DIVERSITY, COMPOSITION AND SEASONALITY

OF WILD BEES (HYMENOPTERA: APOIDEA) IN A

NORTHERN MIXED-GRASS PRAIRIE PRESERVE

by

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ABSTRACT

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Diversity, composition and seasonality of wild bees (Hymenoptera: Apoidea) in a northern mixed-grass prairie preserve.

Major professor: R.E. Roughley

Information deficiencies exist regarding patterns of wild bee (Hymenoptera: Apoidea) diversity and community composition in representative habitats worldwide. The main objective of this study was to characterize the wild bee fauna of mixed-grass prairie in southwestern Manitoba. Weekly sampling of wild bees using two methods, sweep-netting and bee bowls, was conducted over two years (2005-2006) at three sites within the Yellow Quill Mixed-grass Prairie Preserve. Spatial and seasonal patterns in diversity indices, taxonomic composition and ecological composition of the bee fauna were identified and investigated in relation to sampling method, environmental conditions, and floral resource availability.

 A total of 7014 individual bees representing five families, 21 genera and 100 species were collected during the course of this study; however, this assessment is incomplete as taxon accumulation curves did not achieve asymptotes. While the fauna was biogeographically biased toward eastern-distributed taxa, there was nonetheless solid representation of species with central and western affinities. Fifteen species are newly recorded for Manitoba. A total of 23.8% of the taxa were pollen specialists. Miners were the most species-rich nesting guild (50 species); while the bulk of the

individuals were social nesters (75.3%) of the genera *Lasioglossum* and *Bombus*. Representing 11% of the sample, the proportion of parasitic taxa was lower than expected compared to other studies, likely owing to sampling effects or taxonomic difficulties.

Overall, bee catch and species richness were greater in the second year, but diversity was lower. Observed spatial and temporal patterns in the abundance, diversity and composition of the bee community were strongly modified by sampling method. Sweep-net sampling detected more diverse, even and species-rich assemblages, while catch frequencies for each method were reciprocally related to resource availability. That the second year was characterized by high temperatures and deficient rainfall allowed some of the observed patterns to be interpreted within the context of floral resource limitation. While high densities of the exotic invasive plant *Euphorbia esula* altered the diversity and seasonality of the floral resource base at one site, other factors were deemed responsible for supporting a qualitatively species-rich assemblage at that site relative to the other two sites. In both years, seasonal bee diversity values, measured as Hill's effective species richness (N1), peaked in the early part of the season and subsequently declined. Redundancy analysis was used to relate this pattern to high early-season species richness of miners and to an increase in the relative abundance of social nesters over the season.

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INTRODUCTION

As the primary group of pollinating insects, bees (Hymenoptera, Apoidea, Apiformes)

provide valuable environmental services in many natural and agricultural ecosystems.

By facilitating the sexual reproduction of over half of the world's flowering plants

(Kearns and Inouye 1997), bees indirectly contribute to habitat preservation, erosion

prevention, and carbon storage. Bees pollinate over 30% of the crops grown for

human consumption (O'Toole 1993), a service worth over 20 billion dollars (US) per

year in North America (Tommasi *et al.* 2004). Of that, nearly 3.07 billion dollars is

attributable to non-domesticated, wild bees (Losey and Vaughan 2006).

Despite the important role of wild bees in ecosystem functioning and in agricultural

production, bee populations are declining in many habitats around the world.

Widespread declines in the abundance of certain bee populations, particularly of

Bombus (Apidae) species, have been documented in long-term monitoring programs

in Great Britain, the Netherlands, France and Belgium (Biesmeijer *et al.* 2006;

Rasmont *et al.* 2006). In North America, 58 wild bee species have been placed on the

Red List of Insect Pollinators issued by the Xerces Society for Invertebrate

Conservation (Shepherd *et al.* 2005). Pollination deficits (Kevan and Phillips 2001),

reduced genetic variability in certain bee taxa (Zayed *et al.* 2004), and short-term

studies on bee community responses to habitat alteration (Kremen *et al.* 2002;

MacKenzie and Winston 1984) are suggestive of declines in elements of the North

American bee fauna.

Unfortunately, it is difficult to ascertain suspected declines because bee populations characteristically display large fluctuations over time and space (Williams *et al.* 2001), and baseline data regarding population trends and patterns of bee diversity are not available in many habitats (Allen-Wardell *et al.* 1998; Committee on the Status of Pollinators in North America 2007). Lack of standardization among methods used across space and time renders comparisons of bee abundance and species richness patterns at different scales tenuous (LeBuhn *et al.* 2003). Complicating matters further, failure to address adequately the implications of sampling biases associated with different sampling methods and protocols may affect interpretation of observed trends. Without systematic, long-term baseline data, effective status assessments and conservation planning are difficult. As such, baseline data need to be collected at an ecosystem level in a manner that is conducive to comparisons across habitats and temporal scales (Kevan and Phillips 2001; LeBuhn *et al.* 2003).

Knowledge of the bee fauna of northern mixed-grass prairie is poor, particularly for the Canadian prairie provinces. There are few published studies on wild bee diversity from these areas and no species lists are available. What little published information exists arose from a limited number of investigations into wild bees associated with alfalfa (*Medicago sativa* L.) in the 1940s and 1950s amid concerns about declining alfalfa seed yields (Hobbs and Lilly 1954; Peck and Boulton 1946; Stephen 1955). These researchers contributed some data on *Megachile* (Megachilidae) and *Bombus* species; however, there are no published investigations of the northern prairie bee fauna at a whole community level.

Investigation of mixed-grass prairie bees is important for several reasons. First, the mixed-grass prairie is an ecosystem in decline. Widespread agricultural conversion, alteration of fire and grazing regimes and the encroachment of aspen and exotic species have degraded over three-quarters of Canada's share of mixed-grass prairie (Mansell and Moore 1999). A critical step in developing management plans for remnant parcels of mixed-grass prairie is to identify and document the organisms that occupy them and to understand how they contribute to ecosystem processes. Secondly, as a result of extensive habitat loss, biodiversity on the mixed-grass prairie has declined precipitously. Although grasses are the dominant vegetative life form in the prairie in terms of biomass, flowering forbs contribute disproportionately to diversity in the prairies (Bai *et al.* 2001; Collins and Gibson 1990). To the extent that many forbs rely on insects for pollination, bees may be considered a keystone taxon in the maintenance of mixed-grass prairie biodiversity. Finally, from an economic perspective, studying bee communities in an ecosystem that supports extensive agricultural activities provides a strategic starting point in the long-term goal of maintaining pollination services to crops.

The broad objective of my study was to address the information deficit regarding bees of the northern mixed-grass prairie of North America. This is the first systematic, season-long investigation of the diversity and community composition of a wild bee assemblage in Manitoba. The objectives of the study were:

1) to characterize the wild bee community of a managed nature preserve, the Yellow Quill Mixed-grass Prairie (YQMGP), in terms of both taxonomic and ecological composition;

2) to compare the effect of two sampling methods, bee bowls and sweep-netting, on a) bee diversity, b) community composition and c) the relationship between bee catch and resource availability;

3) to describe seasonal patterns in the diversity and composition of wild bees and the floral resource base in the YQMGP;

4) to determine the effect of year, site and bowl colour on capture rates of families, dominant taxa and ecological groups collected with bee bowls;

5) to determine the effect of site, time of day and sweep location relative to grazing on capture rates of families, dominant taxa and ecological groups collected by sweep-netting.

Natural history of bees

While bees share several defining structures and behaviours, they are a tremendously diverse group of insects.   Bees can be divided according to taxonomic groups on the basis of phylogenetic relationships or ecological groups on the basis of natural history attributes such as floral associations, nesting habits and social structure. This section explores the scope of bee diversity, beginning with unifying features and then moving on to examine taxonomic and ecological variation. Unless otherwise specified, remarks pertaining to abundance or species richness refer to adults.

Classification of bees

Bees form a distinct group related to the ants and wasps within the Hymenoptera. They are believed to have arisen from the sphecid wasps, and together, both the Apiformes and the Spheciformes comprise the superfamily Apoidea. Monophyly of the bees is supported by several structural and behavioural characters, many of which are associated with an evolutionary switch from a predatory lifestyle to pollen and nectar feeding (Alexander and Michener 1995; Danforth *et al.* 2004). These characters include branched or plumose hairs, pollen-feeding larvae, broadened basitarsi, reduced larval mandibles and the behaviour of cleaning the foreleg by drawing it through the flexed middle leg (Danforth *et al.* 2004; Michener 2000; Thorp 2000).

While systematists continue to struggle with establishing the higher-level phylogenies (e.g. family, sub-family, tribe), it is generally accepted that the bees can be divided

into two main groups based on mouthpart structure. The first two segments of the labial palpi are unmodified in short-tongued bees, whereas they are long, compressed and form a sheath around the glossa in long-tongued bees (Michener *et al.* 1994). The short-tongued bees are a paraphyletic group that gave rise to the monophyletic long-tongued bees, although it is not certain from which group of short-tongued bees the long-tongued bees are derived (Alexander and Michener 1995; Danforth *et al.* 2004; Roig-Alsina and Michener 1993). Families of short-tongued bees include Colletidae, Stenotrididae, Andrenidae, Halictidae and Melittidae. The long-tongued bees include Megachilidae and Apidae, in which the previously distinct family Anthophoridae is now placed as a sub-family (Alexander and Michener 1995; Danforth *et al.* 2004; Roig-Alsina and Michener 1993).

Taxonomic diversity of bees

There are approximately 17,000 known species of bee worldwide; however, the actual total may be 20,000 to 30,000 species when including estimates of undescribed species (Michener 2000). Globally, the most species rich bee faunas occur in xeric, warm-temperate regions including the Mediterranean basin, the desert regions of the southwestern United States and northern Mexico, central Chile, central Argentina and much of Australia (Michener 1979). Generic diversity appears to be highest in the Neotropical regions (Michener 1979).

In North America, the number of bee species is estimated to be 4000 species (O'Toole and Raw 1991); however, species richness among the main biotic regions appears to vary considerably. The southwestern deserts and Mediterranean area of California contain the richest bee faunas, with regional assemblages of over 800 species.

Species richness progressively declines from the Rocky Mountains, to the North American Plains, the boreal forest, various mixed and soft-wood forest types, and Arctic tundra (Moldenke 1979). There may be up to 500 species of bees in the North American Plains (Moldenke 1979).

Michener (2000) cautioned that comparisons of bee diversity among broad geographic regions may be questionable given large variation in the number and types of surveys conducted in different regions. Also, the taxonomic literature is scarce for many bee taxa and regions, further impairing initiatives to provide complete regional assessments of the bee fauna.

Ecological diversity of bees

The requirement for bee larvae to feed upon pollen provisioned by adult females is associated with unique methods for acquiring, transporting and storing pollen that are characteristically expressed in bees' floral associations, nesting strategies and social relationships.

Floral associations

Pollen, nectar and oils are the main floral rewards collected by bees. Generally, it is only the females of non-parasitic bees that collect pollen, as they provision brood and may require the nutritional protein for egg production (Michener 2000; Proctor *et al.* 1996; Roulston *et al.* 2000). Species that specialize on certain types of nectar or oil also to be pollen specialists (Michener 2000). Most bees forage on nectar from a wider range of plant taxa than they do to meet their pollen needs (Buchmann 1996; Waser *et al.* 1996).

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The extent to which bees specialize in their floral relations varies. Bees that consistently and heritably restrict their pollen foraging to plants within a particular taxon, usually a genus or family, are oligolectic (Linsley 1958; Wcislo and Cane 1996). These species are typically solitary and have a relatively short adult lifespan which must be synchronized with the blooming period of floral hosts (Cane 2001). Oligolecty is most common within in the Rophitinae, Colletidae (excluding Hylaeinae), Andrenidae, Melittidae, Megachilidae and the non-social Apidae (Wcislo and Cane 1996). Exactly why certain bees exhibit specialization is unclear, but hypotheses include structural constraints in accessing floral resources (Michener 2000; Waser *et al.* 1996), differential colour discrimination abilities (Waser *et al.* 1996), nutritional constraints on proper development (Waser *et al.* 1996), spatio-temporal predictability of host availability (Minckley *et al.* 1999), and greater foraging efficiency (Strickler 1979).

Polylectic bees forage more generally for pollen from a range of unrelated or distantly related plant species (Linsley 1958). They tend to visit flowers with complex corollas and many have longer adult phases than oligoleges (Wcislo and Cane 1996). Social species tend to generalize because maintenance of colony life requires that multiple resources be exploited throughout the active season (Michener 2000). Polylectic bees often
 will display flower constancy, in which individual bees restrict their visits to a single flower type on a given foraging trip (Grant 1950; Waser 1986). This is not considered to be specialization in the sense of oligolecty, as it is a learned behaviour. The type of

flower handled can vary within individuals of the same species or colony, and individual foragers can switch to other flower types (Waser 1986).

The relative abundance of oligolectic versus polylectic species varies among biomes. Deserts, in which approximately two-thirds of species are oligolectic, appear to be the only regions in which specialists dominate (Waser *et al.* 1996). Oligoleges typically comprise between 22% and 50% of the fauna in temperate habitats. For example, about 36% of the Great Plains bee species are pollen specialists (Moldenke 1979). At sites within a mixed-deciduous ecotone in southwestern Ontario, 21% of the non-parasitic fauna are oligoleges (Grixti and Packer 2006; MacKay 1970). The lowest proportions of oligolectic species, usually less than 20%, tend to occur in tropical grasslands, tropical forest, tundra and the Rocky Mountains (Moldenke 1979; Waser *et al.* 1996).

Nesting

The non-parasitic bees display a variety of nesting strategies based on the substrates they use and the materials with which they line their brood cells (Krombein 1967; Malyshev 1935; Michener 1964, 2000). Bees can be classified as either burrowers or cavity-nesters, depending on whether or not they excavate their own nests or simply occupy a pre-existing cavity (Bosch *et al.* 2001; Malyshev 1935; O'Toole and Raw 1991). Incorporating considerations of substrates and sociality, five guilds of non-parasitic species are commonly identified including miners, carpenters, masons, leaf-cutters and social nesters (O'Toole and Raw 1991; Potts *et al.* 2005).

Miners excavate burrows in the soil that are terminated by brood cells in which the female deposits larval food of pollen and nectar before laying an egg (Potts *et al.* 2005). All of the Andrenidae, Melittidae, Stenotritididae, the megachilid subfamily Fidelinae, and the majority of the Halictidae, Colletidae and Anthophorinae belong to this guild (Cane 1991; Potts *et al.* 2005). While the burrows are typically unlined, cells may be lined or unlined (Michener 2000). Most colletids line their cells with cellophane-like salivary secretions and are the only taxon to do so (Malyshev 1935). Other taxa use either a fine layer of clay or a lipid-based secretion from the Dufour's gland (Cane 1991; Michener 1964). Cells of the Melittidae and the Fideliinae are unlined (Michener 2000).

Mason bees belong primarily to the Megachilidae, and occupy existing cavities such as hollow plant stems, snail shells, crevasses, abandoned burrows and wood-boring beetle tunnels (Potts *et al.* 2005). Their cell-linings are created with materials from their environment such as resin, pebbles or plant hairs (Malyshev 1935). The local availability of nest-lining and building materials is particularly important for this guild, and may limit their abundances in localized areas (Westrich 1996). Leaf-cutters, specifically *Megachile* spp. (Megachilidae) and *Creightonella* spp. (Megachilidae), are cavity-nesters but distinct in their habit of lining cells with pre-cut pieces of leaves (Krombein 1967; Michener 1953).

Carpenter bees excavate either branched or unbranched nests primarily in wood, but sometimes in other anthropogenic substrates such as styrofoam or fiberboard (Gerling *et al.* 1989; Potts *et al.* 2005). The apid genera *Xylocopa* and *Ceratina* and the megachilid genus *Lithurgus* belong to this guild (Gerling *et al.* 1989; Potts *et al.*

2005). Cells linings may be absent or consist of glandular secretions (Gerling *et al.* 1989; Sakagami and Michener 1987).

Social nesting bees nest as colonies, often in large pre-existing cavities. Bees of this group all belong to the apid tribes Apini, Bombini and Meliponini (Potts *et al.* 2005). Wax secreted from metasomal glands is used to construct clusters of brood cells and food storage structures (Michener 1964).   Within this guild, *Apis* and *Bombus* are primarily progressive brood feeders, providing food to larvae as they grow (Michener 2000). All other bees, except those in the African tribe Allodapini, are mass provisioners, supplying larvae with sufficient food for growth at the time of nest construction (Michener 2000).

There is a trend for species composition outside of the lowland tropics to be biased towards miners. Social nesting species tend to predominate in the tropics (Cane 1997), although *Bombus* reaches peak abundance and species richness in the Holarctic regions (Thorp 2003).   In a mixed-deciduous ecotone in southwestern Ontario, about 73% of the nest-building species were ground-nesters (Grixti and Packer 2006; MacKay 1970). Oerteli *et al.* (2005) found 58% of the total fauna to be comprised of miners in hay meadows and grassland habitats on the southern slopes of the Swiss Alps. Guilds that nest in the ground tend to dominate in open habitats where few alternative substrates occur (Potts *et al.* 2005). For example, in a sandy grassland in central Hungary where few woody resources were available, over 80% of the bee species were ground-nesters (Sarospataki and Fazekas 1995).

Bees exhibit considerable diversity in social behaviour, ranging from solitary to highly eusocial. In solitary systems, an individual foundress is the sole provisioner for the eggs that she lays (Michener 1974; O'Toole and Raw 1991). The female constructs her nest without assistance and typically dies before her offspring emerge. Most solitary bees are either univoltine or bivoltine (Delaplane and Mayer 2000). Some solitary species nest in aggregations, although this is not considered a form of sociality since individual foundresses act independently and do not share nest structures (Michener 2000).

Sociality is a form of organized coexistence characterized by: a) a division of labour between a reproductive caste and a sterile worker caste, b) overlapping generations of workers and, c) cooperative maintenance of cells and progressive provisioning of the colony's young (Michener 1974). Two forms of sociality are recognized in bees. In eusocial species, namely bees of the apid tribes Apini and Melaponini, reproductive females are structurally distinct from workers (Michener 1974). Colonies of highly eusocial bees tend to be permanent. In primitively eusocial bees, the reproductive female and workers are structurally similar, although they may differ in size (Michener 1974). This type of eusociality is apparent in the Bombini and several groups within the Xylocopinae and Halictidae (Michener 1974). Colonies tend to be seasonal, beginning after a single foundress emerges and works in solitude to raise the first generation of daughter workers. These workers then assist her in rearing the next generation of workers. Eventually, the colony produces other reproductive females which mate and overwinter to become the next season's foundresses.

There is a range of parasocial states in which bees display some but not all of the characteristics of eusociality. Communal nesters may share a nest, but females will continue to act independently in cell provisioning (Michener 1974; O'Toole and Raw 1991). This is most common among andrenids and the Agapostemonini (Wcislo and Cane 1996). Quasisociality is characterized by several reproductive females cooperating in nest construction, cell provisioning and egg-laying; but there is no division of labour (Michener 1974; O'Toole and Raw 1991). Semi-social species also exhibit cooperation in nest-construction among females of a single generation; however, there is division of labour in which some females lay eggs while others forage (Michener 1974; O'Toole and Raw 1991).

Attributing a term to describe a species' organizational structure is often difficult. With the exception of the highly eusocial bees, a species can be found at any given organizational state over the development of the colony (Michener 2000). In addition, intraspecific geographic variation in sociality has been documented (Packer 1992). For example, several halictids are socially polymorphic, displaying facultative solitary or eusocial behaviour depending in part on latitude or environmental conditions (Eickwort *et al.* 1996; Soucy and Danforth 2002; Yanega 1993). As such, the term used to describe the sociality of a species often applies to the most complex level of organization it attains (Michener 2000).

The majority of bee species are solitary nesters, particularly in temperate regions (Cane 1991). For example, in grasslands and hay meadows of in the Swiss Alps, 83.2% of species were solitary (Oerteli *et al.* 2005). Masner *et al.* (1979) estimated that 76% of the bee species of North America are solitary and 12% are social or semi-

social. While solitary species may dominate species richness in temperate regions, eusocial species may often dominate in terms of species abundance.

<u>Parasitic bees</u>

Parasitic bees do not build nests, but rather oviposit in nests constructed and provisioned by another bee species, causing mortality of the host species offspring and/or reproductives. While instances of usurpation or robbing may occur among and within species, obligate parasitism has evolved into two main forms: social parasitism and cleptoparasitism (Michener 2000). Social parasites attack social hosts by replacing the queen and causing the host workers to rear parasitic offspring. This type of parasitism is seen primarily in species of *Bombus* (*Psithyrus*), and in several species within the Allodapini (Michener 2000). Cleptoparasites mainly attack solitary hosts or primitively eusocial hosts in the solitary phase of the colony cycle by entering the nest and ovipositing in the absence of the host female (Scott *et al.* 2000; Sick *et al.* 1994; Wcislo and Cane 1996). Once inside the nest, the adult cleptoparasite will either kill the host egg and replace it with her own (as in *Sphecodes* spp.) (Sick *et al.* 1994) or she will hide the egg within the cell wall and leave her offspring to kill the host larvae later (as in *Epeolus* spp. and *Nomada* spp.) (Michener 2000). Cleptoparasitism is more common than social parasitism and occurs in approximately 15%-20% of the bee genera (Scott *et al.* 2000; Wcislo and Cane 1996). Apidae, Halictidae and Megachilidae contain the majority of the cleptoparasitic taxa, although there is one known colletid cleptoparasite in the genus *Hylaeus* (Danforth *et al.* 2004).

Parasitic bees are most abundant in northern and temperate climates, and almost absent from the tropics (Wcislo and Cane 1996). In a mixed-deciduous ecotone in southwestern Ontario, parasitic bees accounted for 22-24% of species (Grixti and Packer 2006; MacKay 1970). Areas that contain otherwise high bee species richness may have a relatively small parasitic component. For example, about 11% of the Mediterranean bee fauna is parasitic (Petanidou and Ellis 1996).

Patterns and determinants of bee diversity

Describing diversity

Diversity refers to the variety and relative abundance of organisms occupying a particular area (Magurran 1988). In ecological applications, diversity can be described at a local level, known as alpha (α) diversity, or compared among areas at an ecosystem level, known as beta (β) diversity. Diversity is one of the most fundamental attributes of a biological community and its characterization is a basic requirement for studying or managing a system. Describing diversity in space and time allows hypotheses about important underlying processes to be developed and tested (Morin 1999). Long-term monitoring of diversity may provide important information about the degree of natural variability among constituents of a particular community against which perturbations to the system can be assessed. This type of information also can assist in determining the level of experimental rigour necessary to detect those changes. For example, if background levels of variation are high, the ability to detect changes will require that more intense sampling schemes be employed over longer periods of time (Williams *et al.* 2001). Changes in the diversity of indicator taxa in response to environmental change are used to predict responses of other system

components (Kerr *et al.* 2000). Examining diversity patterns may provide insights into the efficiency and stability of ecosystem function (Balvanera *et al.* 2004; Tilman and Lehman 2001). Such information may be critical to management of particular habitats or ecosystem services.

Diversity is classically viewed in terms of taxonomic groups; however, it can be used to describe functional or ecological groups (Tilman and Lehman 2001). Diversity based on taxonomic groupings usually refers to species diversity, although it can be applied to any taxonomic level such as genus, family, order, etc. It is contingent on every member of the community in question being assigned to a group on the basis of its taxonomic identity. Functional diversity encompasses the range of species attributes or ecological traits that can be identified within a given area. Examples of functional diversity might include life forms of plants or nesting guilds of bees.

Analyses of functional diversity and taxonomic diversity do not have to be mutually exclusive. Oerteli *et al.* (2005) emphasize the importance of insights that can be made by supplementing information conveyed in simple species diversity indices (see below) with information about functional diversity. Depending on the objective of the study, description of taxonomic diversity at the species level is generally preferable because it is the most inclusive category in terms of the information it can provide (Danks 1996). However, the exponentially greater amount of time and expertise required to collect data at the species level for many insect taxa induce resource-strapped researchers to restrict their analyses to higher taxonomic groupings, or functional groups. Because local communities can comprise dozens to several hundred species, describing community structure in terms of functional components

can become "shorthand" in community level studies. However, for functional groups delineated on the basis of attributes that are not structural features of the organism, analysis of functional diversity may still require that all species in a community be known and that there is sufficient knowledge about the natural history of each species (Cane 2001).

Diversity measures

Whether taxonomic or functional, α diversity can be summarized quantitatively using a variety of indices or more qualitatively to explicitly examine the composition of a community. Quantitative diversity measures most commonly applied to the variety of species in a habitat include a) species richness or b) indices based on relative abundance (Magurran 1988).

Species richness refers to the number of species present in the area of interest. It weights all species equally regardless of rarity or commonness (Magurran 1988). Because the number of species observed increases with sampling effort, taxon sampling curves are recommended to evaluate the effectiveness of a sampling program and to compare species richness among communities (Buddle *et al.* 2005; Gotelli and Colwell 2001). Gotelli and Colwell (2001) identify two main types of taxon sampling curves: species accumulation curves and rarefaction curves. Species accumulation curves represent the increase in the number of species detected as samples or individuals are added to the collection. Alternatively, rarefaction curves represent estimates of the mean number of species that can be expected for each level of sampling effort. These estimates are generated by repeatedly re-sampling individuals or samples from the overall collection, and because the algorithm is

iterative, variance can be estimated. As a result, rarefaction curves can be used to standardize estimates of species richness among different communities to a common level of sampling effort (Buddle *et al.* 2005). Both types of sampling curves can be used to determine the effectiveness of a sampling program, as sampling can be considered complete when the accumulation curve reaches an asymptote (Buddle *et al.* 2005).

Indices based on the relative abundance of species include evenness indices, and diversity indices. Evenness describes the relative distribution of individuals among the groups, such that the higher the evenness value, the more equally distributed individuals are across categories (Magurran 1988; Morin 1999). Species diversity indices, also known as heterogeneity measures, combine species richness and evenness into a single metric (Magurran 1988; Morin 1999; Spellerberg 1993). Based on variations of a basic function derived from information theory, a number of diversity indices have been developed, each with their own properties. For example, the most commonly used diversity indices include the Shannon-Weiner index (H) and the Simpson index (H') (Magurran 1988). While the Shannon-Weiner index tends to be more sensitive to rare species, the Simpson index emphasizes more common species. Hill (1973) proposed non-linear transformations of these two indices, referred to as effective species richness (N1 for the transformed Shannon-Wiener index, and N2 for the transformed Simpson index).

While diversity measures are useful in providing single values by which to describe communities, they can obscure information about community composition, namely how particular species fit into the overall pattern of relative abundances (Belaoussoff

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et al. 2003). This is particularly problematic when the objective is to assess how communities respond to environmental change, as indices tend to confound differences in species diversity and species composition (Belaoussoff *et al.* 2003; Tilman and Lehman 2001).

One alternative for describing community composition is the graphical approach of plotting rank-abundance models, in which the abundance within each species or group is plotted against its rank from highest to lowest abundance (Magurran 1988; Morin 1999; Smith and Smith 2001). To the extent that a particular distribution fits mathematically defined models, such as the geometric series, log-normal distribution, the logarithmic series and the broken stick model, insights into the way that species partition resources in a community may be made (Belaoussoff *et al.* 2003; Magurran 1988; Morin 1999; Smith and Smith 2001).

In addition to information provided by diversity measures and rank abundance models, comparison between assemblages, or estimations of β diversity, can be made using similarity indices (Spellerberg 1993). Similarity indices, commonly including Sorensen or Jaccard's indices, can express the level of similarity between communities as a single metric or be used as a basis for a number of community analysis techniques including cluster analysis and ordination techniques (Magurran 1988; Spellerberg 1993). These techniques can be used to compare different communities in space or the same community over time.

General attributes of bee communities

Most ecological communities are characterized by a few abundant species, several of intermediate abundance and many of low abundance (Fischer *et al.* 1943; Lyons *et al.* 2005). In surveys of bee communities, high proportions of rare species are consistently reported (Marlin and LaBerge 2001; McIntyre and Hostetler 2001; Oerteli *et al.* 2005; Potts *et al.* 2003b; Tommasi *et al.* 2004). Williams *et al.* (2001) found that singletons, species represented by a single individual, make up 15-40% of samples. One possible explanation for this pattern is that sampling programs are insufficient to capture all species. Williams *et al.* (2001) noted that many studies include rarefaction curves that do not meet asymptotes, yet even when they do, high proportions of rare species nonetheless are observed. Alternatively, Potts *et al.* (2005b) suggested that long-range dispersal may account for a certain number of the observed singletons.

Bee communities also exhibit considerable spatio-temporal variation (Williams *et al.* 2001). Temporally, bee communities can vary widely on an annual, seasonal and even diurnal basis. Bee populations can fluctuate by several orders of magnitude between years (Roubik 2001). Seasonally, temporal variation can be the combined result of life history traits and environmental factors. McIntyre and Hostetler (2001) found a nearly complete phenological turnover from September to April in Phoenix, Arizona, which they attributed to most local bees having univoltine life cycles combined with short life spans of six to 21 weeks. Variability in individual species populations can lead to marked changes in composition, dominance patterns and relative abundances (Kremen *et al.* 2002; Lyons *et al.* 2005). In climates with shorter active seasons, spring faunas tend to contain a high relative abundances of andrenids

and *Bombus* queens, whereas the warmer summer season community is characterized by greater proportions of megachilids and halictids (Ginsberg 1983; Petanidou and Ellis 1996; Russell *et al.* 2005). Spatially, bee communities can vary considerably. Several researchers report high levels of variation in local samples. Minkley *et al.* (1999) found less than 40% overlap in the species richness of bees visiting creosote (*Larrea tridentata* (DC) Coville) at sites located within five kilometres of one another.

Sampling bee communities

The extent to which sampling protocols, methods and conditions contribute to observations of community structure cannot be underestimated. Given the temporal and spatial variability inherent in bee populations, accurate representations of community structure in space and time requires highly replicated, intense sampling over several seasons and years (Cane 2001; MacKenzie and Winston 1984; Oerteli *et al.* 2005; Williams *et al.* 2001). This is particularly important for assessing the magnitude of anthropogenic impacts against background levels of variation. Yet, high background variation may preclude detection of impacts that are less than dramatic. Despite the need for intense sampling, care must be taken to minimize the potential that the sampling program may itself alter the community (Tepedino and Stanton 1982; Williams *et al.* 2001).

The choice of sampling methods used to collect bee community data is likely to bias assessments of community composition. The most commonly used methods include netting, pan-trapping and trap-nesting, each having implications in terms of sources of bias and resource requirements. As an active sampling technique, netting can be used

to sub-sample flowers for relative proportions of bee visitors or it can be used for sweep-sampling along transects or in standardized areas (Banaszak 1980; Williams *et al.* 2001). While it has not been tested for bees, studies of other arthropods suggest that netting involves biases of individual collectors (Russell *et al.* 2005), although proper training can minimize collector bias (Banaszak 1980). Net sampling is thought to be biased against certain groups such as parasitic bees, which do not spend long periods of time on flowers, or bees that are too small to be visually detected by the collector (Oerteli *et al.* 2005).

The use of pan-traps, or bee bowls, is gaining popularity because it is a passive technique that eliminates the need for trained collectors. Despite this, few researchers have specifically investigated biases associated with this method (Cane *et al.* 2000; Leong and Thorp 1999). Bowl characteristics such as colour, arrangement and height above the ground may not only affect which species are caught, but also the proportional catches of sexes (Leong and Thorp 1999). Cane *et al.* (2000) suggested that bowls may compete with flowers during full bloom and that their placement on the ground may evade bees that forage in a horizontal stratum; however, this effect may depend on the degree of vertical structure in the habitat. Strong fliers such as bumble bees and honey bees may be underrepresented in pan-traps (Aizen and Feinsinger 1992; Oerteli *et al.* 2005; Sarospataki and Fazekas 1995). The utility of bowls for capturing oligolectic bees is not clear, and the literature is scarce (Cane *et al.* 2000; Leong and Thorp 1999). There is evidence that if the colour of the trap can provide an oligolectic bee with similar stimulus as its floral host, then it may be effective (Leong and Thorp 1999); however, this may be tempered by the relative availability of host bloom (Cane *et al.* 2000).

Solitary cavity nesting bees can be passively sampled with trap-nests, blocks of wood

containing a series of cylindrical holes of varying diameters. Trap-nesting is useful for

providing accounts of parasitism, resource availability and reproductive output.

Assessments of community composition can be affected by the arrangement of the

traps, and variation in the diameters of the tunnels used (Krombein 1967). The extent

to which diversity of trap-nested bees represents overall bee community diversity

appears to have not been studied. As such, it is a technique that may be better suited

to studies of bee biology or to community studies that have specific implications for

this subset of the bee community.

Because any method is likely to be biased towards particular groups of bees, the

choice of sampling methods must therefore correspond to the objective of the study.

For example, the use of more than one method may be most appropriate for

enumeration studies (Cane and Tepedino 2001; Danks 1996), while hand-netting at

flowers may be a more appropriate choice when considering a guild of species

associated with particular plant species. Floral visitation records may allow the range

of possible species to be narrowed to those that are known to visit a particular plant

species (Cane *et al.* 2000).

Selected determinants of bee community patterns

Abiotic conditions

Abiotic factors such as moisture conditions, latitude and temperature regimes are the

most commonly invoked determinants affecting global patterns of bee species

richness and the relative abundances of functional groups. Abiotic conditions may affect bees indirectly by affecting floral resources levels or directly by acting on species' environmental tolerances or biological attributes.

Humidity may affect bee assemblages on global and regional scales. The low proportion of ground-nesting species in the tropic may be related to high humidity which promotes fungal growth and spoils larval food stores (Michener 2000; Wcislo and Cane 1996). Alternatively, high humidity may cause larvae to drown in hygroscopic liquefaction of food provisions (Rozen unpublished in Michener 2000). On a more local scale, Devoto *et al.* (2005) described changes in the composition of the pollinator fauna along a rainfall gradient (mean annual precipitation of 200-2800 mm) in Patagonia that was characterized by minimal changes in altitude (~300m). They observed no changes in overall diversity of pollinator species along the gradient; however, there was a reversal in dominance from bees at the low end of the spectrum to flies (Diptera) in the high end.

Laroca (1999) invoked geological stability as an explanatory factor for global patterns of bee distributions. Regions containing rich bee faunas correspond to areas where tectonic plates are most active, creating greater soil diversity and varied topography. There appears to be little support for this hypothesis elsewhere.

Temperature and the length of the warm season likely affect the composition of bee communities. Bee faunas become increasingly depauperate towards the poles, as the larger, more endothermic bumblebees (*Bombus* spp.) dominate in the Nearctic regions and flies take over from the bees as the major pollinators in Arctic regions (Elberling

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and Olesen 1999; McCall and Primack 1992). The importance of humidity and temperature in affecting bee populations is also apparent in observations of lowered bee activity during cool, cloudy days. Many researchers choose not to sample bees under such conditions.

Floral resources

Floral resources are an obvious and well-studied determinant of bee community diversity and composition. The most common measurements of floral resource availability in community level studies are the per cent cover of flowering plants, plant species diversity, flower abundance, and flower diversity. Bee abundance is positively associated with increasing per cent coverage of flowering plants (Banaszak 1996; Steffan-Dewenter and Tscharntke 2001), whereas bee abundance and diversity have been related to flower abundance (Ginsberg 1983; Potts *et al.* 2003b; Potts *et al.* 2001b; Steffan-Dewenter and Tscharntke 2001) and floral diversity (Potts *et al.* 2001b; Steffan-Dewenter and Tscharntke 2001). Plant species diversity is believed to promote bee diversity because heterogeneity in the resource base supports a greater number of foraging niches. Stanton and Tepedino (1981) found that this diversity relationship also applied at higher taxonomic levels, as a greater contribution of bee family diversity to overall bee diversity was associated with less similar floral types and reward profiles.

Because nectar and pollen are the actual resources sought by bees, their direct measurement may be a more accurate representation of resource levels at any given time (Potts *et al.* 2001b; Zimmerman and Pleasants 1981). Nectar quality and quantity

vary considerably on a daily and seasonal basis (Martins 2004) and over successional stages (Petanidou and Ellis 1996; Potts *et al.* 2001a; Steffan-Dewenter and Tscharntke 2001). Changes in nectar properties can be attributed to such factors as soil moisture, air temperature, air moisture, replenishment rates, flower age and pollination status (Pleasants 1983a; Tepedino and Stanton 1982). Spatial and temporal variation in nectar quality and quantity can interact with differential energy requirements of bees to provide the basis for resource partitioning. The high energetic demands of large bees such as bumble bees or megachilids encourage them to seek out flowers with high nectar volume and sugar content, whereas smaller or solitary bees often specialize on flowers with less but more highly concentrated nectar (Petanidou and Smets 1995; Willmer 1983). While the quality and quantity of nectar resources may interact with individual bee species' biology to impact populations, nectar quality and quantity may be less important at a community level. Rather, in Mediterranean pine woodlands, it is the diversity of nectar resources that may be a greater determinant of bee species richness than overall habitat levels of nectar volume, concentration or sugar content (Potts *et al.* 2003b; Potts *et al.* 2004).

Although critical for bee reproduction, pollen appears to be under-studied in community-level research. In one of few community-level studies to consider pollen resources, Potts *et al.* (2003b) found that the pollen to nectar energy ratio was most influential in determining bee species richness and abundance over pollen energy or grain density. This effect was most notable for the Megachilidae and Halictidae. Pollen protein, or some other nutritional constituent, may be more influential than energy variables.

<u>Nesting resources</u>

The availability and diversity of nesting substrates and building materials are critical in determining the nesting guild structure of bee communities. While floral resources are usually the main predictors of bee community richness, Potts *et al.* (2005) found that 5% of community richness and 10% of dominant species richness in Mediterranean woodland habitat were explained by nesting resource diversity. They also looked at community composition and found that 40% of the variation in the species-abundance pattern of the whole community, and 60% of the guild structure, were attributable to nesting resource diversity. As with flower resources, a greater diversity of nesting resources could support a greater number of nesting guilds.

Nesting resources may even be more or as important as floral resources. For example, in a comparison of bee diversity between urban habitats of Tucson, Arizona and desert scrub, several generalist and specialist species were more abundant on poorer quality creosote (*Larrea* spp.) in the urban habitats, which the author attributed to a greater variety of woody nesting substrates in the older suburbs than in the desert (Cane unpublished in Cane and Tepedino 2001). To the extent that such results can be used to infer the importance of nesting resources in other systems, ecosystem changes likely affect bee communities by altering the relative abundance of different nesting resources, and by extension the bee community.

<u>Competition</u>

While interspecific competition is an oft-cited structuring agent in vertebrate, invertebrate and plant communities, determination of its occurrence and intensity is problematic because demonstration of niche overlap among species is not in itself

evidence that competition exists (Buchmann 1996; Goulson 2003). A pre-requisite for the occurrence of competition is that the shared resources are limited. If they are, there should be a tight link between the abundance and diversity of resources and consumers, as consumers should be continually adjusting to changes in the resource base (MacArthur 1972). Where similarity of species abundance curves of flower and bee species-abundance curves over time have been examined, resource limitation varies temporally and is likely episodic in most communities (Tepedino and Stanton 1981, 1982; Zimmerman and Pleasants 1981). Also, it must be shown that species have reduced fitness as a result of their interaction with another species (Goulson 2003). This, perhaps, is most easily studied in bee species that use trap-nests as reproductive output for several species can be examined concurrently, however, very few studies appear to have addressed this aspect (but see Steffan-Dewenter and Tscharntke 2000).

As competition should place limits on the extent to which species can be alike and continue to coexist (Johnson and Steiner 2000), several forms of resource partitioning have been used as surrogates to infer competition. Factors believed to promote coexistence within bee communities include diurnal or seasonal temporal segregation (Ginsberg 1983; Martins 2004; Parrish and Bazzaz 1979; Pleasants 1983b), floral specialization (Johnson and Steiner 2000; Waser *et al*. 1996), altitudinal segregation (Inouye 1976; Lundburg and Ranta 1980), patch dynamics (Palmer *et al.* 2003), spatio-temporal heterogeneity (Palmer *et al.* 2003; Ranta and Vepsäläinen 1981), core-satellite dynamics (Hanski 1982) and tongue length differences (Hanski 1982; Pleasants 1983b; Ranta 1982). The extent to which observed patterns of resource partitioning affects or is affected by competition dynamics is poorly understood

(Palmer *et al.* 2003), particularly when more than one co-existence mechanism is occurring.

Because of the complexity of interactions occurring at the gross community level and the nature of competition itself, attempts to understand competition in bee communities usually focus on particular guilds. For example, bumble bees have been used as a model taxon for testing hypotheses regarding the role of competition in structuring communities. Several researchers have suggested that upper limits exist on the number of bumblebee species that can coexist. Using tongue length as a surrogate for resource use, it was initially postulated that a maximum of four bumble bee species could inhabit any given local community: a short tongued species, a long tongued species, one with an intermediate length and one robber species (Inouye 1976), each specializing on flowers with corresponding corolla lengths. However, Hanski (1982) suggested that competition was more likely to structure regional species pools than local communities.

Investigations of the impact of managed or feral honey bees on other bees have been largely unsuccessful at proving the effects of competition on wild bee community structure. Theoretically, honey bees are strong competitors because they are generalists; they have wide foraging niches; they enjoy thermal benefits associated with large bodies and heat retention inside colonies; they have the ability to communicate the location of abundant resources; and managed colonies receive supplemental feeding, making them more resilient during periods of resource limitation (Forup and Memmot 2005; Goulson 2003; Thorp 1996). Social, polylectic

bees may to experience the greatest competitive effects from honey bees because of their similar foraging strategies.

Researchers have come up with highly suggestive results for competition between honey bees and native bees. Ginsberg (1983) observed exclusion of *Andrena* species from larger, more nectar-dense flower clusters of yellow rocket (*Barbarea vulgaris* R.Br.)(Brassicaceae) and apple (*Pyrus malus* L.)(Rosaceae) flowers. Similarly, visitation rates of native bees on *Dillwynia juniperina* Lodd. (Fabaceae) were negatively correlated to the presence of honey bees (Gross 2001). Honey bees may reduce the standing crop of nectar to levels that are unprofitable for other species, as on *Agave schottii* Englemann (Agavaceae) (Schaffer and Zeh 1983). Inverse abundance relationships between honey bees and native bees were observed at flowers over a three-year period in a systematic honey bee removal experiment on Santa Cruz Island, California (Thorp 1996). Abundance of halictids, in particular, was negatively correlated with honey bee abundance, suggesting competitive release. Yet, despite evidence of resource competition at flowers, there has been no conclusive confirmation that these interactions produce negative population level impacts for wild bees (Goulson 2003; Roubik and Wolda 2001; Steffan-Dewenter and Tscharntke 2000).

Landscape factors

In landscape level studies of bee communities, landscape context is most commonly quantified by measuring the proportion of suitable habitat or the diversity of habitat types within a defined area. In particularly fragmented or altered landscapes, such as agricultural areas, 'suitable' habitat is most commonly equated to natural or semi-

natural areas. Species richness of bee communities in different landscapes increases

with the proportion of natural or semi-natural habitat (Dauber *et al.* 2003; Kearns and

Inouye 1997; Kremen *et al.* 2004; Kremen *et al.* 2002; Steffan-Dewenter *et al.* 2002).

In Germany, bee species richness in an agricultural setting increased with the

percentage of grassland cover in the surrounding matrix (Dauber *et al.* 2003). Kremen

et al. (2002) found that the amount of natural habitat within a one kilometre radius of

watermelon farms in California was more important in determining bee species

richness, abundance and pollen deposition on crops than whether organic or

conventional farm management systems were being utilized.

Observations of increased richness and abundance in response to landscape level

availability of natural habitat invoke questions regarding the effect of processes that

reduce its availability. For example, habitat fragmentation causes a concurrent

reduction in the total area of suitable habitat and subdivision of the remaining habitat

into smaller, more isolated patches (Noss and Csuti 1997). Because bees deal with

floral and nesting resources that are by nature patchily distributed at a local level, the

extent to which fragmentation represents a problem to bees is not clear (Cane 2001).

Evidence for bee responses to habitat fragmentation is most commonly sought in

species-area relationships and species-isolation relationships (Aizen and Feinsinger

1992; Steffan-Dewenter and Tscharntke 2002; Zanette *et al.* 2005). However, these

relationships have been found in some studies (Steffan-Dewenter and Tscharntke

2002) and not in others (Zanette *et al.* 2005), suggesting that bee responses to

fragmentation are species-specific and context-dependent.

Dispersal capability and life history traits are factors believed to affect a species response to landscape structure (Harris and Johnson 2004; Steffan-Dewenter *et al.* 2002). Dispersal capability governs the scale at which a species interacts with its environment. The connectivity of a landscape decreases as inter-patch distances exceed a species' movement range and the intervening matrix is not hospitable. The average and maximum distances that most bee species can fly are unknown. While there is evidence for a correlation between body size and dispersal capabilities (Cane 2001; Gathmann and Tscharntke 2002; Steffan-Dewenter and Tscharntke 1999), bees probably forage in much smaller ranges than they are capable of flying (Potts *et al.* 2003a). There can be strong variation in the foraging ranges of similar-sized taxa. For example, in a study using mark-recapture techniques on three species of bumble bees, Walther-Hellwig and Frankl (2000) found that *Bombus terrestris* L. could regularly be recaptured up to 1750 m from the nest, whereas *B. muscorum* L. was not found beyond 500 m. Conversely, solitary species are believed to remain relatively local, within 150-600 m for trap-nesting species (Gathmann and Tscharntke 2002) and less than 200 m for smaller solitary species (Potts *et al.* 2001b).

Analysis of bee community responses to the proportion of suitable habitat at several landscape scales has provided empirical evidence for the notion that different groups of bees vary in how they perceive the landscape context. Steffan-Dewenter *et al.* (2002) found that solitary bee richness and abundance of experimental plants correlated most strongly with the proportion of semi-natural habitat within 750 m. Bumble bees, on the other hand, did not respond to the proportion of semi-natural or natural habitats at any scale, suggesting greater flexibility in nesting requirements and/or dispersal capabilities. Therefore, bumble bees, may be less dependent on semi-

natural or natural habitats than other groups of smaller bees. While availability of natural and semi-natural habitats at the landscape level may be more important for groups of smaller bees than larger bees, threshold levels of habitat loss beyond which bee communities can be expected to decline seriously have not been established.

Life history traits may affect bees' perceptions of landscape structure. For example, connectivity between habitat patches may not be as important to generalists as to specialists because generalists are more likely to meet their needs outside of discrete patches of natural habitat (Steffan-Dewenter 2003). Alternatively, specialists that rely on a particular plant taxon that is not available outside of a habitat patch may be restricted to that patch. Likewise, parasitic bees associated with oligoleges or poorly dispersing hosts may be sensitive to decreased connectivity.

Bee communities in mixed-grass prairie

The rise and fall of the mixed-grass prairie

The mixed-grass prairie of North America is a subtype of a much broader biotic system. This system, the grasslands, is found on nearly every major landmass and is one of the globe's main biomes. Grasslands include tropical savannas of Africa, South America, and Australia as well as the temperate grasslands of North America and Eurasia (Coupland 1992b).

Despite their wide geographic distribution, grasslands share similar dominant life forms, flat or rolling topography, comparable climatic patterns, high rates of evapo-transpiration, and similar disturbance regimes (Coupland 1992b). Grasslands have

developed where mean annual precipitation is from 250 to 1000 mm (Tscharntke and Greiler 1995), but it is the characteristic pattern of seasonal rainfall deficiency and periodic drought that has promoted the evolution and dominance of drought-tolerant grasses (Poaceae) (Coupland 1992b). Periodic fire is also important in preventing grasslands from developing into more mesic vegetation types. Dominant animal life forms include grazing and burrowing animals, which have historically contributed to the maintenance of productivity and biodiversity in grasslands.

The Great Plains of North America have been classified according to a number of systems (Carpenter 1940; Clements 1920; Coupland 1992b); however, for ease, these have been generally characterized as having three dominant types: short-grass prairie, mixed-grass prairie and tallgrass prairie (Jones and Cushman 2004; Robertson *et al.* 1997). In Canada, these types occur along a moisture gradient from west to east. Short-grass prairie occurs in the more arid conditions characteristic of southern Alberta and southwestern Saskatchewan. Mixed-grass prairie can be found in more intermediate conditions extending from east-central Alberta, through Saskatchewan to southwestern Manitoba. Tallgrass prairie occurs in the more mesic conditions of southeastern Manitoba, with a relatively small pocket occurring in southern Ontario.

Mixed-grass prairie is considered an ecotone that combines elements of the drought-tolerant short-grass prairie from the west and the tallgrass prairie from the east. Ranging along a north-south gradient from the southern Canadian prairie down through the Dakotas, western Kansas and Texas, its occurrence and composition are determined by a specific combination of geographical and climatic factors, interacting with disturbance by fire and grazing. Soils of the northern mixed-grass prairie reflect

the processes of glacial expansion and retreat that superimposed deposits such as till and loess over granite bedrock (Bragg and Steuter 1995). Most of the northern mixed-grass prairie soils are classified as mollisols, darkened due to a large proportion of decomposed organic matter (Bragg and Steuter 1995). The climate of the northern mixed-grass prairie is considered to be dry-humid to semi-arid and is characterized by strong winds, mean monthly temperatures ranging from -18°C in January to 18°C in July, and mean annual precipitation of 300mm to 450mm (Coupland 1992b). As a disturbance-regulated ecosystem, mixed-grass prairie is heavily influenced by fire and grazing, which are important determinants of plant community composition and structure (Shay *et al.* 2001).

