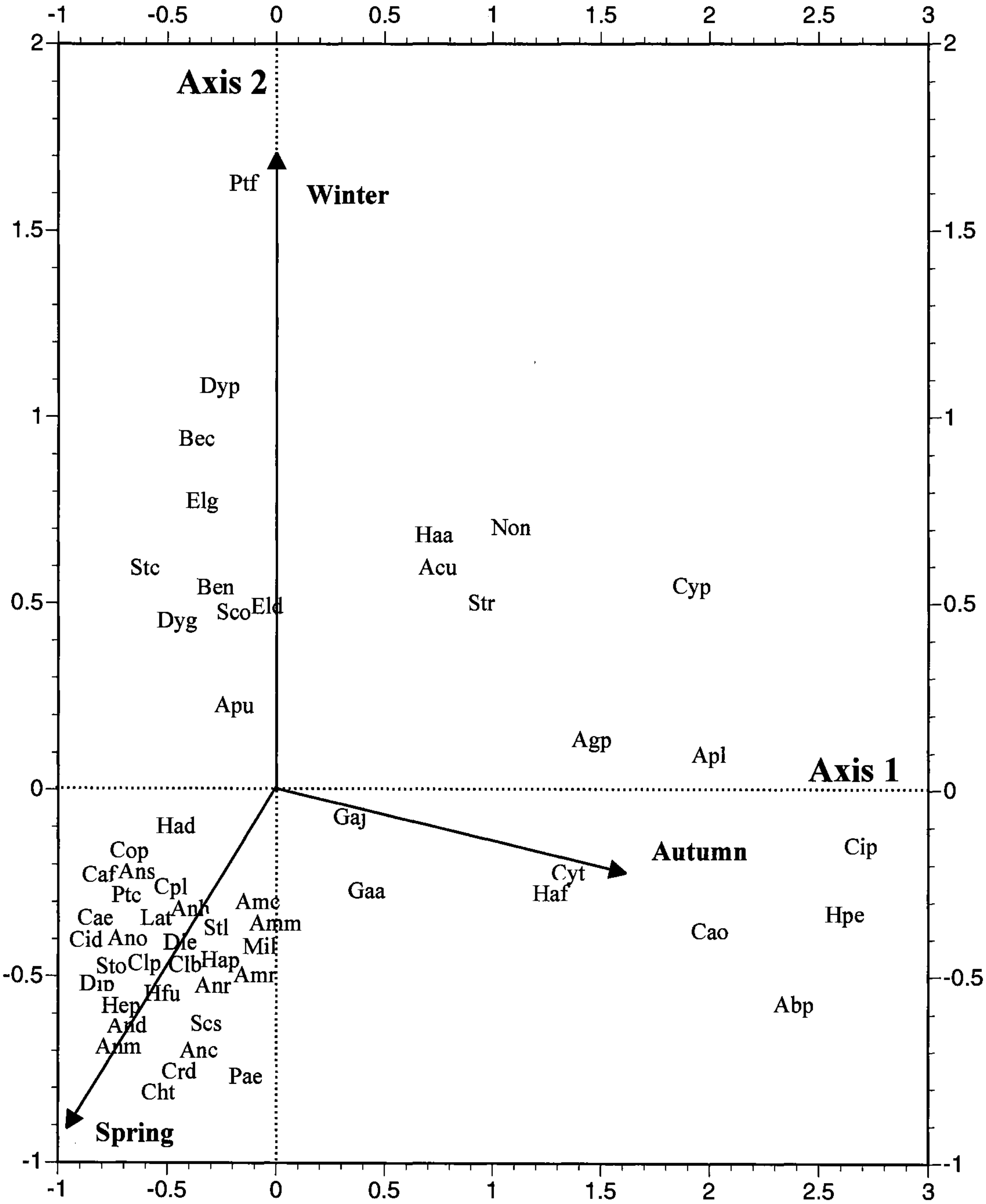

Figure 4. Biplot of ground beetle abundances and seasonal variables from CCA. The abbreviation of species names are plotted and complete names are listed in Table 1. Environmental variables; autumn, winter, and spring are represented by arrows.

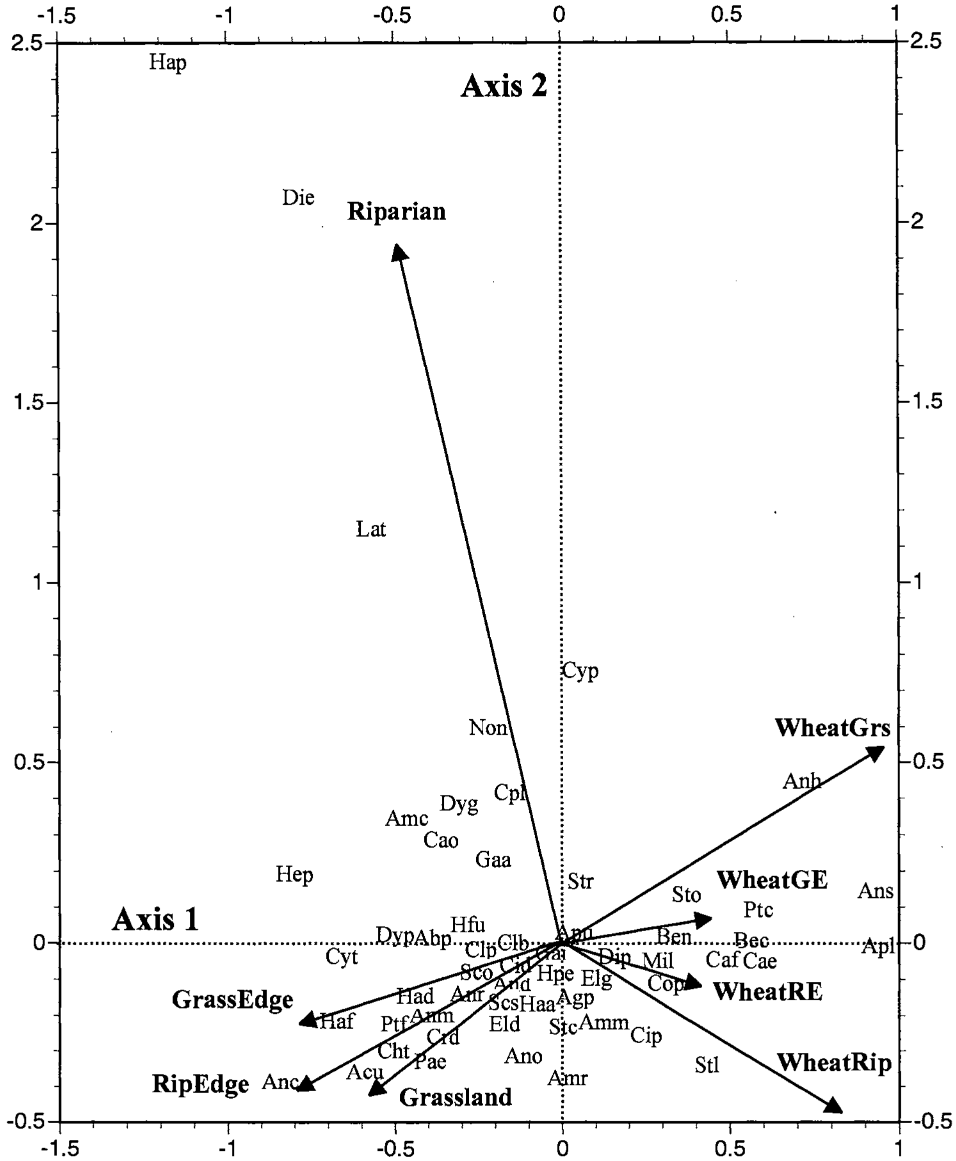

Figure 5. Biplot of ground beetle abundances and independent variables from a partial CCA. The abbreviation of species names are plotted and complete names are listed in Table 1. Environmental variables are represented by arrows. The environmental variables are riparian interior = Riparian, riparian edge = RipEdge, wheat interior adjacent to riparian zones = WheatRip, wheat edge adjacent to riparian zones = WheatRE, grassland interior = Grassland, grassland edge = GrassEdge, wheat interior adjacent to grassland = WheatGrs, wheat edge adjacent to grassland = WheatGE.