Variation in moisture availability is a determining factor in the vegetative composition of mixed-grass prairie, which contains both the warm-season C_4 grasses typical of short-grass prairie and the cool-season C_3 grasses dominant on tallgrass prairie (Bragg and Steuter 1995; Shay *et al.* 2001). Short-grass species are more prevalent in years of drought while tallgrass species dominate in moister years (Coupland 1992b). Coupland (1992b) identified five main vegetative associations in the mixed-grass prairie based on assemblages of the dominant grass genera. These include the *Stipa-Agropyron* association characteristic of mesic deep glacial till; the warm-season, drought resistant *Stipa-Bouteloua* association; the climatically flexible *Stipa-Bouteloua-Agropyron* assemblage; the *Bouteloua-Agropyron* association occupying the most xeric regions; and the assemblage dominated by *Agropyron* and *Koeleria* typical of clay, lacustrine soils. Local vegetation composition is usually dominated by one of these graminoid associations, while interstitial forb species contribute disproportionately to overall species diversity (Collins and Gibson 1990).

Important groups of flowering forbs species include entomophilous asters (Asteraceae) and legumes (Fabaceae) (Smith and Smith 2001). As an ecotone, mixed-grass prairie may harbour higher levels of plant diversity than either short-grass or tallgrass prairie (Bragg and Steuter 1995).

Yet, biodiversity on the mixed-grass prairie has been in decline. Since European settlement, Canada's original 24 million ha of mixed-grass prairie has been reduced to less than a quarter of its original distribution due to fire suppression, agricultural conversion, overgrazing, aspen (*Populus tremuloides* Michx.) encroachment and exotic species invasions (Mansell and Moore 1999). Remnant pockets of mixed-grass prairie occur primarily on marginal sites that are unsuitable for crop production, yet most are surrounded by a matrix of agricultural lands. Some of these remnants are preserves administered by government or by conservation organizations; however, few of these are actively managed. Many remnant prairies are small, isolated fragments in which reduced colonization and increased extinction rates have contributed to the loss of large proportions of original prairie plant species (Leach and Givnish 1996). Plant community diversity is being negatively impacted by invasive plant species including leafy spurge (*Euphorbia esula* L.) (Euphorbiaceae), smooth brome grass (*Bromus inermis* Leysser) (Poaceae), Kentucky bluegrass (*Poa pratensis* L.) (Poaceae) and common juniper (*Juniperus communis* L.) (Cupressaceae) (Belcher and Wilson 1989; Mansell and Moore 1999). These remnant areas support reduced levels of animal biodiversity compared to the original habitat. A disproportionate number of the species listed by the Committee on the Status of Endangered Wildlife in Canada are prairie inhabitants.

Causes of bee community change in the mixed-grass prairie

Natural and anthropogenic sources of habitat alteration can be expected to cause non-random changes in species composition and relative abundances (Balvanera *et al.* 2004; Kremen *et al.* 2002). The extent to which bee communities will be affected by habitat alteration will depend on how it modifies plant communities, nesting habitats, competition interactions and the landscape context. Forms of habitat alteration that are known to impact bee communities include urbanization (McIntyre and Hostetler 2001; Saure 1996; Tommasi *et al.* 2004; Zanette *et al.* 2005), powerline right-of-way management (Russell *et al.* 2005), logging (Cartar 2005), grazing (Mayer 2004; Petanidou and Ellis 1996; Steffan-Dewenter and Leschke 2003), habitat fragmentation (Aizen and Feinsinger 1992; Cane 2001; Harris and Johnson 2004; Steffan-Dewenter 2003), agricultural intensification (Kremen *et al.* 2002; Westphal *et al.* 2003), and fire (Petanidou and Ellis 1996; Potts *et al.* 2001a; Potts *et al.* 2003a). This section will investigate agents of change that are most likely to affect prairie bee communities.

Agricultural practices

Approximately 75% of the mixed-grass prairie region has been converted to crop or rangeland agriculture (Canadian Council on Ecological Areas 2006). Modern cropping systems often involve high tillage, the use of chemical fertilizers and pesticides and planting of either large expanses of monocultures or non-native forage species.   While no one has examined the impact of agriculture on bee communities in mixed-grass prairie specifically, demonstrated responses to habitat loss and fragmentation, cropping systems and pesticide use in other habitats are amenable to comparison.

The primary effect of land conversion on bees has been a reduction in the abundance and diversity of forage plants and nest sites (O'Toole 1993). Not only do bees need floral food, nest sites and nesting materials, but these resources also must be available within flight range of one another (Westrich 1996). Habitat alteration and degradation due to agriculture have created highly fragmented landscapes characterized by small isolated islands of suitable habitat. The subsequently patchy and discontinuous distribution of forage and nesting resources in fragmented agricultural landscapes have made bees increasingly dependent on areas of semi-natural habitat or marginal lands such as shelterbelts and field edges (Calabuig 2000; Westrich 1996). Declines of bumble bee populations in agroecosystems of Germany in the late sixties were attributed to reduced forage availability associated with altered drainage patterns and the removal of marginal lands (Peters 1972 in O'Toole 1993). Field margins may represent nesting refuges from tillage, as greater densities of bees were found nesting in the ground in the field margins surrounding California sunflower fields than inside the fields (Kim *et al.* 2006). Marginal lands around agricultural fields are particularly important if the lifespan of a species exceeds or does not completely overlap with the flowering period of a particular crop (Calabuig 2000; Morandin and Winston 2005) or if a species cannot exploit the crop resources for mechanical or other reasons.

Replacement of natural habitats by large expanses of monocultures has not only reduced habitat area, but also habitat diversity. Primarily wind-pollinated crops, such as grasses, are of little value to bees; however, mass flowering crops can provide highly rewarding concentrations of nectar and pollen that can support large densities of bees. Westphal *et al.* (2003) conducted a study of bumble bee densities on

experimental plots in agricultural landscapes at 12 different spatial scales. Bumble bees did not respond to the proportion of semi-natural habitat at any scale but rather to the availability of mass flowering crops, particularly at the larger spatial scales. Bumble bee abundances were apparently not limited in areas with as little as 2% semi-natural habitat. While the authors asserted that this provided evidence of the value of large monocultures to bumble bees, they may not be as beneficial to other bees. Banaszak (1996) found a negative correlation between bee species density and diversity (H) among 15 different ecosystems in western Polish and Romanian lowlands, which he attributed to the effect of monocultures.

Modern cropping systems often are accompanied by the wide-scale use of insecticides, from which bees may suffer non-target effects. Application of insecticides is frequently implied where higher abundance or diversity of bees is observed in natural settings compared to nearby agricultural areas or where pollen limitation on crops was investigated (Banaszak 1996; Calabuig 2000; MacKenzie and Winston 1984; Scott-Dupree and Winston 1987). Understanding of the impact of pesticides on native bee communities has largely been inferred by what is known about the responses of honey bees and other managed bees to pesticide poisoning. Effects of pesticide poisoning in honey bees vary with the dose, timing of application and type of chemical used, but symptoms include in or near hive mortality, increased aggressiveness, paralysis or peculiar repetitive motions, incorrect performance of communication dances, abnormal patterns of egg laying in queens and supercedure (Johansen 1977; Moffett *et al.* 1970; Schricker and Stephen 1970). Honey bees may take several days to die, during which time they may bring contaminated pollen or pesticide grains back to the hive, killing brood and newly emerged adults (Moffett *et*

al. 1970). Symptoms observed in other managed species including the alfalfa leafcutting bee (*Megachile rotundata* (F.)), the alkali bee (*Nomia melanderi* Cockerell) and some bumble bees may be an indication that susceptibility is correlated with surface area/volume ratios (Torchio 1973).

Differential responses of individual bee species to pesticides can alter community composition.   Kevan *et al.* (1999) described changes in the species-abundance curve of bee communities on commercial blueberry in New Brunswick related to application of fenitrothion on adjacent forests to control spruce budworm (*Choristoneura fumiferana* (Clemens)) infestations. The species-abundance curves of communities before pesticide application and distant from application fit a log-normal model of species composition, whereas, curves from post-application and nearby fields deviated from that pattern. Interestingly, community level effects were detectable only by using the graphical approach of species-abundance curves. There was no difference in single-value indices for diversity and evenness for the respective comparison groups, suggesting the use of simple indices can obscure compositional changes in response to perturbation.

Whether low-impact, pesticide-free methods of agriculture, or organic agriculture, are better able to support diverse and healthy bee communities is only rarely considered. Morandin and Winston (2005) investigated bee abundance and pollen deficits on canola (*Brassica* spp.) among organic, conventional and genetically modified (GM) crops in northern Alberta. While they found that pollen deficits increased and bee abundance declined from organic, to conventional and to GM crops, it is difficult to interpret their results in terms of community impacts because no diversity or

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community composition values were reported. In another study among organic and conventional watermelon crops in California, the finding of greater bee diversity and pollen deposition on organic versus conventional crops was rendered insignificant by a strong impact of proximity to natural habitat of one of the organic farms (Kremen *et al.* 2002).

Grazing

Vertebrate and invertebrate grazers are an integral part of the mixed-grass prairie ecosystem. A substantial role in the emergence of the North American grasslands in the post-Pleistocene era is attributed to grazing by large herbivores, many of which are now extinct (Knapp *et al.* 1999; Robertson *et al.* 1997). For millennia, bison (*Bison bison* L.) held a keystone role in shaping the structure and function of prairie ecosystems until widespread settlement and cultivation of the prairies saw replacement of native bison with domesticated cattle (Knapp *et al.* 1999). As a form of disturbance, grazing can profoundly affect prairie soils and vegetation (Collins and Barber 1985; Coupland 1992a; Kleijn and Steinger 2002). Effects on plant communities may occur directly through removal of biomass, plant reproductive structures or accumulated detritus. Indirect effects may occur through trampling, redistribution of nutrients or removal of competitively dominant species (Collins and Glenn 1988; Coupland 1992a; Kerley *et al.* 1993; Knapp *et al.* 1999). Plant populations may increase or decline in response to grazing depending on such features as chemical composition, life history traits, competitive ability and tolerance to grazing (Kleijn and Steinger 2002). Individual plants may demonstrate changes in productivity, reproductive allocation, propagation method or architecture as a result of grazing (Kerley *et al.* 1993; Kleijn and Steinger 2002; Wallace 1990).

The extent to which population and community level responses occur is primarily a function of the intensity and frequency of grazing, traits of grazers themselves, and interaction with other disturbances (Collins and Glenn 1988). Bison prefer perennial grasses to forbs and woody species, which can significantly reduce the grass to forb cover ratio (Vinton *et al.* 1993). Although cattle prefer grasses, they will feed more frequently on forbs than bison (Steuter and Hidinger 1999). In a comparative study conducted on tallgrass prairie, sites grazed by bison contained greater abundance and richness of annual forbs and higher spatial heterogeneity of biomass and cover than sites grazed by cattle (Knapp *et al.* 1999). Nevertheless, grazing by cattle has been shown to either maintain or increase plant productivity and species diversity at low to mid stocking densities (Collins and Barber 1985; Knapp *et al.* 1999). Conversely, high stocking densities and lack of appropriate rotation are associated with lower plant diversity, decreased spatial heterogeneity and range deterioration (Bai *et al.* 2001; Collins and Barber 1985). The greatest diversity and heterogeneity tends to be observed on grasslands in which moderate levels of grazing and fire interact (Collins and Glenn 1988).

 The impact of grazing on grassland insect communities is linked to its impacts on vegetation, and it varies by taxon (Steffan-Dewenter and Leschke 2003; Tscharntke and Greiler 1995). Kruess and Tscharntke (2002) distinguished between short-term and long-term impacts of grazing on phytophagous insect communities. Short-term impacts include those associated with architectural simplification of plant communities causing a reduction of spatial feeding niches and the replacement of

grazed plant parts with nutrient rich, younger tissues. In the long term, shifts in plant community structure can occur, changing the niche structure.

Research investigating the impact of grazing on bee communities appears to be limited. Taken together, results from the few studies encountered where the impact of grazing on bee communities was examined reveal no clear trends. Among high intensity, low intensity, and ungrazed grasslands in Germany, species richness of solitary bees and wasps collected in trap-nests was higher on ungrazed versus grazed sites (Kruess and Tscharntke 2002). In the same study, grazing intensity appeared to affect only abundance, which was lower in intensively grazed sites than on ungrazed or low-intensity grazed sites. Mean vegetation height, rather than any other vegetation variable including plant species richness and forb/grass ratio, was the best predictor of bee and wasp richness (r^2=0.59). In another study in German orchard meadows, there was no difference in abundance or richness of bee communities among grazed, mowed or abandoned sites despite greater herb species richness in mowed meadows and significantly lower total plant diversity in abandoned meadows (Steffan-Dewenter and Leschke 2003). In lowland scrub communities of the Mediterranean region, the only variable that was positively related to grazing intensity was abundance of the 17 most common bee species (Potts *et al.* 2003b). In South Africa, Mayer (2004) found no difference in bee abundance between a grazed site and an adjacent ungrazed site sampled with Malaise traps and transect walks. A difference in species richness was found only in the Malaise trap dataset, with more species found on the ungrazed lands. Clearly, no generalizations can be made based upon the results of these studies and comparisons are difficult because of the different methods used (Kruess and Tscharntke 2002). The two studies herein that investigated plant

community responses also seemed to indicate a disconnect between plant diversity and bee diversity, which make potential predictions of bee community responses to grazing based on vegetation community responses tenuous.

Fire

Fire is considered to be a main factor in the expansion and maintenance of the North American grasslands, as periodic burning is necessary to prevent encroachment of woody vegetation onto mesic prairie (Anderson *et al.* 1990; Briggs *et al.* 2005; Shay *et al.* 2001). Historically, regular lightning strikes and range management by First Nation peoples maintained fire return intervals of one to four years; however, European settlement in the mixed-grass prairie led to extended periods of fire suppression (Anderson *et al.* 1990; Briggs *et al.* 2005; Shay *et al.* 2001). Modern rangeland and preserve managers commonly employ prescribed burns to control invasive native and non-native species, promote productivity and enhance biodiversity. The response of mixed-grass prairie to fire varies according to the seasonal timing of the burn, time since the burn, grazing history, precipitation and fire temperature (Collins and Gibson 1990).

Insects exhibit a wide variety of responses to fire. Panzer (2002) listed five insect traits associated with negative population responses to fire including 1) dependence on small habitat remnants, 2) inhabitation of upland areas, 3) limited dispersal capability, 4) nonvagility, and 5) univoltine life cycles. In the short-term, fire events can cause high mortality or emigration of many insect populations, though total extirpation of populations is rare (Panzer 2002; Swengel 2001). Soil-dwellers and insects with strong flight capabilities can avoid exposure to intense heat and flames

(Tscharntke and Greiler 1995). The potential for insect populations to recolonize after a fire depends on the suitability of post-fire habitat (Swengel 2001). Immediate post-fire habitats are often characterized by dry soils and low plant diversity and biomass (Anderson *et al.* 1989). These conditions favour insect taxa that are associated with grasses, annual forbs, exposed soil or sunny, xeric conditions (Swengel 2001). Timing of the fire may impact insect responses depending on the lifecycle stage. For example, removal of accumulated litter by an early spring burn may accelerate the rate of soil temperature increase, thereby causing insects that overwinter in the soil to emerge sooner (Anderson *et al.* 1989). Intermediate and long-term impacts of fire on insects are more closely related to changes in plant communities. Generalists and taxa attracted to highly productive post-fire vegetation, such as grasshoppers and some butterflies, have been shown to peak in richness and abundance in early successional stages following fire (Anderson *et al.* 1989; Force 1981; Swengel 2001).

While there is a respectable literature on insect responses to fire, it offers disappointingly few references to bees. The impact of fire on bee community succession has been investigated only in the species-rich Mediterranean shrublands of Greece (Petanidou and Ellis 1996) and Israel (Potts *et al.* 2003a). A chronosequence approach was used in both studies in which bee community structure at the family level was related to turnover in predominant plant life forms and nesting habitat. While Potts *et al.* (2003a) tracked changes over a longer period of time (60+ years), Petanidou and Ellis (1996) had a greater representation of sites in the first few years (2-10) post-fire. A common feature in both studies was that peak bee and plant species richness occurred around two years post-fire. In both cases, this was attributed

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to a plant community turnover from the pioneer annuals to more nectar-rich perennials. Potts *et al.* (2003a) showed subsequent declines in bee species richness from ~10, 16, 25 to 60+ years. In Greece, habitats in the first year after a burn were characterized by exposed soils and a predominance of annual forbs. Pioneer habitats were relatively nectar-poor and dominated by small, short-tongued, ground-nesting bees, especially andrenids. At around seven years post-burn, perennials and a greater number of woody species became dominant. High nectar volumes at these sites were associated with greater abundances and diversity of large-sized, long-tongued bees. Also, the greater availability of woody stems contributed to a concurrent increase in wood and twig-nesting species. While there were common elements in the family associations between the two studies, failure to investigate taxon associations beyond the family level probably obscured important dynamics and points of comparison between the two faunas.

Discussion

An important theme that emerges from this review is that accurately describing patterns in bee communities is critical for determining underlying processes and for assessing community responses to natural and anthropogenic change. Without appropriate baseline data regarding the temporal and spatial patterns of bee diversity, there is a risk of misinterpreting, exaggerating or altogether missing causative factors.

Descriptions of bee community patterns may consider diversity in terms of either taxonomic or functional components; however, approaches that incorporate elements of both provide the greatest insights. The use of an integrated approach for measuring diversity that supplements single-value diversity measures with compositional

information is useful in identifying differential responses of constituent taxa. Yet, there appears to be a heavy reliance on the common parameters of bee species richness and gross bee abundance as the sole response variables. Moreover, when species richness is used to compare across habitats, it is often not standardized with the use of taxon sampling curves. Beyond showing that certain impacts have either a positive of negative impact on species richness or diversity, consideration of community composition informed by solid taxonomy can assist in identifying how the species that make up a community respond to particular impacts.

An ability to describe temporal and spatial trends in bee communities accurately requires that variation be examined over appropriate scales. For example, despite widespread recognition that bee populations are inherently variable over time, few studies actually appear to contain data collected over and entire season, or for longer than three years. Failure to sample adequately over longer temporal scales may obscure the influence of community processes or disturbances in at least two ways. Firstly, the lack of adequate baseline data could conceivably lead to erroneous interpretations of responses associated with an impact that are within the range of natural variation. Secondly, observations of reduced bee species richness or abundance following a particular disturbance may only be a result of short-term impact of the event itself, whereas communities may actually demonstrate resilience in the long term. However, despite the obvious need for more temporally rigorous sampling, specific parameters regarding how often and for how long are generally absent.

In terms of spatial scales, making broad generalizations about patterns among bee communities in different ecosystems is difficult because of the variable approaches taken by bee researchers. The same method is rarely used in exactly the same way, and the lack of standardized sampling across systems makes it very difficult to compare across habitats. Given the biases inherent in specific sampling techniques, complementary use of more than one method may provide the most comprehensive surveys.

The importance of rigorously collected baseline data for detecting change places an impetus on compiling such data in as many habitats as possible. At this point, there is little information to suggest that pollinator declines observed elsewhere apply to mixed-grass prairie bees of southwestern Manitoba; however, this may be due to a paucity of data. As a first step in assessing bee communities in mixed-grass prairie, species lists must be compiled for various localities and spatial and temporal trends over appropriate scales must be identified and interpreted with explicit consideration of biases associated with the sampling methods. As such, my study objective to document species richness, composition, and spatial and seasonal trends in the bee community of the Yellow Quill Mixed-grass Prairie Preserve explicitly incorporates an analysis of the impact of sampling method.

MATERIALS AND METHODS

Study area

Sampling was conducted at the Yellow Quill Mixed-grass Prairie (YQMGP), an 846-ha preserve located in southwestern Manitoba. It is situated approximately 2 km north of the junction of the Souris and Assiniboine rivers in the Rural Municipality of South Cypress (Sveinson *et al.* 2001). The preserve is surrounded by the Assiniboine Corridor Wildlife Management Area to the south, the Canadian Forces Shilo Military Reserve to the east and north, and by cultivated lands to the west.

The YQMGP is found in the Upper Assiniboine Delta physiographic area, formed by deposits left as the Assiniboine River flowed into glacial Lake Agassiz approximately 12,000 years ago (Ehrlich *et al.* 1957; Shay *et al.* 2001). The regional terrain is level to gently rolling, with deep valleys formed by the Assiniboine and Souris Rivers (Bird 1927). The soils of the YQMGP are predominantly classified as Miniota sands, with Stockton fine sandy loams accounting for about 30% of the area (Ehrlich *et al.* 1957; Nature Conservancy of Canada no date). The dominance of sand in these soil types enhances drainage, but renders them susceptible to erosion (Ehrlich *et al.* 1957). Soil fertility and moisture retention are generally low throughout the region (Ehrlich *et al.* 1957), although the introduction of potato (*Solanum tuberosum* L.) (Solanaceae) farming and irrigation have allowed agriculture to expand over time (Sveinson *et al.* 2001).

Approximately half of the land cover in the YQMGP is forest dominated by trembling aspen (*Populus tremuloides* Michx.) (Salicaceae) with pure and mixed stands of bur oak (*Quercus macrocarpa* Michx.) (Fagaceae), white spruce (*Picea glauca* (Moench)) (Pinaceae) and balsam poplar (*Populus balsamifera* L.) (Salicaceae) occurring throughout (Sveinson *et al.* 2001). The remaining vegetative cover is classified as either grass-dominated prairie or shrub-prairie characterized by creeping juniper (*Juniperus horizontalis* Moench) and western snowberry (*Symphoricarpos occidentalis* Hook) (Caprifoliaceae) (Sveinson *et al.* 2001). Dominant grasses at the preserve include porcupine grass (*Stipa spartea* Trin.) (Poaceae), little bluestem (*Andropogon scoparius* Michx.) (Poaceae) and sheep's fescue (*Festuca ovina* L.) (Poaceae). Common forbs include prairie crocus (*Anemone patens* L.) (Ranunculaceae), three-flowered avens (*Geum triflorum* Pursh) (Rosaceae), purple prairie clover (*Dalea purpurea*) (Fabaceae), hairy golden-aster (*Chrysopsis villosa* (Push) Nutt.) (Asteraceae), northern bedstraw (*Galium boreale* L.) (Rubiaceae) and pasture sage (*Artemesia frigida* Willd.) (Asteraceae). Leafy spurge (*Euphorbia esula* L.) (Euphoribaceae) is an invasive, exotic plant of European origin that dominates at some sites.

The regional climate is continental, with warm, dry summers and long, cold winters (Shay *et al.* 2001). Average climatic information for the YQMGP is generalized from data recorded from 1971 to 2000 at the nearest possible meteorological station run by the Canadian Department of Agriculture (CDA) Research Station near Brandon, Manitoba (49°52'N, 99°58'W) (Environment Canada 2007). Mean annual temperature is 2.4°C. The warmest daily mean temperature occurs in July at 18.9°C, and the coldest occurs in January, at -17.9°C. Average annual precipitation is 474

mm, of which approximately 73% falls as rain. Soil moisture in this region of the

mixed-grass prairie is typically depleted by late July (Chhin and Wang 2002).

The YQMGP is owned and managed primarily by the Nature Conservancy of Canada

(NCC), although the western-most and northern-most sections are Manitoba Crown

Lands. Management practices employed at the preserve include twice-over rotational

cattle grazing, controlled burns, trembling aspen control and integrated weed

management for leafy spurge.

Study sites

Sampling was conducted at three 1-ha sites within the YQMGP, shown in Figure 1.

Each site consisted of a 100 m X 100 m fenced-off exclosure located within a 2.56

km^2 grazing paddock. The grazing exclosures were established by NCC in 2000 as

control treatments for a program to monitor the impact of cattle grazing. During both

years of this study, 153 cattle consisting of 75 calf/cow pairs and three bulls were

rotated among the three grazing paddocks such that each paddock was grazed for

approximately two weeks in the spring and another six-week period over the summer.

Each sampling site was named after the section of the legal land description within

Township 16 and Range 8W in which the grazing paddocks were found. Adjacent

study sites were separated by approximately 2 km. Dates during which cattle were

present in each grazing paddock are listed in Appendix A.

The westernmost study site in Section 29 (N 49°40'55.4", W 99°33'40.8") is located

nearest to the boundary of the preserve that borders agricultural land. A field planted

with potatoes in 2005 and wheat in 2006 is located approximately 1.5 kilometres to

the north-west of the sampling site. With the exception of a small aspen bluff approximately 100 metres to the east, Section 29 also contains the least aspen cover within a one-kilometre radius. In addition to other common plants distributed throughout the preserve, this site is dominated in several areas by ground juniper.

 The central study site in Section 28 (N 49°41'27.7", W 99°34'38.7") is characterized by a large, dense stand of leafy spurge, which made it subject to experimental manipulations for the control of leafy spurge in the fall of 2002 including mowing and the spraying of 2,4-D. There is a relatively high proportion of aspen forest within a one-kilometre radius of this site, with the nearest stand occurring within approximately 50 meters to the western edge of the exclosure. This site is located close to a small open-faced sand dune adjacent to a cattle dugout approximately 100 m to the north and west of the site.

The easternmost study site in Section 27 (N 49°40'51.4", W 99°33'15.4") is situated within a relatively open tract of prairie, approximately 300 metres south of the nearest patch of aspen forest. While leafy spurge and ground juniper are present at this site, they occur at relatively low densities compared to the other two sites. In 2006, the areas surrounding the grazing exclosure were subjected to a low-intensity burn in early June.

Field methods

Samples were taken weekly from early May to late September in 2005 (22 weeks) and 2006 (20 weeks). Bees are less active in cool, wet conditions, so an effort was made to sample only on days for which a favourable forecast was reported.

Bee survey

Bee survey methods were based primarily on the standardized monitoring protocol developed by LeBuhn *et al.* (2003) with some modifications. These included:

Bee bowls

Passive sampling of bees was conducted using bee bowls, a modified form of a pan trap. A series of lipless, 177 ml (six ounce) bowls were painted fluorescent yellow, fluorescent blue or white to provide a visual stimulus for foraging bees. Colour pigments and the carrier (Silica Flat) were ordered from Guerra Paint of New York (http://www.guerrapaint.com/tadc.html). White bowls were painted inside and out with two layers of white Zinsser Bull's Eye 1-2-3 all surface bond coat (Product # 02014) obtained locally. This paint also formed the base layer for the yellow bowls. Blue bowls were first painted with a grey (B-20) base layer of the same product.

At each site, 15 bowls were placed along each of two intersecting 50 m transects to create an 'X' configuration, for a total of 30 bowls (Figure 2). Each set of bowls consisted of ten white, ten blue and ten yellow bowls positioned randomly throughout the configuration. The colour positions were randomized independently for each site and maintained from week to week throughout both sampling seasons. Each plot of 30 bowls was centred in its respective grazing exclosure. Bowls were separated by

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3.57 m and bowl stations were marked with 30 cm X 1 cm bamboo stakes tied with a small piece of orange flagging tape. Bowls were positioned approximately 50 cm away from the bamboo stakes and to the left or the right side of the stake alternately from week to week to minimize the effect of trampling on the vegetation. On each sampling date, bowls were filled three-quarters full with soapy water and left out for 24 hours. The soapy water was mixed by squirting approximately 30 ml of Dawn Blue dish soap into a four-litre jug of water. After 24 hours, the contents of the bowls were collected in plastic jars and returned to the lab for pinning. Samples were processed within 36 hours of collection.

On three sampling dates in 2005 (June 1, July 12 and August 30), the bowl contents at one site were collected every two hours to determine changes in bee capture rates throughout the day.

Sweep-netting

Two to three rounds of sweep-netting were conducted at each site depending on weather conditions, one between 8:00am and 12:00pm, another between 12:00pm and 4:00pm and a third between 5:00pm and 9:00 pm. Each round consisted of 15 minutes of sweeping inside the grazing exclosure and 15 minutes of sweeping outside of the grazing exclosure, for a total of 30 minutes. Therefore, each site received either an hour or an hour and a half of sweeping on every sampling date.

The sweepers followed prescribed routes inside and outside of the exclosure at each site. Outside, sweeping was conducted around the perimeter of the exclosure, about 25 m away from the fence line, for a total of 560 m. Inside the exclosure, an effort

was made also to have the sweeper cover approximately 560 m, usually in a series of linear transects from one end of the exclosure to the other. The orientation of the transects (i.e. north-south or east-west) inside the exclosure was varied between sampling rounds to counter any effect of mean daily wind direction. The sequence of the sites sampled in the morning was maintained in subsequent rounds throughout the day, but the sequence was alternated from week to week to control for the potential influence of the time of day. All nets used for sweeping had 45.7 cm (18-inch) bent triangular frames, with 91.4 cm (36-inch) handles and were obtained from Rose Entomology (www.roseentomology.com). Specimens were euthanized with ethyl acetate and stored in labelled plastic bags inside a cooler until they were processed, usually within 48 hours.

In 2005, I conducted all of the sweeping. In 2006, I usually had the assistance of another individual for sweeping of the inside and outside portions of the exclosure at a site concurrently. An effort was made to reduce the effects of collector bias by ensuring that if one collector swept the inside of the exclosure in the morning round, that same collector would sweep on the outside in the afternoon round. No sweep-net samples were taken if it was raining, the vegetation was wet or if the wind was strong enough to turn the net inside out while sweeping.

Bee identifications

Bees were identified to genus using Michener *et al.* (1994) and to species using keys in Mitchell (1960; 1962). Determinations several taxa were verified against specimens in the J.B. Wallis Museum at the University of Manitoba. Dr. John Ascher from the American Museum of Natural History in New York identified all members of the

Andrenidae and also verified specimens of several taxa to create a voucher collection that was used for further identifications. Dr. Robbin Thorp, from the University of California at Davis, verified several specimens of *Bombus* to act as a voucher collection. Jason Gibbs, York University, identified all of the *Lasioglossum* (*Dialictus*) collected in the first year of sampling, which became the voucher collection for the second year. Several specimens of each *Dialictus* species were confirmed by genetic bar coding by J. Gibbs. Most specimens from this study are deposited in the J.B. Wallis Museum in Winnipeg, Canada. A limited number of specimens were deposited at the American Museum of Natural History, New York. Species authorities are printed in Appendix B.

Resource availability

To provide a rough estimate of floral resources available to bees, the numbers of flowering stems per species were counted every week within 46 – 1m X 1 m quadrats at each site (Figure 3). Thirty quadrats were placed inside the grazing exclosures, each centred on a bee bowl.   Another 16 permanent quadrats were placed around the perimeter of the exclosure, 25 meters from the perimeter of the fenced grazing exclosures. These quadrats were arranged such that four stations were systematically spaced along each side of the exclosure, with the position of the first quadrat determined randomly. Common plants that were in bloom in the vicinity but were not recorded in any of the quadrats on a week-to-week basis were also recorded. For example, certain shrub species in the forested portions of the YQMGP would no doubt have been important resources for bees, and were therefore noted. Flowering plants were identified in the field to species using appropriate field guides (Johnson *et al.* 1995; Vance *et al.* 1999) and the assistance of Al Rogosin of the University of

Brandon in 2005. Samples of difficult taxa were collected and later identified by Elizabeth Punter, Department of Botany, University of Manitoba, with reference to herbarium specimens. Plant species authorities are found in Appendix C.

Incident light

On each sampling day, incident light was measured approximately once an hour during daylight hours using a LI-COR-1000 Data Logger attached to 100 cm X 5 cm long LI-COR Line Quantum Sensor (LI COR Inc., Lincoln, Nebraska). At each hour, a series of 20 readings were taken at 10-second intervals. Daily averages were used in analyses.

Analysis

Diversity indices

<u>Bees</u>

Parameters used to assess alpha diversity of wild bees within sites and/or time periods include species richness, species diversity, species evenness and species dominance. Species diversity of bee data was calculated using both the common Shannon-Wiener diversity index (H) and Hill's (1973) reformulation of Renyi's entropy function of order one (N1), sometimes called effective species richness. Shannon-Wiener diversity was calculated as:

$$H = \sum_{i=1}^{S} p_i \log_e p_i$$

where s is the total number of species and p_i is

the proportion of individuals belonging to the ith

species.

N1 was calculated using the following equation:

$$N1 = \exp(H),$$

where p_i is the proportion of individuals

belonging to the ith species.

Kvalseth's (1991) diversity ratio (E6) was chosen to measure species evenness

because it is less sensitive than other common evenness indices to the effect that

variation in sample size has on the number of species. It was calculated according to

the following equation:

$$E6 = (N2-1)/(N1-1),$$

in which N1 is calculated as above and N2 is

calculated as,

$$N2 = [\sum_{i=1}^{s} p_i^2]^{-1}$$

in which p_i is the proportion of individuals of the

ith species and Σ indicates summation from i=1

to $i=s$ with s being the number of species in the

sample.

The Berger-Parker index (d) (Berger and Parker 1970) was calculated to assess

species dominance based on the following equation:

$$d = N_{max}/ N$$

Where N is the total number of individuals and

N_{max} is the number of individuals of the most

abundant species.

Comparison of assemblages among sites and between the two methods were made

using rarefied species richness taken from Coleman rarefaction curves that were

generated using EstimateS 8.0 (Colwell 2006). The resampling procedure in this

program allows standard deviations to be estimated, thereby providing a better idea of

actual differences in diversity between the sites when samples are standardized to the

smallest sample size.

<u>Flowering stems</u>

 Diversity parameters used for the floral environment within sites and/or time periods

include species richness, Hill's N1 effective species richness, and Kvalseth's evenness

ratio. All calculations were performed on the pooled number of flowering stems

within the site and time period of interest.

Ecological classification of bees

Two main classification schemes were used for analyses of ecological composition.

Natural history information upon which these schemes were developed was obtained

from a variety of published sources (Krombein 1967; Krombein *et al.* 1979;

Michener 1964, 1974, 2000; Mitchell 1960, 1962) and consultation with experts.

First, all non-parasitic bees were classified as either pollen specialists or pollen

generalists. Secondly, all bee species were assigned to one of four nesting guilds

chosen to reflect some combination of social status and primary nesting substrate.

Cleptoparasites are bees that do not build nests but which lay eggs in nests

provisioned by other host bees. *Social nesters* are bees for which sociality is

considered to be the common social state, regardless of substrate. Solitary to semi-

social bees that excavate nests primarily below ground are classified as *miners*, while

those that nest above ground are classified as *cavity nesters*.

Univariate analyses

All univariate statistics were performed in SYSTAT 11. When necessary to meet the

assumptions of normality and homogeneity of variances, data were log-transformed

using the equation $y = \log_{10}[x + 1]$. For the bee bowl data, analysis of variance

(ANOVA) was used to determine the effect of bowl position within the experimental

layout by coding bowls from the centre of the "X" configuration to the extremities

and using bowl colour as a blocking variable. ANOVA was performed using the GLM

module of SYTAT to determine the effect of site, year, bowl colour and all possible

interactions on bowl catches for the families, ecological classes and the top ten

species. For this analysis, bowl captures were summed over all the sampling weeks in

a season. When significant results were obtained, analysis of the differences between the levels of the factor of interest was performed using Tukey pairwise comparisons.

For the sweep-netting data, ANOVA was used to investigate the impact of time of day (Morning, Afternoon, Evening) and position either inside or outside of the grazing exclosures (Inside, Outside) on the catch frequency of the bee families, the ten most commonly collected species and the ecological classes. These analyses incorporated the effect of site as a blocking factor rather than an experimental factor because there was a lack of replication within combinations of the factors for any given week. Therefore, interactions involving site could not be examined.

A repeated measures ANOVA was used to examine differences in mean forb flowering stem densities among the sites and position of quadrats either inside the grazing exclosures (inside) or outside of the grazing exclosures (outside). Repeated measures were chosen to account for possibility that individual flowering stems may have been counted over two or more subsequent weeks. Weeks in which no flowering stems were observed were excluded from the analysis.

Examination of the effect of flowering stem density on weekly bee catch was undertaken using multiple regression to account for environmental conditions. Two regressions, one for each method, were performed. Values for mean flowering stem density were log transformed. As light intensity and log daily maximum temperature were positively correlated, only the variable that had the strongest simple correlation with bee catch for the method under consideration was used in multiple regression. Therefore, light intensity was incorporated into the model for the bee bowl data, while

maximum daily temperature was used in the sweep-netting model. To minimize the

effects of seasonal trends in bee catch for each method, a smoothing technique was

first applied to the weekly bee catch data to generate seasonal trends in each year.

Smoothing was performed using the SMOOTH function in SYSTAT 11.0, selecting

options for a mean smoother with an Epanechnikov kernel and a window size based

on 50% of the nearest neighbouring data points. Assuming that deviations from the

seasonal trend would be associated with environmental variables, it was the log-

transformed residuals that were used as the response variable in the multiple

regressions.

Analyses to compare the relative abundances of individuals or species within

particular ecological classes across years, sites and/or seasons were performed using

log linear analysis.

Paired t-tests were used to compare the effect of sampling method on the species

richness, Hill's N1 effective species richness, Shannon-Weiner diversity, Kvalseth's

evenness and the Berger-Parker index for bees within each site-year combination.

Multivariate analyses

 To determine whether linear or non-linear methods were appropriate, initial

ordinations of all datasets were performed using Detrended Correspondence Analysis

(DCA). As each dataset exhibited gradient lengths of fewer than four standard

deviation units along the primary axis, linear methods were chosen.   Principal

Components Analysis (PCA) was primarily used for exploratory purposes and

Redundancy Analysis (RDA) was used for constrained analyses. All ordinations were

performed on log-transformed data and based on the default covariance option in

CANOCO 4.5 (ter Braak and Smilauer 1998). The option for Monte Carlo simulations

(499 permutations) was selected to test the significance of the constrained analyses.

Weighted average scores were used in the plots of the constrained ordinations to

represent site placement in species space rather than environmental space.

Comparison of sampling methods

RDA was used to examine the impact of sampling method on the assessment of the

composition of the bee community. The analysis was performed on the log-

transformed relative abundances of each species by each combination of site (Sections

29, 28 and 27), year (2005 and 2006) and method (Bowls and Sweeps). These data

were then constrained by using 'Bowls' and 'Sweeps' as the environmental variables.

Modelling of seasonal trends

Seasonal modelling of the bee data was performed on a combined dataset derived

from each of the two sampling methods. This approach was taken to minimize the

impact of biases associated with each method and to emphasize compositional

patterns of the overall community. The data were combined by taking the mean of the

species' relative abundances from the two methods. An iterative process involving a

series of PCAs was used to reduce successively the number of time intervals

examined from 22 weeks in 2005 and 20 weeks in 2006 to fewer distinct time periods

which would best represent the seasonal dynamics. Three time periods, called "early-

season", "mid-season" and "late season" were identified in each year and used in

combination with sites (Figure 4). Analyses were performed separately for each year,

as the number of sampling weeks associated with each time period differed between

the years. Therefore the data matrix used for each analysis consisted of nine columns (three sites X three seasonal time periods) and *S* rows, in which *S* represents the number of species collected by both methods in the year under consideration. RDA was then used to constrain the bee data by the flowering stem data. Because the number of flowering species greatly exceeded the number of Site*Season combinations, PCA was first performed on the flowering stem data and the resulting sample scores along the first two axes of the PCA were included as the environmental variables in the RDA.

Climate

Temperature and precipitation data at Brandon, Manitoba acquired from Environment Canada are shown in Table 1. In general, monthly temperatures tended to be higher in 2006 compared to 2005 and the long term average. There was notably less precipitation in 2006 than in 2005, particularly in June and July.

The floral environment

Overall species diversity and stem density

Results of weekly flowering stem counts pooled over all three sites are contained in Table 2. A total of 63 plant taxa in 22 families was observed to produce flowers in the permanent sampling quadrats over the course of the study. A total of 60 species were recorded in 2005 and 52 were recorded in 2006. The majority of the recorded flowering plant taxa were within the Asteraceae and the Fabaceae, making up 33.3% and 12.69% of the total taxa, respectively. Table 3 contains the species richness, diversity, evenness and mean density of flowering stems by site and year. Among the three sites, Section 28 had the lowest overall species richness and Hill's N1 diversity values in both years and the lowest evenness (E6) in 2006. In both years, evenness was greatest in Section 29.

Flowering stem densities between years, sites and location inside or outside of the grazing exclosure are presented in Figure 5. Overall density of flowering stems was significantly higher in 2005 than in 2006 (t = 254, df=275, p=0.01). Although overall

stem density appeared to be highest in Section 28 (Table 3), the difference among sites was not significant in the between subjects results of the repeated measures ANOVA (Table 4) in either year. However, the grazed areas had significantly more flowers than the exclosures. The interaction between these effects was significant only in 2005. The within-subjects effect of week and all interactions terms were significant in all years; therefore, week-to-week patterns of resource availability differed among sites and grazing treatments.

The top ten dominant species in terms of the mean density of flowering stems by site and year are shown in Table 5. *Cerastium arvense* (Caryophyllaceae)*,* an early season perennial, was a prominent flowering plant at all sites in both years. While early season *Androsace septontrionalis* (Primulaceae) was dominant in 2005 in both Section 27 and 28, it was notably less abundant in the second year. Section 28 was primarily characterized in both years by a high density of the early-season exotic invasive, *Euphorbia esula* (Euphorbiaceae). The dominant species in Section 29 was the spring perennial *Lithospermum canescens* (Boraginaceae) in both years.

Seasonal patterns

Stem density

The seasonal pattern in the density of forb flowering stems was qualitatively similar between the two years, with some differences (Figure 6). Overall, flowering was initiated earlier in 2006; however, density during the early season peak was lower than in 2005. Whereas flowering was sustained into mid-September at Sections 27

and 29 in 2005, it ended by early August in 2006. Site-level weekly patterns of the mean density of flowering stems for 2005 and 2006 in grazed areas outside of the exclosures and ungrazed area inside of the exclosures are shown in Figure 7 . In general, the difference between the grazed and ungrazed areas was most pronounced in the early part of the season. There was a general tendency for flowering stem density to decrease at the onset of grazing; however, the magnitude and duration of those dips appear to vary seasonally.

Species diversity

Weekly trends in Hill's (N1) effective species richness of flowering stems by site in both years are shown in Figure 8. Week-to-week N1 values were higher in 2005; however, this effect is most pronounced from July onwards. Whereas diversity patterns follow a similar trajectory in Section 27 and 29 for the first part of the season, 2006 was characterized by a notable dip in N1 values for the latter part of the season. N1 values in Section 28 were consistently lower from week to week than those at the other two sites.

Species composition

There was clear seasonal progression in the floral community but with some variation among the sites and years (PCA, Figure 4). Ordination of the 2005 data captured 64.3% of the total variation along the first two axes (Figure 9). Axis one, which explains 46.5% of the total variation, distinguishes early season assemblages from the mid- and late seasons assemblages, whereas axis two captures the variation related to differences between the mid- and late season. As such, there is a counter-clockwise progression of the seasonal assemblages around the ordination diagram. The early

season assemblages from the three sites, positioned at the far positive end of the first axis, are distinct from other the other assemblages. The early season floral community is most strongly characterized by *Cerastium arvense*, *Androsace septentrionalis* and *Geum triflorum* (Rosaceae). The distinction between the mid- and late season assemblages is less clear, as they are linked by a prolonged progression of species. The mid-season assemblages from Sections 27 and 29, positioned towards the positive end of axis two and the negative end of axis one, are characterized primarily by *Achillea millefolium* (Asteraceae), *Linum lewisii* (Linaceae), *Penstemon gracilis* (Scrophulariaceae), *Gaillardia aristata* (Asteraceae) and *Galium boreale* (Rubiaceae). Species associated with the transition from the mid- to late season are located towards the strong negative end of the first axis. These species include *Campanula rotundifolia* (Campanulaceae), the *Dalea* species, *Aster ptarmicoides* (Asteraceae) and *Chrysopsis villosa* (Asteraceae). The late season assemblages at Section 27 and 29, located in the lower left quadrant of the ordination plot, are characterized primarily by *Aster ericoides* (Asteraceae), but also late-season *Solidago* (Asteraceae) species. Because of the position of the mid- and late season assemblages for Section 28 close to the centre of the ordination diagram, they are only weakly associated with the flowering species that are characteristic of those time periods. In particular, the mid-season assemblage for Section 28 appeared to be more closely associated with the early season assemblages rather than the mid- season assemblage.

Similar trends were apparent in the ordination of the 2006 floral dataset, which explained 69.9% of the total variation (Figure 10). The general placement of the seasonal assemblages in relation to the axes has been maintained; however, the majority of the species are concentrated towards the top half of the ordination,

indicative of a temporal concentration of bloom availability into the early and middle parts of the season. Also, the mid- and late season assemblages from Section 28 are clearly associated with the late season assemblages at Sections 27 and 29.

Overall bee catch

A total of 7014 bees representing five families, 21 genera and 100 species were collected during the course of this study (Appendix B). A limited number of honey bees (*Apis mellifera*) were caught during this study (Figure 11); however, they are excluded from all diversity calculations and analyses. A complete list of the bee taxa by year, method and site, along with ecological classifications, is presented in Table 6.

Bee bowl data

Taxonomic composition

Over both years, 5340 bees representing five families, 20 genera and 80 species were collected in bee bowls. A total of 2212 individuals, 64 species and 18 genera were captured in 2005, while 3128 individuals, 72 species and 18 genera were collected in 2006. Colletidae, Andrenidae, Halictidae, Megachilidae and the Apidae were represented in both years. Bee bowl catches are summarized by family in Table 7. The Halictidae made up the majority of the total catch (71.4%), followed by the Apidae (16.7%). Halictids also accounted for the greatest number of species (25), followed by the Andrenidae (19). The Colletidae made up the smallest proportion of the catch in terms the number of individuals (24) and taxa collected (2 genera, 3 species).

Seventy per cent of the species and 80% of the genera were captured in both years. Aster specialists in the genus *Pseudopanurgus* (Andrenidae) and a cleptoparasite of the genus *Stelis* (Megachilidae) were caught exclusively in the first year. In the second year, the solitary, ground-nesting species, *Calliopsis andreniformis* (Andrenidae), and the primitively eusocial *Augochlorella aurata* (Halictidae) were the sole representatives from their respective genera.   Over both years, the three most speciose genera were *Andrena* (Andrenidae) with 17 species, *Lasioglossum* (Halictidae) with 15 species and *Bombus* (Apidae) with nine species. Six genera (30%) and 16 species (20%) were each represented by a single specimen. The mean number of species shared among the sites in all pairwise comparisons was 63.2%. Sections 27 and 28 shared the fewest species (60.0%), and Sections 27 and 29 shared the greatest percentage of species (66.2%). Approximately 36.3% of the species were captured at one site only, 12.5% were captured at two sites and 50.0% were captured at all three sites.

Over both years, 14 species had a relative abundance of at least one per cent and these represented 83.6 % of the collected individuals (Table 8). *Lasioglossum succinipenne*, from the primitively eusocial subgenus *Dialictus*, was the most commonly collected species at all sites and in both years, representing 43.4% of the total catch from both years. The other common species were *L.*(*Dialictus*) *albipenne* (9.8%), *L.*(*Lasioglossum*) *paraforbesii* (5.6%), *Bombus ternarius* (5.5%), *Andrena geranii* (4.9 %) , *L.* (*Dialictus*) *perpunctatum* (4.0%), *B. rufocinctus* (4.0%), *B. borealis* (2.9%), *L.* (*Dialictus*) *pruinosum* (1.6%), *L.*(*Lasioglossum*) *zonulum* (1.3%), *Osmia distincta* (Megachilidae) (1.3%), *Agapostemon texanus* (Halictidae) (1.2%), *L.* (*Dialictus*) *pruinosiforme* (1.2%), *Melissodes druriella* (Apidae) (1.2%) and *Hoplitis*

(Megachilidae) *pilosifrons* (1.1%). The majority of these taxa, namely species of the genus *Bombus* and the *Lasioglossum* subgenus *Dialictus* are primitively eusocial and present throughout the flight season. Ranging in sociality from solitary to communal, *L. paraforbesii, L. zonulum* and *Agapostemon texanus* were all collected throughout most of the season in both years with the exception of a distinct lag in the middle of the summer. The remaining common species were more temporally restricted. The presence of the vernal bee, *Andrena geranii*, among the most common species is due primarily to its especially high relative abundance in 2005. Cavity-nesting *Osmia distincta* and ground-nesting *Melissodes druriella* were the only pollen specialists represented among the commonly-collected species, being associated with *Penstemon* spp. (Fabaceae) and Asteraceae, respectively. *Hoplitis pilosifrons* is a solitary, twig-nesting species. Though not exceeding one per cent of the total catch, the most commonly collected cleptoparasitic taxon among the bowl samples was *Nomada* sp. (Apidae) 1, which was captured primarily in Section 28.

The top five dominant taxa by site and year are listed in Table 9. There appeared to be greater variation in the dominant taxa among the sites in 2005 compared to 2006. Whereas *B. ternarius* and *A. geranii* co-dominated along with *L. succinipenne* in Sections 27 and 28, *B. rufocinctus* and then *B. ternarius* were the co-dominant species in Section 29. In 2006, *L. succinipenne, L. albipenne* and *L. paraforbesii* were consistently the dominant species at all three sites, in that order.

Diversity indices calculated on the bee bowl data pooled by site and by year are listed in Table 10. Though species richness was higher in 2006 than in 2005, the assemblage captured in 2005 was more diverse in terms of Hill's effective species richness. As

such, the 2006 bee assemblage had a greater Berger-Parker dominance value and, hence, a lower evenness value. Among the sites, Section 29 had the most diverse assemblage in both years despite having the lowest species richness and catch frequency. Section 29 also had the lowest Berger-Parker dominance value and the highest evenness value in both years. Section 28 harboured the least diverse assemblage in both years, owing in part to a large dominance value. Coleman rarefaction curves for the three sites were pooled over both years are shown in Figure 12. When standardized to the number of individuals captured, Section 29 had the highest species richness, whereas there is little to no difference in the rarefied species richness of the other two sites. Also of interest, none of these three curves have attained an asymptote.

Ecological composition

<u>Nesting guilds</u>

 Of all the species captured in bee bowls (Figure 13a), 38 (48%) were miners, 22 (28%) were social nesters, 14 (18%) were cavity nesters and 6 (8%) were cleptoparasites. Disregarding social status, 81% of the non-parasitic taxa nest primarily below ground.

In a log linear analysis examining the effect of year, site and nesting guild on species frequencies, only the term for nesting guild was significant (x^2=94.6, df=3, p<0.005); the proportions of species divided among the nesting guilds were independent of site (nesting guild * site: x^2=4.6, df=6, p=0.59) and year (nesting guild * year: x^2=0.9, df=3, p=0.83). Within the nesting guilds, the cleptoparasites and the miners had the

highest degree of interannual species turnover, with only 50.0% and 57.9%, respectively, of the species in these groups were collected in both years. About 86.0% of the cavity nesters and the miners were represented in both years (Figure 14).

Over three quarters of the total number of individuals captured in bee bowls were social nesters, 18% were miners, 5% were cavity nesters and 1% were cleptoparasites (Figure 13b). A log linear model that simultaneously included the effect of year and site on the relative frequencies of individuals could not be fit. However, in log linear analyses performed on a year-by-year basis, relative abundances of the nesting guilds differed among sites in both years (2005: x^2=54.9, df=6, p<0.005; 2006: x^2=50.1, df=6, p<0.005). When examined on a site-by-site basis, the relative proportions of individuals among the nesting guilds were independent of year only in Section 29 (Section 27: x^2=19.6, df=3, p<0.005; Section 28: x^2=70.8, df=3, p<0.005: Section 29: x^2=5.2, df=3, p=0.16). Therefore, there were significant differences in the relative abundances of the nesting guilds between the years in Sections 27 and 28 only. The proportions of the nesting guilds by site and year are shown in Figure 15. Overall, the relative abundance of social species was higher in 2006 than in 2005. In Section 28, the increased proportion of social nesters in from 2005 to 2006 was accompanied by a relative decrease in all other groups in 2006. In Section 27, the relative proportion of miners decreased from 2005 to 2006, accompanied by increases in the proportions of social nesters, cavity nesters and cleptoparasites in 2006. In terms of site differences, Section 28 hosted the lowest relative abundance of social nesters among the three sites in 2005; however, it contained the highest proportion in 2006. Conversely, the proportion of miners was highest among the sites in Section 28 in 2005, but lowest at this site in 2006. Section 28 contained the highest proportion of cleptoparasitic

species in both years. The proportion of cavity nesters was higher in Section 29 in 2005 than at the other two sites.

Pollen specialists

Among the non-parasitic taxa, 12 (17%) species were pollen specialists. The proportions of specialist taxa did not differ among the sites (x^2=1.18, df=4, p=0.89) or years (x^2=1.12, df=4, p=0.89). Six (50%) of the specialist taxa were detected in both years. In order of decreasing relative abundance these include *Osmia distincta*, *Melissodes druiella, M. agilis, Dufourea maura* (Halictidae), *Colletes brevicornis* (Colletidae), and *M. rustica. Osmia distincta* is a widespread species associated with flowers of *Penstemon* spp. All three of the *Melissodes* species are associated with plants in the Asteraceae. *Colletes brevicornis* is apparently associated with flowers of *Campanula* spp. The host plant of *Dufourea maura* is unknown.

Pollen specialists represented 4% of the non-parasitic individuals captured in bowls. In the the log linear model of the effect of year and site on the proportion of oligolectic individuals, only the interaction term involving site was significant (x^2=60, df=7, p<0.005). Therefore, the proportion of oligolectic taxa was stable between years but not sites. In terms of the relative abundance of specialists among the sites, Section 28 hosted significantly fewer specialists than the other two sites. Over both years, approximately 5% of the individual bees collected in Sections 27 and 29 were oligolectic compared to about 1% in Section 28.

Effect of bowl position on bowl catches

While there was a general trend for bowl catches to increase from the centre of the configuration to the extremities (Figure 16), this effect was not significant in ANOVA ($F_{7, 156}$=1.9, p=0.06). Bowl colour was also included in the model and was significant ($F_{2, 156}$=13.6, p<0.005). There was no significant interaction between position and bowl colour ($F_{14,156}$=1.0, p=0.44). Bowl position therefore was not considered in further analyses.

Effect of time of day on bowl catches

The mean percentages of daily catch captured in two-hour time intervals are shown in Figure 17. Peak bowl catches were collected from late morning to late afternoon, after the six, eight and ten hour time intervals.

Effect of bowl colour, site and year on bowl catches

Results of the ANOVA to test the effects of bowl colour, site and year on catch frequency (bees / bowl) for the total bee catch and for the families are shown in Table 11. Figures are included only for groups for which significant interaction were detected. There were significant main effects on total catch frequency of year, site and bowl colour as well as an interaction between site and bowl colour (Figure 18). Overall, more bees were caught in 2006. The differences among all sites were significant in pair wise comparisons, with the highest catch frequency occurring in Section 28 and the lowest catch frequency in Section 29. In both years, blue bowls yielded the highest catch frequency and yellow bowls the lowest; however, the degree to which the catch frequencies in white bowls approached those in blue or yellow bowls varied among the sites.

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Among the families, the main effects of site, year and bowl colour were all significant for the Apidae, Andrenidae, and Halictidae, but interactions were significant only for apids (Figure 19) and andrenids (Figure 20). While the catch frequency of halictids increased from 2005 to 2006, the catch of andrenids and apids declined. There was a consistent trend for these three families to be captured most frequently in Section 28; however, andrenids and halictids were captured less often at Section 29, while apids were significantly less frequent at Section 27. Site was the only significant effect for megachilids, which were caught more frequently in Section 27 than elsewhere. The Andrenidae were caught consistently more often in blue bowls, while blue bowls and white bowls were equally effective for halictids. While overall catch frequencies of apids were greatest in blue bowls, this varied by site. There was a significant interaction between site and year for the andrenids (Figure 20), owing to a decline from 2005 to 2006 in Sections 27 and 28, but not in Section 29. The interaction between bowl colour and site was the only significant term in the analysis of the Colletidae (Figure 21).

The results of the ANOVAs performed to test the effects of bowl colour, site and year on catch frequency for the ten most common species are shown in Table 12. For six of the ten species, year was a significant factor in determining catch frequency. Whereas catch frequencies of *B. ternarius* and *A. geranii* declined from 2005 to 2006, those for *L. succinipenne*, *L. albipenne*, *L. paraforbesii*, and *L. pruinosum* increased. Site differences were important for eight of the ten species, with catch frequencies typically being highest in either Section 27 or 28 and lowest in Section 29. The only species that was collected most frequently in Section 29 was *B. rufocinctus* ($F_{2,162}=$

9.7, p<0.005). Bowl colour had a significant effect on the catch frequency of seven of the ten species. Most of the species for which bowl colour was important were caught most frequently in blue bowls and least frequently in yellow bowls; however, L. *perpunctatum* was the only species that was captured most frequently in yellow bowls. While bowl colour effects were often consistent across sites and years, interactions between bowl colour and site or bowl colour and year occurred among the top four species. *Lasioglossum albipenne* ($F_{4,162}$= 3.4, p<0.005) and *L. paraforbesii* ($F_{4,162}$= 2.6, p=0.04) were the only two species for which a three-way interaction between year, site and bowl colour was found.

Table 13 contains the results of ANOVAs performed to investigate the effect of site, year and bowl colour on the catch frequency of the ecological groupings. There were significant differences among the sites and bowl colours for each of the nesting guilds. The only group for which there was a significant difference between the years was the social nesters, which increased in catch frequency from 2005 to 2006. This group was caught most frequently in Sections 28 and 27 and in blue bowls compared to the other colours. Cleptoparasites were captured most frequently in Section 28 (Figure 22), and they were the only group for which yellow bowls tended to yield the highest catch frequencies. However, the colour effect was significant in Section 28 only. Cavity nesters were captured more frequently in Section 27 than at the other two sites overall; however, catch frequency was higher at this site in 2006 only (Figure 23). Cavity nesters were caught equally effectively in blue and white bowls, but less often in yellow bowls. Overall, miners were caught least frequently in Section 29 and most often in blue bowls overall; however, they are the only ecological group for which the three-way interaction was significant. Whereas fewer miners were

captured in Section 29 in 2005, there was no difference among the sites in 2006 (Figure 24). The three-way interaction is due to differences among the sites and years in the degree to which catch frequency in white bowls most closely approached that of the blue bowls or the yellow bowls, which were the most and least effective bowl colours, respectively.

In the analysis of variance on the catch frequency of specialists, the effects of year, site and bowl colour were significant, but there were no important interactions. Overall, specialists were caught more frequently in 2006 compared to 2005 and in blue bowls compared to other colours. Section 27 yielded the greatest catches of specialists and Section 28, the fewest.

Sweep-netting data

Taxonomic composition

A total of 1674 individual bees were collected by sweep-netting in both years, representing 79 species and 18 genera in five families over both years. In 2005, sweep-netting yielded 650 bees, 56 species and 17 genera, while in 2006, 1024 individuals, 67 species and 17 genera were collected. A summary of sweep-net catches by family is found in Table 14. Approximately half (51.5%) of the total catch consisted of Halictidae, while about a third (33.6%) were Apidae. Accounting for a total of 22 species, the Andrenidae was the most speciose family. The Apidae followed closely with 20 species. Megachilidae and Colletidae were caught in relatively low numbers (54 individuals); however, colletids were the least rich group in terms of species representation.

Approximately 55% of the species and 89% of the genera were captured in both years. *Pseudopanurgus* spp. were captured only in 2005, while wood-nesting *Anthophora terminalis* (Apidae) was the only representative of this genus in 2006. With 20 species, *Andrena* was the most speciose genus, followed by *Lasioglossum* with 12 species and *Bombus* with 10 species. One genus (6%) and 20 species (25%) were each represented by a single specimen. The mean number of species shared among the three sites in all pairwise comparisons was 51.9%. Section 27 shared 55.8% of its species with each of the other two sites, while Sections 28 and 29 were the least similar, sharing only 44.3% of their taxa. Approximately 36.7% of the species were captured at one site only, 26.6% were captured at two sites and 36.7% were captured at all three sites.

There were 16 species with a relative abundance over one per cent, which accounted for 83.8% of all individuals (Table 15). As with the bowl samples, *L. succinipenne* was the dominant species collected through sweep-netting, representing 17.5% of the catch. Most of the remaining common species are predominantly widespread social taxa, including *L. albipenne* (16.4%), *Bombus ternarius* (11.8%)*, B. borealis* (7.5%), *L. perpunctatum* (7.0%)*, B. rufocinctus* (5.8%)*, B. vagans* (3.0%)*, B. nevadensis* (1.4%)*, L. pectoraloides* (1.2%). Two taxa of communal bees, *L. paraforbesii* (1.3%) and *L. athabascense* (1.1%) were well represented, although the latter was primarily captured in 2006. *Andrena vicina* (2.6%) and *A. geranii* (1.6%) were the most common vernal, polylectic bees. Ground-nesting *Dufourea maura* (2.8%) and *Colletes brevicornis* (1.6%) were the most common specialists collected through sweep-netting. *Sphecodes* sp. 1 (Halictidae) (1.1%) was the most commonly

represented cleptoparasitic taxon. There were no solitary cavity nesters among the most common species; however, *Anthidium clyptodentatum* (Maegachilidae), a carder bee that lines its nest with woolly substances such as trichome hairs, was the most common cavity nester (0.9%).

Relative abundances of the top five species captured with sweep-netting by site and year are listed in Table 16. *Bombus* and social *Lasioglossum* species were the most common taxa at nearly all sites; however, dominance within each site and year tended to be shared among several different species in these genera. Interestingly, the vernally active species *Andrena vicina* was the dominant species captured in Section 28 in 2005 and is the only solitary taxon present among the top five taxa. In general, there was more variability among the sites in the dominant species in 2005. Also, the relative abundances of the most common species at each site were greater in 2006 than in 2005. In both years, Section 29 hosted assemblages with the greatest degree of dominance.

Diversity index values for sweep-net catches by site and year are presented in Table 17. While the overall catch and species richness were higher in 2006 compared to 2005, effective species richness and Kvalseth evenness values were qualitatively higher in 2005. Berger-Parker dominance was higher in 2006. Among the sites, Section 28 hosted the most diverse assemblage in both years as indicated by the high effective species richness and evenness values and the lowest dominance values. Values for the other two sites were qualitatively comparable, although, in both years, dominance was notably higher at Section 29 relative to the other two sites. Coleman rarefaction curves for the three sites pooled over both years are shown in Figure 25.

When standardized to the number of individuals captured, Section 28 had the highest species richness, whereas there was little to no difference in the rarefied species richness of the other two sites. None of the three curves reach an asymptote.

Ecological composition

<u>Nesting guilds</u>

With 38 species, miners accounted for the greatest proportion of species (51%). Sweep-netting also yielded 22 (24%) species of social nesters, 18 species of cavity nesters (15%) and 6 species of cleptoparasite (10%) (Figure 26a). Of the non-parasitic taxa, 83% are primarily ground-nesting species, regardless of social status. The proportions of species distributed among the nesting guilds were independent of site (nesting guild * site: x^2=4.6, df=6, p=0.59) and year (nesting guild * year: x^2=4.5, df=3, p=0.92). Although year did not affect the proportion of species in each category, there was a certain degree of turnover within each category (Figure 27). In particular, only 37.5% of the cleptoparasitic species and 50% of the miner species were collected in both years.

In terms of individuals, social nesters represented 75% of the sweep-netting catch, miners accounted for 20%, cavity nesters represented 3% and cleptoparasites represented 2% (Figure 26b). The relative abundances of the nesting guilds varied among the sites and the years, as indicated by failure to fit either a saturated model (x^2=17.88, df 6, p<0.005) or a reduced model on the data partitioned by year (2005: x^2=47.25, df=6, p<0.005; 2006: x^2=13.61, df=6, p=0.03). When examined on a site-by-site basis, the relative abundance of the nesting guilds differed between years only

in Section 28 (Section 27: x^2=5.88 df=3, p=0.11; Section 28: x^2=21.38.8, df=3,

p<0.005: Section 28: x^2=2.00, df=3, p=0.57). The relative abundances of the nesting

guilds among the sites and years are shown in Figure 28. The large difference

between the years in Section 28 is due to a relative decrease in the proportions of

miners and cleptoparasites in 2006. This effect may be driving the differences among

the sites, as there appears to be comparatively little variation in the proportions

otherwise.

Pollen specialists

A total of 23% (15) of the species captured through sweep-netting were pollen

specialists, and this proportion did not change across sites (x^2=0.41, df=4, p=0.98) or

years (x^2=0.55, df=3, p=0.91). In order of decreasing relative abundance, the

following seven taxa (48%) were detected in both years: *Dufourea maura, Colletes*

brevicornis, C. *susannae*, *Melissodes druiella, Osmia distincta, Andrena*

erythrogaster and *C. robertsonii*. Host-plant associations of *D. maura, C. brevicornis,*

M. druriella and O. *distincta* are discussed in Results Section "Bowl data: Ecological

Composition: Pollen Specialists". Of the remaining species, *A. erythrogaster* is an

early-season specialist on *Salix* spp. (Salicaceae), while *C. susannae* and *C.*

robertsonii are associated with *Dalea* spp.

Among the non-parasitic individuals captured by sweep-netting, 7% were oligolectic.

A saturated model including terms for site, year and pollen use status was fit (x^2=5.92,

df=2, p=0.06) to the data, in which the proportion of specialists was not independent

of site (x^2=12.61, df=3, p=0.01). Further examination indicated that the proportion of

specialists was highest at Site 27.

Effect of site, time of day and grazing on sweep catches

Results for analyses of variance examining the impact of time of day, sweeping

location relative to the grazing exclosure and using site as a blocking factor are shown

in Table 18 for family and Table 19 for species. Separate analyses were conducted for

each year due to the different responses of the overall bee community to resource

levels and environmental conditions identified in the multiple regression model (See

Results: Comparison of methods: Relationship between catch frequency and resource

availability: Sweep-netting data). In both years, the highest catch frequency was

obtained in Section 27. There was no effect of time of day in 2005; however, there

were significantly fewer bees captured during evening sweeps in 2006 (2006:

$F_{2,10}$=13.43, p<0.005). Whether sweeping occurred inside or outside of the exclosure

made no difference on overall catch in either year.

All families except the Colletidae were caught more frequently at particular sites in at

least one year (Table 18). Apids and halictids were captured most frequently in

Section 27 in both years, as were megachilids in 2006. More andrenids and halictids

were captured in the morning and afternoon sweeps relative to the evening sweeps in

both years, as were colletids in 2006. There was no effect of sweeping location

relative to the grazing exclosures on any family, nor was there an important

interaction between time of day and sweeping location.

Among the ten most common taxa, site was an important factor for six taxa in at least

one year (Table 19). Most species were captured most often in Section 27, and

Bombus ternarius and *Dufourea maura* were the only species for which this was

consistent between the years. Few of the tested species showed differences in catch

frequencies depending on time of day. Only *Lasioglossum albipenne* and *L. perpunctatum* in 2005 and *Andrena vicina* in both years were captured more frequently in the morning than at any other time of day. *Lasioglossum perpunctatum* was the only species for which sweeping location affected catch frequency, being captured more frequently outside of the exclosure in 2006.

Among the nesting guilds, site was a factor only for social nesters in both years and for miners in 2006 (Table 20). Social nesters were collected significantly more often in Section 27 in 2005 and in both Sections 27 and 29 in 2006. In 2006, miners were collected most often in Section 27. Catch frequencies decreased throughout the day for social nesters in 2006 and miners in both years, whereas cleptoparasites were captured more frequently in the afternoon rather than the morning or evening in 2005. There were no differences in catch frequency attributable to any of the tested parameters for cavity nesters or pollen specialists.

Comparison of methods

Similarity and missed taxa

At the level of sampling effort undertaken in this study, bee bowls yielded just over three times as many bees as sweep-netting but a similar number of taxa (80 and 79, respectively). Fifty-nine per cent of the 100 species collected in this study were common to both methods. Twenty-one species were collected exclusively in bowls and 20 species exclusively by sweep-netting. No more than one or two specimens of most of these species were collected. However, several (>5) individuals of *Osmia bucephala, Lasioglossum coriaceum, Lasioglossum sp. 1* were collected only in bowls

while several individuals of *Andrena carlini* and *Colletes susannae* were collected only in sweeps. There were no significant differences in the distribution of missed taxa among the nesting guilds (x^2= 3.13, df=3, p= 0.37) or pollen specialization classes (x^2= 2.66, df=1, p= 0.10). Although values for community similarity among the sites were generally lower for sweep-netting (See Results: *Sweep-netting data*) than for the bee bowls data (See Results: *Bee bowl data*), the difference was not significant (paired t=4.30, df=2, p=0.12).

Accumulation curves

There are important qualitative differences in the rarefaction curves for each of the two methods (Figure 29). While both methods captured a similar number of species, the curve for the bowl catches lies well below that for the sweeps. The curve for the sweep-netting increases more steeply, indicating a faster rate of species accumulation relative to the number of individuals captured. Although the curve for the bowl catches appears closest to reaching an asymptote, neither curve achieves one, nor does the curve for both methods combined.

Relationship between catch frequency and resource availability

Bowls

The relationship between flowering stem density and weekly bowl catch was analyzed in a multiple regression model that included weekly catch data from both years combined, but not pooled. This approach was deemed appropriate because a) as shown in Figure 30, the smoothed seasonal patterns in each year were qualitatively similar with a bimodal pattern; b) there were no significant differences in the

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intercepts or the slopes of the lines for the years when analysed using the GLM module of SYSTAT 11, and c) combining but not pooling the data from both years increased the sample size of the regression. As indicated by the coefficient of determination (R^2), the model explained 53.2% of the variation in weekly bee catch beyond seasonal variation ($F_{2,24}=13.7$, $p<0.005$). Log mean light intensity ($t=4.65$, df= 26, $p<0.005$) and log mean flowering stem density ($t=-2.71$, df=26, $p=0.012$) were both significant variables in the regression, although in opposite directions. While weekly bowl catch increased significantly with greater mean light intensity, it decreased with a greater density of flowering stems.

Sweep-netting data

The effect of environmental variables on weekly sweep-netting catches was analyzed for each year separately, as there were notable differences in the smoothed seasonal patterns in each year (Figure 31) and in the regression results. No significant relationship between flowering stem density and weekly bee catches could be detected in 2005. In 2006, maximum temperature ($t=2.78$, df = 15, $p=0.02$) and log mean flower density ($t=3.49$, df=15, $p<0.005$) were significantly and positively correlated to sweep catch residuals in a regression that explained 61.3 % of the variation ($F_{2,13}=10.3$, $p<0.005$).

Seasonal trends in catch per unit effort

Overall weekly catch per unit effort for the two sampling methods is presented in Figure 32. In the first half of 2005 and all of 2006, periods of high bowl catch frequency occurred during periods of relatively low sweep-netting catch frequency, and vice versa. In both years, bee bowl catches initially peaked during the first few

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weeks of May. The low value in the second week of May in 2005 is likely an artefact of cool, wet weather that occurred on that day. Bee bowl catches were then sustained at moderate levels from late May until approximately late July, after which they peak once again until the end of the season. Conversely, sweep-netting catches were initially very low until approximately late May when there was an early season peak from approximately June until the early part of July. In the latter part of 2005, there was a concurrent peak in bee bowl and sweep-net catches.

Comparison of diversity indices

The assemblages of bees collected in the bee bowls had significantly lower values for Kvalseth evenness (paired t=-3.56, df=5, p=0.02), and significantly higher Berger-Parker dominance values (paired t=3.69, df=5, p=0.01) than the assemblages obtained from sweep-netting (Tables 10 and 17). While the values for Hill's effective species richness were lower for the bee bowls, the difference was only marginally significant (paired = -2.55, df=5, p=0.05). However, when testing the difference between methods in the commonly used Shannon-Weaver diversity index (paired t = -2.80, df=5, p=0.04) and rarefied species richness (paired t = -4.11, df=5, p=0.01) the difference was significant.

Ecological composition

In log linear analysis, species frequencies among nesting guilds were independent of sampling method (x^2 = 4.63, df=3, p=0.20). There was no difference in the frequency of species that were pollen specialists between the methods (x^2 = 2.91, df=1, p=0.09).

Taxonomic composition

Redundancy analysis of the bee data constrained by method produced an ordination that explains 44.7% of the species variation, with 26.7% captured along the first axis (Figure 33). One hundred per cent of the variation in the species-environment relation is explained on the first axis. The vectors for each of the methods were of equal length and aligned with the main axis in opposing directions. All of the assemblages sampled using sweep-netting are positioned to the right of the origin, while those sampled using bee bowls are positioned to the left of the origin. Variation along the second axis may roughly reflect year, although the sweep assemblage from Section 27 in 2005 appears to be more closely associated with the assemblages in 2006. Most of the *Andrena* and *Bombus* species fall to the right of the plot; whereas *Lasioglossum* is strongly represented on the left side of the plot. Particular species which appear to be associated with sweep-netting include *Colletes brevicornis*, *B. borealis*, *Megachile melanophaea*, *B. vagans*, *Lasioglossum pectoraloides*, *Dufourea maura*, *B. nevadensis* and *Nomada cuneata*. In particular, the assemblage collected with sweep-netting in Section 28 in 2005 is positioned in the extreme upper right corner, and is surrounded by a distinct assemblage of several *Andrena* species and the less common *Bombus* species such as *B. sandersonii*. Species that were more strongly associated with bowls include *L. paraforbesii*, *L. succinipenne*, *Melissodes druriella*, *L. zonulum*, *L. pruinosiforme*, *Agapostemon texana*, *Osmia bucephala* and *O. distincta*.

Seasonal patterns

Relative abundance of selected taxa

Seasonal patterns in species' mean relative abundance from the two sampling

methods were generated and smoothed for selected taxa including the five most

common social nesters and miners, the three most common cavity nesters and the two

most common cleptoparasites (Figures 34 to 48). A variety of seasonal patterns is

apparent. Several taxa, particularly social nesting species, were present throughout

most of the sampling season, but displayed obvious peaks either early or late in the

season. For example, *Lasioglossum succinipenne* (Figure 34) and *L. albipenne* (Figure

35) had primarily bimodal patterns of relative abundance, with greater second peaks

in both years. The mining bee *L. paraforbesii* (Figure 36) also had a primarily

bimodal curve, but it was separated by several weeks in the middle of the summer

during which no specimens were collected. The relative abundance of *B. rufocinctus*

(Figure 37) peaked in the latter season part of the season, particularly in 2005.

Bombus ternarius (Figure 38) and *L. perpunctatum* (Figure 39) had broad temporal

distributions that peaked either in the early or middle parts of the season; however,

there were no consistent patterns between the years. Most of the other taxa had

narrower temporal distributions, with *Andrena geranii* (Figure 40)*, A. vicina* (Figure

41), the specialist *Osmia distincta* (Figure 42)*, Hoplitis pilosifrons* (Figure 43) and the

two cleptoparasitic taxa (Figures 44 and 45) having the earliest seasonal peaks.

Oligolege *Dufourea maura* (Figure 46) and the cavity nester *Anthidium*

clyptodentatum (Figure 47) had relatively narrow temporal distributions peaking in

the late spring/early summer, while the Asteraceae specialist, *Melissodes druriella,*

(Figure 48) was most prominent in the middle to late part of the season.

Seasonal patterns of community diversity

The seasonal patterns in bee species diversity, as measured by weekly values for Hill's effective species richness (N1) are shown in Figure 49. Weekly N1 values for bees were generated using the mean of the species relative abundances between both sampling methods. Weekly N1 values for bees are generally higher in 2005 than in 2006, but particularly in the early part of the season. In both years, there was a consistent peak in bee diversity at all the sites in the earlier part of the season, around late May to early June, followed by a general trend towards decreased diversity over time.

Ordination of seasonal periods

Diagrams for the ordinations performed on the seasonal bee assemblages in 2005 and 2006 are shown in Figures 50 and 51, respectively. Redundancy analysis of the 2005 bee data classified into three seasonal time periods and constrained by floral resource availability produced an ordination in which 51.0% of the total species variation was explained along the first two axes. A total of 67.3% of the variation in the species-environment relationship was captured along the first axis. For the 2006 data, the ordination captured 57.3% of the total species variation, with 67.1% of the species-environment relationship explained along the first axis. In both years, seasonal variation in the floral community corresponded strongly with seasonal variation in the bee community as Axis 1 from the flower PCA trends significantly with Axis 1 of the RDA, and Axis 2 from the floral PCA trends consistently with Axis 2 of the RDA. In 2006, however, the floral axes were offset from the RDA axes to a greater degree than in 2005. In both years, the first axis appears to be important for separating out the early season assemblages, located on the positive end of the

axis, from the mid- and late season assemblages in the negative region of that axis. The second axis distinguishes between the mid- and late season assemblages, located in the upper left and lower left quadrants of the triplots, respectively.

Whereas the site assemblages representing the different seasonal periods are closely grouped together in 2005, clustering in the left portion of the diagram is looser in 2006. In particular, the mid-season assemblage from Section 28 is placed mid-way between the other mid-season and the late-season assemblages from the other sites.

In 2005, the early part of the season is characterized predominantly by species of *Andrena* and to a lesser extent, *Osmia* and *Nomada*. In particular, *A. forbesii*, *A. geranii*, *A. vicina* and *A. barbilabris* are highly characteristic of the early season, as are *O. bucephala*, *O. simillima* and *N. cuneata*. Many of these taxa were still present in 2006; however, there also appears to be greater representation of *Lasioglossum* species, including *L. perpunctatum*, *L. pectoraloides*, *L. zonulum* and *L. athabascense*.

In both years, the mid-season assemblage was characterized by greater generic representation than the early season; however, there was some turnover in the species that are characteristic of the mid-season. *Andrena persimulata*, *Colletes brevicornis*, *Anthidium clyptodentatum*, *Melissodes agilis*, *Bombus nevadensis* and *Lasioglossum perpunctatum* were highly characteristic of the mid-season in 2005. In 2006, species associated with the mid-season were *A. miranda*, *A. dunningi*, *Megachile melanophoaea*, *Dufourea maura* , *Anthophora teminalis* and *M. brevis*.

The late part of the season in both years was most strongly characterized by an abundance of *Bombus* and *Lasioglossum* species.

Classification of species in the ordination triplot by nesting guild indicates that certain guilds were more stable than others between the two years of the study. While there were more cleptoparasites overall in 2006, this group was associated with the early part of the season in both years. Cavity nesters were most highly concentrated in the early season in both years, although there was strong representation into the middle part of the season in 2005. Mining species were relatively well distributed over the whole season in both years, although there was a greater concentration of miners in the early part of the season in 2005 that was not as apparent in 2006. Whereas the social nesters were clearly associated with the late part of the season in 2005, they appeared to be more temporally distributed over the whole season in 2006.

Table 1. Mean monthly temperature and monthly precipitation accumulations at Brandon, Manitoba in 2005 and 2006 and the long term average.

		Mean max (°C)	Mean (°C)	Mean min (°C)	Precipitation (mm)
October 2004 – April 2005					156.6
2005	May	16.1	2.6	9.3	56.2
	June	21.2	11.4	16.3	216.2
	July	24.9	12.9	18.9	130.2
	August	23.6	9.5	16.6	18.4
	September	20.3	4.7	12.5	10.4
	Seasonal total				431.4
October 2005 – April 2006					187.4
2006	May	18.5	4.7	11.6	41
	June	23.8	10.6	17.2	81.6
	July	27.9	19.9	11.9	7.8
	August	26.6	18.8	11.1	76.4
	September	19.5	12.1	4.6	74.6
	Seasonal total				281.4
Average (1971 – 2000)					
October – April					155.8
	May	19.2	11.8	4.4	52.6
	June	23.5	16.6	9.8	75.7
	July	25.9	18.9	11.9	72.5
	August	25.4	18.0	10.5	69.2
	September	18.8	11.9	4.9	48.3
	Seasonal total				318.3

Climatic data from Environment Canada for the Canadian Department of Agriculture Research Station near Brandon, Manitoba.

Table 2. Mean density (stems / $m^2 \pm$ SEM) of flowering stems of forb species counted weekly within 46 permanent 1m X 1m quadrats at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba by site and year.

	2005				2006			
	Section 27	Section 28	Section 29	Total	Section 27	Section 28	Section 29	Total
Asteraceae								
Achillea millefolium L.	0.27 ± 0.061	0.31 ± 0.054	0.18 ± 0.044	0.26 ± 0.054	0.32 ± 0.074	0.39 ± 0.085	0.12 ± 0.032	0.28 ± 0.069
Agoseris glauca (Pursh) Raf.	0.13 ± 0.048	0.00 ± 0.000	0.00 ± 0.000	0.04 ± 0.029	0.08 ± 0.033	0.00 ± 0.000	0.00 ± 0.000	0.03 ± 0.019
Antennaria neodioica Greene	0.07 ± 0.024	0.30 ± 0.103	0.00 ± 0.000	0.12 ± 0.063	0.13 ± 0.046	0.09 ± 0.044	0.00 ± 0.000	0.08 ± 0.037
Aster ericoides L.	0.28 ± 0.071	0.03 ± 0.013	0.26 ± 0.074	0.19 ± 0.062	0.02 ± 0.010	0.00 ± 0.000	0.02 ± 0.010	0.01 ± 0.008
A. ptarmicoides (Nees) Torr. & A. Gray	0.14 ± 0.046	0.00 ± 0.000	0.25 ± 0.066	0.13 ± 0.048	0.03 ± 0.016	0.00 ± 0.000	0.08 ± 0.036	0.04 ± 0.023
Chrysopsis villosa (Pursh) Nutt.	0.40 ± 0.068	0.01 ± 0.009	0.32 ± 0.056	0.25 ± 0.057	0.41 ± 0.063	0.00 ± 0.000	0.10 ± 0.026	0.17 ± 0.046
Echinacea angustifolia DC	0.00 ± 0.000	0.00 ± 0.000	0.06 ± 0.025	0.02 ± 0.015	0.00 ± 0.000	0.00 ± 0.000	0.06 ± 0.024	0.02 ± 0.014
Erigeron glabellus Nutt.	0.10 ± 0.034	0.01 ± 0.009	0.05 ± 0.024	0.05 ± 0.025	0.13 ± 0.044	0.04 ± 0.024	0.07 ± 0.026	0.08 ± 0.032
Erigeron sp. 1	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000	0.18 ± 0.063	0.03 ± 0.020	0.04 ± 0.024	0.08 ± 0.041
Erigeron sp. 2	0.24 ± 0.060	0.12 ± 0.024	0.20 ± 0.047	0.19 ± 0.047	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000
Erigeron sp. 3	0.12 ± 0.048	0.00 ± 0.000	0.07 ± 0.034	0.06 ± 0.035	0.03 ± 0.020	0.00 ± 0.000	0.00 ± 0.000	0.01 ± 0.012
Gaillardia arista Pursh	0.13 ± 0.043	0.00 ± 0.000	0.10 ± 0.031	0.08 ± 0.031	0.11 ± 0.043	0.00 ± 0.000	0.15 ± 0.043	0.09 ± 0.036
Helianthes laetiflorus Pers.	0.19 ± 0.054	0.00 ± 0.000	0.07 ± 0.033	0.09 ± 0.039	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000
Lactuca pulchella (Pursh)	0.00 ± 0.000	0.00 ± 0.000	0.05 ± 0.026	0.02 ± 0.015	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000
Liatris punctata Hook.	0.00 ± 0.000	0.00 ± 0.000	0.10 ± 0.030	0.03 ± 0.019	0.00 ± 0.000	0.00 ± 0.000	0.02 ± 0.010	0.01 ± 0.006
Senecio plattensis Nutt.	0.03 ± 0.013	0.01 ± 0.009	0.11 ± 0.037	0.05 ± 0.024	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000
Solidago missouriensis Nutt.	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000	0.06 ± 0.038	0.00 ± 0.000	0.00 ± 0.000	0.02 ± 0.022
S. nemoralis Ait.	0.46 ± 0.086	0.00 ± 0.000	0.02 ± 0.015	0.16 ± 0.060	0.17 ± 0.042	0.00 ± 0.000	0.07 ± 0.026	0.08 ± 0.030
Solidago sp. 1	0.00 ± 0.000	0.00 ± 0.000	0.04 ± 0.021	0.01 ± 0.012	0.08 ± 0.029	0.00 ± 0.000	0.09 ± 0.040	0.06 ± 0.029
Taraxacum officinale G.H. Webber ex Wiggers	0.00 ± 0.000	0.00 ± 0.000	0.01 ± 0.009	0.00 ± 0.005	0.00 ± 0.000	0.08 ± 0.029	0.00 ± 0.000	0.03 ± 0.017
Tragopogon dubius Scop.	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000	0.02 ± 0.010	0.00 ± 0.000	0.00 ± 0.000	0.01 ± 0.006
Boraginaceae								
Lithospermum canescens (Michx.) Lehm	0.08 ± 0.025	0.01 ± 0.009	0.32 ± 0.093	0.14 ± 0.059	0.07 ± 0.026	0.06 ± 0.028	0.41 ± 0.101	0.18 ± 0.066
L. incisum Lehm	0.00 ± 0.000	0.02 ± 0.015	0.01 ± 0.009	0.01 ± 0.010	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000
Onosmodium hispidissimum MacKenzie	0.00 ± 0.000	0.03 ± 0.013	0.00 ± 0.000	0.01 ± 0.008	0.00 ± 0.000	0.03 ± 0.014	0.00 ± 0.000	0.01 ± 0.008

Table 2. continued

	2005				2006			
	Section 27	**Section 28**	**Section 29**	**Total**	**Section 27**	**Section 28**	**Section 29**	**Total**
Brassicaceae								
Arabis holboellii var. collinsii (Fern.) Rollins	0.00 ± 0.000	0.08 ± 0.031	0.00 ± 0.000	0.03 ± 0.019	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000
Arabis sp.	0.14 ± 0.045	0.01 ± 0.009	0.12 ± 0.040	0.09 ± 0.036	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000
Brassica sp. 1	0.05 ± 0.023	0.07 ± 0.026	0.00 ± 0.000	0.04 ± 0.020	0.04 ± 0.019	0.06 ± 0.028	0.00 ± 0.000	0.03 ± 0.019
Erysimum asperum (Nutt.) DC.	0.17 ± 0.037	0.05 ± 0.022	0.04 ± 0.016	0.09 ± 0.028	0.03 ± 0.014	0.00 ± 0.000	0.00 ± 0.000	0.01 ± 0.008
Erysimum inconspicum (Watson) McMill.	0.00 ± 0.000	0.04 ± 0.017	0.00 ± 0.000	0.01 ± 0.010	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000
Campanulaceae								
Campanula rotundifolia L.	0.39 ± 0.078	0.00 ± 0.000	0.44 ± 0.093	0.27 ± 0.076	0.35 ± 0.077	0.00 ± 0.000	0.32 ± 0.072	0.22 ± 0.064
Caryophyllaceae								
Cerastium arvense L.	0.38 ± 0.107	0.37 ± 0.106	0.25 ± 0.083	0.33 ± 0.099	0.26 ± 0.086	0.46 ± 0.122	0.21 ± 0.066	0.31 ± 0.094
Euphorbiaceae								
Euphorbia esula L.	0.18 ± 0.034	0.94 ± 0.126	0.22 ± 0.049	0.44 ± 0.095	0.10 ± 0.034	0.92 ± 0.144	0.22 ± 0.051	0.42 ± 0.104
Fabaceae								
Astragalus crassicarpus Nutt.	0.03 ± 0.013	0.08 ± 0.026	0.13 ± 0.042	0.08 ± 0.029	0.09 ± 0.033	0.11 ± 0.040	0.20 ± 0.044	0.13 ± 0.039
Dalea candida Michx. Ex Willd.	0.07 ± 0.023	0.00 ± 0.000	0.21 ± 0.052	0.09 ± 0.035	0.18 ± 0.054	0.04 ± 0.019	0.30 ± 0.091	0.17 ± 0.063
D. purpurea Vent.	0.33 ± 0.069	0.22 ± 0.060	0.37 ± 0.077	0.30 ± 0.069	0.29 ± 0.090	0.12 ± 0.040	0.24 ± 0.078	0.22 ± 0.072
Medicago lupulina L.	0.00 ± 0.000	0.03 ± 0.013	0.00 ± 0.000	0.01 ± 0.008	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000
Medicago sativa L.	0.00 ± 0.000	0.04 ± 0.016	0.00 ± 0.000	0.01 ± 0.009	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000
Oxytropis splendens Dougl. ex Hook.	0.00 ± 0.000	0.01 ± 0.009	0.00 ± 0.000	0.00 ± 0.005	0.00 ± 0.000	0.08 ± 0.036	0.00 ± 0.000	0.03 ± 0.021
Psoralea esculenta Pursh	0.00 ± 0.000	0.00 ± 0.000	0.01 ± 0.009	0.00 ± 0.005	0.03 ± 0.016	0.00 ± 0.000	0.00 ± 0.000	0.01 ± 0.009
Vicia americana Mull. ex Willd.	0.00 ± 0.000	0.00 ± 0.000	0.01 ± 0.009	0.00 ± 0.005	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000	0.00 ± 0.000
Iridaceae								
Sisyrinchium montanum Greene	0.09 ± 0.034	0.08 ± 0.033	0.05 ± 0.019	0.07 ± 0.029	0.02 ± 0.010	0.06 ± 0.041	0.08 ± 0.038	0.05 ± 0.032
Lamiaceae								
Monarda fistulosa L.	0.21 ± 0.065	0.00 ± 0.000	0.18 ± 0.069	0.13 ± 0.056	0.21 ± 0.075	0.00 ± 0.000	0.22 ± 0.072	0.14 ± 0.061
Linaceae								
Linum lewisii Pursh	0.05 ± 0.029	0.00 ± 0.000	0.20 ± 0.058	0.09 ± 0.039	0.17 ± 0.053	0.00 ± 0.000	0.25 ± 0.069	0.14 ± 0.052

Table 2. continued

	2005				2006			
	Section 27	**Section 28**	**Section 29**	**Total**	**Section 27**	**Section 28**	**Section 29**	**Total**
Onagraceae								
Oenothera nuttallii Sweet	0.00 ± 0.000	0.00 ± 0.000	0.03 ± 0.013	0.01 ± 0.008	0.00 ± 0.000	0.00 ± 0.000	0.03 ± 0.014	0.01 ± 0.008
O. serrulata Nutt.	0.18 ± 0.040	0.00 ± 0.000	0.00 ± 0.000	0.06 ± 0.027	0.09 ± 0.030	0.00 ± 0.000	0.02 ± 0.010	0.04 ± 0.019
Primulaceae								
Androsace septentrionalis L.	0.25 ± 0.083	0.58 ± 0.132	0.20 ± 0.072	0.34 ± 0.101	0.00 ± 0.000	0.04 ± 0.029	0.00 ± 0.000	0.01 ± 0.017
Ranunculaceae								
Anemone cylindrica Gray	0.01 ± 0.009	0.00 ± 0.000	0.05 ± 0.019	0.02 ± 0.013	0.04 ± 0.019	0.03 ± 0.016	0.06 ± 0.028	0.04 ± 0.021
Ranunculus rhomboideus Goldie	0.00 ± 0.000	0.00 ± 0.000	0.03 ± 0.013	0.01 ± 0.008	0.00 ± 0.000	0.00 ± 0.000	0.03 ± 0.014	0.01 ± 0.008
Rosaceae								
Potentilla argentea L.	0.02 ± 0.015	0.16 ± 0.051	0.07 ± 0.023	0.09 ± 0.034	0.00 ± 0.000	0.06 ± 0.020	0.00 ± 0.000	0.02 ± 0.012
P. arguta Pursh	0.03 ± 0.021	0.00 ± 0.000	0.00 ± 0.000	0.01 ± 0.013	0.05 ± 0.022	0.07 ± 0.030	0.00 ± 0.000	0.04 ± 0.022
Prunus pumila L.	0.17 ± 0.055	0.00 ± 0.000	0.00 ± 0.000	0.06 ± 0.034	0.07 ± 0.047	0.00 ± 0.000	0.00 ± 0.000	0.02 ± 0.027
Rosa arkansana Porter	0.00 ± 0.000	0.04 ± 0.021	0.00 ± 0.000	0.01 ± 0.012	0.03 ± 0.014	0.02 ± 0.010	0.02 ± 0.010	0.02 ± 0.011
Geum triflorum Pursh	0.08 ± 0.036	0.08 ± 0.040	0.07 ± 0.037	0.07 ± 0.037	0.03 ± 0.016	0.11 ± 0.042	0.16 ± 0.055	0.10 ± 0.041
Rubiaceae								
Galium boreale L.	0.20 ± 0.051	0.03 ± 0.013	0.25 ± 0.072	0.16 ± 0.053	0.39 ± 0.109	0.02 ± 0.010	0.19 ± 0.059	0.20 ± 0.074
Santalaceae								
Houstonia longifolia Gaertn.	0.00 ± 0.000	0.14 ± 0.048	0.21 ± 0.061	0.12 ± 0.046	0.25 ± 0.078	0.32 ± 0.097	0.30 ± 0.087	0.29 ± 0.086
Comandra umbellata (L.) Nutt.	0.01 ± 0.009	0.10 ± 0.051	0.17 ± 0.051	0.09 ± 0.042	0.04 ± 0.019	0.00 ± 0.000	0.15 ± 0.049	0.06 ± 0.031
Saxifragaceae								
Heuchera richardsonii R. Br.	0.05 ± 0.026	0.00 ± 0.000	0.01 ± 0.009	0.02 ± 0.016	0.00 ± 0.000	0.00 ± 0.000	0.02 ± 0.010	0.01 ± 0.006
Scrophulariaceae								
Orthocarpus luteus Nutt.	0.23 ± 0.059	0.00 ± 0.000	0.00 ± 0.000	0.08 ± 0.038	0.19 ± 0.062	0.00 ± 0.000	0.04 ± 0.029	0.08 ± 0.040
Penstemon gracilis Nutt.	0.09 ± 0.035	0.01 ± 0.009	0.14 ± 0.046	0.08 ± 0.034	0.11 ± 0.042	0.00 ± 0.000	0.09 ± 0.034	0.07 ± 0.031
Violaceae								
Viola pedatifida G. Don	0.03 ± 0.013	0.00 ± 0.000	0.03 ± 0.013	0.02 ± 0.011	0.00 ± 0.000	0.00 ± 0.000	0.02 ± 0.010	0.01 ± 0.006
Total taxa	40	32	45	60	39	24	38	52

Table 3. Mean density (stems / m^2 ± SEM), species richness, Hill's effective species richness (N1), and Kvalseth evenness (E6) of forb flowering stems counted weekly within 46 permanent 1 m X 1 m quadrats at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba by site and year.

	2005				2006			
	Section 27	Section 28	Section 29	Overall	Section 27	Section 28	Section 29	Overall
Density (stems / m^2)	1.98 ± 0.206	2.64 ± 0.375	1.88 ± 0.206	2.17 ± 0.248	1.44 ± 0.146	2.39 ± 0.362	1.33 ± 0.139	1.72 ± 0.215
Species richness	40	32	45	60	39	24	38	52
Hill's N1 diversity	17.89	6.49	21.65	19.17	17.27	4.85	16.58	16.22
Kvalseth E6 evenness	0.55	0.65	0.70	0.56	0.63	0.57	0.67	0.58

Table 4. Results of a repeated measures ANOVA performed on the density of forb flowering stems at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba by year. Data were log transformed prior to analysis. Significant p-values are in bold.

	2005			2006		
Between subjects	df	F-ratio	P-value	df	F-ratio	P-value
Site	2	0.14	0.87	2	1.85	0.16
Exclosure	1	13.84	**<0.005**	1	23.34	**<0.005**
Site * Exclosure	2	5.06	**0.01**	2	1.02	0.36
Error	132			132		
Within Subjects						
Week	18	74.63	**<0.005**	18	88.77	**<0.005**
Week * Site	36	7.09	**<0.005**	36	8.87	**<0.005**
Week * Exclosure	18	18.65	**<0.005**	18	6.90	**<0.005**
Week * Exclosure * Site	36	2.47	**<0.005**	36	1.89	**0.01**
Error	2376			2376		

Table 5. Mean density (stems / m^2) of flowering stems of the ten most common flowering forb species counted weekly within 46 permanent 1 m X 1 m quadrats at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba by site and year.

Section 27	Stems / m^2	Section 28 Species	Stems / m^2	Section 29 Species	Stems / m^2	Overall Species	Stems / m^2
vense	0.41	Androsace septentrionalis	0.69	Lithospermum canescens	0.18	Androsace septentrionalis	0.31
eptentrionalis	0.16	Euphorbia esula	0.64	Campanula rotundifolia	0.16	Cerastium arvense	0.29
noralis	0.13	Cerastium arvense	0.32	Cerastium arvense	0.14	Euphorbia esula	0.23
otundifolia	0.10	Antennaria neodioica	0.28	Dalea purpurea	0.08	Antennaria neodioica	0.10
illosa	0.07	Dalea purpurea	0.04	Galium boreale	0.08	Campanula rotundifolia	0.09
es	0.07	Achillea millefolium	0.04	Androsace septentrionalis	0.08	Dalea purpurea	0.07
rea	0.07	Comandra umbellata	0.04	Aster ericoides	0.07	Lithospermum canescens	0.06
ulosa	0.06	Potentilla argentea	0.03	Monarda fistulosa	0.07	Aster ericoides	0.05
efolium	0.05	Houstonia longifolia	0.02	Aster ptarmicoides	0.05	Solidago nemoralis	0.04
2	0.04	Geum triflorum	0.02	Chrysopsis villosa	0.05	Monarda fistulosa	0.04
ale	0.25	Euphorbia esula	0.84	Lithospermum canescens	0.19	Euphorbia esula	0.29
rea	0.14	Cerastium arvense	0.49	Houstonia longifolia	0.13	Cerastium arvense	0.22
vense	0.12	Houstonia longifolia	0.19	Dalea candida	0.13	Houstonia longifolia	0.13
ulosa	0.08	Achillea millefolium	0.10	Dalea purpurea	0.09	Galium boreale	0.10
otundifolia	0.08	Geum triflorum	0.02	Campanula rotundifolia	0.07	Dalea purpurea	0.08
ngifolia	0.08	Androsace septentrionalis	0.02	Monarda fistulosa	0.07	Lithospermum canescens	0.07
efolium	0.06	Antennaria neodioica	0.02	Linum lewisii	0.06	Achillea millefolium	0.06
illosa	0.06	Sisyrinchium montanum	0.01	Cerastium arvense	0.05	P.etalostemon candida	0.05
luteus	0.04	Dalea purpurea	0.01	Galium boreale	0.03	Campanula rotundifolia	0.05
1	0.04	Astragalus crassicarpus	0.01	Geum triflorum	0.03	Monarda fistulosa	0.05

Table 6. Ecological classification of the bee species and the number of individuals collected by bee bowls and sweep-netting at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba by year and site.