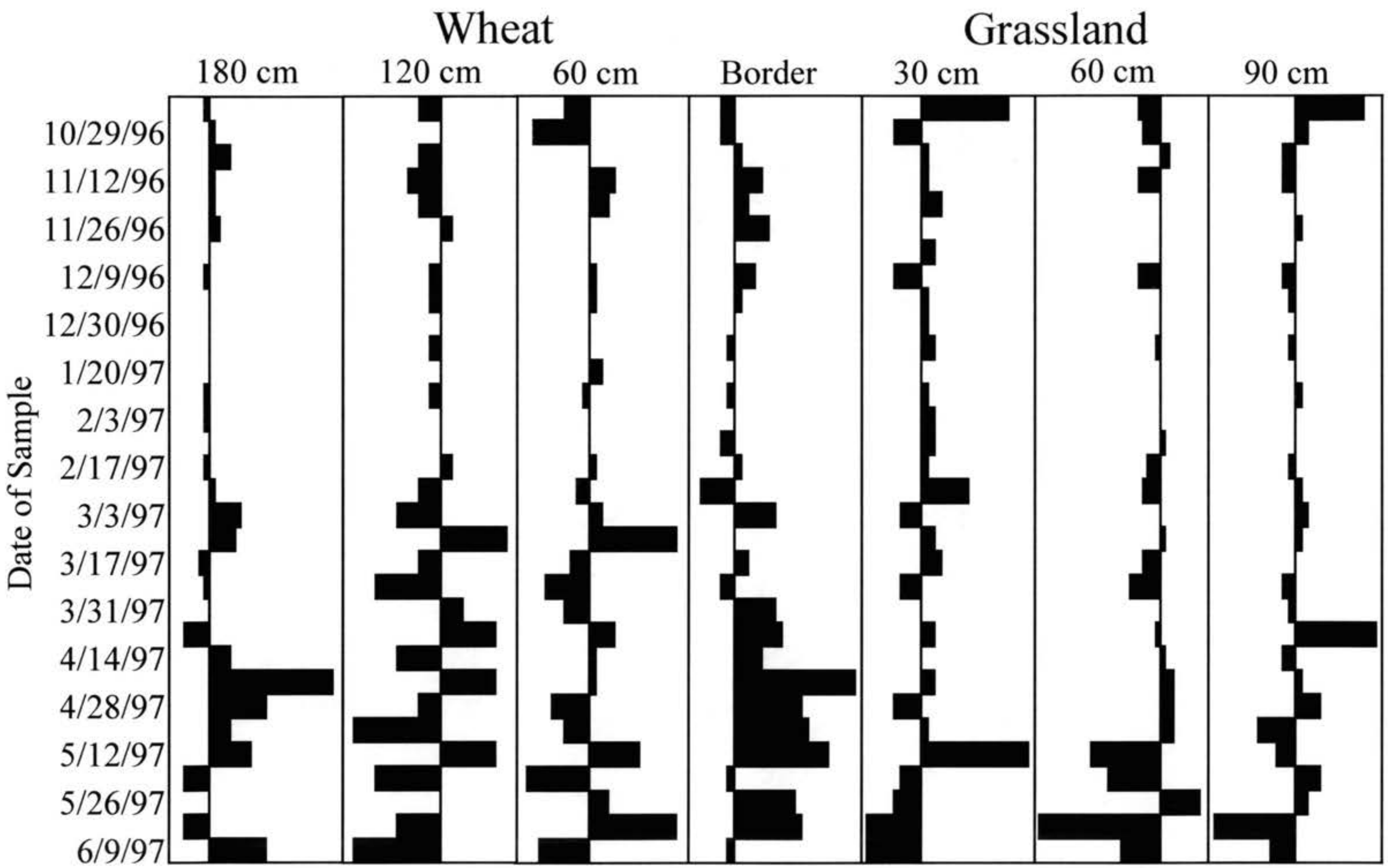

Figure 6. Net dispersal of ground beetles from traps positioned in the grassland edge and wheat field edge. Direction of bars indicate net direction of dispersal.

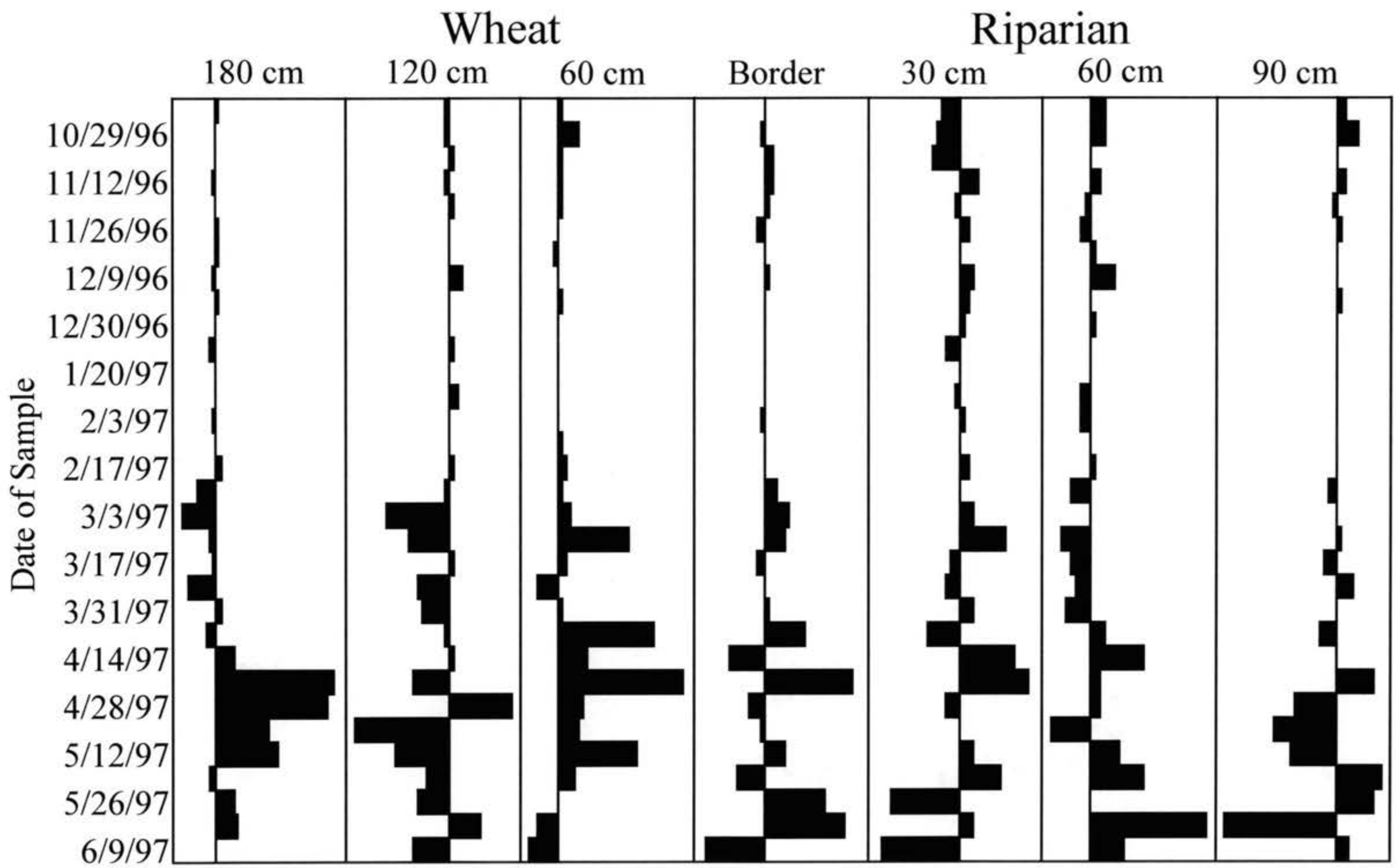

Figure 7. Net dispersal of ground beetles from traps positioned in the riparian edge and wheat field edge. Direction of bars indicate net direction of dispersal.