	Classes		2005 bowls			2005 sweeps			2006 bowls			2006 sweeps			Totals		
	Guild[a]	Pollen[b]	S27	S28	S29	S27	S28	S29	S27	S28	S29	S27	S28	S29	2005	2006	Grand
Andrenidae																	
Andrena (Andrena) thaspii Graenicher	M	G	0	0	0	0	1	0	1	0	0	0	0	0	1	1	2
A. (Euandrena) geranii Robertson	M	G	70	120	22	1	1	5	10	31	8	3	6	10	219	68	287
A. (Gonandrena) persimulata Viereck	M	S	0	0	0	1	0	1	0	0	0	0	0	0	2	0	2
A. (Leucandrena) barbilabris (Kirby)	M	G	16	18	1	2	3	0	3	10	1	1	1	1	40	17	57
A. (Melandrena) carlini Cockerell	M	G	0	0	0	0	6	1	0	0	0	0	0	2	7	2	9
A. (Melandrena) dunningi Cockerell	M	G	0	1	0	1	0	0	0	0	0	2	0	1	2	3	5
A. (Melandrena) nivalis Smith	M	G	1	0	0	0	2	0	2	0	0	1	2	0	3	5	8
A. (Melandrena) regularis Malloch	M	G	0	0	0	0	5	0	0	1	0	0	0	0	5	1	6
A. (Melandrena) vicina Smith	M	G	10	5	3	8	19	7	9	0	2	5	2	3	52	21	73
A. (Parandrena) wellesleyana Robertson	M	S	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1
A. (Rhacandrena) robertsonii Dalla Torre	M	G	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
A. (Scaphandrena) arabis Robertson	M	S	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1
A. (Scrapteropsis) imitatrix Cresson	M	G	1	0	2	0	0	1	0	0	0	0	0	0	4	0	4
A. (Thysandrena) medionitens Cockerell	M	G	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1
A. (Trachandrena) ceanothi Viereck	M	G	1	0	0	0	0	0	0	1	0	0	0	2	1	3	4
A. (Trachandrena) cyanophila Cockerell	M	G	0	0	0	0	0	0	3	1	2	4	1	3	0	14	14
A. (Trachandrena) forbesii Robertson	M	G	0	0	2	1	2	0	3	1	0	5	0	0	5	9	14
A. (Trachandrena) mariae Robertson	M	S	0	1	0	0	1	0	0	0	0	0	0	0	2	0	2
A. (Trachandrena) miranda Smith	M	G	0	0	2	0	3	0	1	0	2	4	0	0	5	7	12
A. (Trachandrena) sigmundi Cockerell	M	S	0	1	0	1	0	1	0	0	0	0	0	0	3	0	3
A. (Tylandrena) erythrogaster (Ashmead)	M	S	0	0	0	0	2	0	0	0	0	0	1	0	2	1	3
Andrena sp. 1	M	?	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
Andrena sp. 2	M	?	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1
Calliopsis (Calliopsis) andreniformis Smith	M	G	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1
Pseudopanurgus (Heterosarus) nebrascensis (Crawford)	M	S	0	0	0	2	0	0	0	0	0	0	0	0	2	0	2
P. (Heterosarus) renimaculatus (Cockerell)	M	S	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1
P. (Heterosarus) simulans (Swenk and Cockerell)	M	S	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1

Table 6. continued

	Classes		2005 bowls			2005 sweeps			2006 bowls			2006 sweeps			Totals		
	Guild[a]	Pollen[b]	S27	S28	S29	S27	S28	S29	S27	S28	S29	S27	S28	S29	2005	2006	Grand
Apidae																	
Anthophora (Clisodon) terminalis Cresson	C	G	0	2	9	0	0	0	7	2	3	0	0	1	11	13	24
Bombus (Bombias) nevadensis Cresson	S	G	6	3	1	7	0	6	3	0	1	7	2	2	23	15	38
B. (Bombus) terricola Kirby	S	G	0	1	1	1	1	0	1	1	1	0	1	0	4	4	8
B. (Cullumanobombus) rufocinctus Cresson	S	G	30	29	60	30	1	47	17	33	44	12	5	3	197	114	311
B. (Fervidobombus) fervidus (Fabricius)	S	G	2	0	0	2	0	0	2	0	0	0	0	0	4	2	6
B. (Pyrobombus) bimaculatus Cresson	S	G	0	0	0	0	0	0	0	0	0	2	0	0	0	2	2
B. (Pyrobombus) sandersoni Franklin	S	G	4	2	4	1	5	3	0	1	0	0	5	2	19	8	27
B. (Pyrobombus) ternarius Say	S	G	76	75	49	47	10	27	28	23	17	83	14	17	284	182	466
B. (Pyrobombus) vagans Smith	S	G	3	9	8	12	12	7	5	7	13	4	10	5	51	44	95
B. (Separatobombus) griseocollis (DeGeer)	S	G	1	2	1	9	0	3	1	2	2	1	0	0	16	6	22
B. (Subterraneobombus) borealis Kirby	S	G	31	33	21	34	7	25	25	19	26	35	7	18	151	130	281
Epeolus sp. 1	P	N/A	0	0	0	1	0	0	0	0	0	0	0	1	1	1	2
Melissodes (Eumelissodes) agilis Cresson	M	S	0	0	1	0	0	0	7	3	8	1	0	5	1	24	25
M. (Eumelissodes) druriella (Kirby)	M	S	8	5	14	1	1	1	13	14	10	1	1	1	30	40	70
M. (Eumelissodes) menuachus Cresson	M	S	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1
M. (Eumelissodes) rustica (Say)	M	S	0	1	0	0	0	0	0	2	0	0	0	0	1	2	3
Melissodes sp. 1	M	?	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1
Nomada (Nomada) cressonii Robertson	P	N/A	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1
N. (Nomada) cuneata (Robertson)	P	N/A	0	0	0	1	1	0	0	0	0	3	0	0	2	3	5
N. (Nomada) maculata Cresson	P	N/A	0	0	1	0	0	0	6	1	1	2	0	0	1	10	11
N. (Nomada) pygmaea Cresson	P	N/A	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1
Nomada sp. 1	P	N/A	0	30	1	0	5	0	0	16	1	0	0	0	36	17	53
Nomada sp. 2	P	N/A	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1
Colletidae																	
Colletes andrewsi Cockerell	M	S	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1
C. brevicornis Robertson	M	S	3	1	3	4	4	7	0	0	4	3	5	3	22	15	37
C. kincaidii Cockerell	M	G	1	0	0	0	0	2	0	1	2	2	1	4	3	10	13
C. robertsonii Dalla Torre	M	S	0	0	0	0	1	1	0	0	0	0	1	0	2	1	3
C. susannae Swenk	M	S	0	0	0	0	1	0	0	0	0	1	6	0	1	7	8
C. willistoni Robertson	M	S	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
Hylaeus (Hylaeus) mesillae (Cockerell)	C	G	0	3	0	1	0	0	4	0	2	1	1	3	4	11	15

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Table 6. continued

| | Classes | | 2005 | | | | | | 2006 | | | | | | Totals | | |
| | | | bowls | | | sweeps | | | bowls | | | sweeps | | | | | |
	Guild[a]	Pollen[b]	S27	S28	S29	S27	S28	S29	S27	S28	S29	S27	S28	S29	2005	2006	Grand
Halictidae																	
Agapostemon (Agapostemon) sericeus (Förster)	M	G	2	1	0	0	0	0	0	0	2	0	1	0	3	3	6
A. (Agapostemon) splendens (Lepeletier)	M	G	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1
A. (Agapostemon) texanus Cresson	M	G	5	5	6	2	0	3	19	17	12	0	2	0	21	50	71
Augochlorella (Augochlorella) aurata (Smith)	S	G	0	0	0	0	0	0	3	0	0	0	0	0	0	3	3
Dufourea (Halictoides) maura (Cresson)	M	S	8	1	0	22	1	0	4	0	1	19	1	4	32	29	61
Halictus (Nealictus) parallelus Say	S	G	1	0	0	0	0	0	1	0	0	0	0	1	1	2	3
H. (Protohalictus) rubicundus (Christ)	S	G	6	2	1	2	1	1	13	0	1	6	4	1	13	25	38
H. (Seladonia) confusus Smith	S	G	0	1	0	0	0	0	0	3	0	0	0	0	1	3	4
Lasioglossum (Dialictus) albipenne (Robertson)	S	G	48	17	22	31	8	21	150	206	81	94	37	83	147	651	798
L.(Dialictus) pectoraloides (Cockerell)	M	G	0	4	0	2	2	0	6	3	0	7	7	2	8	25	33
L. (Dialictus) perpunctatum (Ellis)	S	G	43	43	36	5	10	10	49	29	15	57	17	18	147	185	332
L.(Dialictus) pictum (Crawford)	S	G	1	16	0	0	0	0	1	26	1	0	4	0	17	32	49
L. (Dialictus) pruinosiforme (Crawford)	S	G	14	8	22	0	1	1	10	8	2	1	0	0	46	21	67
L. (Dialictus) pruinosum (Robertson)	S	G	2	0	0	0	0	0	21	36	27	7	3	2	2	96	98
L. (Dialictus) sp. 1	S	G	0	0	0	0	0	0	0	9	0	0	0	0	0	9	9
L. (Dialictus) sp. 2	S	G	0	0	0	0	0	0	2	1	0	0	0	0	0	3	3
L. (Dialictus) succinipenne (Ellis)	S	G	312	407	93	32	15	23	552	690	263	130	51	42	882	1728	2610
L. (Dialictus) vierecki (Crawford)	S	G	0	3	0	0	0	0	0	7	1	0	0	1	3	9	12
L. (Lasioglossum) athabascense (Sandhouse)	M	G	1	0	0	0	0	0	3	1	0	14	4	0	1	22	23
L. (Lasioglossum) coriaceum (Smith)	M	G	0	0	0	0	0	0	2	3	4	0	0	0	0	9	9
L. (Lasioglossum) leuzoconium (Schrank)	M	G	1	3	0	0	1	0	5	3	4	0	0	0	5	12	17
L.(Lasioglossum) paraforbesii McGinley	M	G	45	48	27	11	2	1	66	70	46	2	4	4	134	192	326
L.(Lasioglossum) zonulum (Smith)	M	G	5	24	5	3	1	0	15	10	13	0	2	0	38	40	78
Sphecodes sp.1	P	N/A	0	1	0	2	4	2	0	5	1	4	6	0	9	16	25
Sphecodes sp. 2	P	N/A	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1
Megachilidae																	
Anthidium (Anthidium) clypeodentatum Swenk	C	G	1	6	17	0	1	4	5	5	3	1	0	1	29	15	44
Hoplitis (Alcidamea) pilosifrons (Cresson)	C	G	17	5	2	2	1	0	17	5	6	3	0	1	27	32	59
H. (Androicus) cylindrica (Cresson)	C	G	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1
H. (Monumetha) albifrons (Kirby)	C	G	0	2	0	0	0	0	0	1	0	0	0	0	2	1	3
Megachile (Litomegachile) brevis Say	C	G	5	1	2	2	0	1	1	0	2	0	0	1	11	4	15

Table 6. continued

	Classes		**2005**						**2006**						**Totals**		
			bowls			sweeps			bowls			sweeps					
	Guild[a]	Pollen[b]	S27	S28	S29	S27	S28	S29	S27	S28	S29	S27	S28	S29	2005	2006	Grand
Megachilidae (cont'd)																	
M. (Megachile) inermis Provancher	C	G	0	3	4	1	0	0	0	1	1	1	0	2	8	5	13
M. (Megachile) relativa Cresson	C	G	0	0	0	0	0	0	0	0	0	2	2	0	0	4	4
M. (Xanthosarus) frigida Smith	C	G	0	0	1	0	1	1	0	0	0	2	0	0	3	2	5
M. (Xanthosarus) latimanus Say	C	G	0	0	1	0	0	0	0	0	2	0	0	0	1	2	3
M. (Xanthosarus) melanophaea Smith	M	G	0	1	0	0	1	3	0	1	0	8	0	3	5	12	17
M. (Xanthosarus) perihirta Cockerell	M	G	0	1	0	0	0	0	0	1	0	0	0	1	1	2	3
Osmia (Chenosmia) sp. 1	C	?	1	0	0	0	0	0	0	2	1	0	1	0	1	4	5
O.(Melanosmia) atriventris Cresson	C	G	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
O. (Melanosmia) bucephala Cresson	C	G	2	12	2	0	0	0	0	0	1	0	0	0	16	1	17
O. (Melanosmia) distincta Cresson	C	S	11	1	2	2	0	0	38	2	14	1	0	1	16	56	72
O.(Melanosmia)simillima Smith	C	G	3	4	0	0	1	0	3	12	1	1	0	0	8	17	25
Stelis (Stelis) lateralis Cresson	P	N/A	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1
Total individuals			799	963	450	288	145	217	1140	1331	657	547	220	257	2862	4152	7014
Total taxa			40	47	37	37	39	30	47	51	47	46	37	39	76	90	100

[a] Guild Classes: C = cavity nester, M = miner, P = parasitic, S = social nester.
[b] Pollen classes: G= generalist, S = specialist.

Table 7. Summary of the number of individuals, genera and species collected in bee bowls at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba by family and year.

Family	2005			2006			Total		
	# of individuals	# of genera	# of species	# of individuals	# of genera	# of species	# of individuals	# of genera	# of species
Andrenidae	279	2	13	95	2	13	374	3	19
Apidae	524	4	15	369	4	18	893	4	18
Colletidae	11	2	3	13	2	3	24	2	3
Halictidae	1290	5	19	2525	6	25	3815	6	25
Megachilidae	108	5	14	126	4	13	234	5	15
Total	2212	18	64	3128	18	72	5340	20	80

Table 8. List of common taxa, for which relative abundance exceeded one per cent of the total catch in bee bowls at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba in 2005 and 2006.

Rank	Taxon	# of specimens	% of catch
1	*Lasioglossum succinipenne*	2317	43.4
2	*Lasioglossum albipenne*	524	9.8
3	*Lasioglossum paraforbesii*	302	5.7
4	*Bombus ternarius*	268	5.0
5	*Andrena geranii*	261	4.9
6	*Lasioglossum perpunctatum*	215	4.0
7	*Bombus rufocinctus*	213	4.0
8	*Bombus borealis*	155	2.9
9	*Lasioglossum pruinosum*	86	2.4
10	*Lasioglossum zonulum*	72	1.3
11	*Osmia distincta*	68	1.3
12	*Lasioglossum pruinosiforme*	64	1.1
13	*Agapostemon texana*	64	1.1
14	*Melissodes druriella*	64	1.1
	Total of common taxa	4673	87.5
	Total specimens collected	5340	100.0

Table 9. List of the top five dominant bee taxa in terms of relative abundance captured in bee bowls at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba by site and year.

Year	Rank	Section 27 Species	% / #	Section 28 Species	% / #	Section 29 Species	% / #	0verall Species	% / #
2005	1	*Lasioglossum succinipenne*	39.0	*Lasioglossum succinipenne*	42.3	*Lasioglossum succinipenne*	20.7	*Lasioglossum succinipenne*	43.4
	2	*Bombus ternarius*	9.5	*Andrena geranii*	12.5	*Bombus rufocinctus*	13.3	*Andrena geranii*	9.8
	3	*Andrena geranii*	8.8	*Bombus ternarius*	7.8	*Bombus ternarius*	10.9	*Bombus ternarius*	5.7
	4	*Lasioglossum albipenne*	6.0	*Lasioglossum paraforbesii*	5.0	*Lasioglossum perpunctatum*	8.0	*Lasioglossum perpunctatum*	5.0
	5	*Lasioglossum paraforbesii*	5.6	*Lasioglossum perpunctatum*	4.5	*Lasioglossum paraforbesii*	6.0	*Lasioglossum paraforbesii*	4.9
	n		**799**		**963**		**450**		**3128**
2006	1	*Lasioglossum succinipenne*	48.4	*Lasioglossum succinipenne*	51.8	*Lasioglossum succinipenne*	40.0	*Lasioglossum succinipenne*	48.1
	2	*Lasioglossum albipenne*	13.2	*Lasioglossum albipenne*	15.5	*Lasioglossum albipenne*	12.3	*Lasioglossum albipenne*	14.0
	3	*Lasioglossum paraforbesii*	5.8	*Lasioglossum paraforbesii*	5.3	*Lasioglossum paraforbesii*	7.0	*Lasioglossum paraforbesii*	5.8
	4	*Lasioglossum perpunctatum*	4.3	*Lasioglossum pruinosum*	2.7	*Bombus rufocinctus*	6.7	*Bombus rufocinctus*	3.0
	5	*Osmia distincta*	3.3	*Bombus rufocinctus*	2.5	*Lasioglossum pruinosum*	4.1	*Lasioglossum perpunctatum*	3.0
	n		**1140**		**1331**		**657**		**2212**

Table 10. Catch totals, catch per unit effort, species richness, Hill's effective species richness, Shannon-Weiner diversity, Kvalseth's evenness and Berger-Parker dominance of bees captured in bee bowls at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba by site and year.

	2005			2006			Pooled		
	Section 27	Section 28	Section 29	Section 27	Section 28	Section 29	2005	2006	Grand
No. individuals	799	963	450	1140	1331	657	3128	2212	5340
Bees per bowl (Mean ± SEM)	26.6 ± 1.72	32.1 ± 1.75	15.0 ± 1.13	38.0 ± 2.3	44.4± 2.83	21.9 ± 1.71	24.6 ± 1.17	34.8 ± 1.66	29.9 ± 1.08
Species richness	40	48	37	47	51	47	62	72	80
Hill's N1 effective species richness	10.99	10.33	15.82	9.01	7.56	11.39	12.91	9.46	11.58
Shannon-Weiner diversity H	2.40	2.34	2.76	2.19	2.02	2.43	2.56	2.25	2.45
Kvalseth E6 evenness	0.44	0.40	0.64	0.35	0.36	0.41	0.42	0.34	0.35
Berger-Parker dominance	0.39	0.42	0.21	0.48	0.52	0.40	0.37	0.48	0.43

Table 11. Results of ANOVAs testing the effect of year (2005 and 2006), site (Sections 27, 28 and 29), bowl colour (Blue, Yellow or White) and all interactions on the catch frequency of bees in bowls overall and by family (mean ± SEM) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. Bold p-values indicate significant differences at p≤0.05. Superscript letters indicate which factor levels were significantly different from one another in Tukey pairwise comparisons.

	Bees per bowl (mean ± SEM)					
	Total	Andrenidae	Apidae	Colletidae	Halictidae	Megachilidae
2005	24.6 ± 1.17^a	3.1 ± 0.33^a	5.8 ± 0.38^a	0.1 ± 0.04	14.3 ± 0.83^a	1.2 ± 0.12
2006	34.8 ± 1.66^b	1.0 ± 0.14^b	4.1 ± 0.30^b	0.1 ± 0.04	28.1 ± 1.52^b	1.4 ± 0.16
$F_{1,162}$	41.26	56.31	21.98	0.24	113.15	0.08
p	**<0.005**	**<0.005**	**<0.005**	0.62	**<0.005**	0.77
S27	32.3 ± 1.61^a	2.2 ± 0.30^a	4.6 ± 0.49^a	0.1 ± 0.04	23.6 ± 1.46^a	1.7 ± 0.19^a
S28	38.2 ± 1.83^b	3.2 ± 0.44^a	5.3 ± 0.36^b	0.1 ± 0.04	28.6 ± 1.85^a	1.1 ± 0.16^b
S29	18.5 ± 1.11^c	0.8 ± 0.12^b	5.0 ± 0.44^b	0.2 ± 0.06	11.3 ± 0.94^b	1.1 ± 0.15^b
$F_{2,162}$	88.38	26.29	3.55	1.43	90.62	5.47
p	**<0.005**	**<0.005**	**0.031**	0.24	**<0.005**	**0.01**
Blue	36.8 ± 1.93^a	2.6 ± 0.41^a	7.9 ± 0.39^a	0.2 ± 0.06	24.6 ± 1.95^a	1.5 ± 0.19
White	27.8 ± 1.66^b	1.6 ± 0.23^b	4.2 ± 0.27^b	0.1 ± 0.04	20.6 ± 1.66^{ab}	1.3 ± 0.15
Yellow	24.4 ± 1.67^c	2.1 ± 0.35^b	2.8 ± 0.32^c	0.1 ± 0.04	18.3 ± 1.50^b	1.1 ± 0.16
$F_{2,162}$	33.61	3.16	78.10	2.65	8.91	2.28
p	**<0.005**	**0.05**	**<0.005**	0.07	**<0.005**	0.11
$F_{2,162}$	0.06	4.56	0.76	2.06	0.25	2.01
p	0.94	**0.01**	0.47	0.13	0.78	0.14
$F_{2,162}$	0.69	1.01	3.38	1.70	0.76	1.92
p	0.51	0.37	0.36	0.19	0.47	0.15
$F_{4,162}$	4.59	1.19	7.33	3.34	2.18	0.20
p	**<0.005**	0.32	**<0.005**	**0.01**	0.73	0.94
$F_{4,162}$	1.04	1.59	0.57	1.4	0.60	1.23
p	0.39	0.18	0.68	0.24	0.67	0.30

Table 12. Results of ANOVAs testing the effect of year (2005 and 2006), site (Sections 27, 28 and 29), bowl colour (Blue, Yellow or White) and all interactions on the catch frequency of the ten most common bee species (mean ± SEM) at the Yellow Quill Mixed-grass Prairie Preserve, Manitoba. Bold p-values indicate significant differences at $p \leq 0.05$. Superscript letters indicate which factor levels were significantly different from one another in Tukey pairwise comparisons.

		Bees per bowl (mean ± SEM)				
		Lasioglossum succinipenne	*Lasioglossum albipenne*	*Lasioglossum paraforbesii*	*Bombus ternarius*	*Andrena geranii*
	2005	9.0 ± 0.68^a	1.0 ± 0.12^a	1.3 ± 0.15^a	2.2 ± 0.21^a	2.4 ± 0.27^a
	2006	16.7 ± 1.06^b	4.9 ± 0.38^b	2.0 ± 0.19^b	0.8 ± 0.11^b	0.5 ± 0.12^b
	$F_{1,162}$	76.32	13.10	9.85	49.50	51.48
	p	**p<0.005**	**p<0.005**	**p<0.005**	**p<0.005**	**p<0.005**
	S27	14.4 ± 0.99^a	3.3 ± 0.34^a	1.8 ± 0.18^a	1.7 ± 0.25^a	1.3 ± 0.23^a
	S28	18.3 ± 1.27^b	3.7 ± 0.58^b	2.0 ± 0.26^a	1.6 ± 0.23^a	2.5 ± 0.38^b
	S29	5.9 ± 0.65^c	1.7 ± 0.26^c	1.2 ± 0.18^b	1.1 ± 0.18^b	0.5 ± 0.11^c
	$F_{2,162}$	68.45	12.86	4.51	3.56	21.49
	p	**p<0.005**	**p<0.005**	**0.01**	**0.03**	**p<0.005**
Colour	Blue	16.6 ± 1.41^a	2.6 ± 0.35	1.7 ± 0.18^{ab}	2.3 ± 0.25^a	2.3 ± 0.34^a
	White	12.0 ± 1.10^b	3.0 ± 0.43	2.1 ± 0.28^a	1.4 ± 0.20^b	0.9 ± 0.20^b
	Yellow	10.0 ± 0.89^b	3.1 ± 0.49	1.2 ± 0.16^b	0.8 ± 0.17^c	1.2 ± 0.27^b
	$F_{2,162}$	19.52	0.82	5.61	17.33	10.42
	p	**p<0.005**	0.44	**p<0.005**	**p<0.005**	**p<0.005**
Site	$F_{2,162}$	1.55	14.03	0.18	0.95	8.31
	p	0.22	**p<0.005**	0.98	0.38	**p<0.005**
Colour	$F_{2,162}$	4.28	0.68	6.80	1.33	0.29
	p	**0.02**	0.51	**p<0.005**	0.27	0.75
Colour	$F_{4,162}$	2.68	3.47	3.3	2.96	0.92
	p	**0.03**	**p<0.005**	**0.01**	**0.02**	0.45
Site*Colour	$F_{4,162}$	1.33	3.41	2.62	1.22	0.49
	p	0.26	**p<0.005**	**0.04**	0.3	0.74

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Figure 12. continued

		Bees per bowl (mean ± SEM)				
		Lasioglossum perpunctatum	*Bombus rufocinctus*	*Bombus borealis*	*Lasioglossum pruinosum*	*Lasioglossum zonulum*
	2005	1.4 ± 0.16	1.3 ± 0.16	0.9 ± 0.11	0.0 ± 0.02^a	0.4 ± 0.07
	2006	1.0 ± 0.12	1.0 ± 0.13	0.8 ± 0.11	0.9 ± 0.12^b	0.4 ± 0.06
	$F_{2,161}$	2.83	2.33	1.43	60.40	0.25
	p	0.09	0.13	0.23	**<0.005**	0.61
	S27	1.5 ± 0.20^a	0.8 ± 0.16^a	0.9 ± 0.15	0.4 ± 0.10	0.3 ± 0.07^a
	S28	1.2 ± 0.16^{ab}	1.0 ± 0.14^a	0.9 ± 0.14	0.6 ± 0.13	0.6 ± 0.10^b
	S29	0.9 ± 0.16^b	1.7 ± 0.21^b	0.8 ± 0.11	0.5 ± 0.13	0.3 ± 0.06^a
	$F_{2,161}$	4.25	9.74	0.38	1.19	3.62
	p	**0.02**	**p<0.005**	0.68	0.31	**0.03**
Colour	Blue	0.9 ± 0.13^a	1.9 ± 0.22^a	1.6 ± 0.17^a	0.5 ± 0.11	0.4 ± 0.09
	White	0.9 ± 0.14^a	0.9 ± 0.13^b	0.6 ± 0.10^b	0.4 ± 0.09	0.4 ± 0.08
	Yellow	1.8 ± 0.23^b	0.7 ± 0.14^b	0.4 ± 0.08^b	0.6 ± 0.15	0.3 ± 0.07
	$F_{2,161}$	10.00	17.76	27.44	1.19	0.62
	p	**p<0.005**	**p<0.005**	**<0.005**	0.32	0.54
Site	$F_{2,161}$	1.98	1.30	1.73	1.95	8.46
	p	0.14	0.28	0.18	0.146	**<0.005**
Colour	$F_{2,161}$	1.18	2.79	0.513	1.52	2.11
	p	0.31	0.06	0.60	0.22	0.12
Colour	$F_{4,161}$	0.76	1.23	0.56	1.64	1.24
	p	0.55	0.30	0.69	0.17	0.30
Site*Colour	$F_{4,161}$	0.60	0.65	1.00	1.63	0.30
	p	0.66	0.63	0.42	0.16	0.88

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Table 13. Results of ANOVAs testing the effect of year (2005 and 2006), site (Sections 27, 28 and 29), bowl colour (Blue, Yellow or White) and all interactions on the catch frequency of bees in bowls by ecological group (mean ± SEM) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. Bold p-values indicate significant differences at p≤0.05. Superscript letters indicate which factor levels were significantly different from one another in Tukey pairwise comparisons.

Factor		Bees per bowl (mean ± SEM)				
		Cleptoparasites	Cavity nesters	Miners	Social nesters	Specialists
Year	2005	0.4 ± 0.11	1.3 ± 0.13	5.7 ± 0.41	17.2 ± 0.90^a	0.7 ± 0.11^a
	2006	0.4 ± 0.09	1.6 ± 0.17	5.3 ± 0.33	27.6 ± 1.44^b	1.4 ± 0.16^b
	$F_{1,162}$	0.07	0.51	0.18	56.83	18.05
	p	0.79	0.48	0.66	**<0.005**	**<0.005**
Site	S27	0.1 ± 0.04^a	1.9 ± 0.20^a	5.9 ± 0.42^a	24.4 ± 1.39^a	1.6 ± 0.21^a
	S28	0.9 ± 0.18^b	1.2 ± 0.17^b	7.0 ± 0.50^a	29.2 ± 1.71^a	0.5 ± 0.12^b
	S29	0.1 ± 0.04^a	1.3 ± 0.16^b	3.5 ± 0.31^b	13.6 ± 0.89^b	1.0 ± 0.15^c
	$F_{2,162}$	26.78	5.8	26.55	62.31	14.74
	p	**<0.005**	**<0.005**	**<0.005**	**<0.005**	**<0.005**
Bowl Colour	Blue	0.1 ± 0.07^a	1.6 ± 0.19^a	7.2 ± 0.47^a	28.0 ± 1.72^a	1.9 ± 0.21^a
	White	0.4 ± 0.11^b	1.6 ± 0.18^a	5.1 ± 0.38^b	20.8 ± 1.43^b	0.8 ± 0.14^b
	Yellow	0.7 ± 0.15^c	1.1 ± 0.17^b	4.2 ± 0.42^c	18.4 ± 1.42^b	0.5 ± 0.10^b
	$F_{2,162}$	14.20	3.31	22.96	23.65	30.41
	p	**<0.005**	**0.04**	**<0.005**	**<0.005**	**<0.005**
Year*Site	$F_{2,162}$	1.89	3.69	7.15	0.96	1.43
	p	0.16	**0.03**	**<0.005**	0.38	0.24
Year*Colour	$F_{2,162}$	0.49	1.30	1.506	0.08	0.02
	p	0.61	0.27	0.22	0.92	0.98
Site*Colour	$F_{4,162}$	4.75	0.59	3.11	2.16	1.65
	p	**<0.005**	0.66	**0.02**	0.08	0.16
Year*Site*Colour	$F_{4,162}$	1.17	1.14	4.39	0.40	0.9
	p	0.32	0.39	**<0.005**	0.81	0.46

Table 14. Summary of the number of individuals, genera and species of bees collected in by sweep-netting at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba by family and year.

Family	2005			2006			Total		
	# of individuals	# of genera	# of species	# of individuals	# of genera	# of species	# of individuals	# of genera	# of species
Andrenidae	80	2	18	62	1	13	142	2	22
Apidae	308	4	13	254	5	18	562	5	20
Colletidae	21	2	5	33	2	7	54	2	7
Halictidae	220	5	12	642	5	17	862	5	18
Megachilidae	21	4	8	33	4	12	54	4	12
Total	650	17	56	1024	17	67	1674	18	79

Table 15. List of common bee taxa for which relative abundance exceeded one per cent of the total sweep-netting catch at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba in 2005 and 2006.

Rank	Taxon	#of specimens	% of catch
1	*Lasioglossum succinipenne*	293	17.5
2	*Lasioglossum albipenne*	274	16.4
3	*Bombus ternarius*	198	11.8
4	*Bombus borealis*	126	7.5
5	*Lasioglossum perpunctatum*	117	7.0
6	*Bombus rufocinctus*	98	5.9
7	*Bombus vagans*	50	3.0
8	*Dufourea maura*	47	2.8
9	*Andrena vicina*	44	2.6
10	*Andrena geranii*	26	1.6
11	*Colletes brevicornis*	26	1.6
12	*Bombus nevadensis*	24	1.4
13	*Lasioglossum paraforbesii*	24	1.4
14	*Lasioglossum athabascense*	20	1.2
15	*Lasioglossum pectoraloides*	18	1.1
16	*Sphecodes* sp. 1	18	1.1
	Total of common taxa	1403	83.8
	Total specimens collected	1674	100.0

Table 16. List of the top five dominant bee taxa captured by sweep-netting in terms of relative abundance by site and year at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.

Year	Rank	Section 27 Species	% / #	Section 28 Species	% / #	Section 29 Species	% / #	0verall Species	% / #
2005	1	*Bombus ternarius*	16.3	*Andrena vicina*	13.1	*Bombus rufocinctus*	21.7	*Bombus ternarius*	12.9
	2	*Bombus borealis*	11.8	*Lasioglossum succinipenne*	10.3	*Bombus ternarius*	12.4	*Bombus rufocinctus*	12.0
	3	*Lasioglossum succinipenne*	11.1	*Bombus vagans*	8.3	*Bombus borealis*	11.5	*Lasioglossum succinipenne*	10.8
	4	*Lasioglossum albipenne*	10.8	*Bombus ternarius*	6.9	*Lasioglossum succinipenne*	10.6	*Bombus borealis*	10.2
	5	*Bombus rufocinctus*	10.4	*Lasioglossum perpunctatum*	6.9	*Lasioglossum albipenne*	9.7	*Lasioglossum albipenne*	9.2
	n		**288**		**145**		**217**		**650**
2006	1	*Lasioglossum succinipenne*	23.8	*Lasioglossum succinipenne*	23.2	*Lasioglossum albipenne*	32.3	*Lasioglossum succinipenne*	21.8
	2	*Lasioglossum albipenne*	17.2	*Lasioglossum albipenne*	16.8	*Lasioglossum succinipenne*	16.3	*Lasioglossum albipenne*	20.9
	3	*Bombus ternarius*	15.2	*Lasioglossum perpunctatum*	7.7	*Bombus borealis*	7.0	*Bombus ternarius*	11.1
	4	*Lasioglossum perpunctatum*	10.4	*Bombus ternarius*	6.4	*Lasioglossum perpunctatum*	7.0	*Lasioglossum perpunctatum*	9.0
	5	*Bombus borealis*	6.4	*Bombus vagans*	4.5	*Bombus ternarius*	6.6	*Bombus borealis*	5.9
	n		**547**		**220**		**257**		**1024**

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Table 17. Catch totals, catch per unit effort, species richness, Hill's effective species richness, Shannon-Weiner diversity Kvalseth's evenness and Berger-Parker dominance of bees captured by sweep-netting at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba by site and year.

	2005			2006			Pooled		
	Section 27	Section 28	Section 29	Section 27	Section 28	Section 29	2005	2006	Grand
No. individuals	288	145	217	547	220	257	650	1024	1674
Bees / 15 min sweep (Mean ± SEM)	3.20 ± 0.39	1.60 ± 0.32	2.41 ± 0.30	5.92 ± 0.81	2.37 ± 0.33	2.77 ± 0.35	2.40 ± 0.20	3.69 ± 0.33	3.05 ± 0.19
Species richness	37	39	30	46	37	39	56	67	79
Hill's N1 effective species richness	16.44	23.81	14.30	13.33	17.28	13.46	21.54	16.28	20.39
Shannon-Weiner diversity H	2.80	3.17	2.66	2.59	2.85	2.60	3.07	2.79	3.02
Kvalseth E6 evenness	0.67	0.70	0.65	0.55	0.54	0.46	0.62	0.49	0.52
Berger-Parker dominance	0.16	0.13	0.22	0.24	0.23	0.32	0.13	0.22	0.18

Table 18. Results of ANOVAs testing the effects of sweep round (Morning, Afternoon or Evening) and location relative to the grazing exclosure (Inside or Outside) using site as a blocking variable (Sections 27, 28 and 29) on the catch frequency (mean ± SEM) overall and by family collected by sweep-netting at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. Analyses were performed separately for 2005 and 2006. Bold p-values indicate significant differences at p≤0.05. Superscript letters indicate which factor levels were significantly different from one another in Tukey pairwise comparisons.

		Number of bees per 15 minutes of sweep-netting (mean ± SEM)							
		Total		Andrenidae		Apidae		Colletidae	
Factor		2005	2006	2005	2006	2005	2006	2005	2006
Site	S27	3.20 ± 0.39^a	5.92 ± 0.81^a	0.20 ± 0.08	0.28 ± 0.08	1.62 ± 0.30^a	1.66 ± 0.37^a	0.06 ± 0.03	0.09 ± 0.03
	S28	1.60 ± 0.32^b	2.37 ± 0.33^b	0.51 ± 0.21	0.15 ± 0.06	0.47 ± 0.11^b	0.50 ± 0.11^b	0.07 ± 0.03	0.15 ± 0.04
	S29	2.41 ± 0.30^b	2.77 ± 0.35^b	0.23 ± 0.10	0.27 ± 0.08	1.32 ± 0.22^{ab}	0.59 ± 0.11^b	0.11 ± 0.03	0.12 ± 0.05
	$F_{2,10}$	7.24	12.42	3.31	1.49	5.32	15.56	1.03	1.40
	p	**0.01**	**<0.005**	0.08	0.27	**0.03**	**<0.005**	0.39	0.29
Round	Morning	2.59 ± 0.35	5.42 ± 0.71^a	0.63 ± 0.19^a	0.34 ± 0.09^a	0.88 ± 0.18	1.17 ± 0.23	0.10 ± 0.03	0.19 ± 0.05^a
	Afternoon	2.52 ± 0.31	3.72 ± 0.47^a	0.15 ± 0.04^b	0.26 ± 0.07^{ab}	1.38 ± 0.23	0.89 ± 0.25	0.05 ± 0.02	0.13 ± 0.04^b
	Evening	1.80 ± 0.35	1.53 ± 0.31^b	0.02 ± 0.02^b	0.06 ± 0.03^b	1.17 ± 0.30	0.64 ± 0.23	0.09 ± 0.05	0.03 ± 0.02^c
	$F_{2,10}$	1.78	13.43	17.44	6.93	0.77	2.67	0.74	8.42
	p	0.21	**<0.005**	**<0.005**	**0.01**	0.48	0.12	0.50	**0.01**
Exclosure	Inside	2.52 ± 0.26	3.49 ± 0.49	0.36 ± 0.12	0.25 ± 0.07	1.13 ± 0.16	1.07 ± 0.25	0.09 ± 0.03	0.12 ± 0.03
	Outside	2.29 ± 0.30	3.88 ± 0.43	0.27 ± 0.11	0.22 ± 0.05	1.14 ± 0.21	0.77 ± 0.12	0.07 ± 0.02	0.12 ± 0.04
	$F_{1,10}$	0.51	0.26	0.48	0.23	0.00	2.75	0.86	0.06
	p	0.49	0.62	0.50	0.64	0.97	0.12	0.37	0.81
Round* Exclosure	$F_{2,10}$	0.17	1.87	0.53	4.26	0.07	0.17	1.51	1.61
	p	0.84	0.20	0.60	0.05	0.92	0.84	0.26	0.24

Table 18. continued

Factor		Number of bees per 15 minutes of sweep-netting (mean ± SEM)			
		Halictidae		Megachilidae	
		2005	2006	2005	2006
Site	S27	1.24 ± 0.21^a	3.71 ± 0.65^a	0.08 ± 0.03	0.21 ± 0.06^a
	S28	0.51 ± 0.10^b	1.55 ± 0.26^b	0.04 ± 0.03	0.03 ± 0.02^b
	S29	0.69 ± 0.11^c	1.72 ± 0.27^b	0.06 ± 0.03	0.10 ± 0.04^{ab}
	$F_{2,10}$	9.67	6.82	1.07	4.53
	p	**<0.005**	**0.01**	0.38	**0.04**
Round	Morning	0.90 ± 0.16^a	3.59 ± 0.59^a	0.08 ± 0.03	0.13 ± 0.05
	Afternoon	0.91 ± 0.12^a	2.28 ± 0.35^a	0.04 ± 0.02	0.16 ± 0.05
	Evening	0.46 ± 0.17^b	0.82 ± 0.20^b	0.06 ± 0.03	0.04 ± 0.03
	$F_{2,10}$	4.83	9.67	1.06	2.31
	p	**0.03**	**<0.005**	0.68	0.15
Exclosure	Inside	0.86 ± 0.13	1.98 ± 0.37	0.08 ± 0.03	0.10 ± 0.03
	Outside	0.77 ± 0.11	2.67 ± 0.36	0.04 ± 0.02	0.12 ± 0.04
	$F_{1,10}$	0.77	1.57	2.75	0.30
	p	0.39	0.24	0.13	0.59
Round* Exclosure	$F_{2,10}$	0.36	1.69	0.06	0.30
	p	0.70	0.23	0.95	0.75

Table 19. Results of ANOVAs testing the effects of sweep round (Morning, Afternoon or Evening) and location relative to the grazing exclosure (Inside or Outside) using site as a blocking variable (Sections 27, 28 and 29) on the catch frequency (mean ± SEM) of the ten most common species collected by sweep-netting at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. Analyses were performed separately for 2005 and 2006. Bold p-values indicate significant differences at p≤0.05. Superscript letters indicate which factor levels were significantly different from one another in Tukey pairwise comparisons

		Number of bees per 15 minutes of sweep-netting (mean ± SEM)							
		Lasioglossum succinipenne		*Lasioglossum albipenne*		*Bombus ternarius*		*Bombus borealis*	
Factor		2005	2006	2005	2006	2005	2006	2005	2006
Site	S27	0.36 ± 0.10	1.41 ± 0.46^a	0.34 ± 0.08^a	1.02 ± 0.22	0.52 ± 0.12^a	0.90 ± 0.23^a	0.38 ± 0.10^a	0.38 ± 0.14
	S28	0.17 ± 0.06	0.55 ± 0.13^b	0.09 ± 0.04^b	0.40 ± 0.11	0.11 ± 0.06^b	0.15 ± 0.04^b	0.08 ± 0.03^b	0.08 ± 0.03
	S29	0.26 ± 0.06	0.46 ± 0.07^b	0.23 ± 0.07^a	0.90 ± 0.21	0.30 ± 0.08^b	0.18 ± 0.05^b	0.28 ± 0.08^a	0.20 ± 0.05
	$F_{2,10}$	0.85	4.65	5.22	3.72	4.93	9.72	6.66	3.10
	p	0.46	**0.04**	**0.03**	0.06	**0.03**	**<0.005**	**0.02**	0.09
Round	Morning	0.31 ± 0.08	1.21 ± 0.42	0.21 ± 0.07	1.34 ± 0.25^a	0.24 ± 0.07	0.60 ± 0.18	0.21 ± 0.06	0.24 ± 0.07
	Afternoon	0.27 ± 0.06	0.82 ± 0.14	0.27 ± 0.06	0.54 ± 0.11^b	0.42 ± 0.10	0.41 ± 0.14	0.28 ± 0.09	0.19 ± 0.09
	Evening	0.13 ± 0.08	0.29 ± 0.13	0.15 ± 0.05	0.38 ± 0.13^b	0.24 ± 0.10	0.18 ± 0.07	0.24 ± 0.07	0.23 ± 0.12
	$F_{2,10}$	2.07	3.79	1.41	9.08	0.96	2.66	0.27	0.11
	p	0.17	0.06	0.29	**0.01**	0.41	0.19	0.77	0.90
Exclosure	Inside	0.25 ± 0.06	0.72 ± 0.29	0.21 ± 0.05	0.73 ± 0.16	0.30 ± 0.08	0.49 ± 0.14	0.30 ± 0.07	0.28 ± 0.10
	Outside	0.27 ± 0.06	0.90 ± 0.14	0.23 ± 0.06	0.82 ± 0.14	0.33 ± 0.07	0.33 ± 0.09	0.19 ± 0.05	0.15 ± 0.04
	$F_{1,10}$	0.01	0.44	0.18	0.09	0.22	1.13	2.61	2.00
	p	0.94	0.52	0.68	0.77	0.65	0.31	0.14	0.19
Round* Exclosure	$F_{2,10}$	1.45	0.83	1.01	1.42	0.31	0.03	0.66	0.71
	p	0.27	0.46	0.40	0.28	0.74	0.97	0.54	0.52

Table 19. continued

Factor		Number of bees per 15 minutes of sweep-netting (mean ± SEM)							
		Lasioglossum perpunctatum		*Bombus rufocinctus*		*Bombus vagans*		*Dufourea maura*	
		2005	2006	2005	2006	2005	2006	2005	2006
Site	S27	0.06 ± 0.04	0.62 ± 0.24	0.33 ± 0.10[a]	0.13 ± 0.05	0.13 ± 0.05	0.04 ± 0.02	0.24 ± 0.12[a]	0.21 ± 0.08[a]
	S28	0.11 ± 0.04	0.18 ± 0.07	0.01 ± 0.01[b]	0.05 ± 0.03	0.13 ± 0.05	0.11 ± 0.04	0.01 ± 0.01[b]	0.01 ± 0.01[b]
	S29	0.11 ± 0.04	0.20 ± 0.08	0.52 ± 0.13[a]	0.03 ± 0.02	0.08 ± 0.03	0.05 ± 0.03	0.00 ± 0.00[c]	0.04 ± 0.02[b]
	$F_{2,10}$	0.78	3.56	4.61	1.59	1.48	0.75	4.89	6.72
	p	0.49	0.07	**0.04**	0.25	0.27	0.49	**0.03**	**0.01**
Round	Morning	0.15 ± 0.04[a]	0.54 ± 0.17	0.10 ± 0.04	0.09 ± 0.03	0.11 ± 0.04	0.08 ± 0.03	0.10 ± 0.08	0.14 ± 0.07
	Afternoon	0.08 ± 0.04[b]	0.35 ± 0.17	0.42 ± 0.11	0.04 ± 0.02	0.08 ± 0.03	0.08 ± 0.04	0.05 ± 0.03	0.07 ± 0.03
	Evening	0.00 ± 0.00[c]	0.05 ± 0.03	0.41 ± 0.15	0.09 ± 0.06	0.19 ± 0.07	0.04 ± 0.03	0.13 ± 0.13	0.05 ± 0.03
	$F_{2,10}$	5.99	4.01	2.14	0.47	2.76	0.50	0.38	1.27
	p	**0.02**	0.05	0.17	0.64	0.11	0.62	0.69	0.322
Exclosure	Inside	0.11 ± 0.03	0.16 ± 0.06[a]	0.27 ± 0.07	0.05 ± 0.02	0.11 ± 0.03	0.09 ± 0.03	0.15 ± 0.08	0.06 ± 0.03
	Outside	0.07 ± 0.03	0.51 ± 0.16[b]	0.31 ± 0.09	0.09 ± 0.04	0.12 ± 0.03	0.04 ± 0.02	0.02 ± 0.01	0.12 ± 0.05
	$F_{1,10}$	0.77	5.38	0.01	0.79	0.08	1.66	3.46	1.42
	p	0.40	**0.04**	0.93	0.39	0.87	0.23	0.09	0.26
Round* Exclosure	$F_{2,10}$	1.33	0.64	0.53	0.10	0.88	0.42	0.56	0.44
	p	0.31	0.55	0.60	0.90	0.44	0.67	0.59	0.66

Table 19. continued

Factor		Number of bees per 15 minutes of sweep-netting (mean ± SEM)			
		Andrena vicina		*Andrena geranii*	
		2005	2006	2005	2006
Site	S27	0.09 ± 0.05	0.05 ± 0.03	0.01 ± 0.01	0.03 ± 0.02
	S28	0.21 ± 0.11	0.02 ± 0.02	0.01 ± 0.01	0.07 ± 0.05
	S29	0.08 ± 0.06	0.03 ± 0.02	0.06 ± 0.03	0.11 ± 0.04
	$F_{2,10}$	2.78	3.19	1.42	1.18
	p	0.11	0.08	0.28	0.34
Round	Morning	0.26 ± 0.11[a]	0.07 ± 0.03[a]	0.04 ± 0.02	0.08 ± 0.04
	Afternoon	0.06 ± 0.03[b]	0.03 ± 0.02[ab]	0.03 ± 0.02	0.08 ± 0.04
	Evening	0.00 ± 0.00[b]	0.00 ± 0.00[b]	0.00 ± 0.00	0.04 ± 0.03
	$F_{2,10}$	13.64	18.33	1.16	0.47
	p	**<0.005**	**<0.005**	0.35	0.67
Exclosure	Inside	0.13 ± 0.07	0.04 ± 0.02	0.02 ± 0.01	0.07 ± 0.03
	Outside	0.13 ± 0.06	0.04 ± 0.02	0.03 ± 0.02	0.07 ± 0.03
	$F_{1,10}$	1.42	0.01	0.09	0.01
	p	0.26	0.97	0.77	0.95
Round* Exclosure	$F_{2,10}$	0.43	1.39	0.63	2.08
	p	0.65	0.29	0.55	0.18

Table 20. Results of ANOVAs testing the effects of sweep round (Morning, Afternoon or Evening) and location relative to the grazing exclosure (Inside or Outside) using site as a blocking variable (Sections 27, 28 and 29) on the catch frequency (mean ± SEM) of bees by ecological category by sweep-netting at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. Analyses were performed separately for 2005 and 2006. Bold p-values indicate significant differences at p≤0.05. Superscript letters indicate which factor levels were significantly different from one another in Tukey pairwise comparisons.