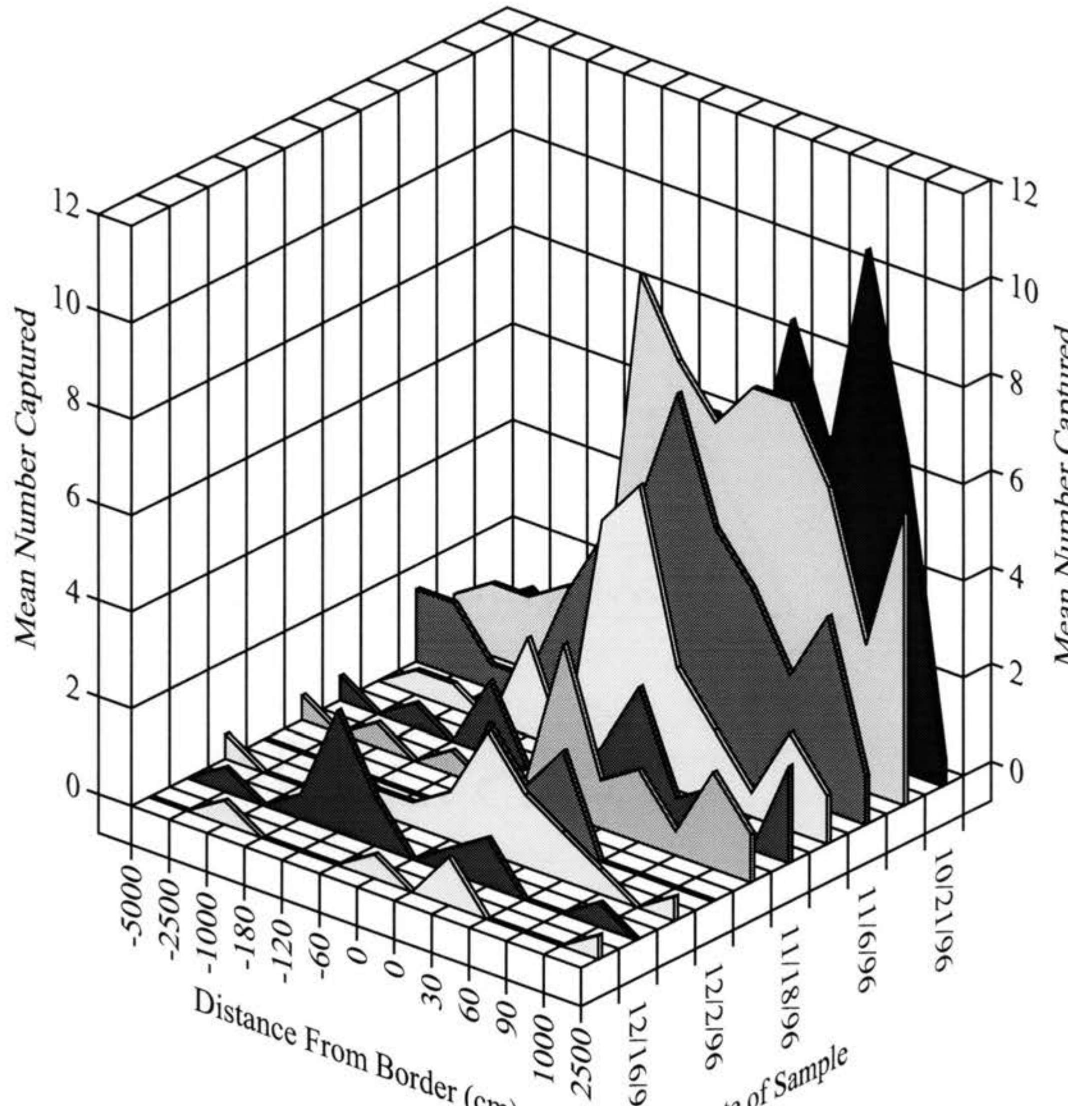

Figure 8. Mean number of ground beetles per site dispersing into grasslands ("+" values) and wheat fields ("-" values) during autumn. Data are from traps facing the border.

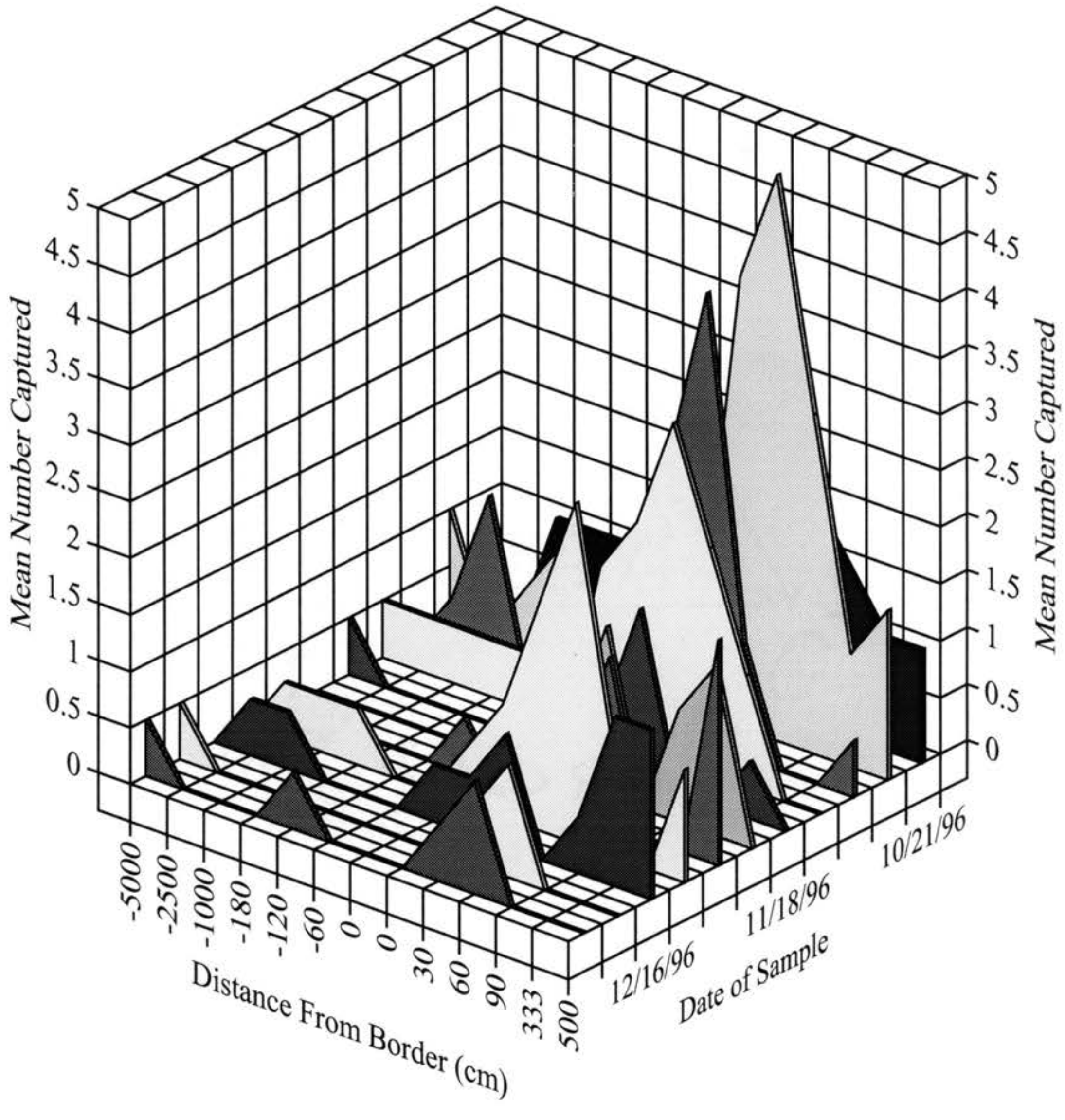

Figure 9. Mean number of ground beetles per site dispersing into riparian zones ("+" values) and wheat fields ("-" values) during autumn. Data are from traps facing the border.

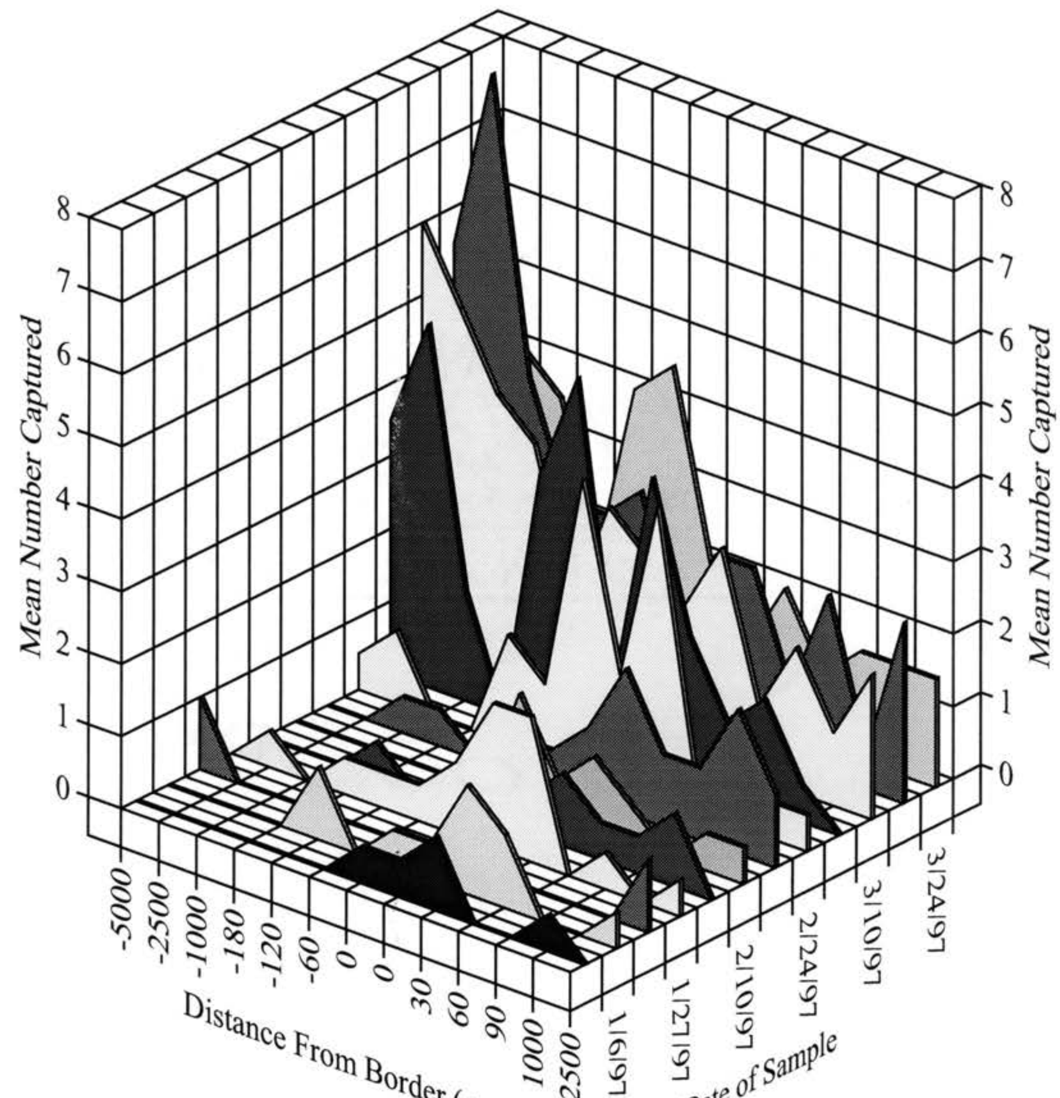

Figure 10. Mean number of ground beetles per site dispersing into grasslands ("+" values) and wheat fields ("-" values) during winter. Data are from traps facing the border.

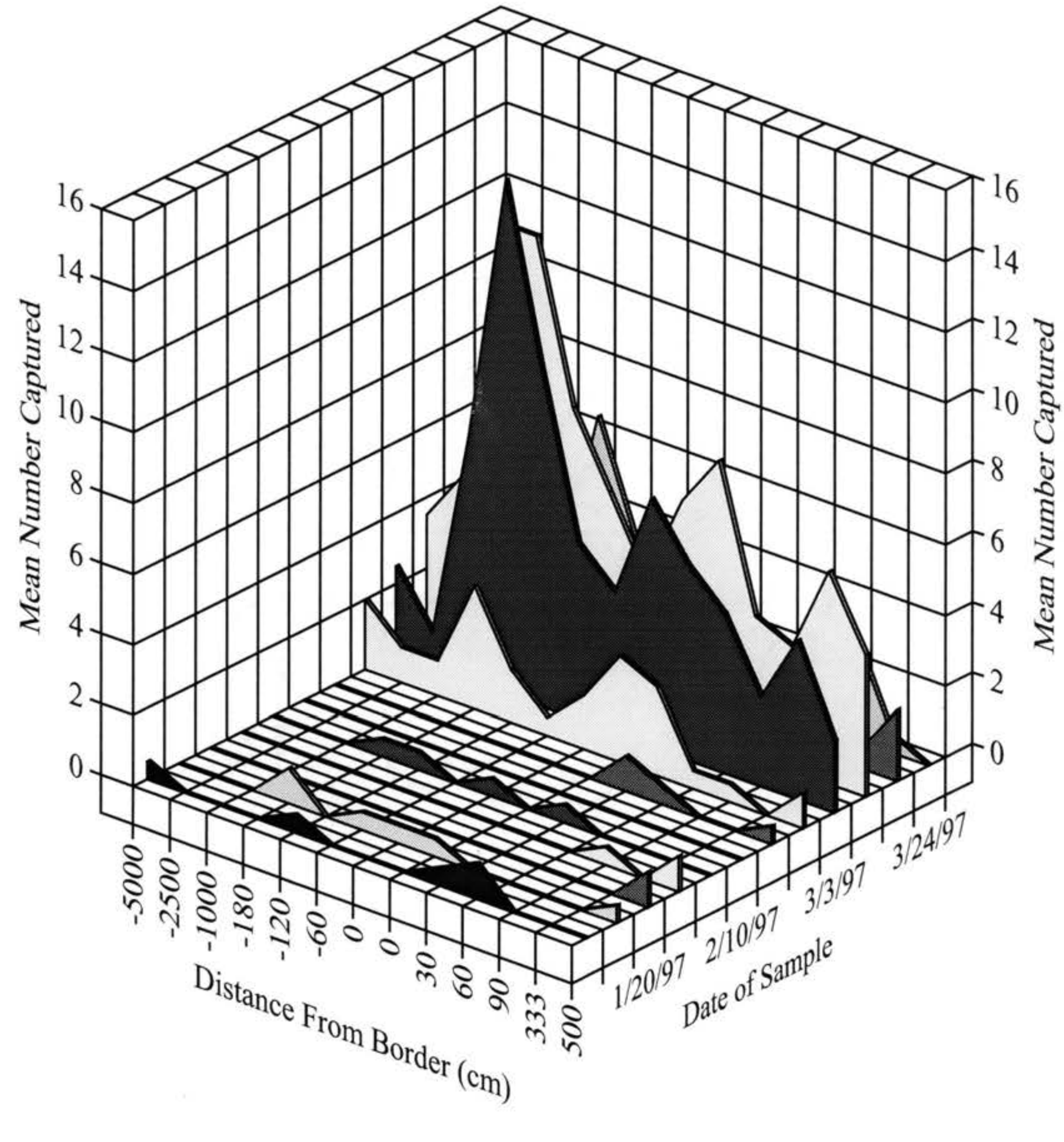

Figure 11. Mean number of ground beetles per site dispersing into riparian zones ("+" values) and wheat fields ("-" values) during winter. Data are from traps facing the border.