Factor		Number of individual bees per 15 minutes of sweep-netting (mean ± SEM)							
		Social nesters		Miners		Cavity nesters		Cleptoparasites	
		2005	2006	2005	2006	2005	2006	2005	2006
Site	S27	2.37 ± 0.34^a	4.77 ± 0.74^a	0.70 ± 0.17	0.91 ± 0.17^a	0.09 ± 0.03	0.14 ± 0.05	0.04 ± 0.03	0.12 ± 0.05
	S28	0.79 ± 0.16^b	1.74 ± 0.25^b	0.67 ± 0.21	0.53 ± 0.10^b	0.04 ± 0.02	0.04 ± 0.02	0.10 ± 0.04	0.08 ± 0.03
	S29	1.93 ± 0.26^c	2.12 ± 0.28^b	0.39 ± 0.11	0.55 ± 0.13^b	0.07 ± 0.03	0.11 ± 0.04	0.02 ± 0.02	0.01 ± 0.01
	$F_{2,10}$	8.13	16.67	1.28	4.42	1.28	0.82	2.60	2.33
	p	**<0.005**	**<0.005**	0.32	**0.04**	0.32	0.46	0.12	0.15
Round	Morning	1.56 ± 0.22	4.34 ± 0.64^a	0.92 ± 0.21^a	0.89 ± 0.17^a	0.09 ± 0.03	0.13 ± 0.05	0.03 ± 0.02^a	0.06 ± 0.03
	Afternoon	1.96 ± 0.29	2.72 ± 0.38^b	0.40 ± 0.07^b	0.77 ± 0.13^a	0.05 ± 0.02	0.13 ± 0.04	0.11 ± 0.04^b	0.11 ± 0.04
	Evening	1.44 ± 0.32	1.28 ± 0.29^c	0.30 ± 0.17^c	0.26 ± 0.07^c	0.06 ± 0.03	0.03 ± 0.02	0.00 ± 0.00^a	0.03 ± 0.02
	$F_{2,10}$	0.89	10.66	5.29	12.19	1.00	1.30	7.80	1.65
	p	0.44	**<0.005**	**0.03**	**<0.005**	0.40	0.01	**0.01**	0.24
Exclosure	Inside	1.70 ± 0.20	2.71 ± 0.44	0.69 ± 0.16	0.65 ± 0.11	0.08 ± 0.03	0.09 ± 0.03	0.04 ± 0.02	0.06 ± 0.03
	Outside	1.69 ± 0.25	3.04 ± 0.36	0.48 ± 0.12	0.68 ± 0.12	0.05 ± 0.02	0.10 ± 0.04	0.07 ± 0.03	0.08 ± 0.03
	$F_{1,10}$	0.01	0.26	2.18	0.02	0.43	0.01	0.60	0.28
	p	0.94	0.62	0.17	0.88	0.53	0.92	0.46	0.61
Round* Exclosure	$F_{2,10}$	0.01	1.14	0.68	3.64	1.29	0.24	1.40	0.28
	p	0.99	0.36	0.53	0.06	0.32	0.79	0.29	0.76

Table 20. continued

Factor		Number of individual bees per 15 minutes of sweep-netting (mean ± SEM)	
		Specialists	
		2005	2006
Site	S27	0.38 ± 0.15	0.29 ± 0.10
	S28	0.12 ± 0.04	0.16 ± 0.05
	S29	0.12 ± 0.03	0.16 ± 0.06
	$F_{2,10}$	2.78	1.57
	p	0.11	0.26
Round	Morning	0.27 ± 0.09	0.27 ± 0.09
	Afternoon	0.14 ± 0.04	0.20 ± 0.06
	Evening	0.22 ± 0.17	0.14 ± 0.05
	$F_{2,10}$	0.49	1.28
	p	0.65	0.32
Exclosure	Inside	0.30 ± 0.10	0.18 ± 0.04
	Outside	0.12 ± 0.03	0.23 ± 0.07
	$F_{1,10}$	3.43	0.37
	p	0.09	0.56
Round* Exclosure	$F_{2,10}$	0.82	1.03
	p	0.46	0.39

Table 21. List of possible new records for Manitoba, with known distributional ranges taken from Krombein *et al*. (1979) and number of specimens collected. An asterisk beside a species name indicates a possible new record for Canada.

Family	Species	Distribution	Number
Andrenidae	*Andrena* (*Scaphandrena*) *arabis* Robertson *	NY to NC, west to MI & IL	1
	Andrena (*Trachandrena*) *cyanophila* Cockerell	BC, AB, south to CA, NV & AZ	14
	Calliopsis (*Calliopsis*) *andreniformis* Smith	Southeastern CND & Maritimes, to FL west to MT, SD CO, UT, OK, TX	1
	Pseudopanurgus (*Pseudopanurgus*) *nebrascensis* (Cockerell)	ME to NJ, west to CO & AB	2
	Pseudopanurgus (*Pseudopanurgus*) *renimaculatus* Mitchell*	ND, WY, NE, CO, NM, TX	1
	Pseudopanurgus (*Pseudopanurgus*) *simulans* (Swenk and Cockerell)*	ND, NE	1
Apidae	*Melissodes* (*Eumelissodes*) *menuachus* Cresson	BC, AB & ND south to CA, TX & IL & Mexico	1
	Melissodes (*Eumelissodes*) *rustica* (Say)	NS to SK, south to GA, LA, NM & southern Mexico	3
	Nomada (*Nomada*) *pygmaea* Cresson	MN to ME south to VA & CO	1
Halictidae	*Dufourea* (*Halictoides*) *maura* (Cresson)*	ND, WY, ID, NE, CO, NM	61
	Lasioglossum (*Dialictus*) *pruinosiforme* (Crawford)	AB, SD, IA, NE, NM, TX, AZ, NV, CA	67
	Lasioglossum (*Dialictus*) *pruinosum* (Robertson)	New England, south to NJ, west to AB and AZ	98
	Lasioglossum (*Dialictus*) *succinipenne* (Ellis)*	CO	2610
Megachilidae	*Hoplitis* (*Androicus*) *cylindrica* (Cresson)	QC & NS to FL, west to NWT, BC, Colo	1
	Megachile (*Xanthosarus*) *perihirta* Cockerell	AB to NE & TX west to BC & CA	3
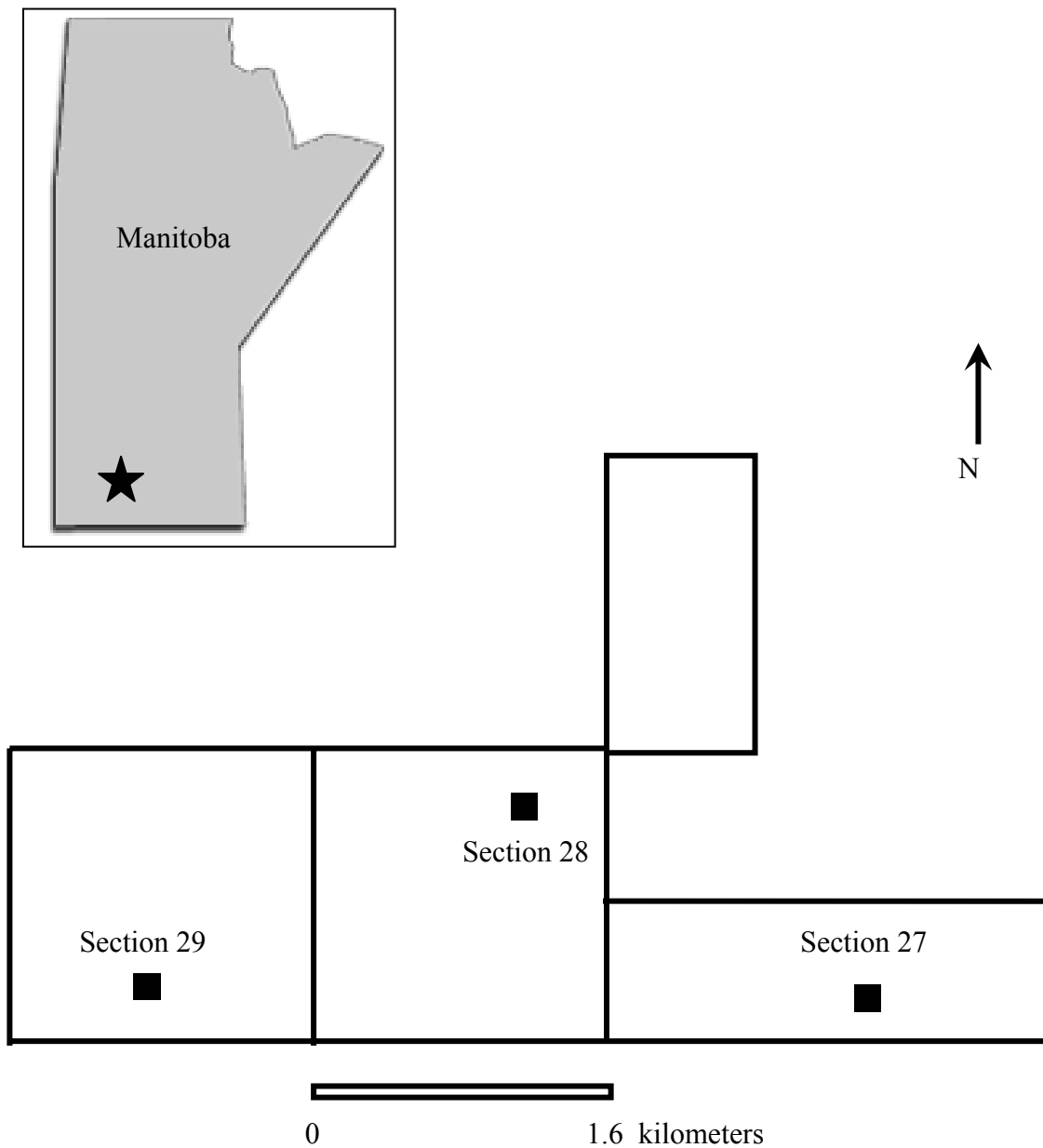
Figure 1. General location (inset) and outline of the Yellow Quill Mixed Grass Prairie (YQMGP) Preserve near Treesbank, Manitoba. The location of the YQMGP in the province of Manitoba is indicated by a star in the inset to the upper right. The three 1-ha grazing exclosures where sampling occurred are indicated by the solid black squares.
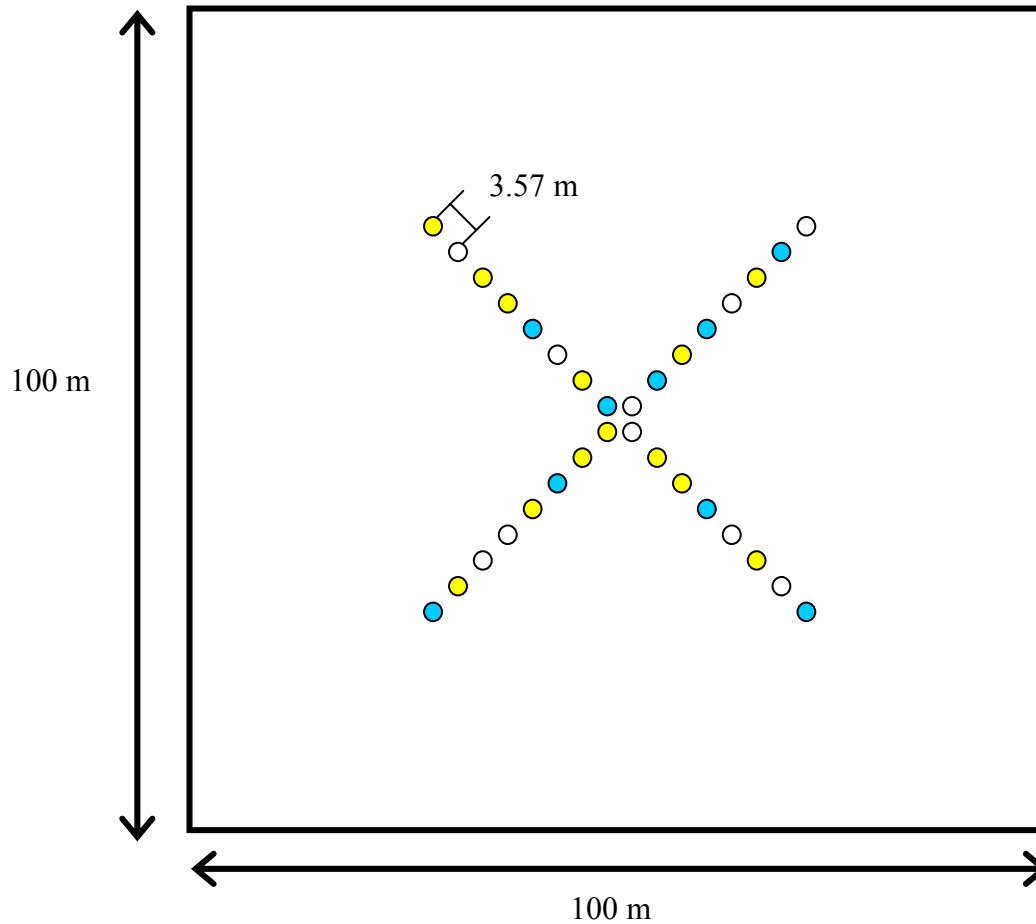
Figure 2. Configuration of the bee bowl array used to sample wild bees within 1-ha grazing exclosures at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. Ten bowls each of the colours white (white circles), fluorescent yellow (light grey circles) and fluorescent blue (grey circles) were randomized throughout the configuration.
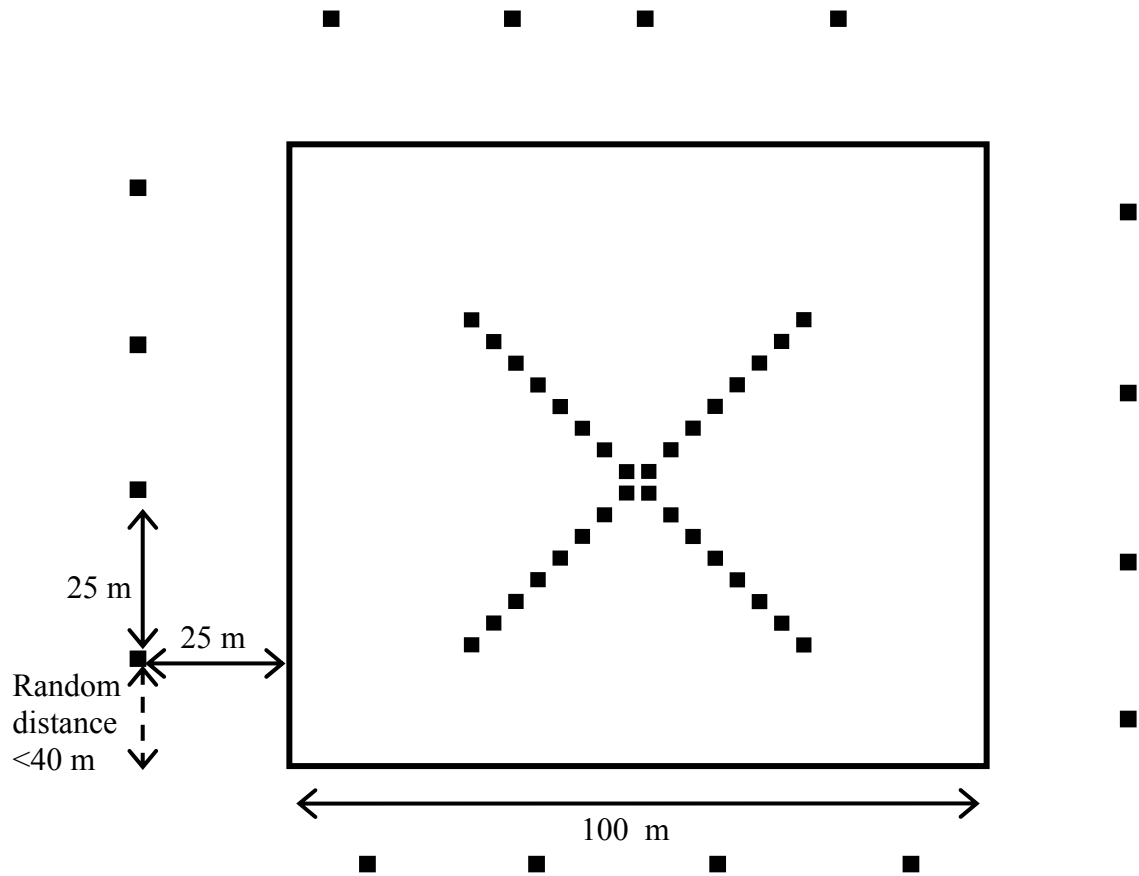
Figure 3. Configuration of the 46 - 1 m X 1 m permanent forb flowering stem counting stations in relation to the grazing exclosures at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.
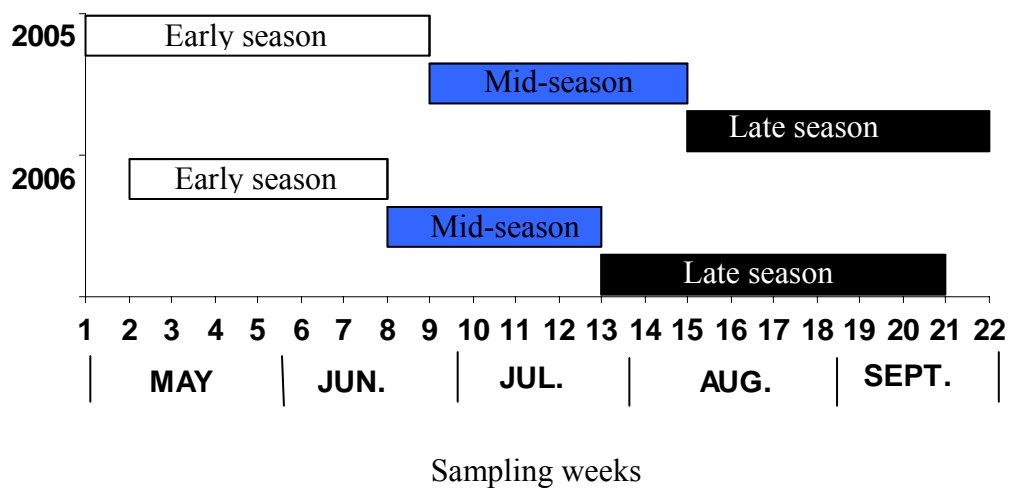
Figure 4. Representation of the sampling weeks in 2005 and 2006 that were grouped to form three seasonal times periods of "early," "mid," and "late" used in the multivariate modeling of seasonal trends for bees and flowering stems in the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.
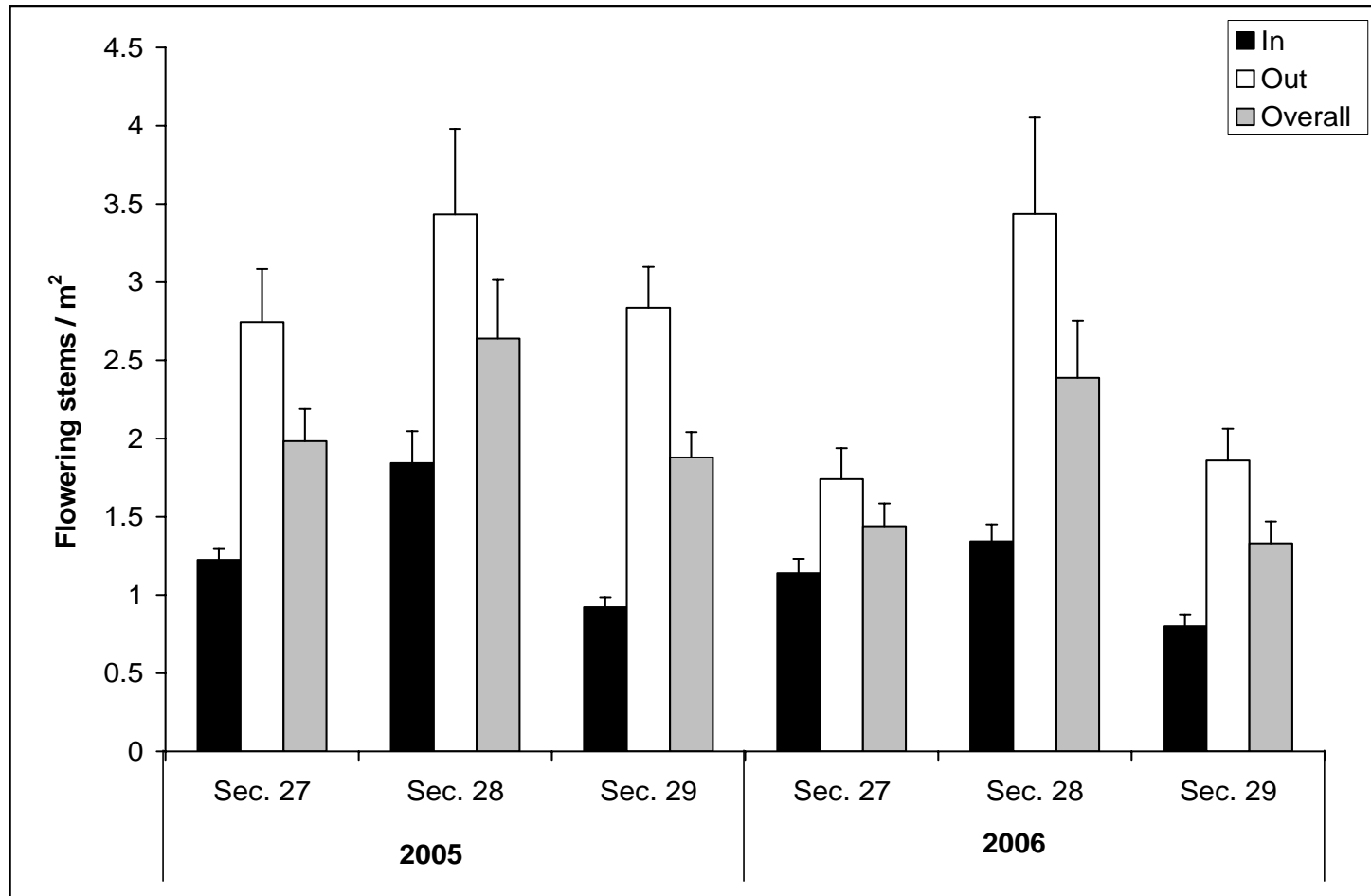
Figure 5. Mean density (mean ± SEM) of forb flowering stems counted inside permanent 1m X 1m quadrats located inside (n=30) and outside (n=16) of the grazing exclosures at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba by site and year.
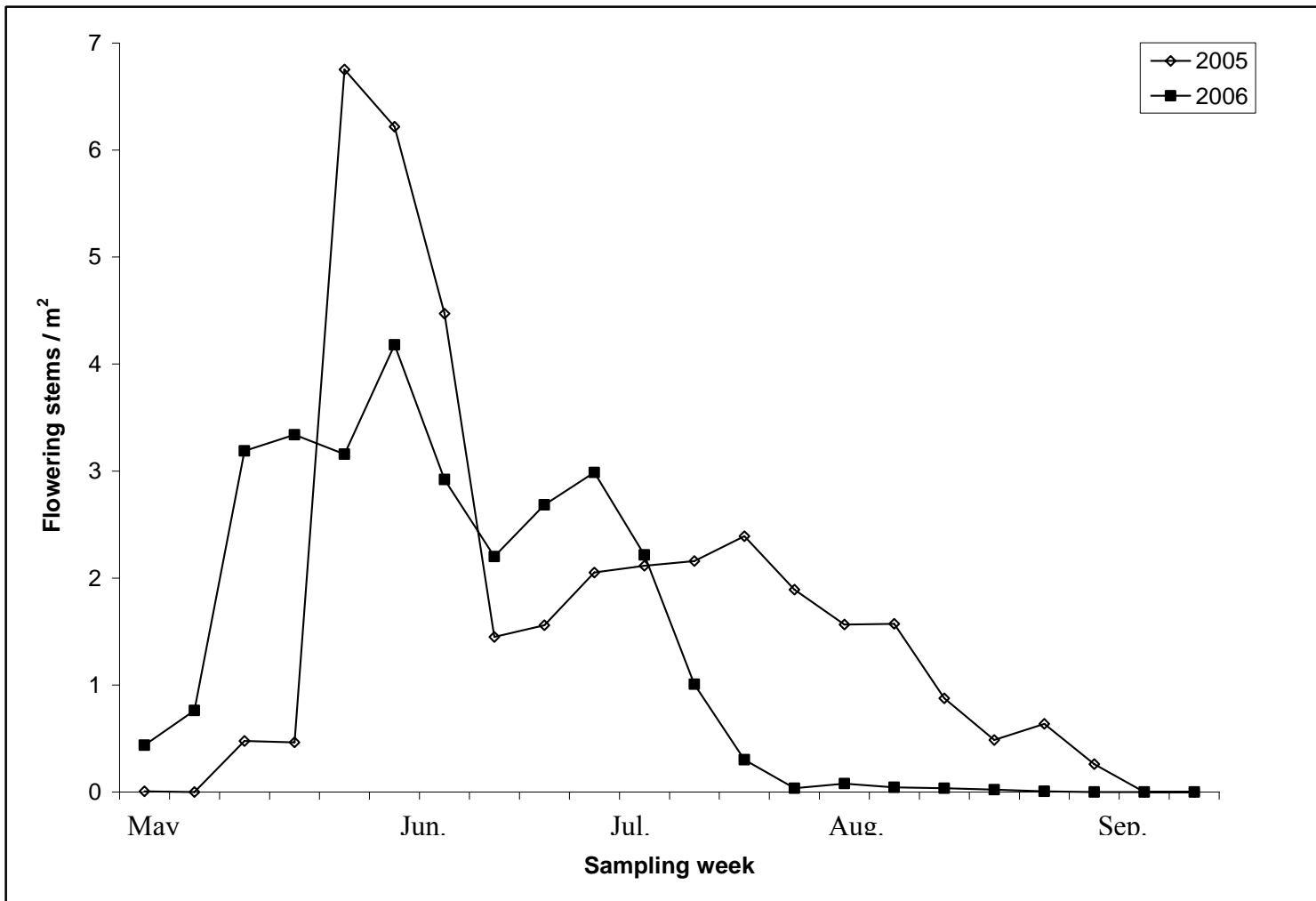
Figure 6. Seasonal pattern in mean density of forb flowering stems at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba in 2005 (empty diamonds) and 2006 (solid squares).
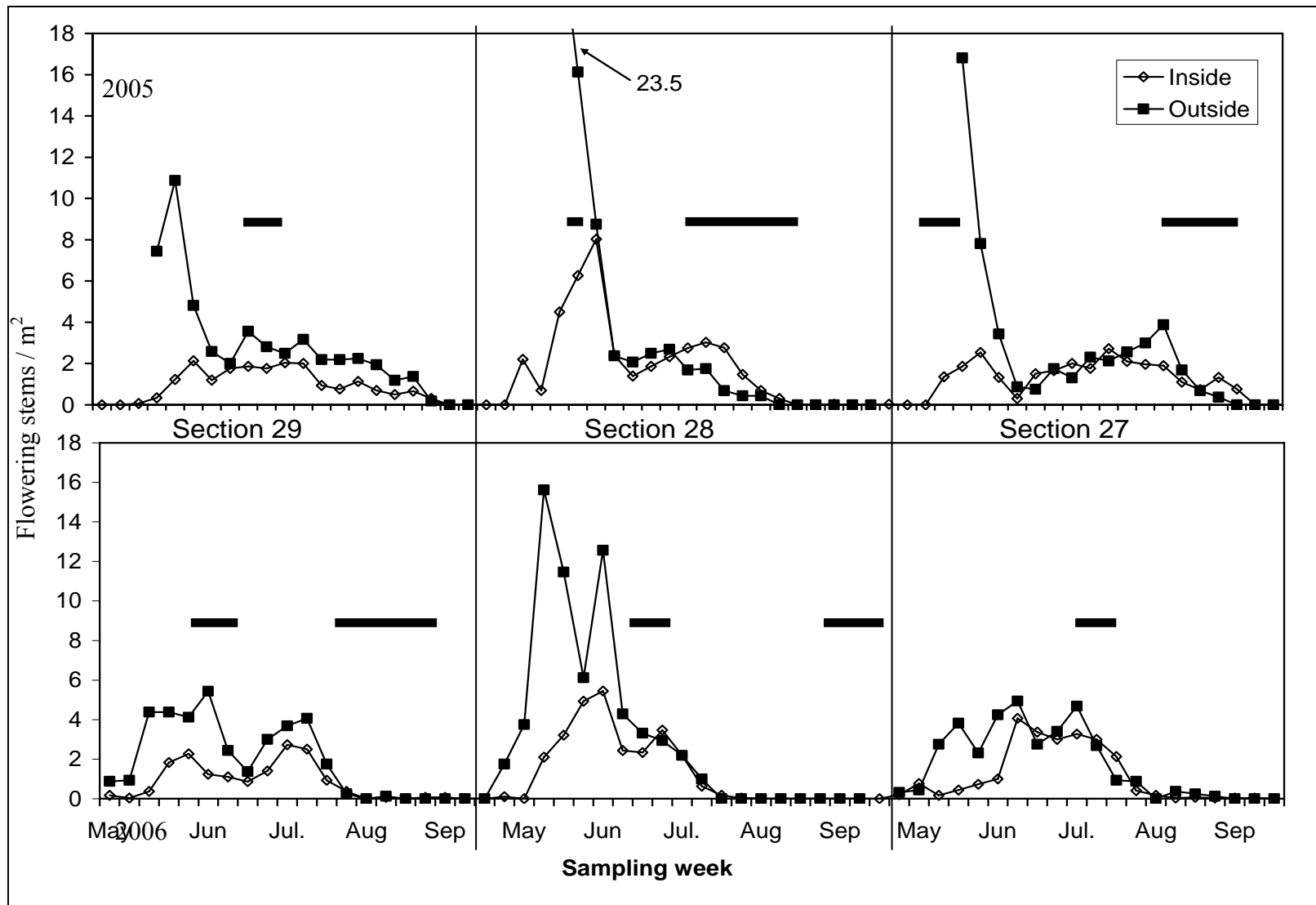
Figure 7. Seasonal pattern in the density of forb flowering stems by site, year (top panel = 2005, bottom panel =2006) and location relative to the grazed area outside of the exclosure ('outside') or in the ungrazed areas inside of the exclosure ('inside') at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. Floating black bars inside the plots indicate periods when grazing cattle were present at each site.
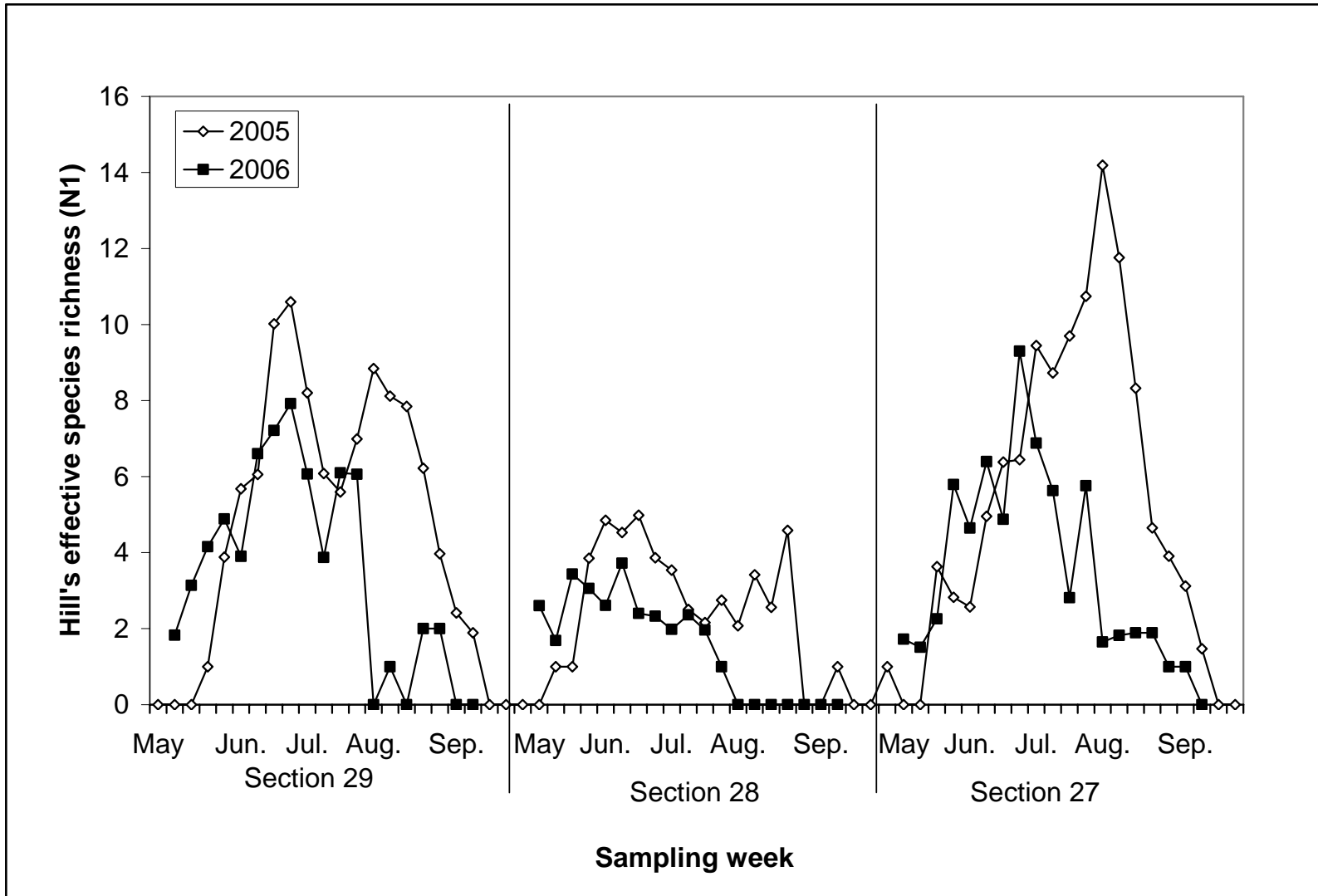
Figure 8. Weekly values for Hill's effective species richness (N1) of forb flowering stems counted inside 46 permanent 1m X 1m quadrats at three sites at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba in 2005 (empty diamonds) and 2006 (solid squares).

Figure 9. Principle Components Analysis ordination diagram of flowering forb species (Δ) and sites (■) associated with three seasonal periods at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba in 2005. The suffix '_1' after site labels refers to early-season assemblages, the suffix '_2' refers to the mid-season assemblages, and the suffix '_3' refers to the late-season assemblages.

Species codes: Ach_mill = *Achillea millefolium*, Ago_gla = *Agoseris glauca*, All_tex = *Allium textile*, And_sep = *Androsace septentrionalis*, Ane_cyl = *Anemone cylindrica*, Ant_neo = *Antennaria neodioica*, Ara_hob = *Arabis holboellii var. collinsii*, Ara_sp. = *Arabis* sp., Ast_cra = *Astragalus crassicarpus*, Ast_eri = *Aster ericoides*, Ast_pta = *Aster ptarmicoides*, Bra_sp1 = *Brassica* sp. 1, Cam_rot = *Campanula rotundifolia*, Cer_arv = *Cerastium arvense*, Chr_vil = *Chrysopsis villosa*, Com_umb = *Comandra umbellata*, Ech_ang = *Echinacea angustifolia*, Eri_glab = *Erigeron glabellus*, Eri_sp2 = *Erigeron* sp. 2, Eri_sp3 = *Erigeron* sp. 3, Ery_asp = *Erysimum asperum*, Ery_inc = *Erysimum inconspicum*, Eup_esu = *Euphorbia esula*, Gai_ari = *Gaillardia arista*, Gal_bor = *Galium boreale*, Geu_tri = *Geum triflorum*, Hel_lae = *Helianthus laetiflorus*, Heu_ric = *Heuchera richardsonii*, Hou_lon = *Houstonia longifolia*, Lac_pul = *Lactuca pulchella*, Lia_pun = *Liatris punctata*, Lil_phi = *Lilium philadelphicum*, Lin_lew = *Linum lewisii*, Lit_can = *Lithospermum canescens*, Lit_inc = *Lithospermum incisum*, Med_lup = *Medicago lupulina*, Med_sat = *Medicago sativa*, Mon_fis = *Monarda fistulosa*, Oen_nut = *Oenothera nuttallii*, Oen_ser = *Oenothera serrulata*, Ono_his = *Onosmodium hispidissimum*, Ort_lut = *Orthocarpus luteus*, Oxy_spl = *Oxytropis splendens*, Pen_gra = *Penstemon gracilis*, Pet_can = *Dalea candida*, Pet_pur = *Dalea purpurea*, Pot_agn = *Potentilla argentea*, Pot_arg = *Potentilla arguta*, Pru_pum = *Prunus pumila*, Pso_esc = *Psoralea esculenta*, Ran_rho = *Ranunculus rhomboideus*, Ros_ark = *Rosa arkansana*, Sen_pla = *Senecio plattensis*, Sis_mon = *Sisyrinchium montanum*, Sol_nem = *Solidago nemoralis*, Sol_sp1 = *Solidago* sp. 1, Sym_occ = *Symphoricarpos occidentalis*, Tar_off = *Taraxacum officinale*, Vic_ame = *Vicia americana*, Vio_ped = *Viola pedatifida*.
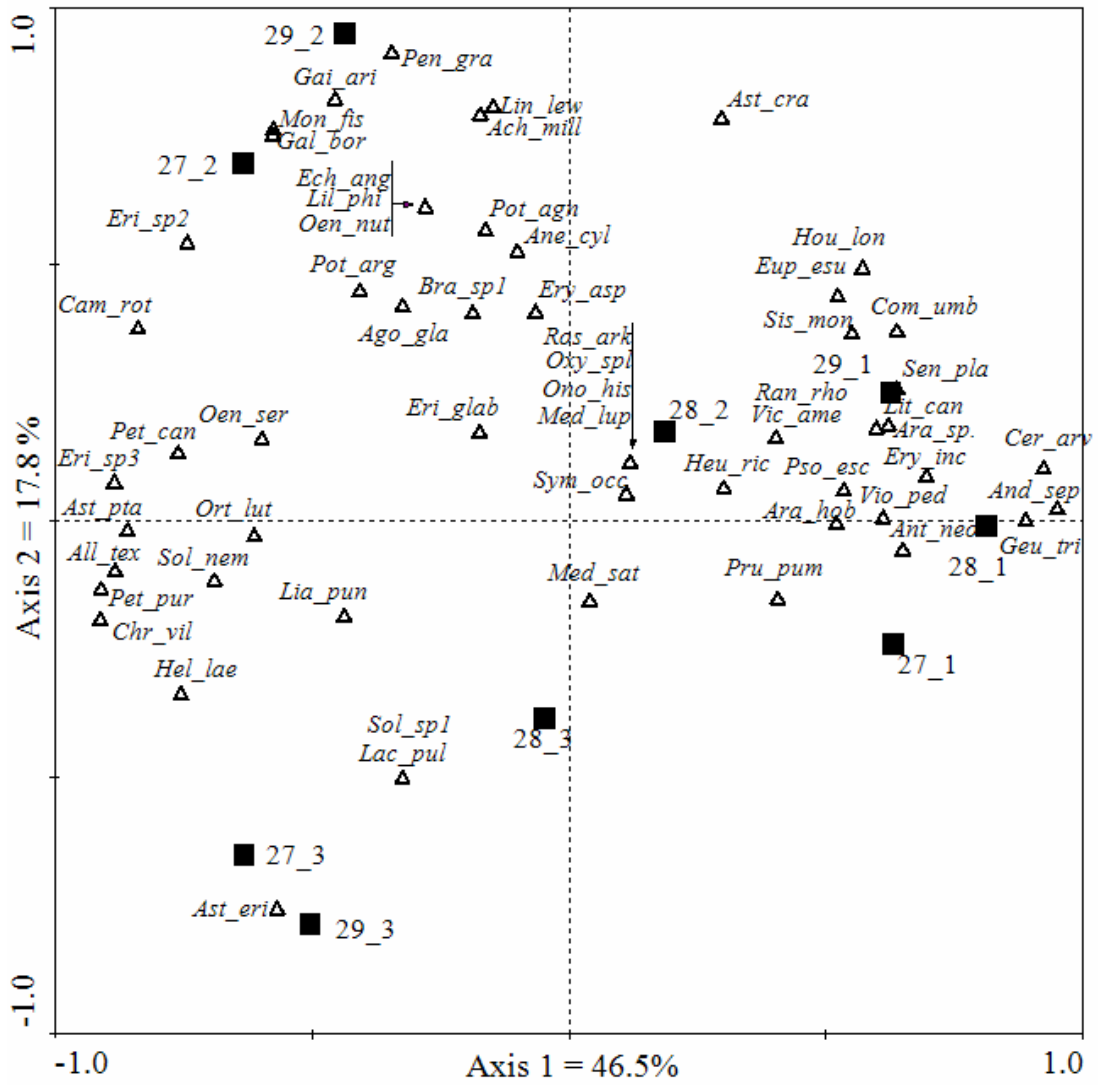
Figure 10. Principle Components Analysis ordination diagram of flowering forb species (Δ) and sites (■) associated with three seasonal periods at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba in 2006. The suffix '_1' after site labels refers to early-season assemblages, the suffix '_2' refers to the mid-season assemblages, and the suffix '_3' refers to the late-season assemblages.

Species codes: Ach_mill = *Achillea millefolium*, Ago_gla = *Agoseris glauca*, All_tex = *Allium textile*, And_sep = *Androsace septentrionalis*, Ane_cyl = *Anemone cylindrica*, Ant_neo = *Antennaria neodioica*, Ast_cra = *Astragalus crassicarpus*, Ast_eri = *Aster ericoides*, Ast_pta = *Aster ptarmicoides*, Bra_sp1 = *Brassica* sp. 1, Cam_rot = *Campanula rotundifolia*, Cer_arv = *Cerastium arvense*, Chr_vil = *Chrysopsis villosa*, Com_umb = *Comandra umbellata*, Ech_ang = *Echinacea angustifolia*, Eri_glab = *Erigeron glabellus*, Eri_sp3 = *Erigeron* sp. 3, Ery_asp = *Erysimum asperum*, Ery_inc = *Erysimum inconspicum*, Eup_esu = *Euphorbia esula*, Gai_ari = *Gaillardia arista*, Gal_bor = *Galium boreale*, Geu_tri = *Geum triflorum*, Heu_ric = *Heuchera richardsonii*, Hou_lon = *Houstonia longifolia*, Lia_pun = *Liatris punctata*, Lil_phi = *Lilium philadelphicum*, Lin_lew = *Linum lewisii*, Lit_can = *Lithospermum canescens*, Mon_fis = *Monarda fistulosa*, Oen_nut = *Oenothera nuttallii*, Oen_ser = *Oenothera serrulata*, Ono_his = *Onosmodium hispidissimum*, Ort_lut = *Orthocarpus luteus*, Oxy_spl = *Oxytropis splendens*, Pen_gra = *Penstemon gracilis*, Pet_can = *Dalea candida*, Pet_pur = *Dalea purpurea*, Pot_agn = *Potentilla argentea*, Pot_arg = *Potentilla arguta*, Pru_pum = *Prunus pumila*, Pso_esc = *Psoralea esculenta*, Ran_rho = *Ranunculus rhomboideus*, Ros_ark = *Rosa arkansana*, Sis_mon = *Sisyrinchium montanum*, Sol_nem = *Solidago nemoralis*, Sol_sp1 = *Solidago* sp. 1, Sym_occ = *Symphoricarpos occidentalis*, Tar_off = *Taraxacum officinale*, Vio_ped = *Viola pedatifida*.