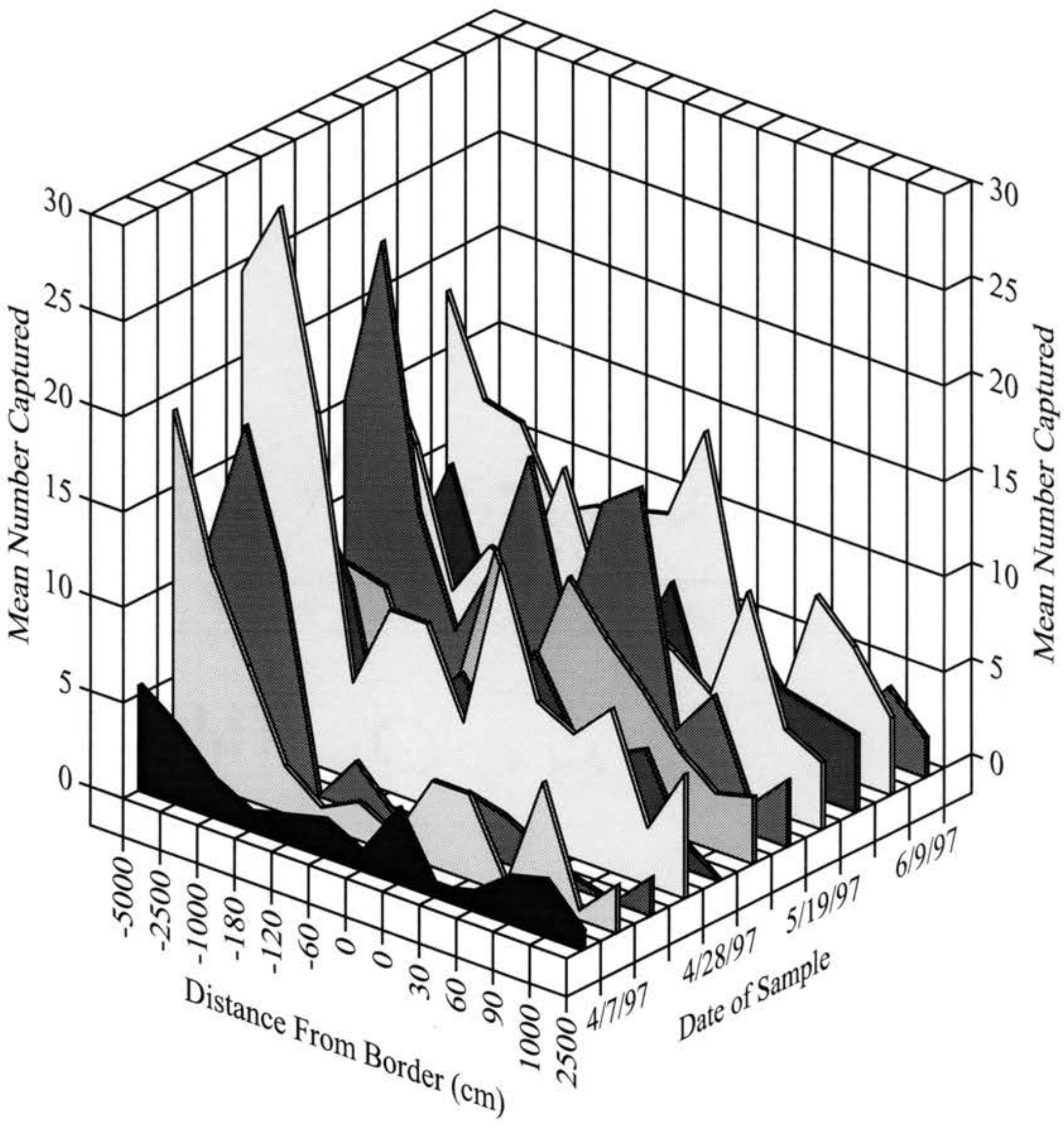

Figure 12. Mean number of ground beetles per site dispersing into grasslands ("+" values) and wheat fields ("-" values) during spring. Data are from traps facing the border.

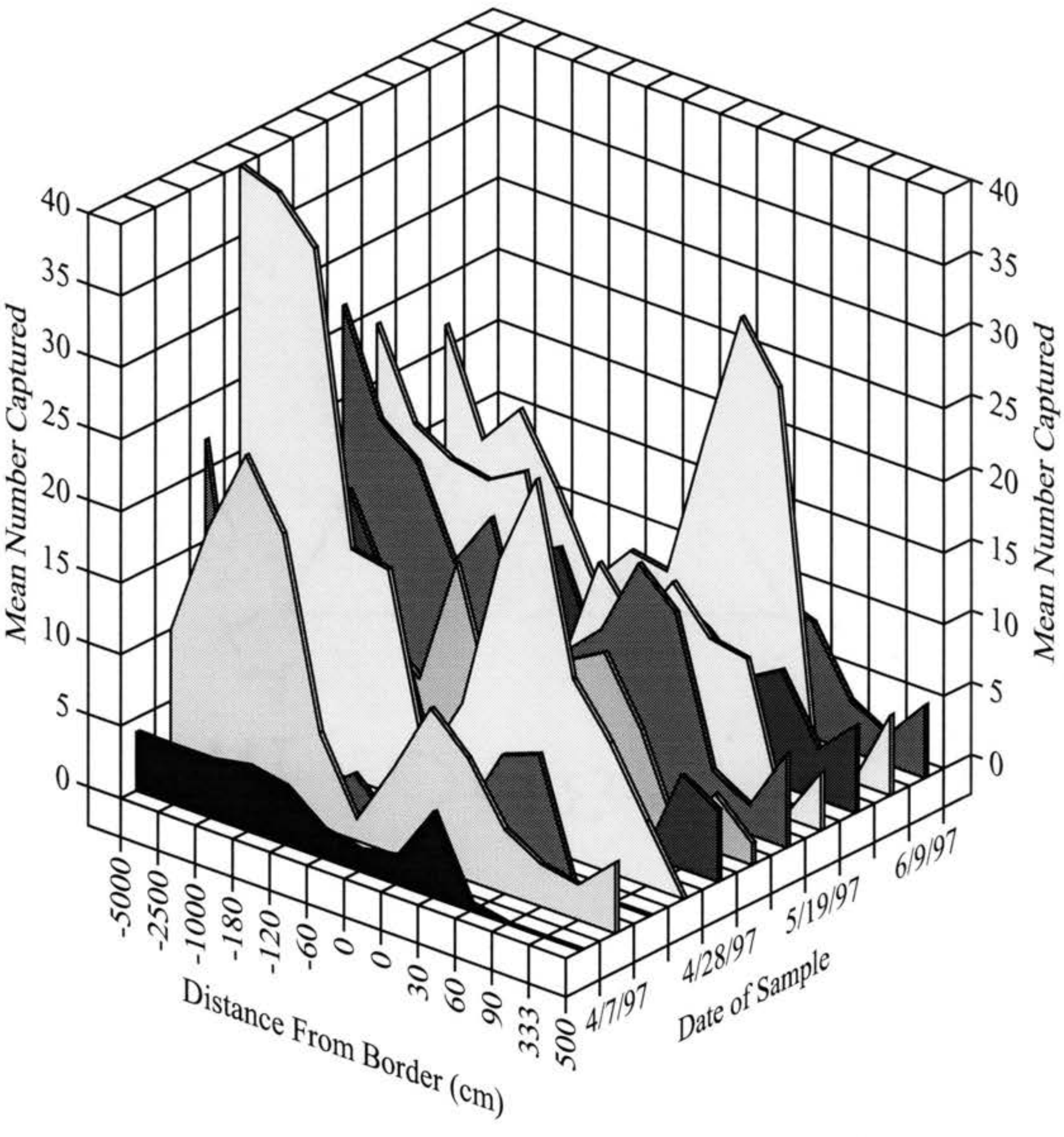

Figure 13. Mean number of ground beetles per site dispersing into riparian zones ("+" values) and wheat fields ("-" values) during spring. Data are from traps facing the border.

CHAPTER VII

SUMMARY

Ground beetles are polyphagous predators and prey upon many invertebrate pests of agricultural crops. Consequently, ground beetles play an important role in the biological control of insect pests in some crops. Ground beetles were captured in agricultural landscapes using pitfall traps. In Oklahoma agricultural landscapes, winter wheat is grown in a mosaic of grasslands and riparian zones. The primary focus of this project was on ground beetle assemblages and abundances in wheat fields and how farm management practices and landscape structure affected these beetles. Different approaches were used to obtain this information. In the Oklahoma panhandle, an individual field scale approach was taken where I focused on the effects of reverting Conservation Reserve Program (CRP) lands back into wheat and livestock production. Here the focus was on the influence of within-field differences in management practices, particularly crop selection and tillage. Highly erodible lands are enrolled in the CRP for 10 years and are planted with native or exotic grasses for erosion control. In this study, more ground beetles were captured in no-tillage wheat (WNT) and managed Old World bluestem (OWBM) plots than in minimum-tillage wheat (WMT) and unmanaged Old World bluestem plots (OWBUM). The WNT and OWBM are intermediate disturbance levels between WMT and OWBUM, and had the greatest effect on ground beetle assemblages. However, species were affected differently by the apparent difference in disturbance levels; some species were more abundant in the WMT plots than in the other cropping systems.

At a broader (landscape) scale, grasslands and riparian zones were examined for their effects on ground beetle assemblages in adjacent wheat fields. These natural habitats are believed to be sources for ground beetles to disperse into wheat fields. Elsewhere it has been determined that ground beetles overwinter in grassy and wooded edges surrounding cereal fields and disperse into the fields under favorable conditions. In Oklahoma, winter wheat is the primary cereal crop and therefore the autumn and winter assemblages of ground beetles may be particularly important as biological control agents. Seasons were the primary factors separating ground beetle assemblages. Ground beetles were separated into autumn, winter, and spring assemblages. Spring assemblages consisted of more species and greater abundance, followed by autumn and winter assemblages. I found distinct assemblages of ground beetles inhabiting the interiors and edges of contiguous wheat fields, grasslands, and riparian strips. The assemblages in wheat fields adjacent to grasslands were different from those in wheat fields adjacent to riparian strips. The net number of ground beetles captured from the grassland and riparian edges showed no consistent pattern of dispersal into and out of the wheat fields. However, mark-recapture studies revealed that several species routinely crossed the wheat field-grassland and wheat field-riparian boundaries. Presumably, the beetles crossing the boundaries resulted in the increase in numbers captured in the wheat field interiors in late winter through spring.

These studies were limited by the use of a single method, pitfall traps, to collect ground beetles. Future studies should employ additional methods of collecting ground beetles. For example, emergence traps could be used to determine the overwintering strategies of ground beetles. Sticky traps or window pane traps could be used to catch flying ground beetles. The many studies on ground beetle dispersal into cereal fields have been at higher latitudes where winters are harsh, and have focused on ground beetles that are univoltine and have an obligate period of diapause in their life cycle. In more southern latitudes where winters are fairly mild, ground beetles may be bivoltine or multivoltine and have a facultative period of diapause. Thus, different research techniques and strategies may be necessary to understand the interactions of ground beetle assemblages in agricultural landscapes in Oklahoma than have been used elsewhere.

A final note on this study; overall, 125 species of ground beetles were collected (Appendix B). Many species were captured repeatedly in different studies, whereas others were captured in only one study (Appendix C). A few species dominated in abundance in each season and habitat, the most common of which were *Agonum punctiforme, Anisodactylus dulcicollis, Bembidion castor, B. nigripes, Galerita janus, Harpalus pensylvanicus, Pasimachus elongatus,* and *Pterostichus chalcites*. These species and others may have responded to microclimatic differences across boundaries as temperatures are known to vary (Appendix D). The species collected in this study in relation to season and habitat type provide a rich database for more detailed research on the ecology and life history of individual species. Like most scientific investigations, this one provides more questions than answers.

APPENDICES

APPENDIX A

EFFECTS OF INSECTICIDAL CATTLE EAR TAGS ON GROUND BEETLE CAPTURES

To determine the effects of insecticidal ear tags on ground beetle captures, 5 paired pitfall traps with metal guides (see Chapter II) were established in a winter wheat field on 1 January 1996. Tags were randomly assigned to one of the pair of traps. Traps were emptied weekly for seven weeks. The number of beetles captured were transformed to natural logarithms. The numbers captured between the traps with tags and traps without tags were not significantly different ($t = 0.80$, $df = 35$, $P > 0.05$). It is concluded that insecticidal ear tags had no effect on beetle captures in any of the studies reported here.

APPENDIX B

SCIENTIFIC NAMES AND AUTHORITIES OF ALL SPECIES OF GROUND BEETLES CAPTURED

No.	Species	Authority
1	*Abacidus permundus*	Say
2	*Acupalpus indistinctus*	Dejean
3	*Acupalpus partiarius*	Say
4	*Acupalpus testaceus*	Dejean
5	*Agonum decorum*	Say
6	*Agonum extensicolle*	Say
7	*Agonum nutans*	Say
8	*Agonum octopunctatum*	Fabricius
9	*Agonum pallipes*	Fabricius
10	*Agonum placidum*	Say
11	*Agonum punctiforme*	Say
12	*Amara carinata*	LeConte
13	*Amara convexa*	LeConte
14	*Amara cupreolata*	Putzeys
15	*Amara exarata*	Dejean
16	*Amara impuncticollis*	Say
17	*Amara musculis*	Say
18	*Amara obesa*	Say
19	*Amara pennsylvanica*	Hayward
20	*Amara rubrica*	Haldeman
21	*Amphasia interstitialis*	Say
22	*Anisodactylus carbonarius*	Say
23	*Anisodactylus dulcicollis*	LaFerté
24	*Anisodactylus harpaloides*	LaFerté
25	*Anisodactylus merula*	Germar
26	*Anisodactylus opaculus*	LeConte
27	*Anisodactylus ovularis*	Casey
28	*Anisodactylus rusticus*	Say
29	*Anisodactylus sanctaecrucis*	Fabricius
30	*Anisodactylus verticalis*	Say
31	*Apenes sinuata*	Say
32	*Apristus latens*	LeConte
33	*Atranus pubescens*	Dejean
34	*Badister notatus*	Hayward
35	*Bembidion castor*	Lindroth
36	*Bembidion impotens*	Casey
37	*Bembidion levigatum*	Say
38	*Bembidion nigripes*	Kirby
39	*Bembidion texanum*	Chaudoir
40	*Brachinus fumans*	Fabricius
41	*Brachinus rugipennis*	Chaudoir

No.	Species	Authority
42	*Brachinus tenuicollis*	LeConte
43	*Bradycellus tantillus*	Dejean
44	*Calathus opaculus*	LeConte
45	*Calosoma affine*	Chaudoir
46	*Calosoma externum*	Say
47	*Calosoma sayi*	Dejean
48	*Calosoma scrutator*	Fabricius
49	*Calosoma wilcoxi*	LeConte
50	*Catogenus rufus*	Fabricius
51	*Chlaenius emarginatus*	Say
52	*Chlaenius erythropus*	Germar
53	*Chlaenius nemoralis*	Say
54	*Chlaenius pennsylvanicus*	Say
55	*Chlaenius platyderus*	Chaudoir
56	*Chlaenius sericeus*	Forst
57	*Chlaenius tomentosus*	Say
58	*Chlaenius vafer*	LeConte
59	*Cicindela denverensis*	Casey
60	*Cicindela punctulata*	Olivier
61	*Cicindela scutellaris*	Say
62	*Clivina bipustulata*	Fabricius
63	*Clivina postica*	LeConte
64	*Colliuris pensylvanica*	L.
65	*Cratacanthus dubius*	Beauvois
66	*Cyclotrachelus constrictus*	Say
67	*Cyclotrachelus seximpressus*	LeConte
68	*Cyclotrachelus torvus*	LeConte
69	*Cymindis laticollis*	Say
70	*Cymindis pilosa*	Say
71	*Dicaelus elongatus*	Bonelli
72	*Discoderus parallelus*	Haldeman
73	*Dyschiriodes abbreviatus*	Putzeys
74	*Dyschiriodes globulosus*	Say
75	*Dyschiriodes pilosus*	LeConte
76	*Elaphropus dolosus*	LeConte
77	*Elaphropus granarius*	Dejean
78	*Euryderus grossus*	Say
79	*Galerita atripes*	LeConte
80	*Galerita janus*	Fabricius
81	*Geopinus incrassatus*	DeGeer
82	*Harpalus amputatus*	Say
83	*Harpalus caliginosus*	Fabricius

No.	Species	Authority
84	*Harpalus compar*	LeConte
85	*Harpalus desertus*	LeConte
86	*Harpalus faunus*	LeConte
87	*Harpalus fulgens*	Csiki
88	*Harpalus katiae*	Battoni
89	*Harpalus longicollis*	LeConte
90	*Harpalus paratus*	Say
91	*Harpalus pensylvanicus*	DeGeer
92	*Helluomorphoides praeustus bicolor*	Harris
93	*Helluomorphoides texanus*	LeConte
94	*Lebia analis*	Dejean
95	*Lebia atriventris*	Say
96	*Lebia pulchella*	Say
97	*Lebia solea*	Hentz
98	*Lebia tricolor*	Say
99	*Lebia viridis*	Say
100	*Micrixys distincta*	LeConte
101	*Microlestes linearis*	LeConte
102	*Notiobia terminata*	Say
103	*Notiophilus novemstriatus*	LeConte
104	*Olisthopus parmatus*	Say
105	*Omophron americanum*	Dejean
106	*Panagueus fasciatus*	Say
107	*Pasimachus elongatus*	LeConte
108	*Patrobus longicornis*	Say
109	*Pterostichus chalcites*	Say
110	*Pterostichus femoralis*	Kirby
111	*Pterostichus lucublandus*	Say
112	*Rhadine larvalis*	LeConte
113	*Scaphinotus cavicollis*	Say
114	*Scarites subterraneus*	Fabricius
115	*Selenophorus opalinus*	LeConte
116	*Selenophorus planipennis*	LeConte
117	*Semiardistomis viridis*	Say
118	*Stenolophus comma*	Fabricius
119	*Stenolophus conjunctus*	Say
120	*Stenolophus dissimilis*	Dejean
121	*Stenolophus lineola*	Fabricius
122	*Stenolophus ochropezus*	Say
123	*Stenolophus rotundatus*	LeConte
124	*Stenomorphus californicus*	LeConte
125	*Tetragonoderus fasciatus*	Haldeman