Axis 1 = 40.2 %

Axis 2 = 29.7 %

1.0

-1.0

-1.0

1.0

Gal_bor *Gai_ari*
Lin_lew
Cam_rot
Pen_gra *Ast_cra*
27_2
Mon_fis
Ane_cyl *Eri_glab*
Ros_ark
29_2
Ach_mill
Pet_can
Oen_ser
Oen_nut
Ech_ang
27_1
Ort_lut
Eri_sp1 *Tra_dub*
Heu_ric
Ago_gla
Hou_lon
Pet_pur
Lil_phi
All_tex
Pso_esc *Pot_arg* *Com_umb*
29_1
Chr_vil
Pru_pum
Cer_arv
Bra_sp1
Lit_can *Geu_tri*
Ery_asp
Sol_sp1
Ast_pta
Ant_neo
Ran_rho
Sis_mon
Vio_ped
Eup_esu
Oxy_spl
And_sep.
28_1
Ono_his
Sym_acc
Pot_agn
Lia_pun
28_2
Eri_sp3
Sol_mis
Ast_eri
29_3
Sol_nem
27_3
28_3

Figure 11. Seasonal patterns of *Apis mellifera* catches at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba by site in 2005 (top panel) and 2006 (bottom panel).
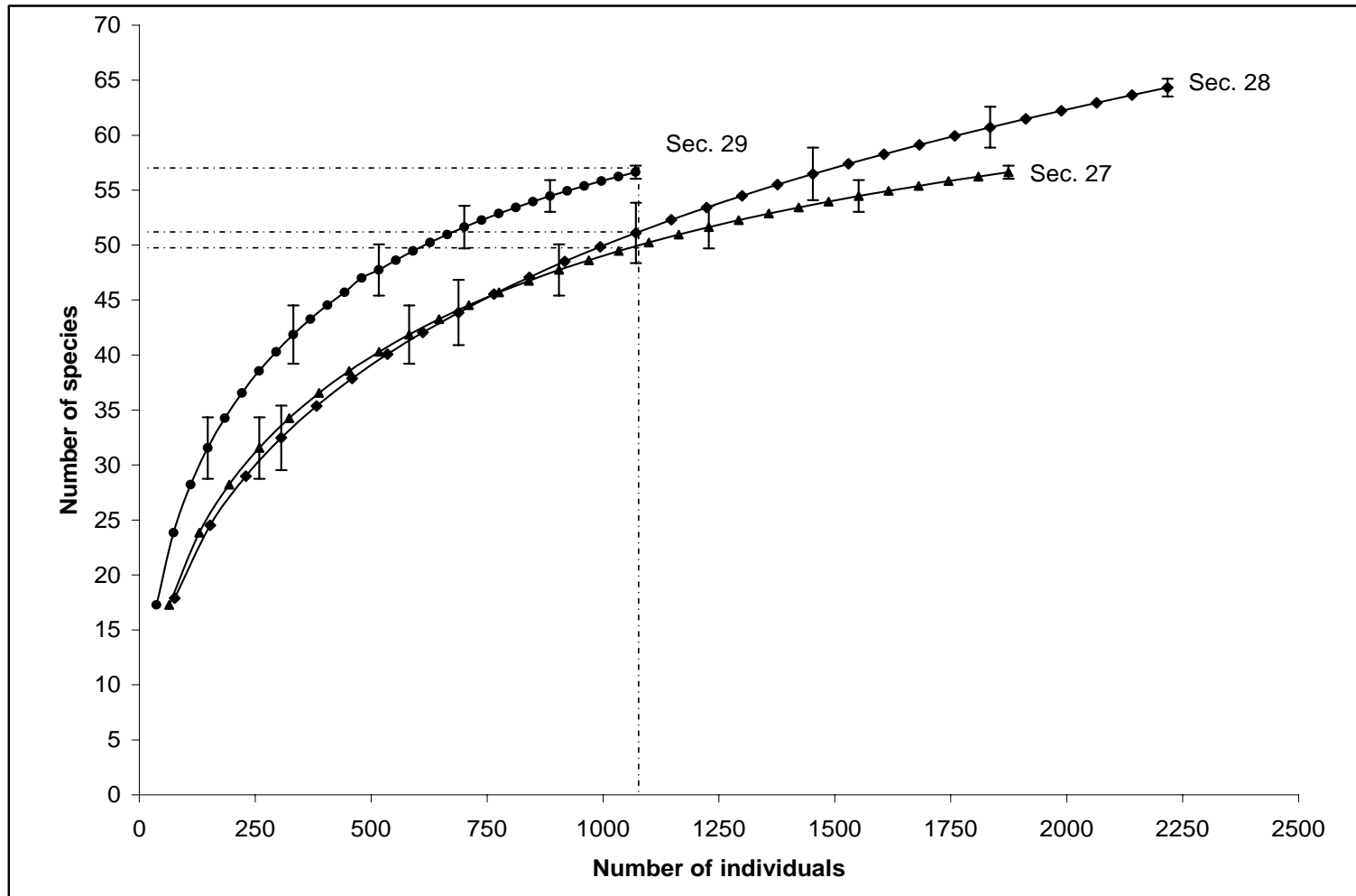
Figure 12. Coleman rarefaction curves of bee bowl sampling for each of three sites at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. Error bars, representing one standard deviation, are included for every fifth data point. The broken lines represent the level at which estimates of rarefied species richness are compared. Sampling occurred weekly during the frost free season of 2005 and 2006.

a)

Social nesters
27%

Miners
47%

Cavity nesters
18%

Cleptoparasites
8%

b)

Cavity nesters
5%

Cleptoparasites
1%

Social nesters
76%

Miners
18%
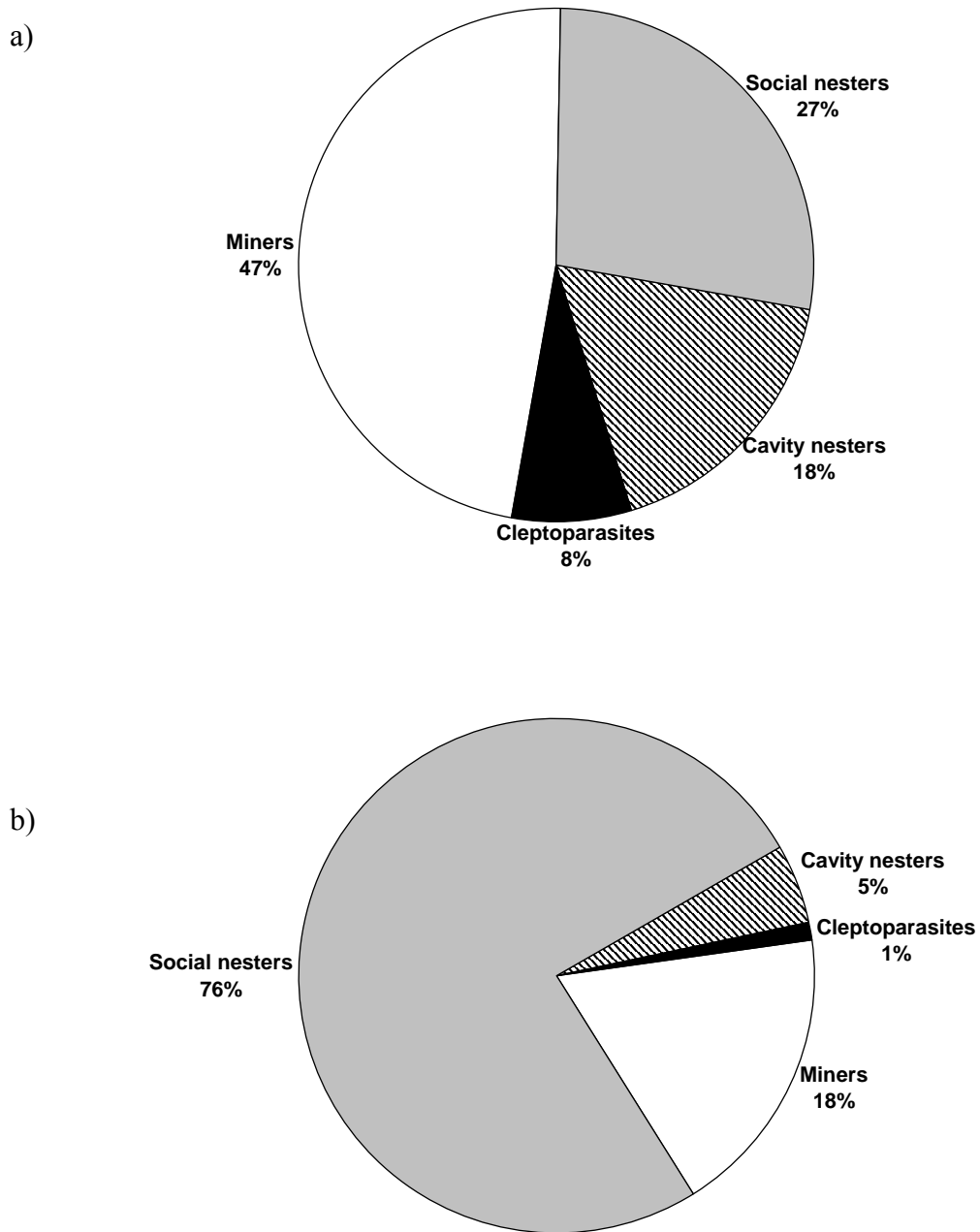
Figure 13. Percentages of a) species and b) individuals captured in bee bowls in 2005 and 2006 that belong to each of the four nesting guilds at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.
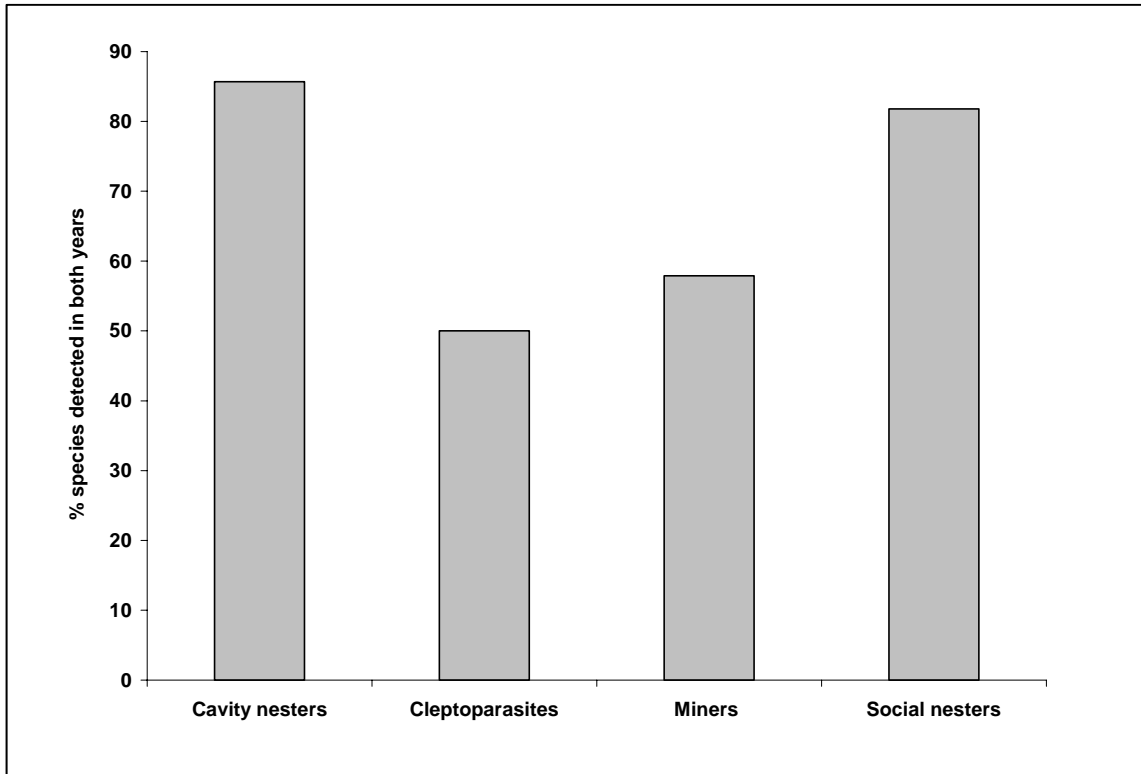
Figure 14. Levels of species turnover between 2005 and 2006 within each nesting guild detected by bee bowls at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. Low values for the percentage of species collected in both year, shown on the y-axis, indicate high levels of species turnover.
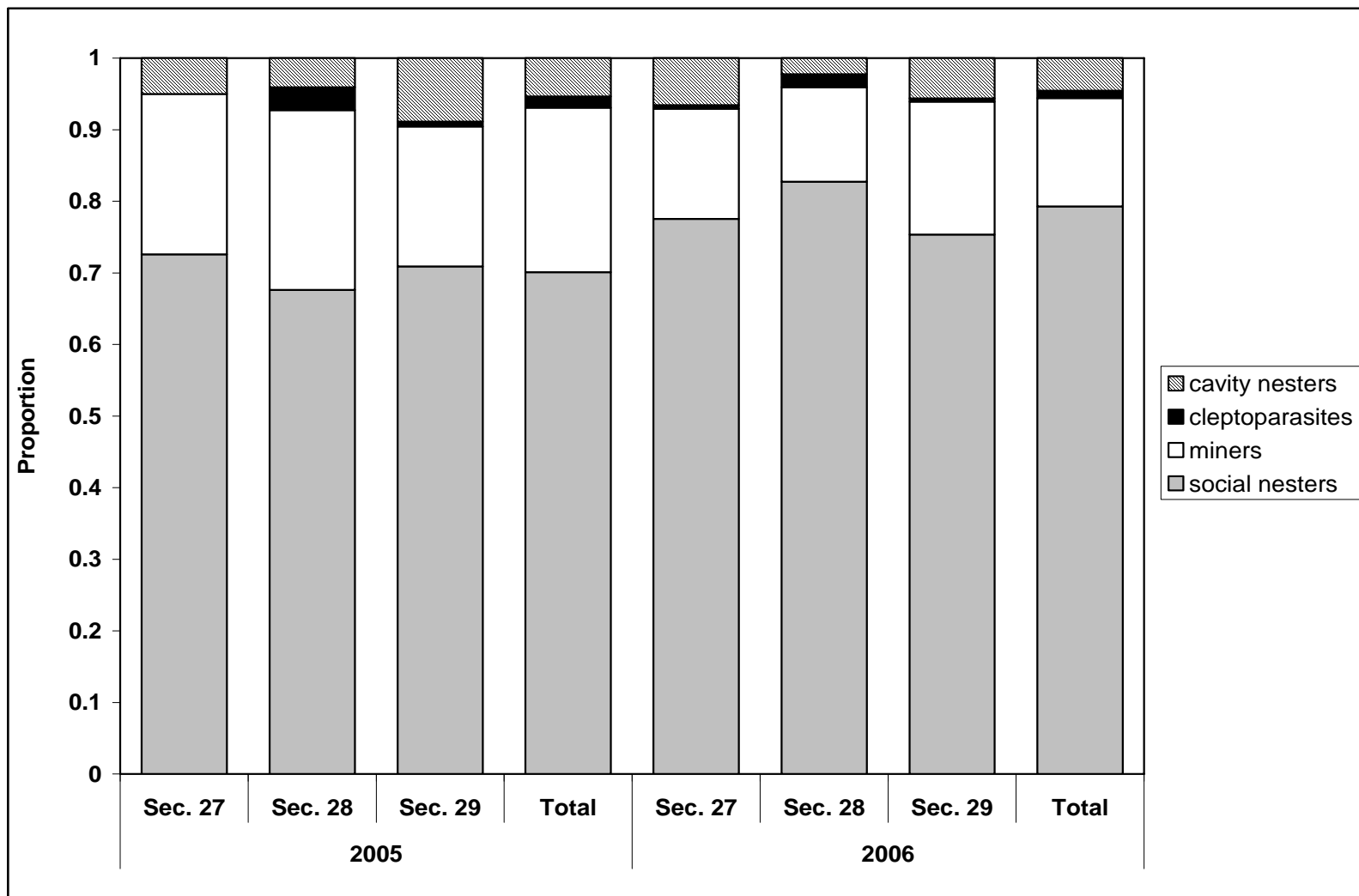
Figure 15. Relative abundance of wild bee individuals among four nesting guilds captured in bee bowls at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba by site and year.
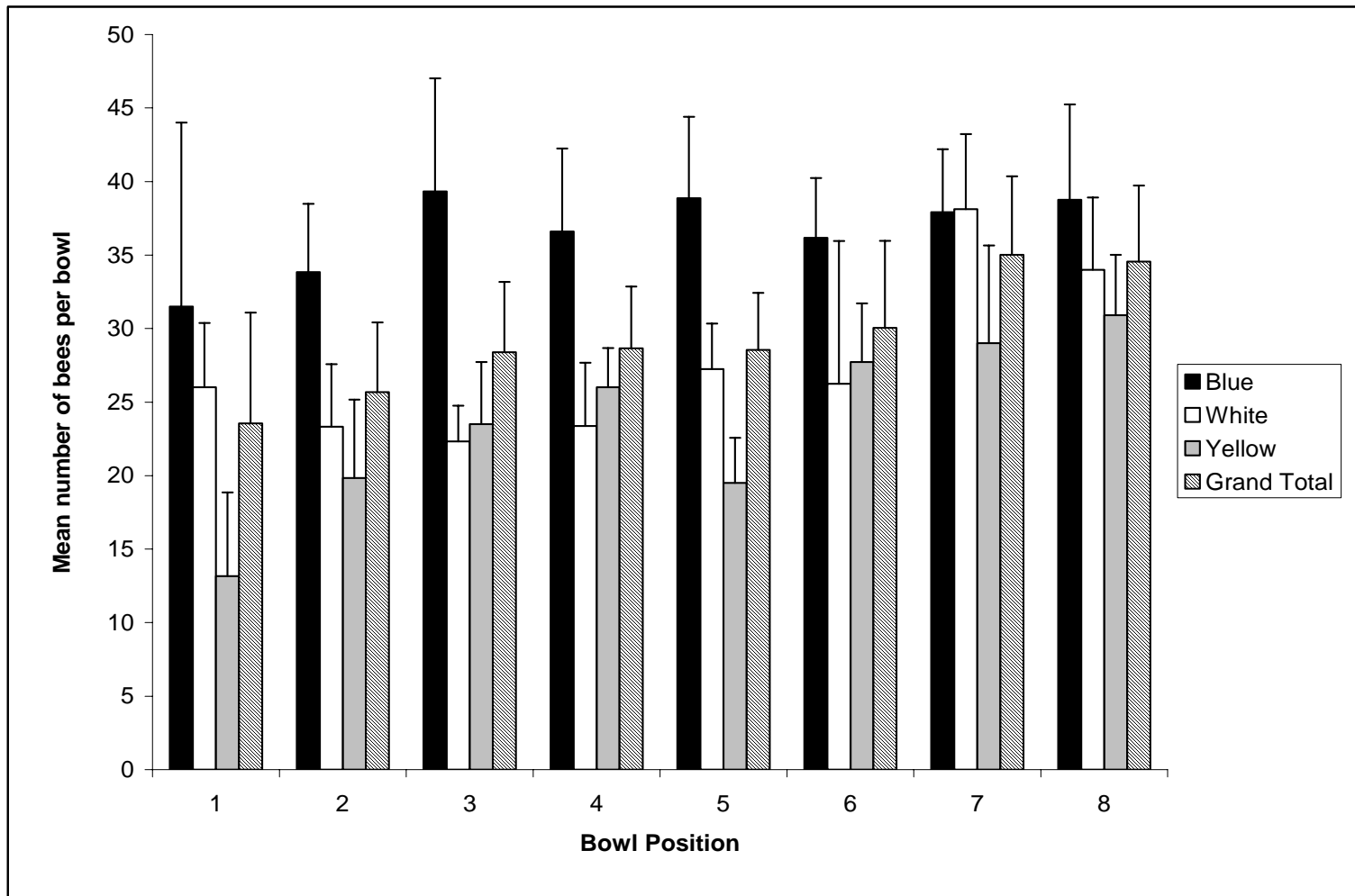
Figure 16. Mean bee bowl catch by bowl colour and position within the experimental 'X' configuration at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. Bowl position numbers on the x-axis increase from the centre to the extremities of the configuration. Error bars represent the standard error of the mean.
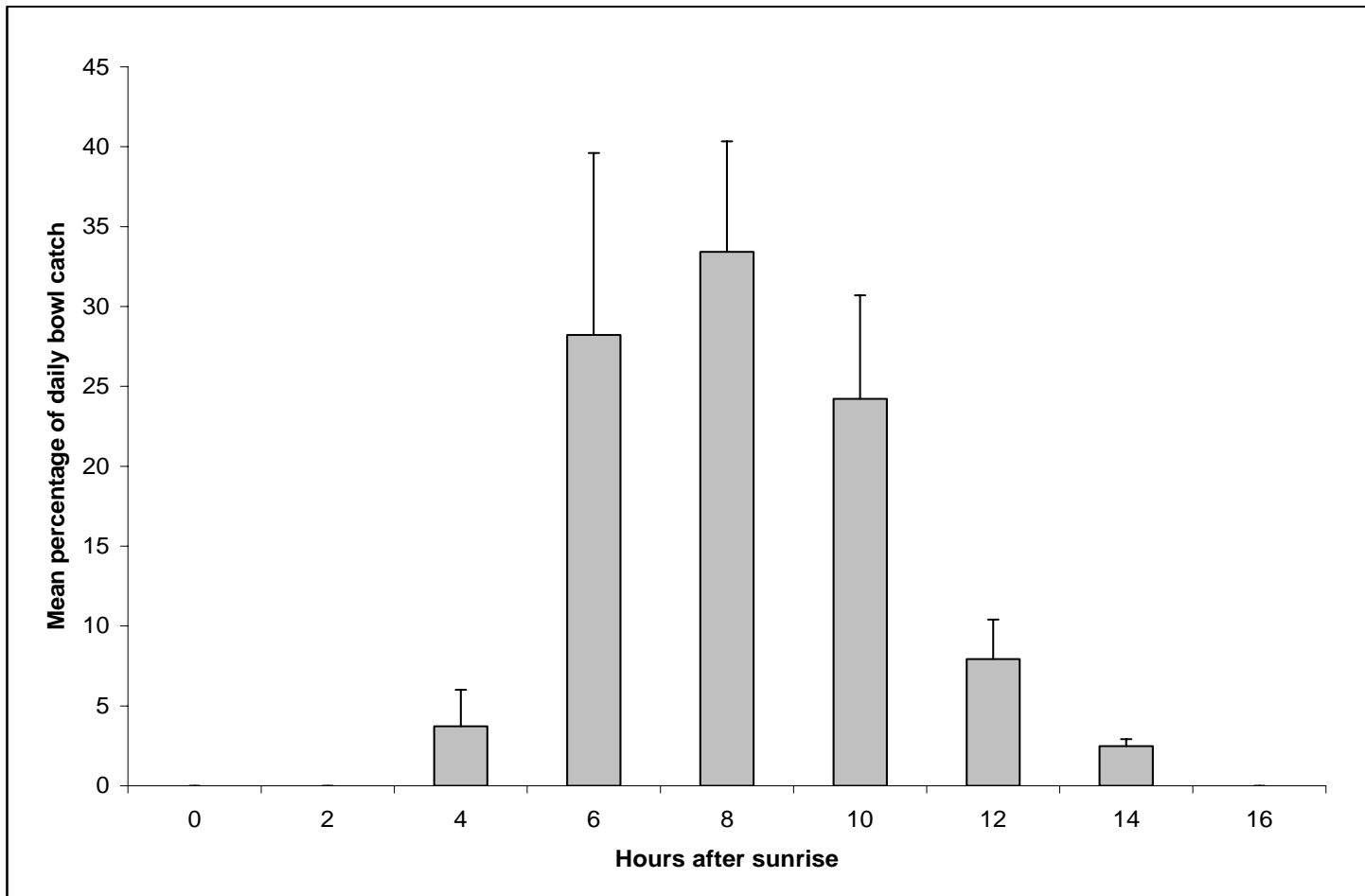
Figure 17. Mean percentage of daily catch captured in two-hour time intervals after sunrise over the course of three days in 2005 at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. Sampling dates were May 5, July 12 and August 30. The error bars represent the standard error of the mean.
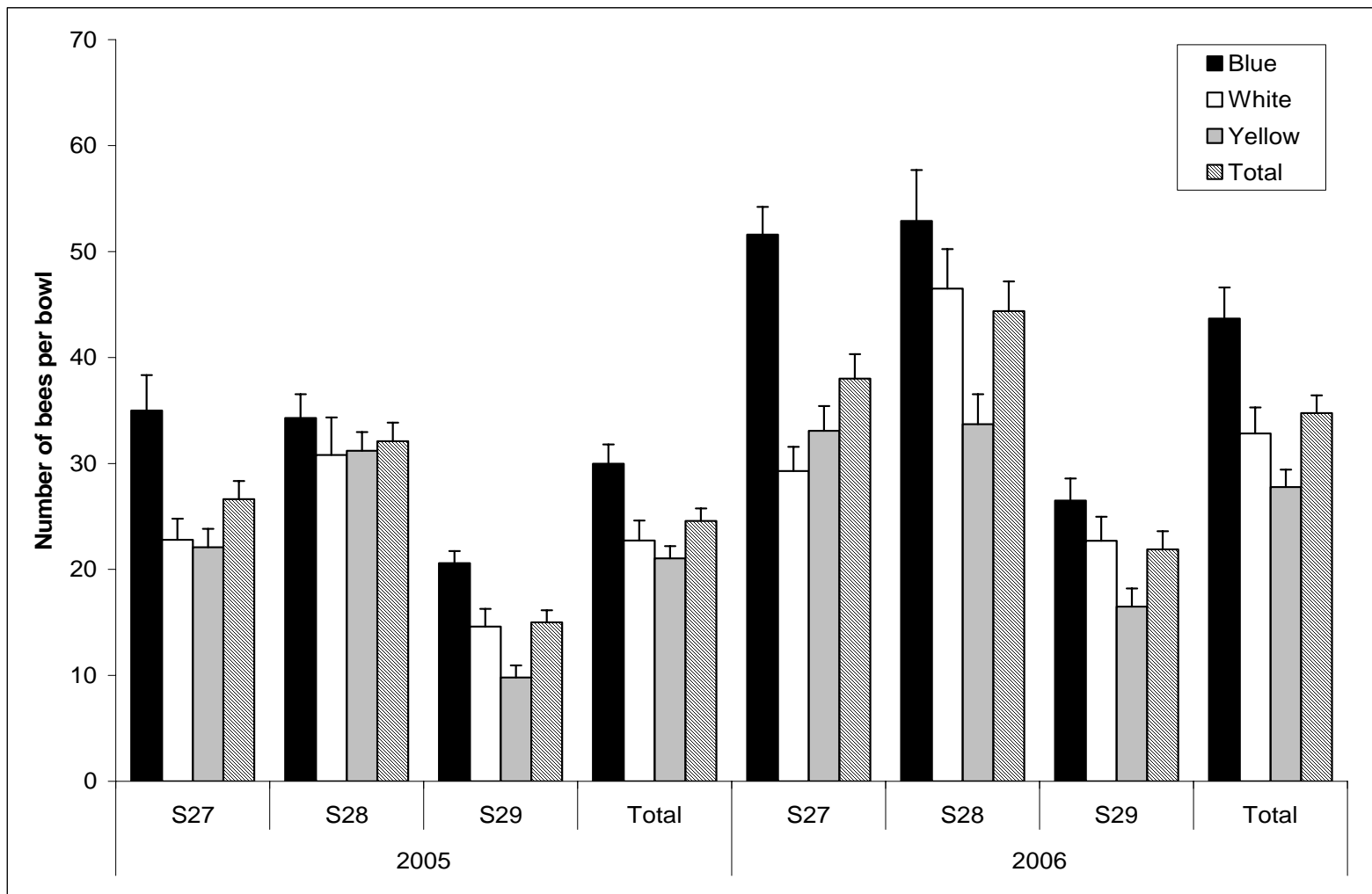
Figure 18. Mean overall bowl catch by year, site and colour at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. The error bars represent the standard error of the mean.
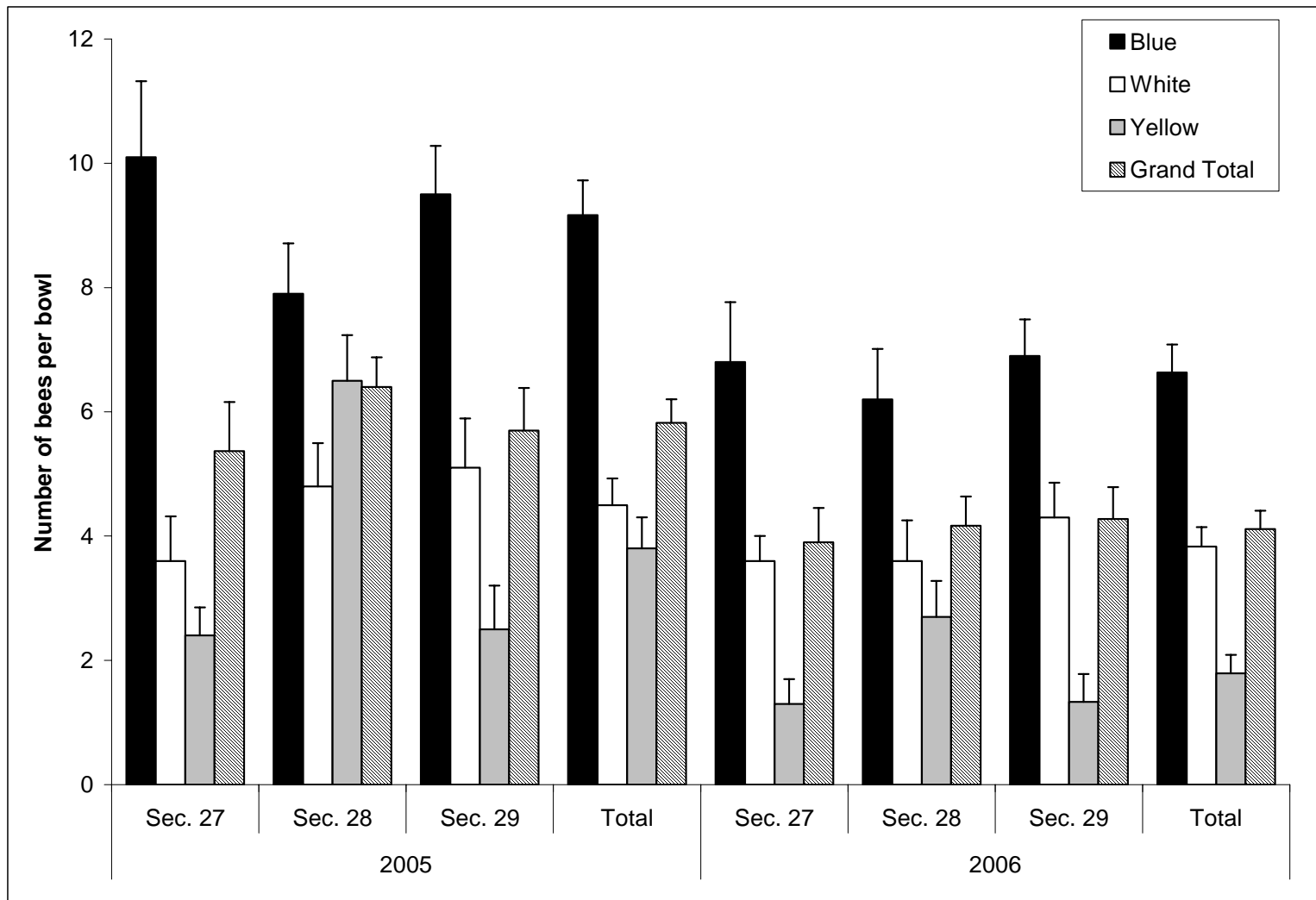
Figure 19. Mean overall bowl catch frequency of apids (Hymenoptera: Apidae, excluding *Apis*) by year, site and bowl colour at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. The error bars represent the standard error of the mean.
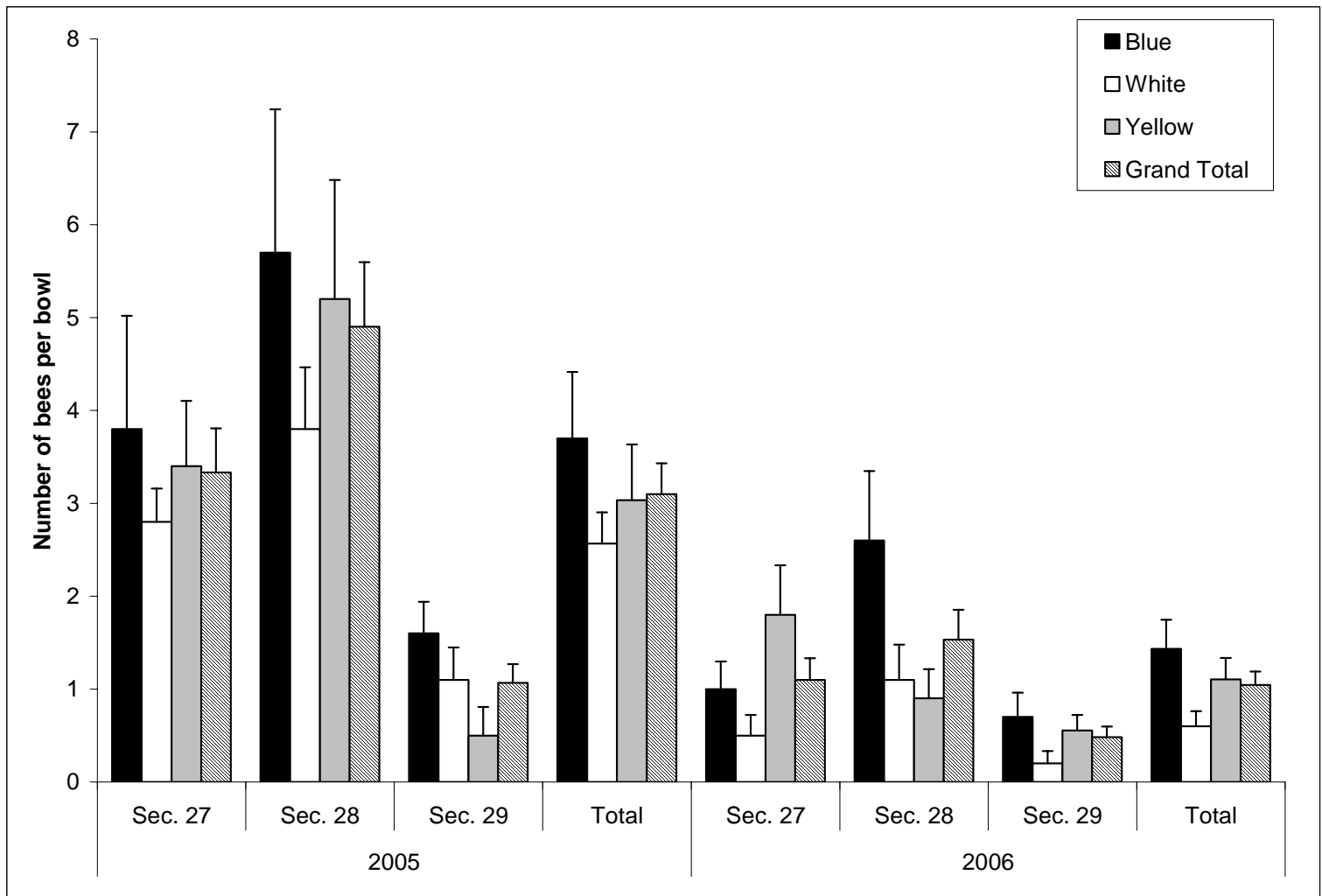
Figure 20. Mean overall bowl catch frequency of andrenids (Hymenoptera: Andrenidae) by year, site and bowl colour at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba The error bars represent the standard error of the mean.
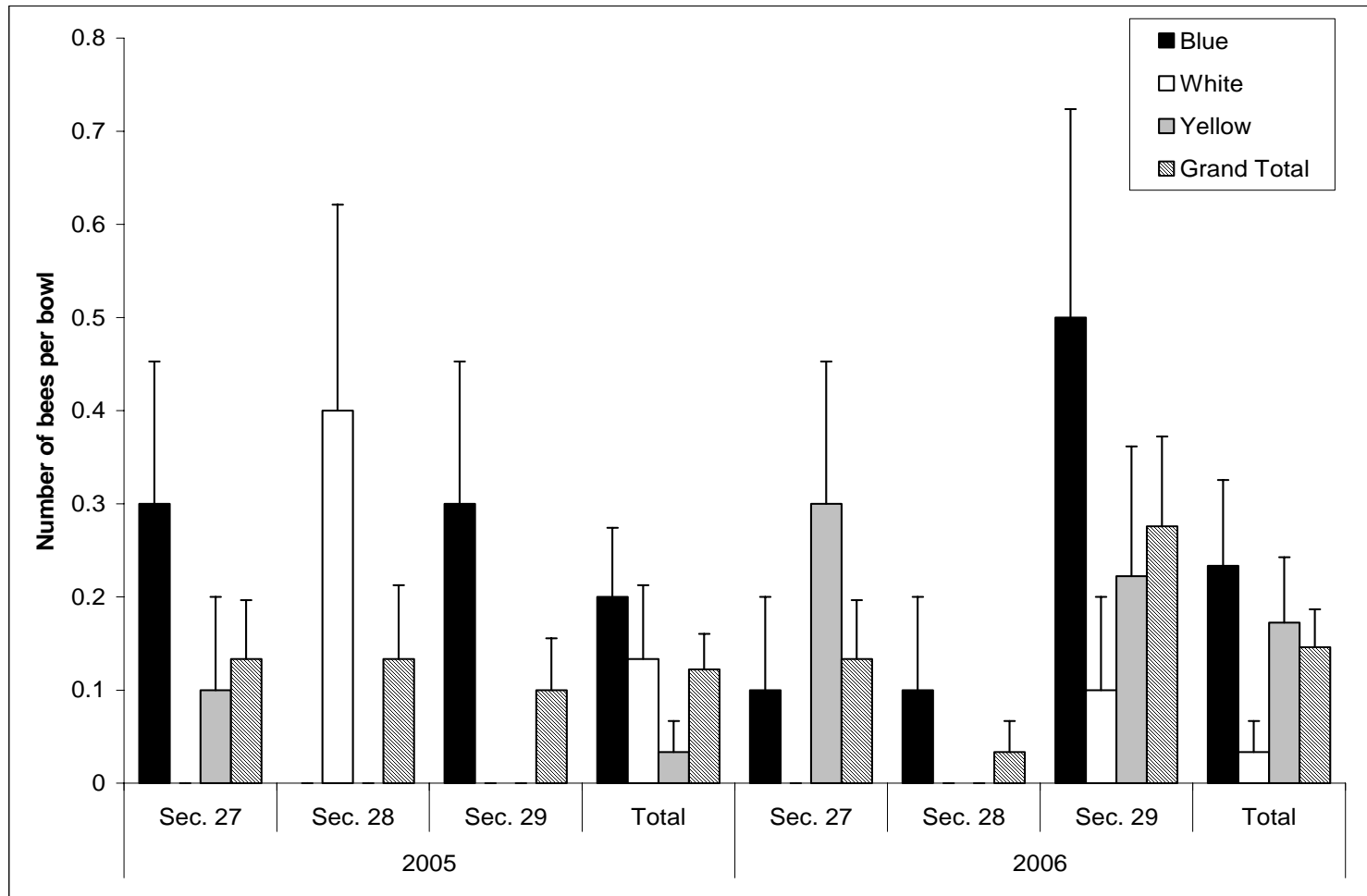
Figure 21. Mean overall bowl catch frequency of colletids (Hymenoptera: Colletidae) by year, site and bowl colour at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. The error bars represent the standard error of the mean.
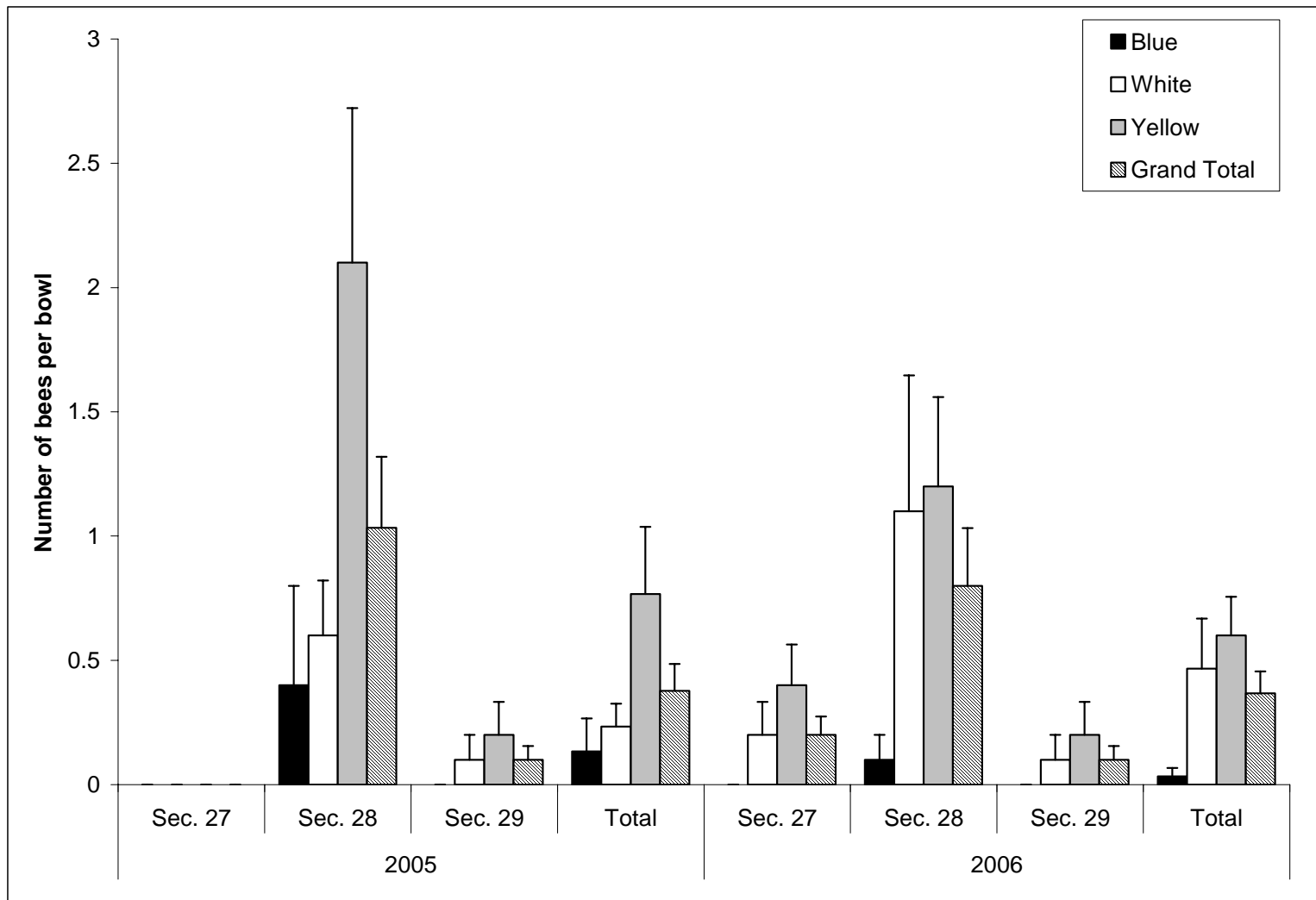
Figure 22. Mean overall bowl catch frequency of cleptoparasitic bees by year, site and bowl colour at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. The error bars represent the standard error of the mean.
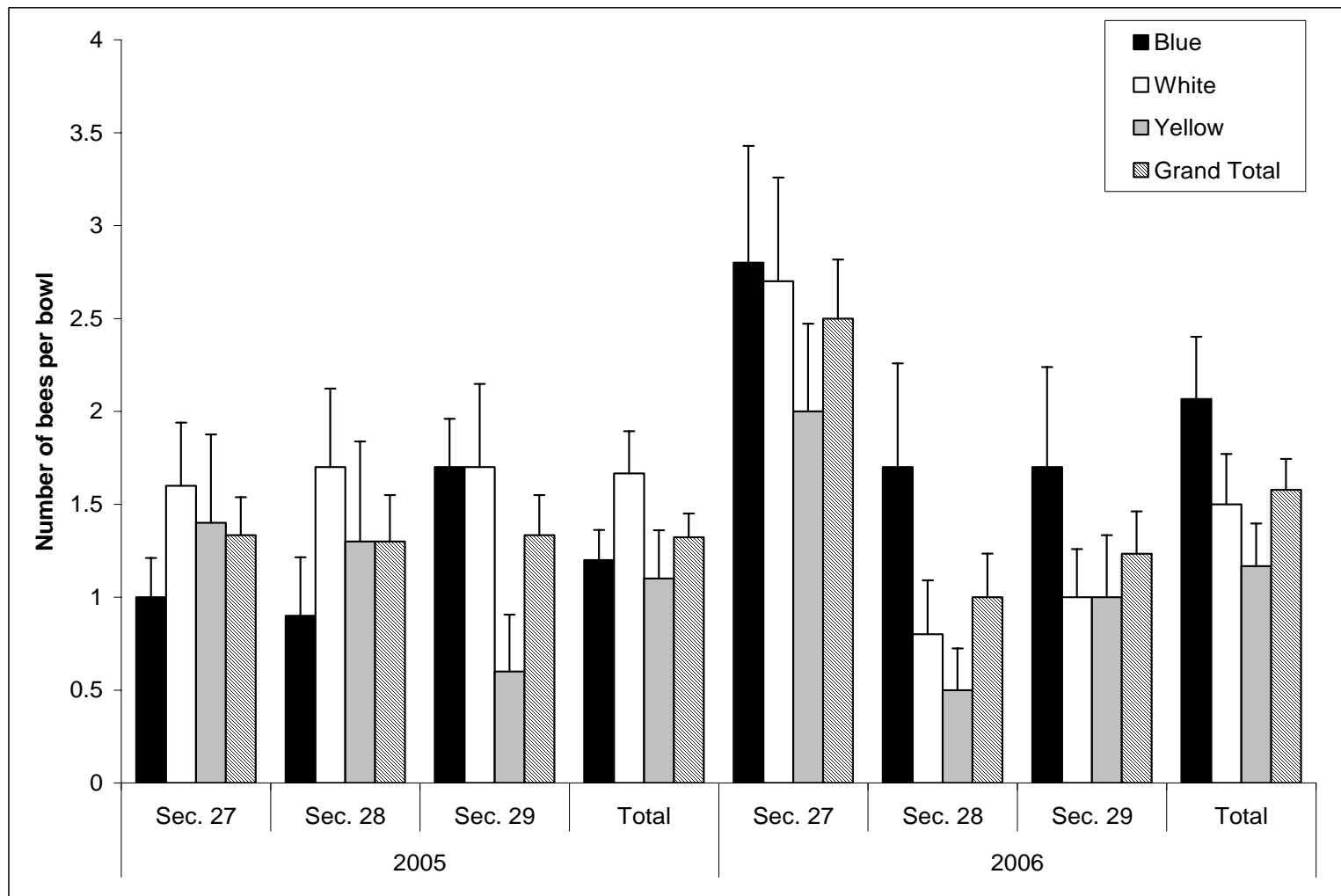
Figure 23. Mean overall bowl catch frequency of cavity nesting bees by year, site and bowl colour at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. The error bars represent the standard error of the mean.
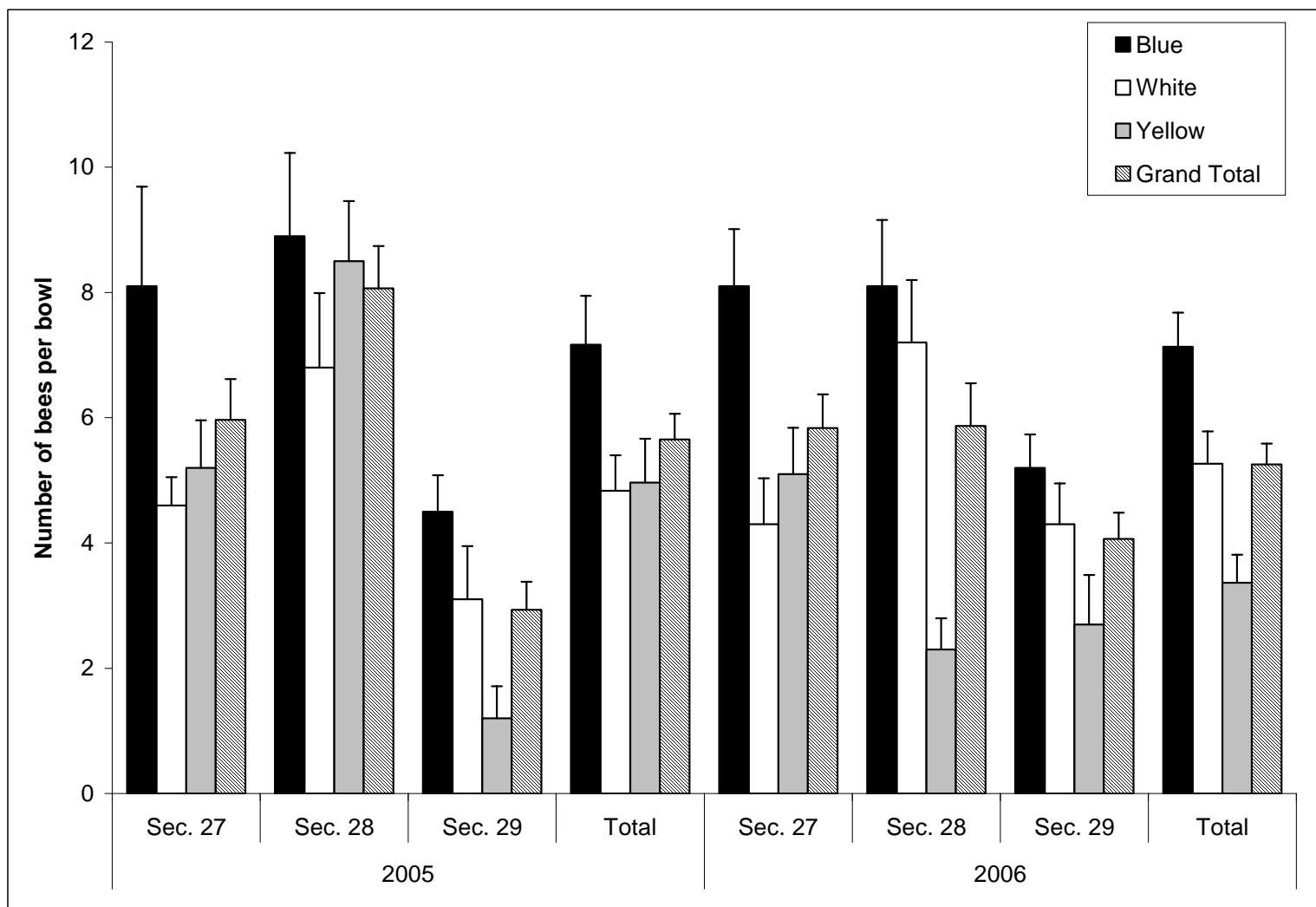
Figure 24. Mean overall bowl catch frequency of mining bees by year, site and bowl colour at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. The error bars represent the standard error of the mean.
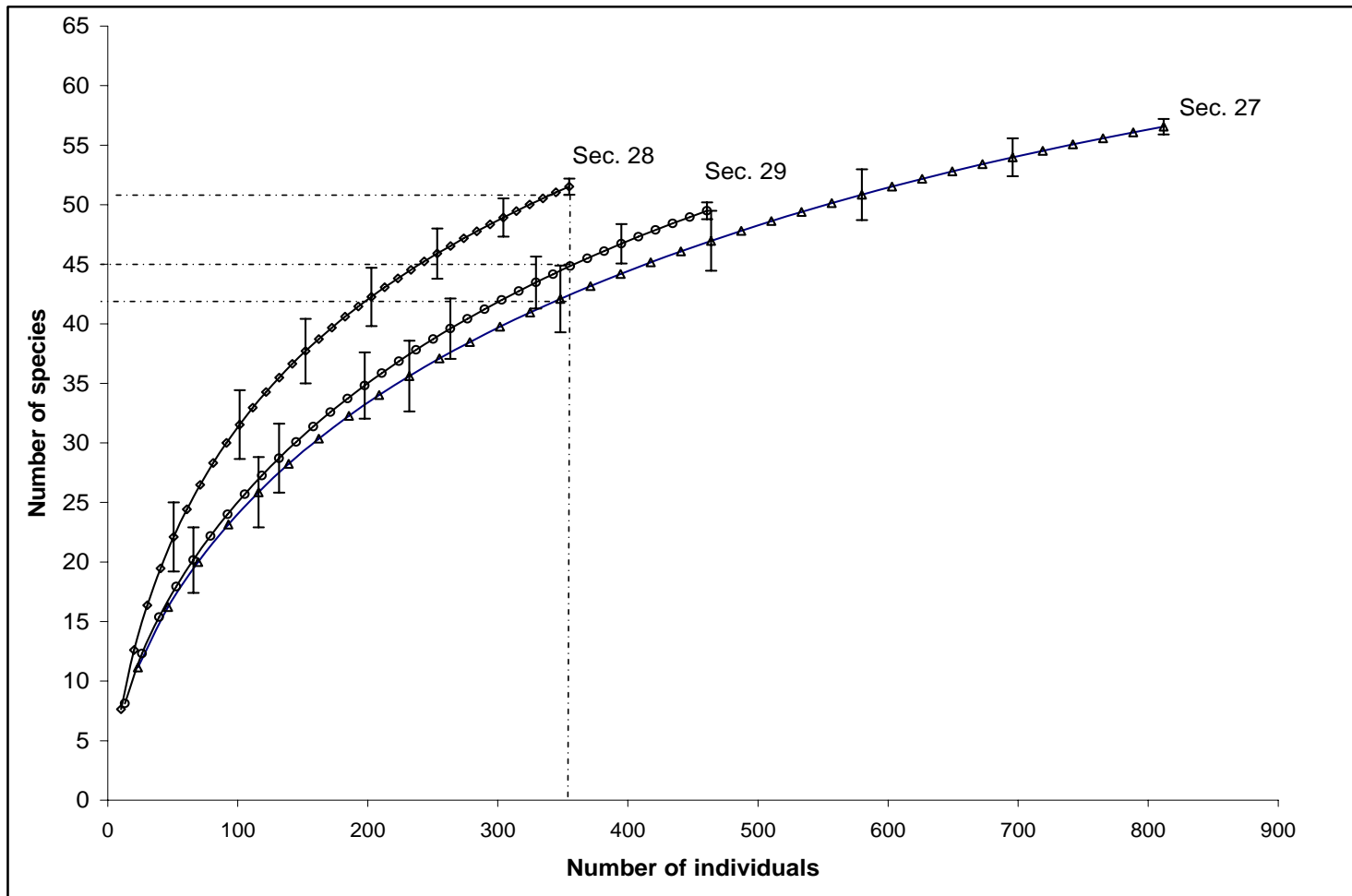
Figure 25. Coleman rarefaction curves of bee sweep-netting for each of three sites at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. Error bars, representing one standard deviation, are included for every fifth data point. The broken lines represent the level at which estimates of rarefied species richness are compared. Sampling occurred weekly during the frost free season of 2005 and 2006.