APPENDIX C

SCIENTIFIC NAMES OF GROUND BEETLES

CAPTURED BY YEAR AND STUDY

No.	Grass 93 & 94 Species	CRP 95 & 96 Species	Grs/ Rip 96 & 97 Species
1	*Abacidus permundus*	*Acupalpus indistinctus*	*Abacidus permundus*
2	*Agonum pallipes*	*Acupalpus partiarius*	*Acupalpus testaceus*
3	*Agonum punctiforme*	*Agonum decorum*	*Agonum decorum*
4	*Amara convexa*	*Agonum pallipes*	*Agonum nutans*
5	*Amara cupreolata*	*Agonum placidum*	*Agonum octopunctatum*
6	*Amara impuncticollis*	*Agonum punctiforme*	*Agonum pallipes*
7	*Amara musculis*	*Amara carinata*	*Agonum punctiforme*
8	*Amara obesa*	*Amara convexa*	*Amara convexa*
9	*Amara pensylvanica*	*Amara cupreolata*	*Amara cupreolata*
10	*Amara rubrica*	*Amara impuncticollis*	*Amara impuncticollis*
11	*Anisodactylus carbonarius*	*Amara musculis*	*Amara musculis*
12	*Anisodactylus dulcicollis*	*Amara obesa*	*Amara obesa*
13	*Anisodactylus harpaloides*	*Amara pensylvanica*	*Amara pensylvanica*
14	*Anisodactylus merula*	*Amara rubrica*	*Amara rubrica*
15	*Anisodactylus ovularis*	*Amphasia interstitialis*	*Amphasia interstitialis*
16	*Anisodactylus rusticus*	*Anisodactylus carbonarius*	*Anisodactylus carbonarius*
17	*Anisodactylus sanctaecrucis*	*Anisodactylus dulcicollis*	*Anisodactylus dulcicollis*
18	*Atranus pubescens*	*Anisodactylus harpaloides*	*Anisodactylus harpaloides*
19	*Bembidion castor*	*Anisodactylus merula*	*Anisodactylus merula*
20	*Bembidion nigripes*	*Anisodactylus ovularis*	*Anisodactylus ovularis*
21	*Calathus opaculus*	*Anisodactylus rusticus*	*Anisodactylus rusticus*
22	*Calosoma affine*	*Anisodactylus sanctaecrucis*	*Anisodactylus sanctaecrucis*
23	*Calosoma externum*	*Bembidion castor*	*Anisodactylus verticalis*
24	*Chlaenius nemoralis*	*Bembidion nigripes*	*Apenes sinuata*
25	*Chlaenius pensylvanicus*	*Calathus opaculus*	*Apristus latens*
26	*Chlaenius platyderus*	*Calosoma affine*	*Atranus pubescens*
27	*Chlaenius sericeus*	*Calosoma externum*	*Badister notatus*
28	*Chlaenius tomentosus*	*Calosoma scrutator*	*Bembidion castor*
29	*Chlaenius vafer*	*Chlaenius nemoralis*	*Bembidion nigripes*
30	*Clivina bipustulata*	*Chlaenius pensylvanicus*	*Bembidion texanum*
31	*Colliuris pensylvanica*	*Chlaenius tomentosus*	*Calathus opaculus*
32	*Cratacanthus dubius*	*Cicindela denverensis*	*Calosoma affine*
33	*Cyclotrachelus torvus*	*Cicindela punctulata*	*Calosoma externum*
34	*Cymindis pilosa*	*Cicindela scutellaris*	*Calosoma sayi*
35	*Dicaelus elongatus*	*Clivina bipustulata*	*Calosoma scrutator*
36	*Discoderus parallelus*	*Clivina postica*	*Calosoma wilcoxi*
37	*Elaphropus granarius*	*Colliuris pensylvanica*	*Catogenus rufus*
38	*Galerita janus*	*Cratacanthus dubius*	*Chlaenius emarginatus*
39	*Harpalus amputatus*	*Cyclotrachelus constrictus*	*Chlaenius nemoralis*
40	*Harpalus caliginosus*	*Cyclotrachelus torvus*	*Chlaenius pensylvanicus*
41	*Harpalus faunus*	*Cymindis laticollis*	*Chlaenius platyderus*

No.	Grass 93 & 94 Species	CRP 95 & 96 Species	Grs/ Rip 96 & 97 Species
42	*Harpalus fulgens*	*Discoderus parallelus*	*Chlaenius sericeus*
43	*Harpalus pensylvanicus*	*Dyschiriodes abbreviatus*	*Chlaenius tomentosus*
44	*Notiophilus novemstriatus*	*Dyschiriodes globulosus*	*Cicindela denverensis*
45	*Pasimachus elongatus*	*Dyschiriodes pilosus*	*Cicindela punctulata*
46	*Pterostichus chalcites*	*Elaphropus dolosus*	*Cicindela scutellaris*
47	*Scaphinotus cavicollis*	*Elaphropus granarius*	*Clivina bipustulata*
48	*Scarites subterraneus*	*Galerita janus*	*Clivina postica*
49	*Semiardistomis viridis*	*Geopinus incrassatus*	*Colliuris pensylvanica*
50	*Stenolophus comma*	*Harpalus amputatus*	*Cratacanthus dubius*
51	*Stenolophus conjunctus*	*Harpalus caliginosus*	*Cyclotrachelus constrictus*
52		*Harpalus desertus*	*Cyclotrachelus torvus*
53		*Harpalus faunus*	*Cymindis laticollis*
54		*Harpalus fulgens*	*Cymindis pilosa*
55		*Harpalus katiae*	*Dicaelus elongatus*
56		*Harpalus paratus*	*Discoderus parallelus*
57		*Harpalus pensylvanicus*	*Dyschiriodes globulosus*
58		*Helluomorphoides praeustus bicolor*	*Dyschiriodes pilosus*
59		*Helluomorphoides texanus*	*Elaphropus dolosus*
60		*Lebia viridis*	*Elaphropus granarius*
61		*Microlestes linearis*	*Galerita atripes*
62		*Notiophilus novemstriatus*	*Galerita janus*
63		*Omophron americanum*	*Harpalus amputatus*
64		*Pasimachus elongatus*	*Harpalus caliginosus*
65		*Pterostichus chalcites*	*Harpalus desertus*
66		*Pterostichus femoralis*	*Harpalus faunus*
67		*Rhadine larvalis*	*Harpalus fulgens*
68		*Scarites subterraneus*	*Harpalus paratus*
69		*Selenophorus planipennis*	*Harpalus pensylvanicus*
70		*Stenolophus comma*	*Helluomorphoides praeustus bicolor*
71		*Stenolophus conjunctus*	*Lebia analis*
72		*Stenolophus lineola*	*Lebia atriventris*
73		*Stenomorphus californicus*	*Lebia solea*
74			*Lebia tricolor*
75			*Lebia viridis*
76			*Micrixys distincta*
77			*Microlestes linearis*
78			*Notiobia terminata*
79			*Notiophilus novemstriatus*
80			*Olisthopus parmatus*
81			*Omophron americanum*

No.	Grass 93 & 94 Species	CRP 95 & 96 Species	Grs/ Rip 96 & 97 Species
82			*Panagueus fasciatus*
83			*Pasimachus elongatus*
84			*Pterostichus chalcites*
85			*Pterostichus femoralis*
86			*Pterostichus lucublandus*
87			*Scaphinotus cavicollis*
88			*Scarites subterraneus*
89			*Selenophorus opalinus*
90			*Semiardistomis viridis*
91			*Stenolophus comma*
92			*Stenolophus conjunctus*
93			*Stenolophus lineola*
94			*Stenolophus ochropezus*
95			*Stenolophus rotundatus*
96			*Stenomorphus californicus*

No.	Spring Rip 95 Species	Rip 95 & 96 Species
1	*Abacidus permundus*	*Abacidus permundus*
2	*Agonum extensicolle*	*Acupalpus partiarius*
3	*Agonum nutans*	*Acupalpus testaceus*
4	*Agonum octopunctatum*	*Agonum decorum*
5	*Agonum pallipes*	*Agonum extensicolle*
6	*Agonum punctiforme*	*Agonum octopunctatum*
7	*Amara convexa*	*Agonum pallipes*
8	*Amara cupreolata*	*Agonum punctiforme*
9	*Amara exarata*	*Amara convexa*
10	*Amara impuncticollis*	*Amara cupreolata*
11	*Amara musculis*	*Amara exarata*
12	*Amara obesa*	*Amara impuncticollis*
13	*Amphasia interstitialis*	*Amara musculis*
14	*Anisodactylus carbonarius*	*Amara obesa*
15	*Anisodactylus dulcicollis*	*Amara pensylvanica*
16	*Anisodactylus harpaloides*	*Amara rubrica*
17	*Anisodactylus merula*	*Amphasia interstitialis*
18	*Anisodactylus ovularis*	*Anisodactylus carbonarius*
19	*Anisodactylus rusticus*	*Anisodactylus dulcicollis*
20	*Anisodactylus sanctaecrucis*	*Anisodactylus harpaloides*
21	*Anisodactylus verticalis*	*Anisodactylus merula*
22	*Badister notatus*	*Anisodactylus ovularis*
23	*Bembidion castor*	*Anisodactylus rusticus*
24	*Bembidion laevigatum*	*Anisodactylus sanctaecrucis*
25	*Bembidion nigripes*	*Anisodactylus verticalis*
26	*Brachinus rugipennis*	*Apenes sinuata*
27	*Calathus opaculus*	*Apristus latens*
28	*Calosoma affine*	*Badister notatus*
29	*Calosoma externum*	*Bembidion castor*
30	*Calosoma wilcoxi*	*Bembidion impotens*
31	*Chlaenius emarginatus*	*Bembidion laevigatum*
32	*Chlaenius erythropus*	*Bembidion nigripes*
33	*Chlaenius nemoralis*	*Brachinus fumans*
34	*Chlaenius platyderus*	*Brachinus rugipennis*
35	*Chlaenius tomentosus*	*Brachinus tenuicollis*
36	*Cicindela denverensis*	*Calathus opaculus*
37	*Cicindela punctulata*	*Calosoma affine*
38	*Cicindela scutellaris*	*Calosoma externum*
39	*Clivina bipustulata*	*Catogenus rufus*
40	*Clivina postica*	*Chlaenius emarginatus*
41	*Colliuris pensylvanica*	*Chlaenius nemoralis*

No.	Spring Rip 95 Species	Rip 95 & 96 Species
42	*Cratacanthus dubius*	*Chlaenius platyderus*
43	*Cyclotrachelus seximpressus*	*Chlaenius sericeus*
44	*Cyclotrachelus torvus*	*Chlaenius tomentosus*
45	*Cymindis pilosa*	*Cicindela denverensis*
46	*Dicaelus elongatus*	*Cicindela punctulata*
47	*Discoderus parallelus*	*Cicindela scutellaris*
48	*Dyschiriodes globulosus*	*Clivina bipustulata*
49	*Dyschiriodes pilosus*	*Clivina postica*
50	*Elaphropus dolosus*	*Colliuris pensylvanica*
51	*Elaphropus granarius*	*Cratacanthus dubius*
52	*Euryderus grossus*	*Cyclotrachelus seximpressus*
53	*Galerita atripes*	*Cyclotrachelus torvus*
54	*Galerita janus*	*Cymindis laticollis*
55	*Harpalus amputatus*	*Cymindis pilosa*
56	*Harpalus faunus*	*Dicaelus elongatus*
57	*Harpalus fulgens*	*Discoderus parallelus*
58	*Harpalus paratus*	*Dyschiriodes globulosus*
59	*Harpalus pensylvanicus*	*Dyschiriodes pilosus*
60	*Helluomorphoides praeustus bicolor*	*Elaphropus dolosus*
61	*Lebia solea*	*Elaphropus granarius*
62	*Microlestes linearis*	*Euryderus grossus*
63	*Notiophilus novemstriatus*	*Galerita atripes*
64	*Omophron americanum*	*Galerita janus*
65	*Pasimachus elongatus*	*Geopinus incrassatus*
66	*Pterostichus chalcites*	*Harpalus amputatus*
67	*Pterostichus lucublandus*	*Harpalus caliginosus*
68	*Scaphinotus cavicollis*	*Harpalus desertus*
69	*Scarites subterraneus*	*Harpalus faunus*
70	*Semiardistomis viridis*	*Harpalus fulgens*
71	*Stenolophus comma*	*Harpalus longicollis*
72	*Stenolophus conjunctus*	*Harpalus paratus*
73	*Stenolophus lineola*	*Harpalus pensylvanicus*
74	*Tetragonoderus fasciatus*	*Helluomorphoides praeustus bicolor*
75		*Lebia analis*
76		*Lebia atriventris*
77		*Lebia pulchella*
78		*Lebia solea*
79		*Lebia tricolor*
80		*Micrixys distincta*
81		*Microlestes linearis*
82		*Notiobia terminata*
83		*Notiophilus novemstriatus*

No.	Spring Rip 95 Species	Rip 95 & 96 Species
84		*Olisthopus parmatus*
85		*Panagueus fasciatus*
86		*Pasimachus elongatus*
87		*Patrobus longicornis*
88		*Pterostichus chalcites*
89		*Pterostichus lucublandus*
90		*Scaphinotus cavicollis*
91		*Scarites subterraneus*
92		*Selenophorus planipennis*
93		*Semiardistomis viridis*
94		*Stenolophus comma*
95		*Stenolophus conjunctus*
96		*Stenolophus dissimilis*
97		*Stenolophus lineola*
98		*Stenolophus ochropezus*
99		*Stenolophus rotundatus*
100		*Tetragonoderus fasciatus*

APPENDIX D

SOIL SURFACE TEMPERATURE MEASUREMENTS

In order to measure the gradient in temperature across a grassland-wheat field and riparian zone-wheat field boundary a Cambell Scientific CR10 Micrologger mounted on a CM10 tripod with an SM192 storage module and an SC532 interface was used to gather data on ground temperatures during the winter wheat growing season. Temperature sensors, 107B, were placed approximately 1 m from the border in the grassland and wheat habitats in 1993 – 1994 and in the riparian and wheat habitats in 1995 – 1996. An additional sensor was added at the grassland-wheat field border in 1996 – 1997. In the 1996 – 1997 riparian zone-wheat field study, temperature sensors were placed in both directions from the border at 0 cm, 183 cm, 366 cm, 549 cm, and 732 cm into the riparian zone and wheat fields. Each sensor was set approximately 1 cm beneath the soil surface, and a piece of white guttering mounted on a wooden stake was used to shade the sensor. Temperatures were recorded each minute and averaged over each hour of the day by the CR10. In this appendix, mean minimum and maximum temperatures are reported by year and season.

In the grassland-wheat field studies, the greatest variation in temperatures consistently occurred in the wheat fields (Table 1). Temperatures in grasslands had the lowest range of extremes, while border temperatures were generally in between the grassland and wheat field temperatures. Even during winter where the average minimum temperatures dropped below freezing in wheat fields, the grassland temperatures remained above freezing. With minimum winter temperatures remaining above the border and wheat field temperatures, grassland edges, as previously shown for more northern latitudes, may provide overwintering refuges for ground beetles. Note also that wheat field mean maximum temperatures were greater, by several degrees, than grassland temperatures during winter. Temperatures were not monitored in early autumn and thus the greater similarity to winter temperatures rather than to spring temperatures.

A similar pattern was observed in the riparian zone-wheat field studies. One exception was during winter in 1995 – 1996, when temperatures varied more in the riparian habitat than in the wheat field (Table 2). In 1996-1997, there appeared to be a gradient with winter minimum temperatures from the riparian zone into the wheat field. Mean minimum temperatures increased from 732 cm to 183 cm into the riparian zone, decreased at the border, then increased again from 183 cm to 549 cm into the wheat field. This pattern occurred in winter and spring. The minimum temperature at 732 cm into the wheat field was higher than all other minimum temperatures in the wheat field during winter and spring. Maximum temperatures differed with respect to distance from the border, with no general trend detectable. However, maximum temperatures were greater in the wheat fields than in the riparian zones during both winter and spring. In contrast, minimum temperatures were greater in the riparian zones during winter, but not during spring.

Table 1. Mean maximum and minimum temperatures (°C) at ground surface in grasslands, wheat fields, and at their borders by year of study and season.

		Autumn		Winter		Spring	
Year	Habitat	Max	Min	Max	Min	Max	Min
1993 – 1994	Grass	10.67	2.82	8.64	1.76	14.36	8.07
	Wheat	11.11	1.44	14.24	-1.89	21.98	5.66
1996 – 1997	Grass	7.95	4.78	6.93	3.74	16.68	12.44
	Border	9.43	2.04	9.02	1.93	19.99	11.40
	Wheat	9.80	1.54	9.06	1.79	19.57	13.33

Table 2. Mean maximum and minimum temperatures (^oC) at ground surface in riparian zones, wheat fields, and at their borders by year of study and season. Distances (cm) from the border are indicated for the 1996 – 1997 study.

	Autumn		Winter		Spring	
	Max	Min	Max	Min	Max	Min
1995 – 1996						
Riparian	21.56	6.34	14.86	-0.08	29.67	12.89
Wheat	23.35	5.31	14.03	0.54	33.96	12.94
1996 – 1997						
Riparian 732	.	.	8.43	2.34	17.54	10.81
Riparian 549	.	.	7.42	3.04	16.22	11.24
Riparian 366	.	.	7.68	3.30	16.50	12.25
Riparian 183	.	.	7.47	3.71	16.34	12.76
Border	.	.	10.09	2.30	18.32	11.95
Wheat 183	.	.	9.16	3.35	16.95	12.45
Wheat 366	.	.	9.31	2.85	19.48	12.29
Wheat 549	.	.	9.77	1.91	20.07	11.50
Wheat 732	.	.	8.81	3.50	19.26	13.02

VITA

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