a)

b)
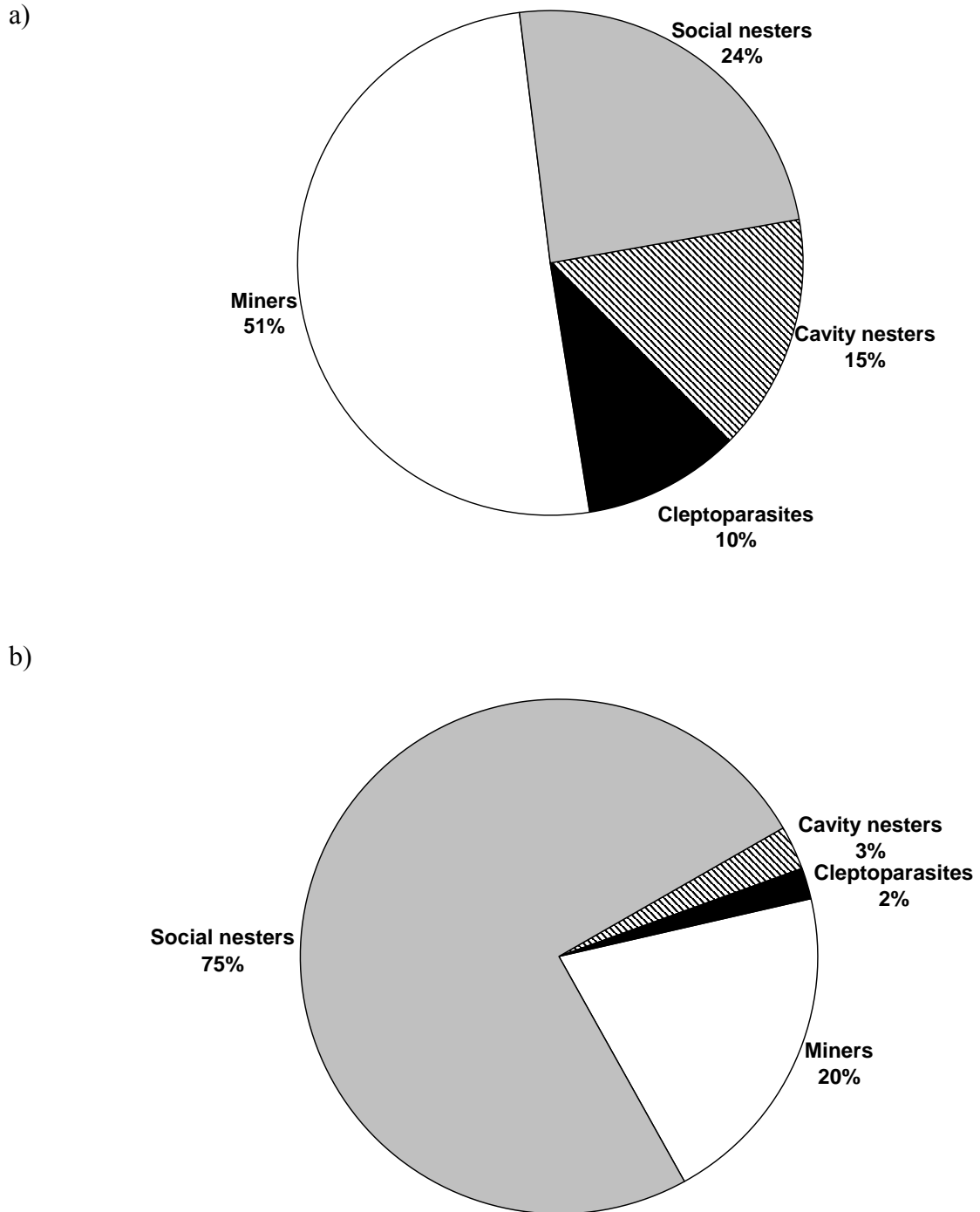
Figure 26. Percentages of bee a) species and b) individuals captured in 2005 and 2006 by sweep-netting that belong to each of the four nesting guilds at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.
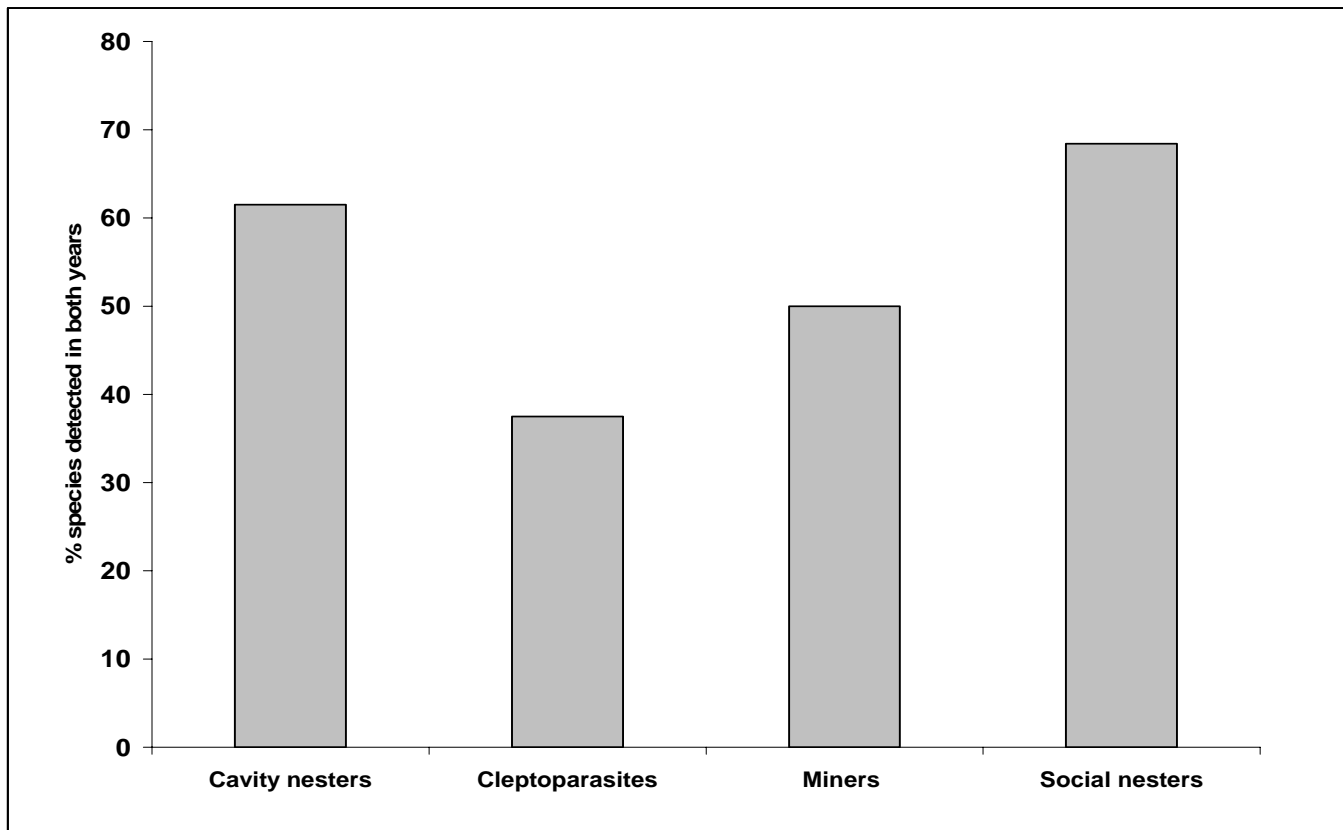
Figure 27. Levels of species turnover between 2005 and 2006 within each nesting guild detected by sweep-netting at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. Low values for the percentage of species collected in both year, shown on the y-axis, indicate high levels of species turnover.
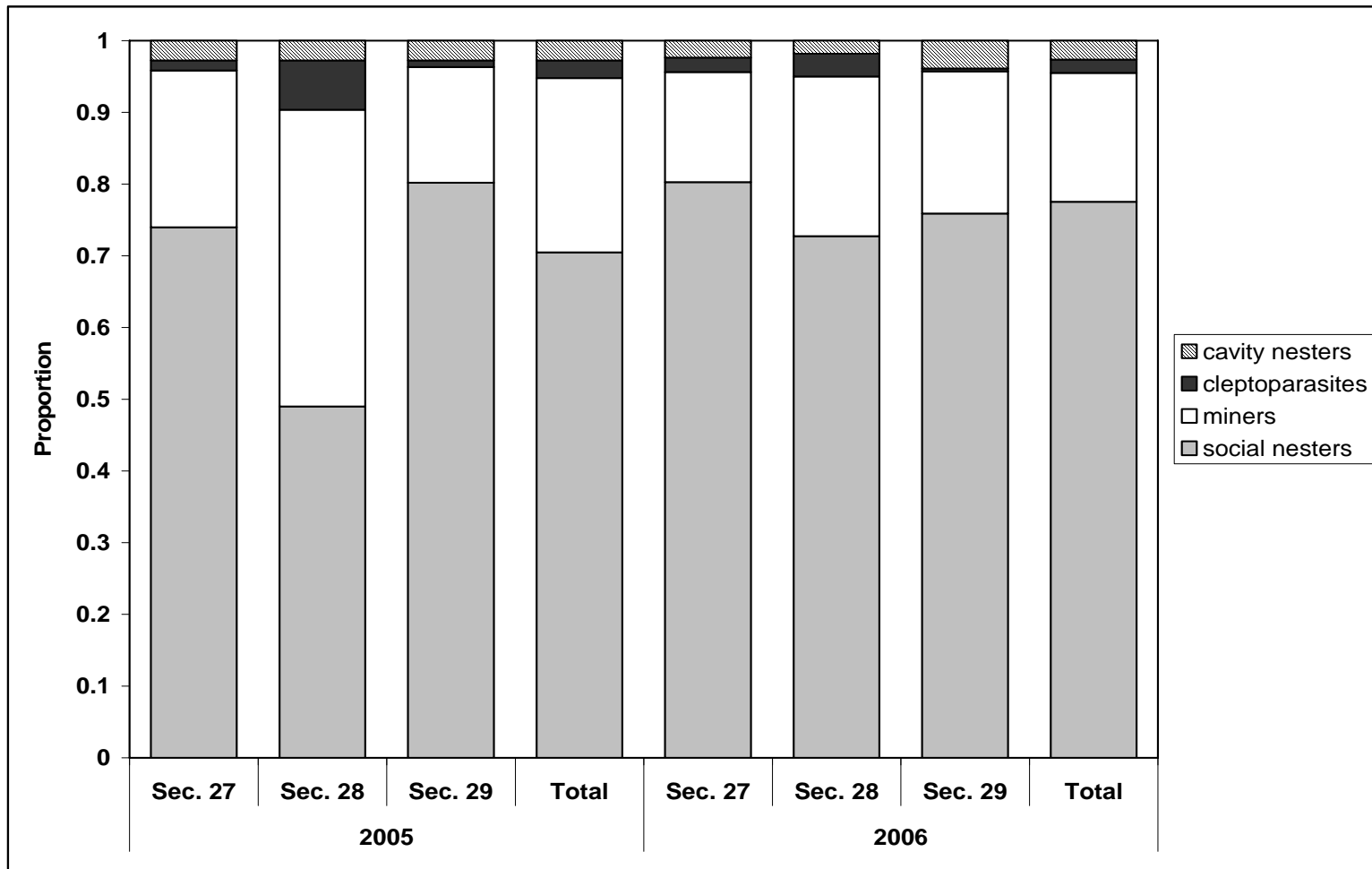
Figure 28. Relative abundance of wild bee individuals among four nesting guilds captured by sweep-netting at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba by site and year.
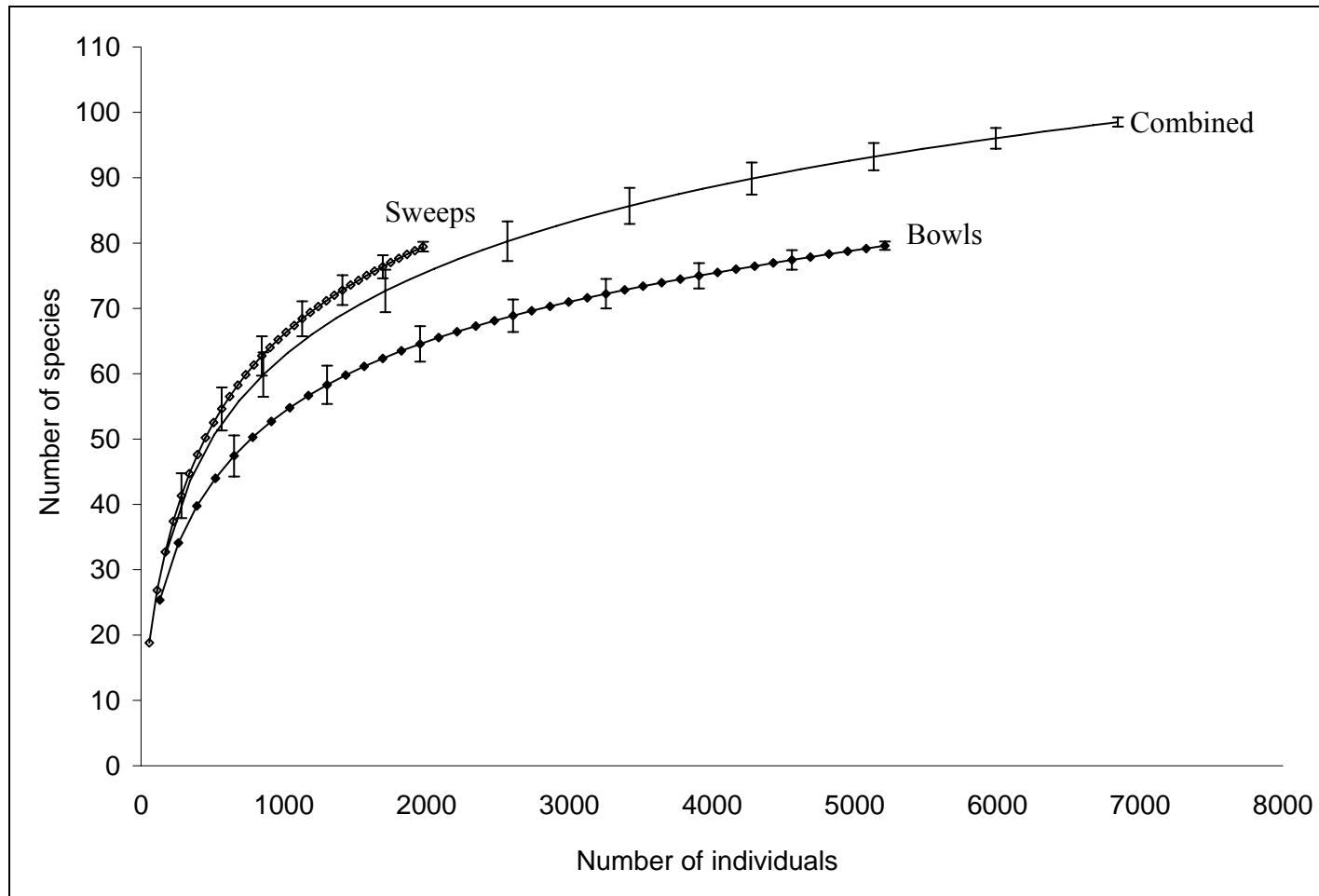
Figure 29. Coleman rarefaction curves for two bee sampling methods, bee bowls (solid diamonds) and sweep-netting (empty diamonds), and the combined catch (no symbol) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. Error bars, representing one standard deviation, are included for every fifth data point. Sampling occurred weekly during the frost free season of 2005 and 2006.

a)

b)
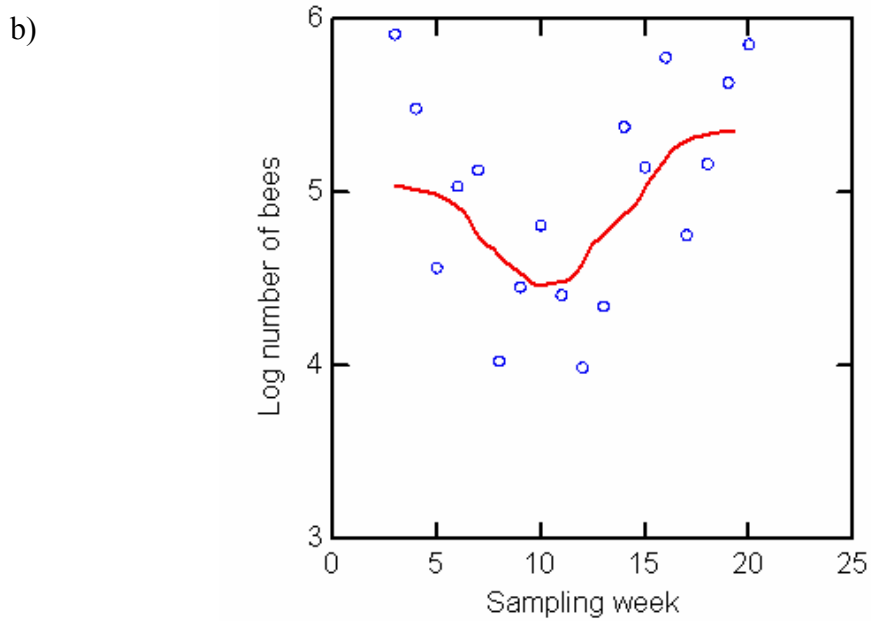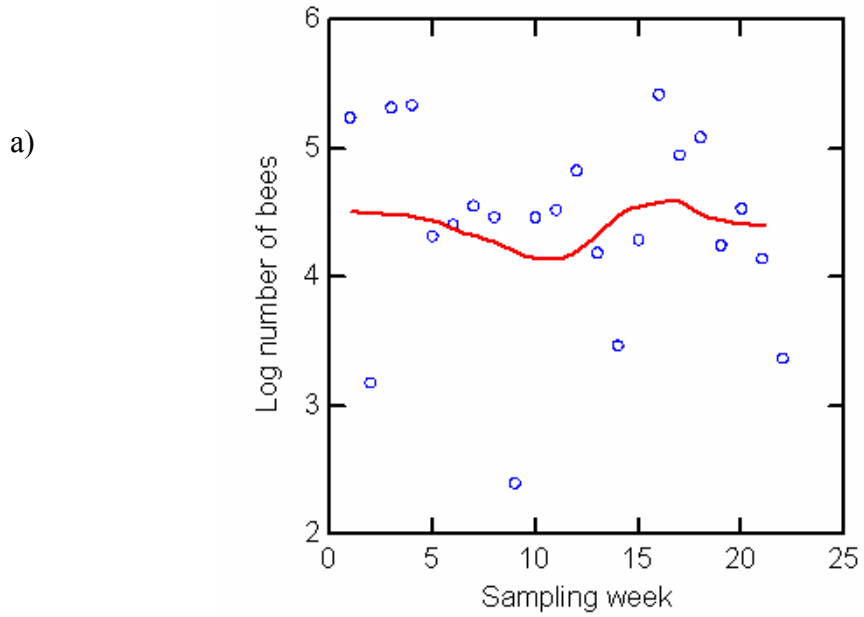
Figure 30. Smoothed seasonal pattern of bee bowl catch summed over all bowls (n=30) at each of three sites (log-transformed) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba for a) 2005 and b) 2006.

a)
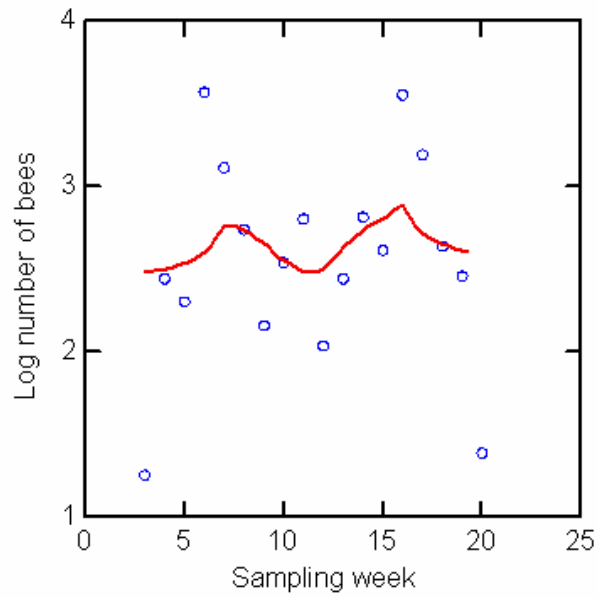
b)
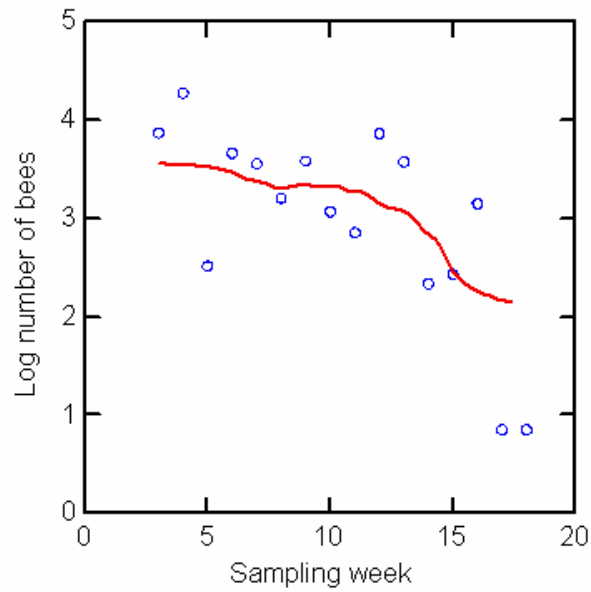
Figure 31. Smoothed seasonal pattern of sweep-netting catch averaged over three round of sweeping per site (log-transformed) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba for a) 2005 and b) 2006.
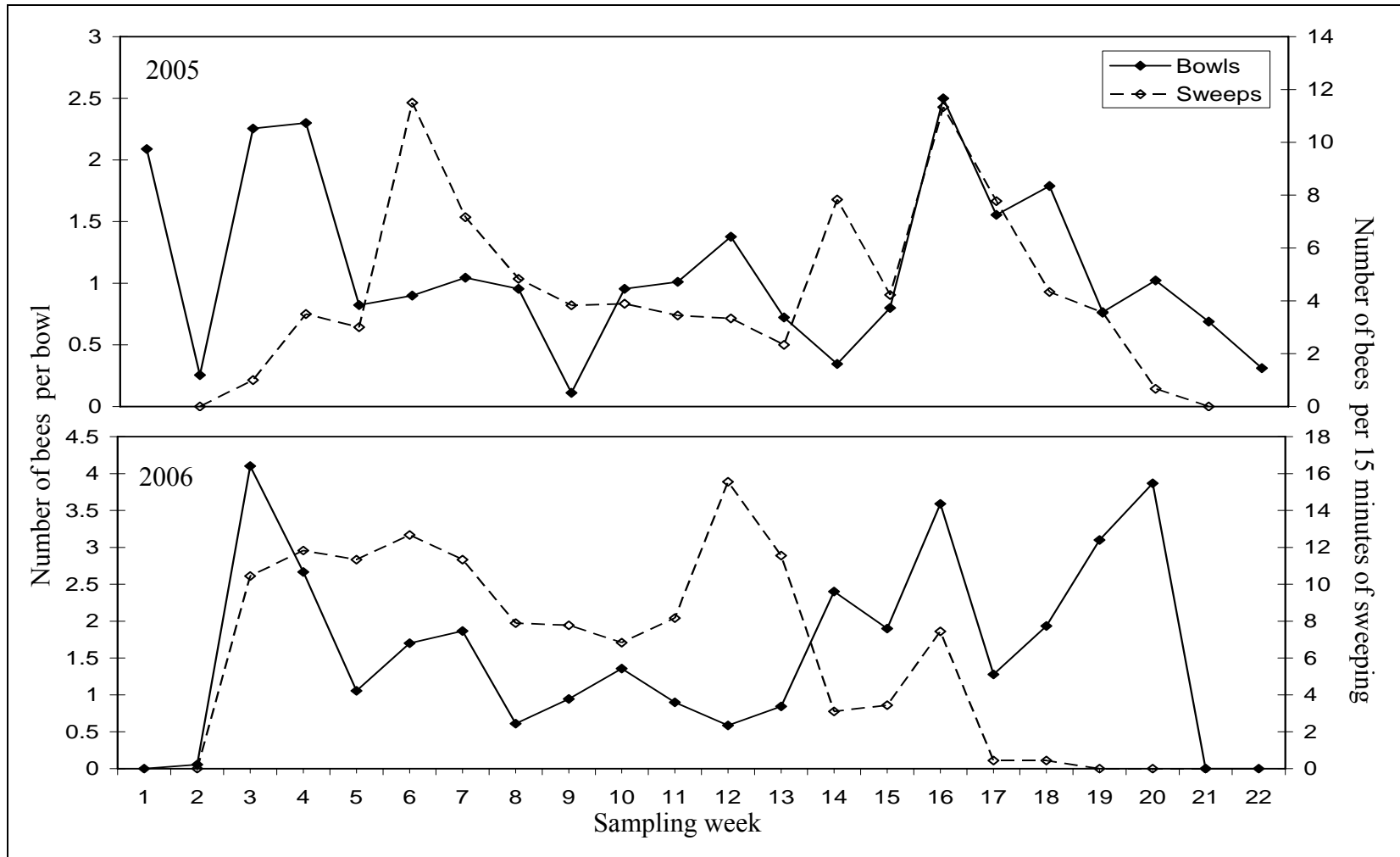
Figure 32. Seasonal patterns in catch per unit effort by sampling method for 2005 (top panel) and 2006 (bottom panel) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. The y-axis on the left corresponds to bee bowl catches (solid line) and the axis on the right corresponds to sweep net catches (broken line).

Figure 33. Redundancy analysis ordination diagram of sites (■) and species (Δ) sampled at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba in two years constrained by sampling method (arrows). For clarity, labels are given only for the 30 species for which the greatest percentage of variation was captured by the ordination.

Species labels include: And_car = *Andrena carlini*, And_cya = *Andrena cyanophila*, And_dun = *Andrena dunningi*, And_ery = *Andrena erythrogaster*, And_mar = *Andrena mariae*, And_niv = *Andrena nivalis*, And_reg = *Andrena regularis*, And_tha = *Andrena thaspii*, And_vic = *Andrena vicina*, Bom_bor = *Bombus borealis*, Bom_nev = *Bombus nevadensis*, Bom_san = *Bombus sandersoni*, Bom_ter = *Bombus terricola*, Bom_vag = *Bombus vagans*, Col_bre = *Colletes brevicornis*, Col_kin = *Colletes kincaidii*, Col_rob = *Colletes robertsonii*, Las_alb = *Lasioglossum albipenne*, Las_par = *Lasioglossum paraforbesii*, Las_prf = *Lasioglossum pruinosiforme*, Las_pru = *Lasioglossum pruinosum*, Las_suc = *Lasioglossum succinipenne*, Las_zon = *Lasioglossum zonulum*, Meg_fri = *Megachile frigida*, Meg_mel = *Megachile melanophaea*, Mel_dru = *Melissodes druriella*, Nom_sp1 = *Nomada* sp. 1, Osm_dis = *Osmia distincta*, Sph_tbd = *Sphecodes* sp. 1.
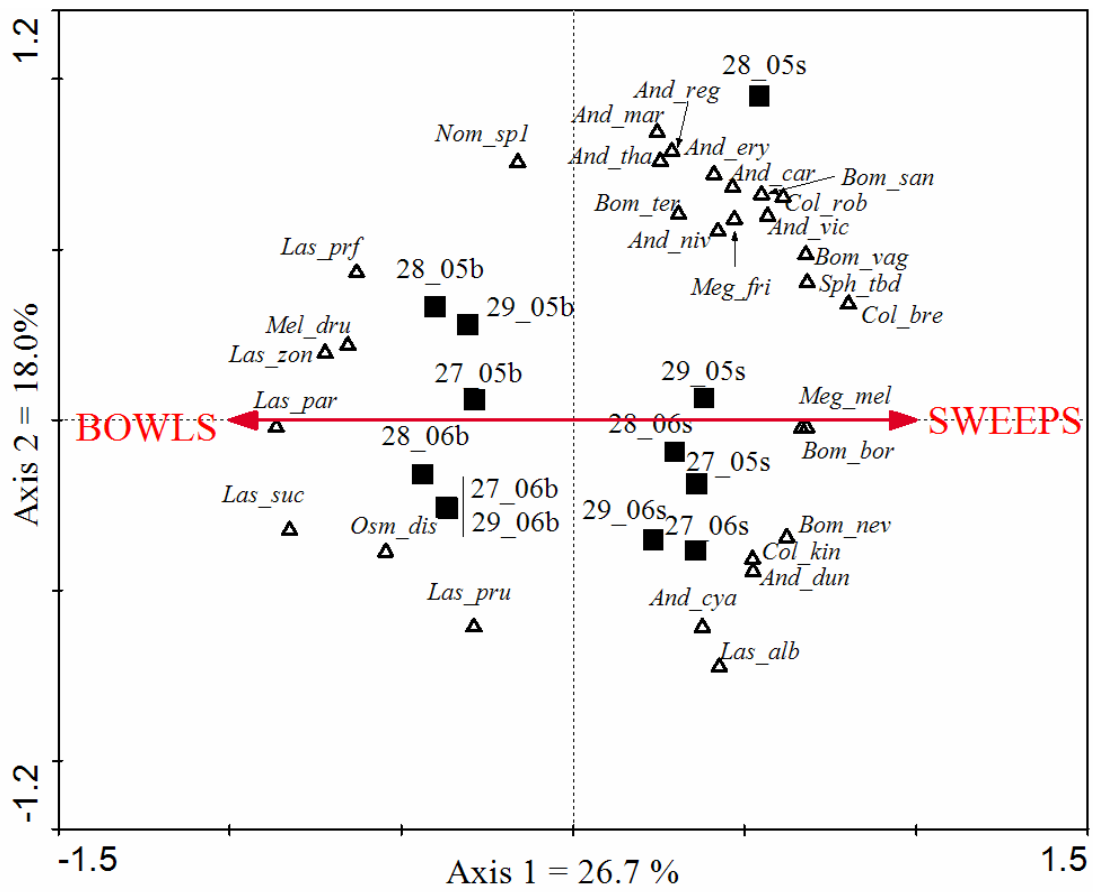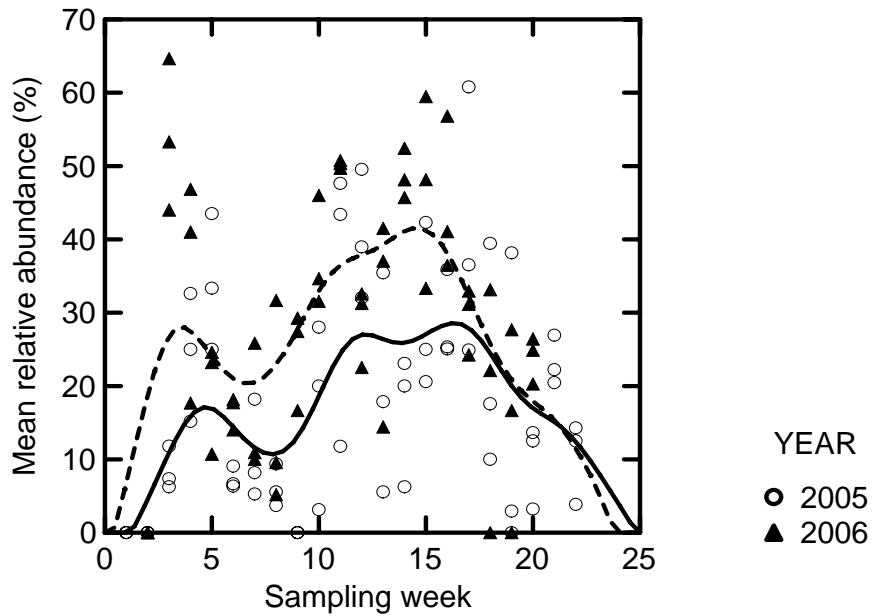
Figure 34. Seasonal patterns in the mean relative abundance of social nester *Lasioglossum succinipenne* (Ellis) (Hymenoptera: Halictidae) in 2005 (solid line, open circles) and 2006 (dashed line, solid triangles) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.
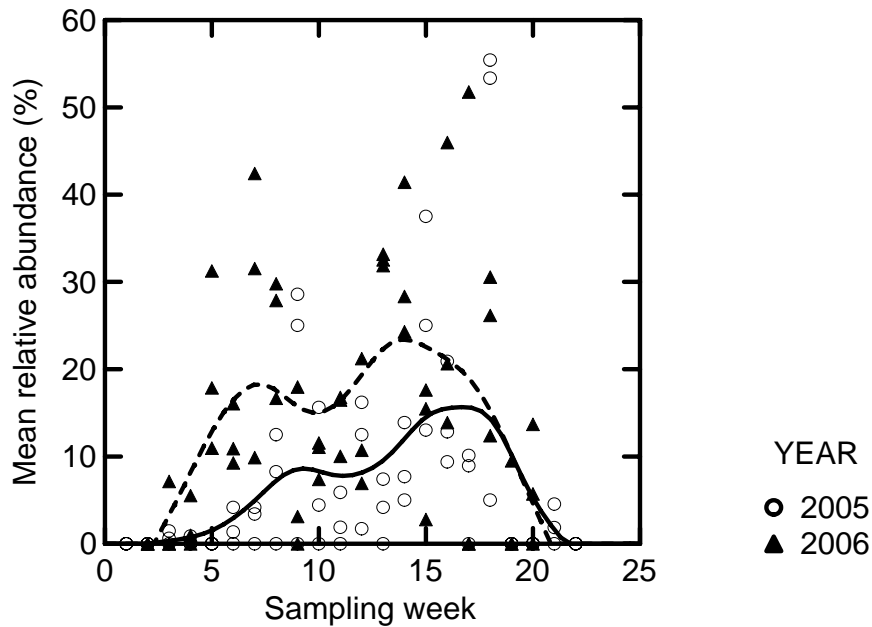
Figure 35. Seasonal patterns in the mean relative abundance of social nester *Lasioglossum albipenne* (Robertson) (Hymenoptera: Halictidae) in 2005 (solid line, open circles) and 2006 (dashed line, solid triangles) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.
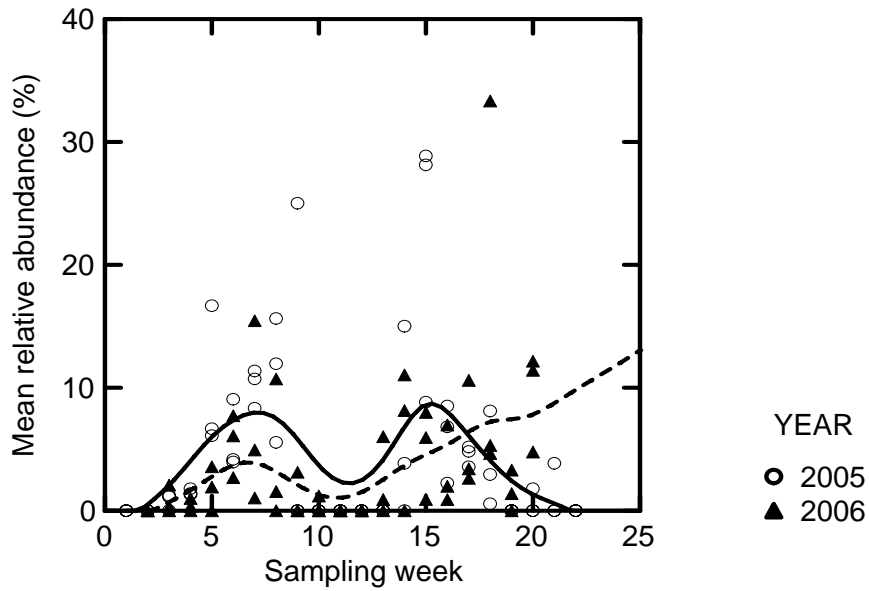
Figure 36. Seasonal patterns in the mean relative abundance of miner *Lasioglossum paraforbesii* McGinley (Hymenoptera: Halictidae) in 2005 (solid line, open circles) and 2006 (dashed line, solid triangles) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.
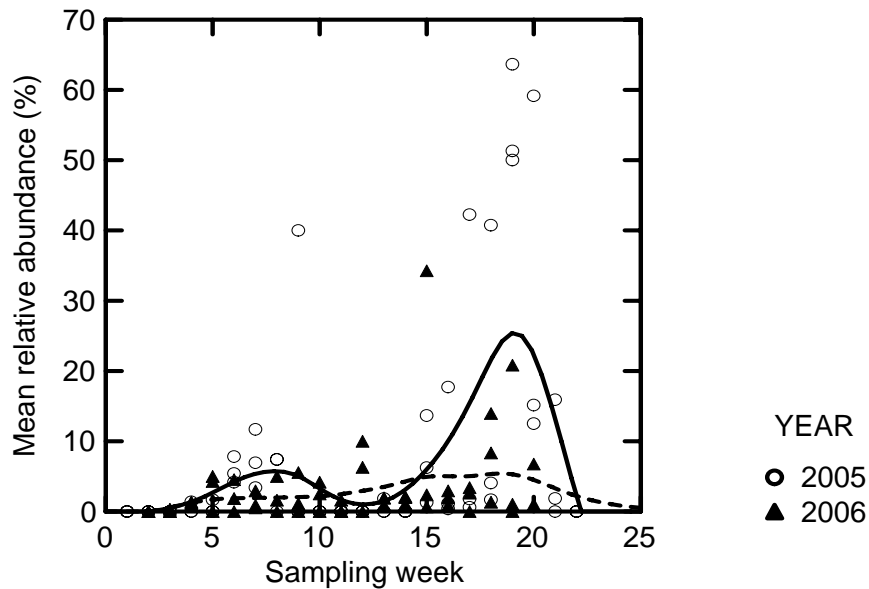
Figure 37. Seasonal patterns in the mean relative abundance of social nester *Bombus rufocinctus* Cresson (Hymenoptera: Apidae) in 2005 (solid line, open circles) and 2006 (dashed line, solid triangles) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.

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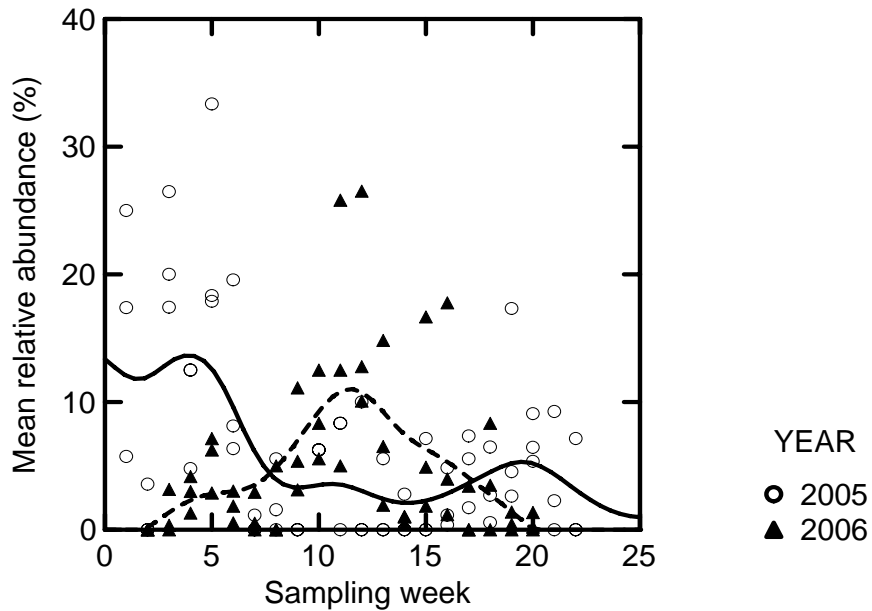
Figure 38. Seasonal patterns in the mean relative abundance of social nester *Bombus ternarius* Say (Hymenoptera: Apidae) in 2005 (solid line, open circles) and 2006 (dashed line, solid triangles) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.
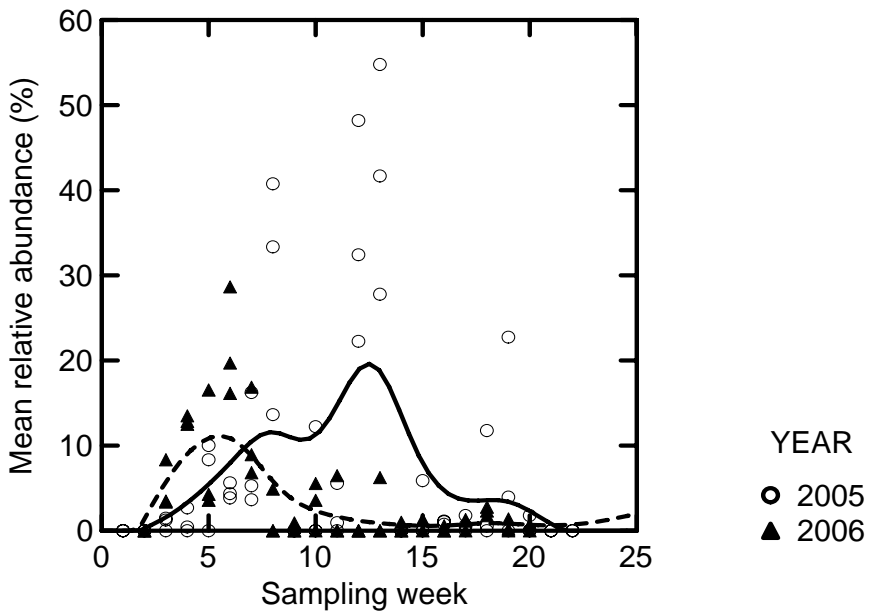
Figure 39. Seasonal patterns in the mean relative abundance of social nester *Lasioglossum perpunctatum* (Ellis) (Hymenoptera: Halictidae) in 2005 (solid line, open circles) and 2006 (dashed line, solid triangles) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.

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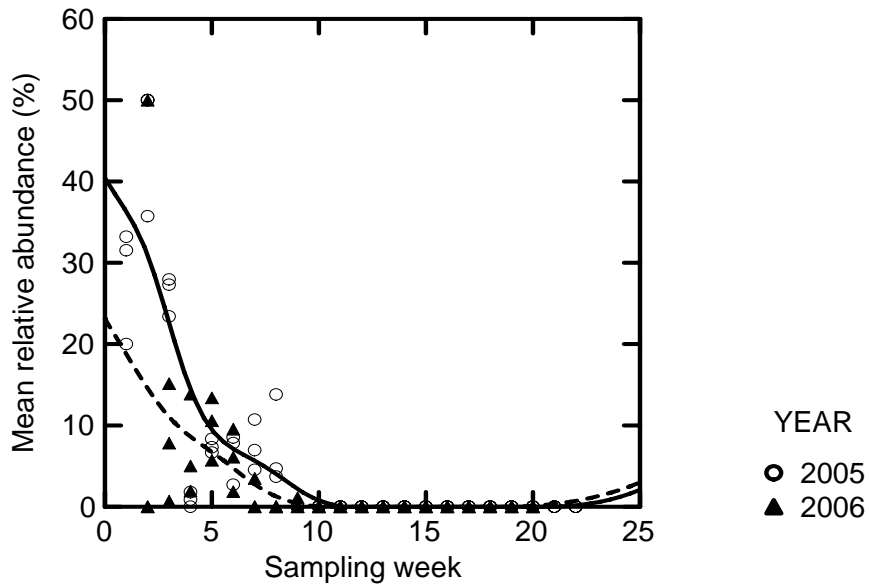
Figure 40. Seasonal patterns in the mean relative abundance of miner *Andrena geranii* Robertson (Hymenoptera: Andrenidae) in 2005 (solid line, open circles) and 2006 (dashed line, solid triangles) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.
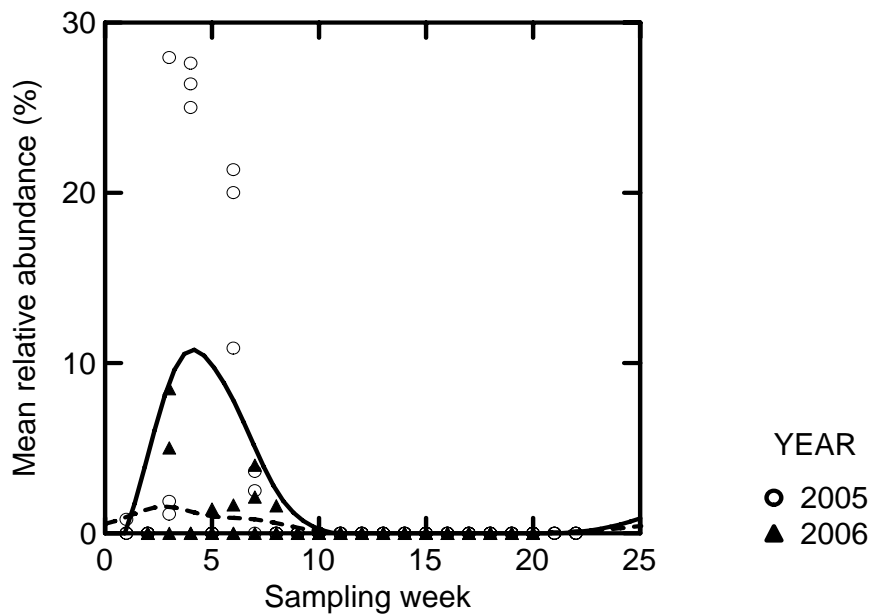
Figure 41. Seasonal patterns in the mean relative abundance of miner *Andrena vicina* Smith (Hymenoptera: Andrenidae) in 2005 (solid line, open circles) and 2006 (dashed line, solid triangles) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.
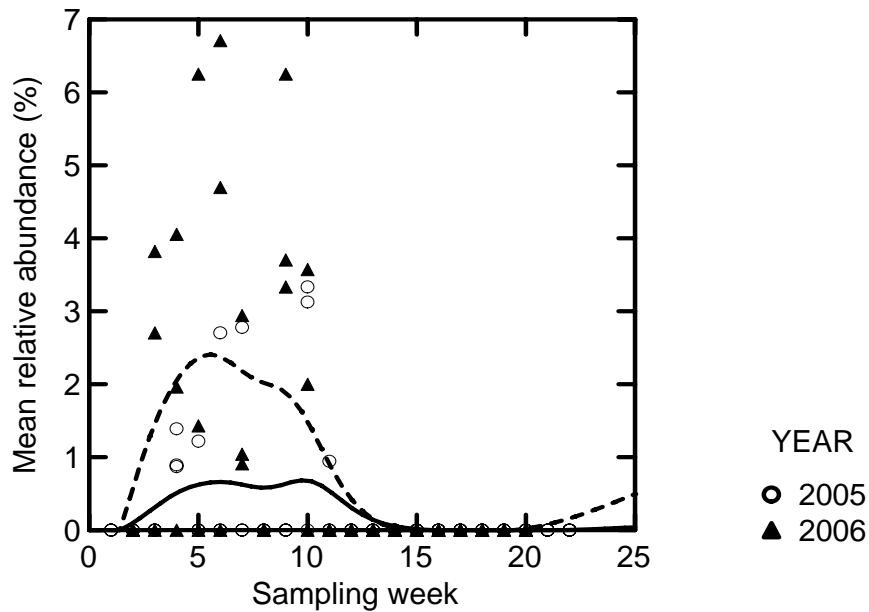
Figure 42. Seasonal patterns in the mean relative abundance of cavity nester and specialist *Osmia distincta* Cresson (Hymenoptera: Megachilidae) in 2005 (solid line, open circles) and 2006 (dashed line, solid triangles) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.
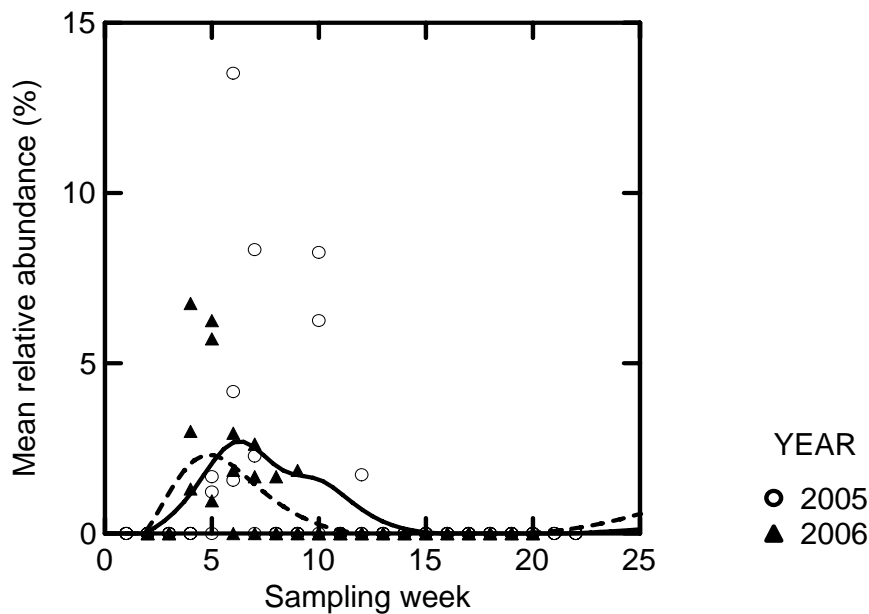
Figure 43. Seasonal patterns in the mean relative abundance of cavity nester *Hoplitis pilosifrons* (Cresson) (Hymenoptera: Megachilidae) in 2005 (solid line, open circles) and 2006 (dashed line, solid triangles) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.

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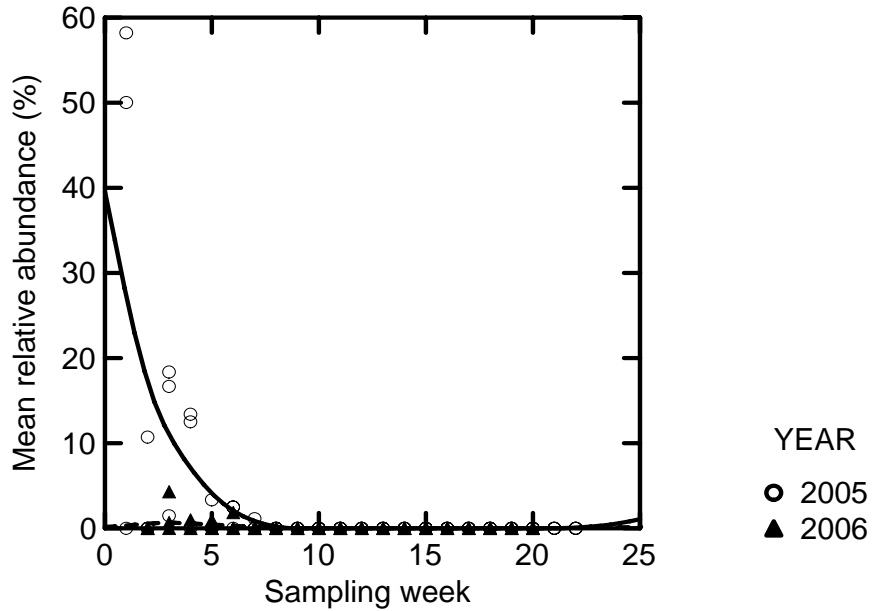
Figure 44. Seasonal patterns in the mean relative abundance of cleptoparasite *Nomada* sp. 1 (Hymenoptera: Apidae) in 2005 (solid line, open circles) and 2006 (dashed line, solid triangles) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.
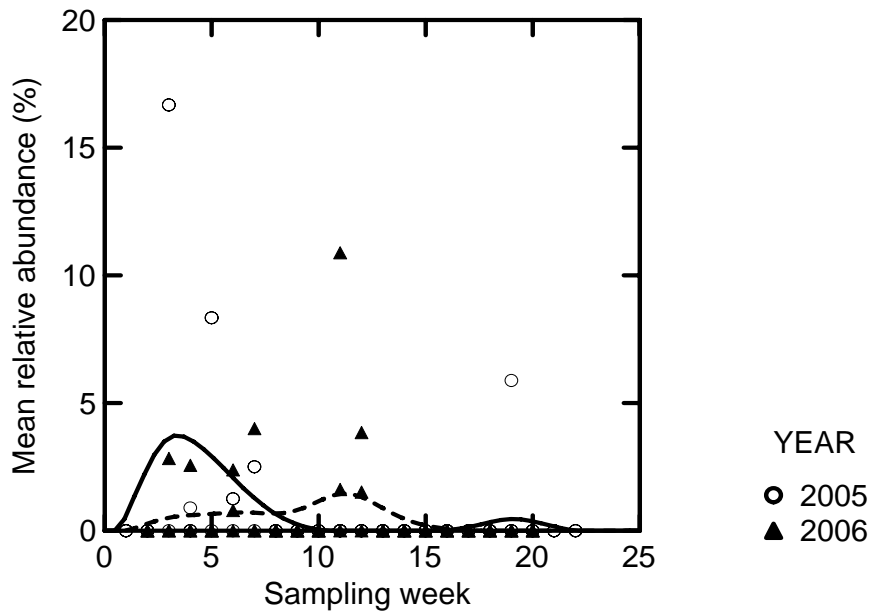
Figure 45. Seasonal patterns in the mean relative abundance of cleptoparasite *Sphecodes* sp. 1 (Hymenoptera: Halictidae) in 2005 (solid line, open circles) and 2006 (dashed line, solid triangles) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.

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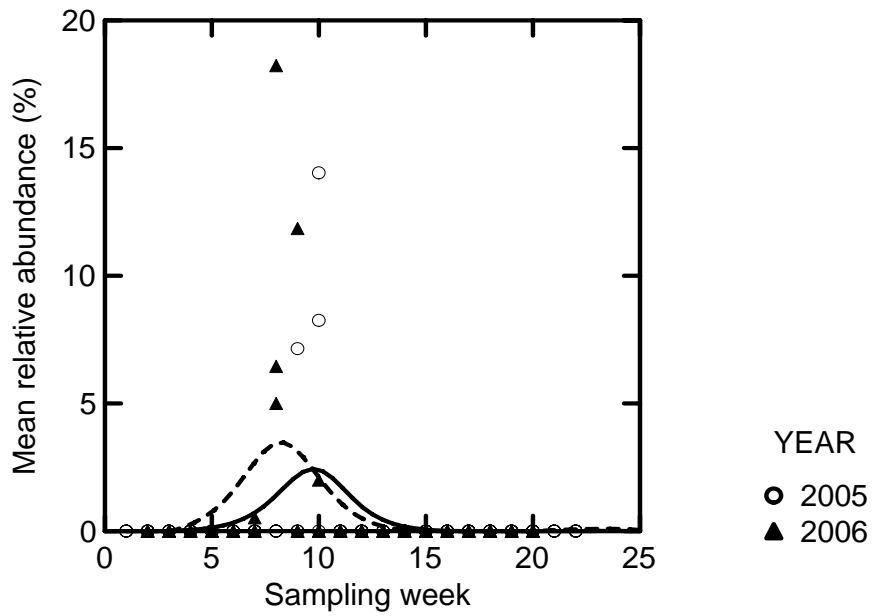
Figure 46. Seasonal patterns in the mean relative abundance of miner and pollen specialist *Dufourea maura* (Cresson) (Hymenoptera: Halictidae) in 2005 (solid line, open circles) and 2006 (dashed line, solid triangles) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.
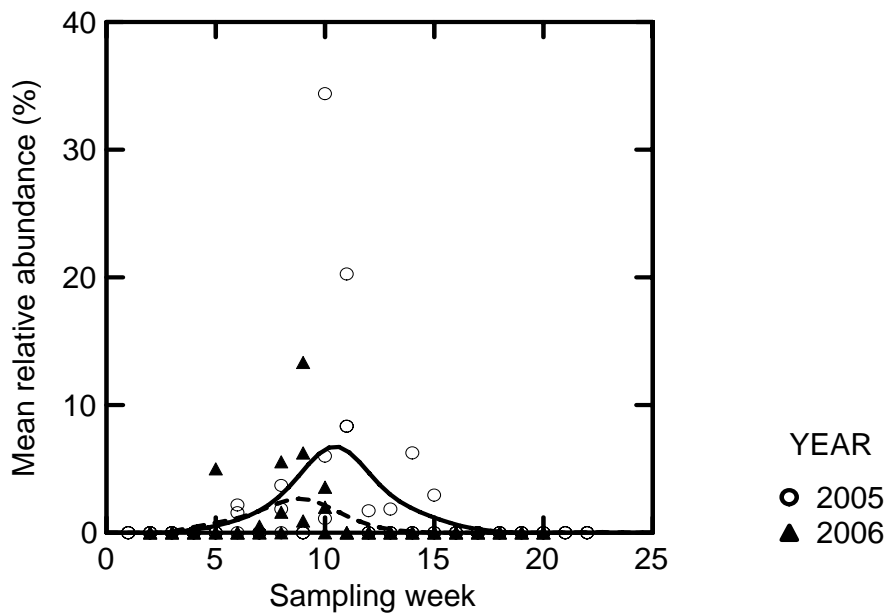
Figure 47. Seasonal patterns in the mean relative abundance of cavity nester *Anthidium clyptodentatum* Swenk (Hymenoptera: Megachilidae) in 2005 (solid line, open circles) and 2006 (dashed line, solid triangles) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.

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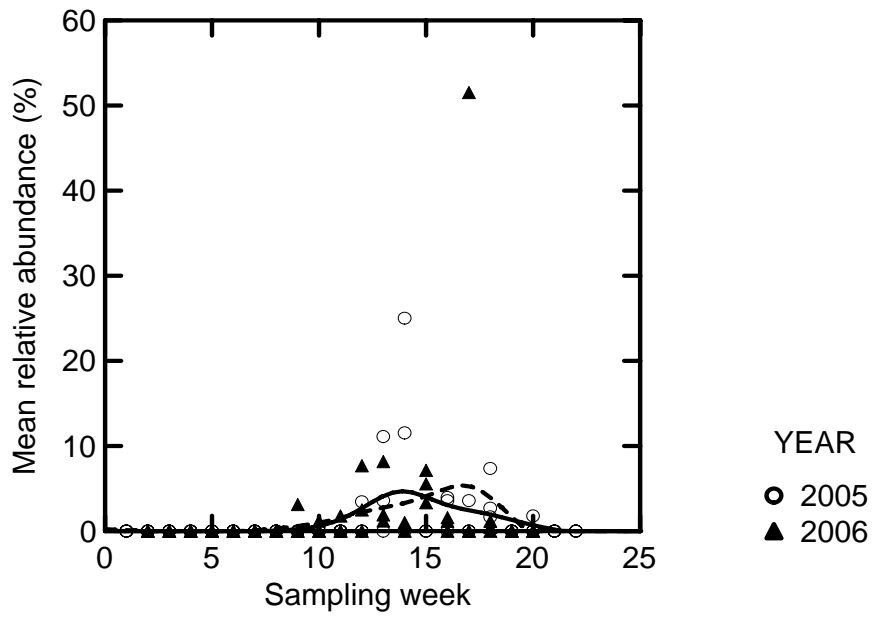
Figure 48. Seasonal patterns in the mean relative abundance of miner *Melissodes druriella* (Kirby) (Hymenoptera: Apidae) in 2005 (solid line, open circles) and 2006 (dashed line, solid triangles) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba.
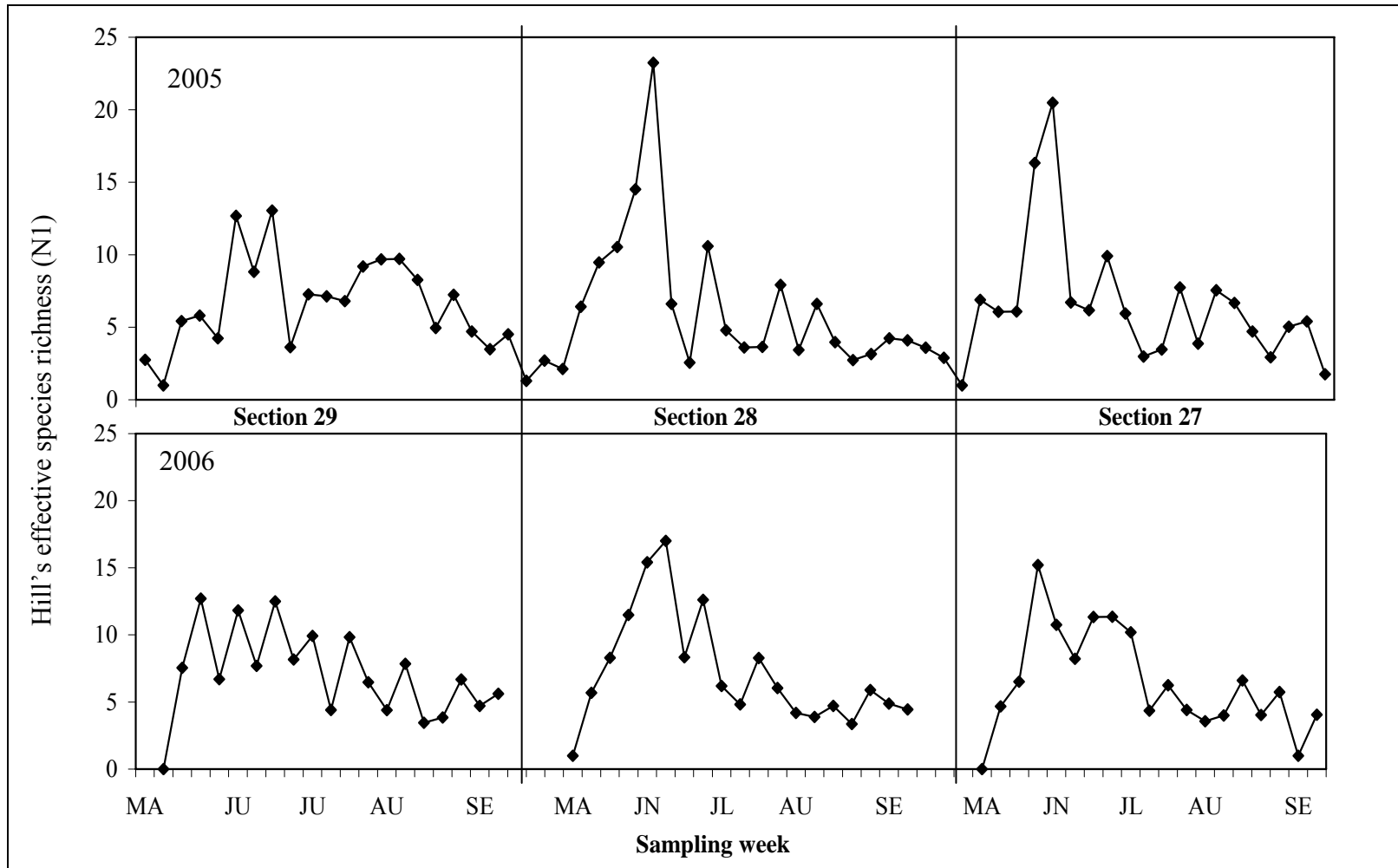
Figure 49. Seasonal patterns of Hill's N1 effective species richness for bees at each of three sites (from right to left) at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba in 2005 (top panel) and 2006 (bottom panel). N1 values on the bee data were calculated using the mean of the species' relative abundances from two methods, sweep-netting and bee bowls.

Figure 50. Redundancy analysis ordination diagram of the seasonal bee assemblages at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba in 2005 classified by nesting guild and constrained by seasonal assemblages of flowering plants (arrows). Samples are coded by site (■) with the suffix of '_1', '_2' or '_3' referring to early, mid or late season assemblages respectively. Species symbols are classified according to nesting guild and are given in the legend. For clarity, labels are given only for the 30 species for which the greatest percentage of variation was captured by the ordination.

Species labels include: And_bar =*Andrena barbilabris*, And_car =*Andrena carlini*,And_for =*Andrena forbesii*, And_ger =*Andrena geranii*, And_per =*Andrena persimulata*, And_sig =*Andrena sigmundi*, And_vic =*Andrena vicina*, Ant_cly =*Anthidium clypeodentatum*, Ant_ter =*Anthophora terminalis*, Bom_bor =*Bombus borealis*, Bom_gri =*Bombus griseocollis*, Bom_nev =*Bombus nevadensis*, Bom_ruf =*Bombus rufocinctus*, Col_bre =*Colletes brevicornis*, Col_kin =*Colletes kincaidii*, Hal_rub =*Halictus rubicundus*, Las_alb =*Lasioglossum albipenne*, Las_cor =*Lasioglossum coriaceum*, Las_per =*Lasioglossum perpunctatum* Las_prf =*Lasioglossum pruinosiforme*, Meg_bre =*Megachile brevis*, Meg_lat = *Megachile latimanus*, Mel_agi =*Melissodes agilis*, Mel_dru =*Melissodes druriella*, Nom_cun =*Nomada cuneata*, Osm_buc =*Osmia bucephala*, Osm_sim =*Osmia simillima*, Pse_sim =*Pseudopanurgus simulans*, Sph_tbd =*Sphecodes* sp.1

SPECIES

+ Cleptoparasites

◇ Cavity nesters

○ Social nesters

△ Miners

SAMPLES

■
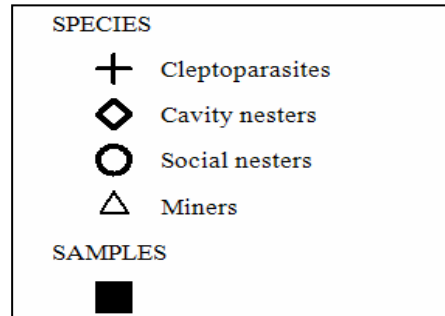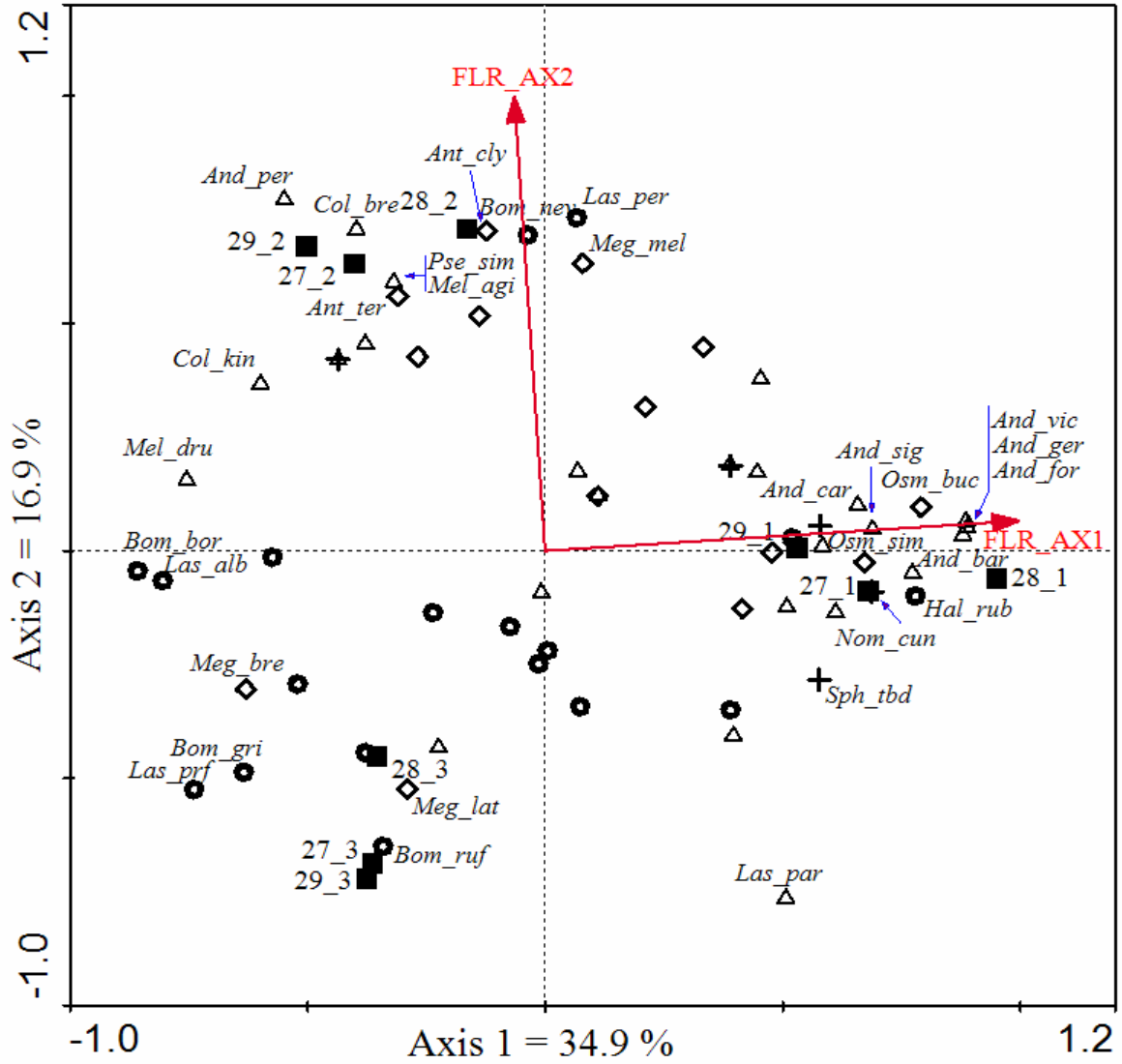
Figure 51. Redundancy analysis ordination diagram of the seasonal bee assemblages at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba in 2006 classified by nesting guild and constrained by seasonal assemblages of flowering plants (arrows). Samples are coded by site (■) with the suffix of '_1', '_2' or '_3' referring to early, mid or late season assemblages respectively. Species symbols are classified according to nesting guild and are given in the legend. For clarity, labels are given only for the 30 species for which the greatest percentage of variation was captured by the ordination.

Species labels include: Aga_tex =*Agapostemon texanus*, And_bar =*Andrena barbilabris*, And_cya =*Andrena cyanophila*, And_dun = *Andrena dunningii*, And_ger =*Andrena geranii*, And_mir =*Andrena miranda*, And_per =*Andrena persimulata*, And_vic =*Andrena vicina*, Ant_ter =*Anthophora terminalis*, Bom_bor =*Bombus borealis*, Bom_ruf =*Bombus rufocinctus*, Bom_trn =*Bombus ternarius*, Col_kin =*Colletes kincaidii*, Duf_mau =*Dufourea maura*, Hop_pil =*Hoplitis pilosifrons*, Hyl_mes =*Hylaeus mesillae*, Las_alb =*Lasioglossum albipenne*, Las_ath =*Lasioglossum athabascense*, Las_cor =*Lasioglossum coriaceum*, Las_pec =*Lasioglossum pectoraloides*, Las_per =*Lasioglossum perpunctatum*, Las_prf =*Lasioglossum pruinosiforme*, Las_zon = *Lasioglossum zonulum*, Meg_bre = *Megachile brevis*, Meg_mel =*Megachile melanophaea*, Mel_dru =*Melissodes druriella*, Nom_mac =*Nomada maculata*, Osm_dis =*Osmia distincta*, Osm_sim =*Osmia simillima*, Osm_tbd =*Osmia* sp. 1.
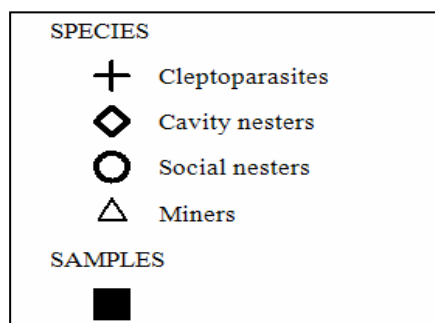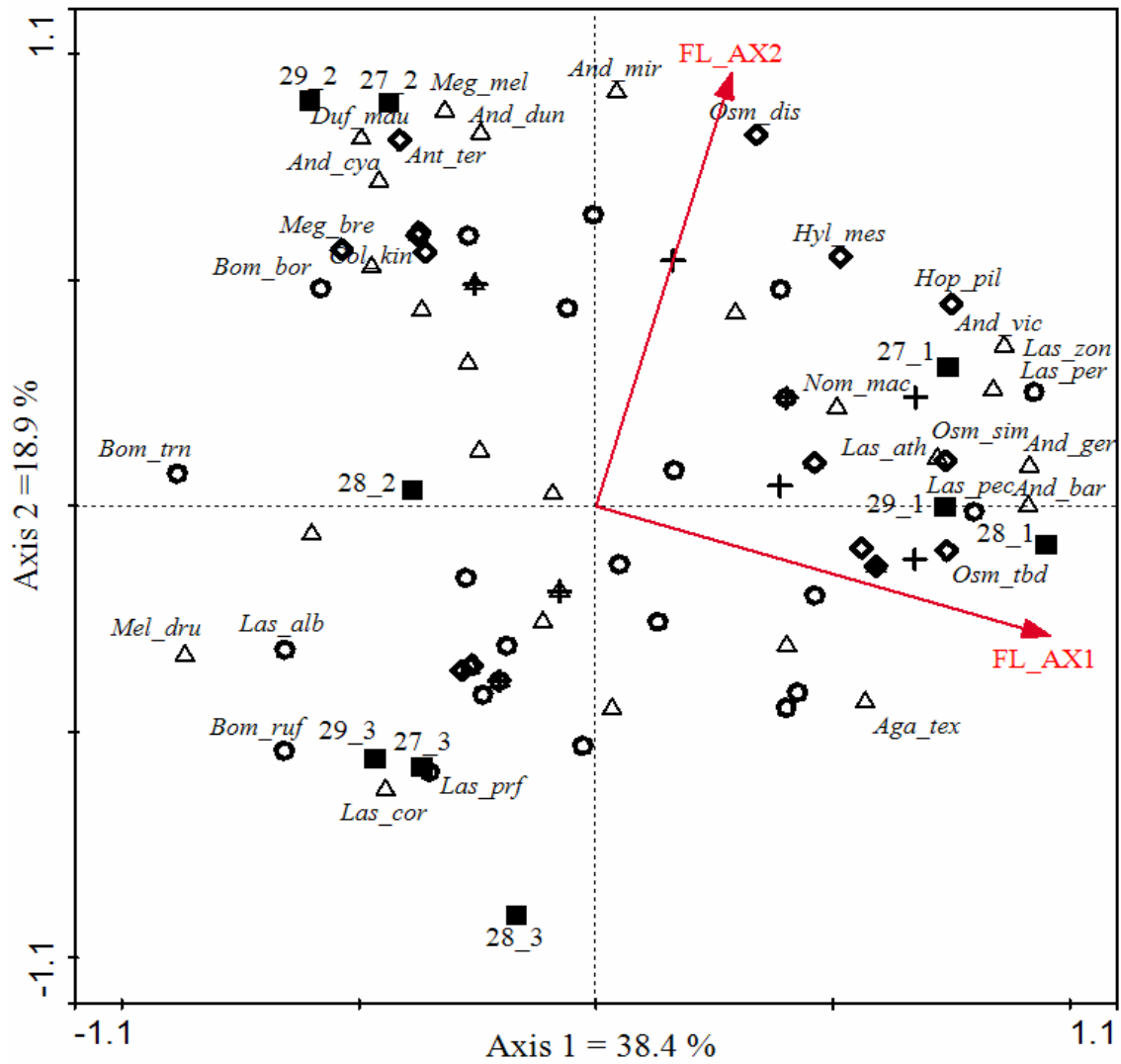
To address information deficiencies regarding patterns of wild bee diversity in key habitats, I sought to characterize the bee fauna of mixed-grass prairie in southwestern Manitoba. To do so, I examined patterns in the diversity and composition of wild bees among three sites within the Yellow Quill Mixed-grass Prairie (YQMGP) sampled over two years. In the first section of this discussion, relevant distributional, ecological and biological features of the fauna collected at the YQMGP will be detailed. In the second section, the relative effectiveness of the two sampling methods used in this study will be considered in light of the implementation of sampling and monitoring programs. The third section of this discussion addresses other factors that were found to affect the diversity and composition of the wild bee community and the floral resource base in the YQMGP. Discussion of results pertaining to the floral environment is incorporated into relevant sections. Major conclusions and directions of future research, which appear throughout the discussion, are summarized briefly at the end.

Characterization of the fauna

Moldenke (1979) estimated that approximately 500 species of bee occur in the Great Plains; however, local faunas are expected to be less diverse, particularly at more northern latitudes. The localized bee fauna of the YQMGP was found to contain at least 100 species. That the overall rarefaction curve failed to reach an asymptote suggests that species richness may have been underestimated (Figure 29). The high number of rare taxa represented by single specimens may be the result of insufficient sampling intensity. Certain aspects of the sampling program may not have been

conducive to capturing all taxa. For example, the sites sampled in this study were located strictly in areas of open prairie. Adjacent habitats types such as aspen forests or riparian areas were not sampled. If such areas contained unique features or microhabitats, unique taxa may have been missed. Dispersers from these local areas or from farther away (Williams *et al.* 2001) may have contributed to the high proportion of numerically rare taxa captured in this study. Alternatively, some of these taxa may be genuinely rare. The addition of more sites or sampling dates may have allowed a greater accumulation of species; however, considerations of feasibility and the potential impact of sampling activities on local populations precluded a more intensive approach. Failure to reach asymptotes in taxon accumulation curves and high levels of numerically rare taxa in sampling collections are nonetheless common in wild bee studies (Williams *et al.* 2001).

It is difficult to compare species richness in this study with that found at other northern prairie sites or even in other habitats for two main reasons. First, there is a paucity of published, peer-reviewed inventories of northern prairie bees against which to compare the degree of effectiveness of the sampling program. Secondly, species richness in other habitats at similar latitudes is inevitably a function of sampling effort, which varies considerably among studies. Nevertheless, comparisons to existing data, however incomplete, provide a starting point for building a picture of the regional bee fauna.

Two unpublished, one-year surveys represent the most comparable results in terms of geographic proximity and habitat type, although both studies included more sampling sites. Using bee bowls at eight managed prairies in Spruce Woods Provincial Park,

Manitoba in conjunction with this project, I detected 75 taxa. The YQMGP is located

approximately 60 km west of SWPP, and the two locations shared 49 species (39%).

Another non-peer reviewed survey of non-parasitic bees in eight Minnesota prairie

remnants reported a total of 123 species, of which 40 species (23%) were shared with

this study (Reed 1993). Although neither of these datasets is a complete

representation of the local fauna, the decreasing number of shared species with

increased distance from the YQMGP is consistent with large-scale spatial patterns

observed in studies in which similar habitat types are sampled over greater distances

(Williams *et al.* 2001).

Among peer-reviewed publications, the number of bee species in this study appears to

be less than local faunas in similar habitats or in different habitats at similar latitudes.

For example, 144 and 150 species were collected in short-grass prairie sites sampled

by hand-netting in Wyoming (Tepedino and Stanton 1981). A two-year study of the

bee fauna in mixed wood-boreal transition zone in southern Ontario yielded 150

species, excluding Bombus *spp.*, at an old-field locality sampled weekly by hand-

netting (Grixti and Packer 2006). A four-year survey of wild bees in longleaf pine

savannas, another xeric habitat type, in Louisiana uncovered 125 species

(Bartholomew 2001). Finally, a sandy grassland site in central Hungary, with climatic

parameters similar to southern Manitoba, contained 96 species when it was sampled

on a biweekly basis; however, only white pan-traps were used in that study

(Sarospataki and Fazekas 1995).

Biogeographically, the fauna of the YQMGP appears to be dominated by eastern and

widespread species (Krombein *et al.* 1979); however, there is nonetheless strong

representation of species with western and central distributions. I shall proceed by considering noteworthy observations followed by a distributional characterization of the fauna on the basis of ecological groupings.

New records

As far as is known, I collected 15 new records for Manitoba, five of which are also new for Canada (Table 21). Some of these species, such as *Hoplitis cylindrica*, are fairly widespread and their discovery in Manitoba likely fills a distributional gap. Other species, for which discovery in Manitoba may reflect a distribution extension, appear to be balanced between being more western or eastern in affinity. For example, the polylectic species *Andrena cyanophila* is known from British Columbia, Alberta and several western states; and this record likely represents a range extension for this species. Also western in affinity are aster specialist *Melissodes menuachus*, cavity nester *Megachile perihirta* and primitively eusocial *Lasioglossum pruinosiforme*, of which several specimens were recorded. Interestingly, *L. succinipenne*, the most commonly collected species in this study, is known only from Colorado. Initial examination of this species indicated that it was structurally similar to *L. pilosum*; however, genetic barcoding undertaken by J. Gibbs at York University indicated that it was actually *L. succinipenne*.

New records of YQMGP species that are more eastern in affinity include commonly-collected *L. pruinosum*, *Calliopsis andreniformis*, cleptoparasite *Nomada pygmaea*, aster specialists *P. nebrascensis* and *Melissodes rustica*, and the crucifer specialist *Andrena arabis*, which may be new for Canada. Aster specialists *P. renimaculatus* and *P. simulans* are rather narrowly distributed in the central regions, particularly the

latter species which is only known from North Dakota and Nebraska. Both of these species appear to be new records for Canada. Another central-ranging species that represents a potential new record for Canada is the oligolege, *Dufourea maura*.

Pollen specialists

With a total of 20 species, the percentage of known pollen specialists among the non-parasitic bees (23.8%) was within the range expected in comparison to other surveys (See Chapter 1: *Pollen specialists*). Pollen specialists were found in all families. As expected, most of the oligolectic species were andrenids; however, colletids included a large number of oligoleges relative to the number of taxa they represented overall. Few specialists were captured in large numbers; therefore, they did not make an important contribution to the overall catch in terms of individuals. However, this group contributed strongly to overall diversity and to expanding the knowledge of northern mixed grass prairie bees. For example, this category contained a disproportionate number of the new records for Manitoba (7 of 15 species). In addition, six species were found that may rely on prairie habitat, as they are restricted to the central Plains region and associated with prairie host plants. These include *Dalea* associates *Colletes robertsonii* and *C. susannae*, and Asteraceae associates *Pseudopanurgus simulans* and *P. renimaculatus*. One specimen of *C. andrewsii*, a specialist on *Heuchera* (Saxifragaceae), was an interesting discovery given that these plants were represented by only one sparsely-distributed species, *H. richardsonii*. Another potential prairie-specific oligolege is *D. maura*, which was fairly common over a two to three week period in late June to early July. While *Dufourea* spp. are known to be specialists, the host of *D. maura* is not known. Visitation records suggest that it may be associated with *Campanula* spp. (Krombein *et al.* 1979);

however, in this study, *D. maura* was temporally and spatially associated with high densities of *Monarda fistulosa* (Lamiaceae). This association would not be unlikely given that a congener from adjacent states, *D. marginata marginata* (Cresson), is known to be a specialist of *Monarda*. The YQMGP may provide an excellent opportunity for studies of host plant associations of this species. Given the relatively narrow range of these six pollen specialists, their rarity in this inventory and their host associations, further investigation regarding the extent to which these species are dependent on remnant prairie habitats may be warranted. The remainder of the pollen specialists are primarily eastern in affinity, with the exception of Asteraceae associate *Melissodes menuachus*, which appears to meet the eastern edge of its range in Illinois, but which has not previously been recorded in Manitoba.

Cavity nesters

The 15 cavity nesting species collected in this study were primarily megachilids; however, apids and colletids were represented by *Anthophora terminalis* and *Hylaeus mesillae*, respectively. The percentage (15%) of cavity nesters is somewhat low compared to other studies in which such data are presented. Including solitary bees nesting above ground in typically woody substrates, this group represented 27% of the taxa in a southern Ontario old field (Grixti and Packer 2006), 32.5% in a small grassland sites in the Swiss Alps (Oerteli *et al.* 2005), and about 20% in a New York forest preserve (Giles and Ascher 2006). The YQMGP contains nearly 50% aspen forest cover, which might be expected to contain no shortage of cavities and woody substrates; however, availability may still be relatively low in this prairie environment compared with the more densely forested or structurally variable habitats in the other studies. The vast majority of the cavity nesters encountered in this study are widely

distributed throughout North America. Only *Anthidium clypeodentatum* is primarily a western species, while *O. atriventris* and *Penstemon* specialist, *Osmia distincta*, are primarily eastern in affinity.

Miners

Representing half of the species detected in this study, and belonging to all five families, miners were the most species rich ecological group. Andrenids, which made up the bulk of this group, were characterized primarily by species with widespread and eastern distributions. *Andrena medionitens* was the only western ranging andrenid while *Pseudopanurgus simulans* and *P. renimaculatus* have relatively restricted distributions in the central regions, but have not been recorded previously from Manitoba. Certain early flying species may have been missed given that some of the more common early emergents such as *A. geranii, A. vicina,* and *A. barbilabris* were being caught in respectable numbers in the first few sampling periods of the season. Although most *Andrena* species occur in the spring, it is notable that no late season *Andrena* were collected in this study. As late-occurring *Andrena* are often specialists on Asteraceae, it is possible that the low availability of floral resources in the latter part of the season at the YQMGP in 2006 may have limited opportunities to collect such bees. However, this did not prevent the emergence of Asteraceae specialists in the genus *Pseudopanurgus*. The latest *Andrena* species collected was the crucifer-specialist, *A. arabis,* of which only one specimen was collected in the third week of July.

Among the halictids, ground-nesters belonged to three genera including *Agapostemon*, *Lasioglossum* and *Dufourea*. Most of the mining *Lasioglossum* species

collected in this study belong to this genus in its strict sense; however, a non-metallic black *Dialictus* (i.e. non-carinate *Evylaeus* in the sense of Michener 2000) species, L. (*Dialictus*) *pectoraloides*, was included among the miners. This was also the only species among the mining halictids that is western in affinity. Several ground-nesting halictids are known to display communal behaviour including the Holarctic *Lasioglossum zonulum*, three widespread species: *Agapostemon texanus, Lasioglossum athabascense* and *L. paraforesii*, and two primarily eastern species: *A. sericeus* and *L. coriaceum*. Females of *Agapostemon texanus* are indistinct from their congener *A. angelicus* Cockerell, with which their range overlaps in western regions. Therefore determination of *A. texanus* in this study was made primarily on the basis of male structure.

Apid miners were eucerines exclusively in the genus *Melissodes*. Males from this tribe are distinct because of their long antennae, from which the common name 'long-horned bees' arises. This group contained the common eastern species *M. druriella* and close associate *M. rustica*, widespread *M. agilis* and western-ranging *M. menuachus*. Miners of the Colletidae were represented primarily by specialists in the genus *Colletes*, which are discussed above (See Discussion section: Characterization of the fauna: *Pollen specialists*); however, widespread *C. kincaidii* was the only polylectic member of this genus. Two members of the Megachilidae, *Megachile melanophaea* and *M. perihirta*, are primarily ground-nesting.

Social nesters

Social nesters of the genera *Bombus* and *Lasioglossum* were numerically dominant in this study; however, a small number of specimens of primarily eastern-distributed

Augochlorella aurata and *Halictus parallelus* were also collected in this study. Representing 23% of the species and 75% of the individuals overall, the dominance of this group is consistent with other studies in grasslands or other habitats at similar latitudes (Grixti and Packer 2006; Oerteli *et al.* 2005; Sarospataki and Fazekas 1995).

All nine primitively eusocial *Lasioglossum* taxa in this study belong to the subgenus *Dialictus* and represent a balance of eastern- and western- ranging species. Despite its widespread distribution and dominance in many habitats, the taxonomy of the *Dialictus* subgenus is not well established. For example, two taxa in this study could not be identified to species. For analytical purposes, they were assumed to be eusocial given the dominance of this strategy among *Dialictus*; however, this may be erroneous. Nonetheless, given that these two taxa represented so few specimens, such an error would have not affected the results of analyses based on nesting guilds. Also, I uncovered an interesting distributional mystery in that the most common species of bee in this study, *L. succinipenne*, is previously recorded only in Colorado (See Section: *New records*). The similarity of this species to the common eastern *L. pilosum* suggests that there may be a distributional turnover between these species from east to the most central regions of North America, which brings the distribution and status of specimens historically identified as these taxa into question. Another common species in this study, *L. albipenne*, is widespread across the more northern parts of the US, but is locally common primarily in the east. It was the only taxon of its genus that appeared to be more frequently captured in sweep-netting than in bee bowls. The more easterly-distributed taxon, *L. perpunctatum,* was the only common non-parasitic taxon that was associated with yellow rather than blue bowls. The centrally distributed species, *L. pictum*, is associated with sandy prairie habitats, and

along with the eastern species, *L. vierecki*, is distinct from other *Dialictus* species due its red to orange-coloured abdomen. *Lasioglossum pruinosiforme* and the western-distributed *L. pruinosum* represent new records for Manitoba.

There were ten species of *Bombus* recorded in this study. Most of these species are distributed quite widely throughout North America; however, *B. sandersonii*, *B. bimaculatus* and *B. terricola* have a primarily eastern distribution and *B. nevadensis* is primarily western in affinity (Krombein *et al.* 1979). Some specimens of *B. sandersonii* that were not preserved in the first year of this study may have been misidentified as *B. vagans* due to subtle differences in appearance that were not understood until the second year of the study. Unfortunately, under-representation of *B. sandersonii* for this reason is apparently not uncommon in inventory-type studies (Giles and Ascher 2006).

Though not a new record, the low number of *Bombus terricola* found in this study (eight) is noteworthy when examining results of the only other study of wild bees published in Manitoba. In a study of the bee pollinators of alfalfa (*Medicago sativa*), Stephen (1955) reported *B. terricola* to be the most common wild bee recorded, outnumbering any other species by a ratio of 2.4 to 1. *Bombus terricola* is considered to be a common eastern counterpart of the western-distributed *B. occidentalis* (Thorp and Shepherd 2005). Both species belong to the subgenus *Bombus* which has been recorded to be in decline across North America since the late 1990's (Thorp and Shepherd 2005). Unfortunately, it is difficult to assess the historical status of *B. terricola* on the basis of one study, especially given that only one crop was examined and that sampling sites were variable and poorly documented. However, the contrast

between this study and that of Stephen (1955) is nonetheless striking enough to warrant consideration of *B. terricola* as a potential candidate for status assessment and further study.

Parasitic taxa

The proportion of parasitic taxa collected in this study is low. Their contribution to species richness was only 11%, compared to values of around 20 to 25% observed in other studies at similar latitudes (See Literature review section: Natural history of bees: *Parasitic bees*). Of particular interest is the lack of social parasites, *Bombus* subgenus *Psithyrus*. *Psithyrus* spp. are parasitic on other *Bombus* species, and they are expected to be present wherever available hosts occur. Species that are associated with hosts captured in this study and that might have been expected to occur at the YQMGP include *B.* (*Psithyrus*) *ashtoni* which associates with *B. terricola, B.* (*Ps.*) *citrinus* which associates with *B. vagans* and *B. nevadensis, B.* (*Ps.*) *fernaldae* associated with *B. rufocinctus* and *B. terricola*, and B. (*Ps.) insularis* which parasitizes *B. nevadensis, B. rufocinctus*, and *B. terricola,* among others (Krombein *et al.* 1979). Of these, *B.* (*Ps.*) *ashtoni, fernaldae* and *insularis* have been recorded in Manitoba; whereas *B.* (*Ps.*) *citrinus* has been recorded in North Dakota (Krombein *et al.* 1979). It is possible that the lack of parasitic bees in this study is the result of low sampling intensity. Alternatively, some feature of their biology, such as host searching behaviour, may render them less likely to be captured by the methods used in this study. That cleptoparasites, and *Nomada* spp. in particular, were nearly the only group of bees in this study that were caught frequently in yellow bowls suggests that they respond to colour stimuli differently than other taxa. Unfortunately, there is very little literature on sensory perception, feeding requirements or host-search

behaviour in this group. Another possible explanation for the low proportion of parasitic bees collected in this study is that there were several morphospecies that could not be identified to species. For example, *Sphecodes* sp. 1 was relatively common among the sweep-samples; however, the peculiar seasonal pattern in its relative abundance (Figure 45) suggests that this "species" may, in fact, represent several, distinct species.

Of the parasitc taxa that were collected and identified, most are either widespread or eastern in affiliation. The only exception is *Epeolus ainsliei*, an apid parasitic on *Colletes* spp., which appears to be restricted to the central region of North America. Unfortunately, the host taxa and distribution of the most common cleptoparasite collected in this study cannot be determined, as it was not identified to species. For convenience, this taxon was called *Nomada* sp. 1, and it occurred nearly exclusively in yellow bowls in Section 28. Its association with *Andrena* species may be inferred, however, given that that site contained the greatest diversity of *Andrena* species and that the other four *Nomada* species collected in this study, including *N. cressoni*, *N. cuneata*, *N. maculata* and *N. pygmaea*, are known to be associated with *Andrena*. *Stelis lateralis*, a widely-distributed megachilid cleptoparasite, was the only taxon detected that is parasitic on cavity nesters.

Comparison of the sampling methods

Interpretation of results must explicitly acknowledge biases associated with sampling methods. Non-similar trends in peak bee catch frequency, diversity indices, compositional patterns and the relationship to floral availability were detected using the two methods employed in this study. Given that two methods were used to

sample the same bee community, the assumption that sweep-netting and bee bowls are unbiased estimators of community parameters must be rejected.

Assemblages collected in bee bowls had greater dominance values, and consequently lower evenness values. This is probably due to the high affinity that *Lasioglossum* spp., particularly the small-bodied bees in the subgenus *Dialictus*, appeared to display for bowls. This is consistent with other studies in which high numbers of *L. (Dialictus)* bees were captured in bowls (Giles and Ascher 2006; Leong and Thorp 1999). The extent to which dominance in bowl samples reflects actual abundance is unclear. In this study, *L. (Dialictus)* spp. were very commonly collected using both methods, but dominance in the bowl samples was exaggerated relative to that in sweep-net samples. There is speculation in the literature that body size may affect susceptibility to being captured in bee bowls (Cane *et al.* 2000; Giles and Ascher 2006). For example, the small body size and low flying habit of *L. (Dialictus)* spp. may make them less likely to be visually detected when sweep-netting and more prone to succumbing to drowning. Conversely, certain *Bombus* spp. were also common, but were more strongly associated with sweep-sampling in the ordination diagram (Figure 33). Although some researchers have suggested that the large body size of *Bombus* may prevent them from drowning in the bee bowls, several large specimens of *Bombus* were collected in bowls in this study. Behavioural factors may be at play, as *Bombus* species are flower constant on any given foraging trip (Grant 1950; Waser 1986). Lower relative abundances in bee bowl may reflect a reduced tendency towards experimentation with a new and unfamiliar flower type. Regardless of the basis for the bias, it is difficult to say which method best represented actual abundance levels of *Bombus* spp.

Although no statistical difference was detected in the Hill's N1 effective species richness, comparison of the more commonly used Shannon-Weaver index showed sweep-netting to detect higher diversity than bee bowl samples. The lack of difference found for the N1 may have had to do with a small sample size relative to the magnitude of the variation in the values among the sites. Further evidence that sweep-netting yielded more diverse assemblages in this study comes from the rarefaction curves, in which the steepness of a curve indicates a more diverse assemblage (Buddle *et al.* 2005). The rarefaction curves produced for each of the methods (Figure 29) indicated that sweep-netting had a greater rate of species accumulation per individual than bee bowls. Not only did sweep-netting produce steeper curves, but rarefaction curves generated on a site-by-site basis (Figures 12 and 25) showed that the methods differed in their representation of the most diverse community. For the bee bowl samples, the steepest curve occurred for Section 29 (Figure 12). Conversely, Section 28 contained the most diverse assemblage based on sweep-netting data (Figure 25). These different results may be reflective of an interaction between actual compositional differences between sites and taxon-specific responses to the particular methods. For example, the tendency for bee bowls to exaggerate the dominance of *Lasioglossum* spp. would have been less pronounced at Section 29, which yielded the lowest catch frequencies of the most common species in this genus. Alternatively, Section 28 contained a greater variety of taxa that tended to be over-represented in sweeps relative to bowls, such as the large variety of *Andrena* spp.. This would have had the effect of enhancing the degree of evenness at this site, and hence, diversity.

That sweep-netting has a greater rate of species accumulations per individual than bee bowls has implications for the perceived efficiency of either method. Sampling with bee bowls is largely regarded as simpler and more efficient than netting because it is a passive sampling technique, and bowls can be deployed and collected with minimum effort (Bartholomew and Prowell 2005; Cane *et al.* 2000). Sweep-netting requires a greater number of person-hours in the field and often limits the number of sites that can be sampled in a day. However, considerations of the efficiency of either method rarely acknowledge processing time. It is widely acknowledged among entomologists that there is a large ratio of hours spent in the lab to hours spent in the field when conducting faunal surveys (Danks 1996). To examine, sort, mount, label and identify specimens requires significant time and financial resources. If sweep-netting can capture a similar or greater number of species per individual than bee bowls, then fewer individuals need to be processed in the lab to obtain a similar level of information on species richness, depending on sampling effort.

Plotting of seasonal trends in catch per unit effort revealed that, during the early part of 2005 and all of 2006, peak catch frequencies in one method occurred during periods of low catch frequencies in the other method (Figure 32). When incorporating findings of seasonal stem densities (Figure 6), bee bowls were more effective in the context of low floral resource availability, while sweep-netting may be more effective during high resource availability. Also, in multiple regression analysis, bee bowl catches were negatively related to floral resource availability in both years, when controlling for seasonality and incident light. Conversely, sweep-net catches were positively related to bee bowl catches in 2006, when controlling for seasonality and maximum temperature.

The negative response of bee bowl catch frequency to floral resource availability is consistent with the suggestion by Cane *et al.* (2000) that a competitive interaction between flowers and bee bowls was responsible for poor capture rates of bees associated with a single host plant, *Larrea tridentata*. However, evidence in this study applies to the whole habitat level. Behavioural factors, such as the tendency for some species to forage in a horizontal stratum, were not tested in this project and therefore cannot be entirely excluded here. However, the prairie habitat sampled in my study had minimal vertical structure compared to other habitats such as forest or tallgrass prairie. It is difficult to suggest why such competition might occur, as there has been little research to indicate how individual bees respond to bowls. Clearly, it is presumed that the bowls present a strong visual stimulus; however, the lack of appropriate chemical stimuli may detract from the bowls when flowers are present.

The relationship between sweep-netting and resource availability was less clear. Sweep-netting catch frequency was positively correlated with floral resource availability in 2006, but not in 2005. The difference in this relationship among years is consistent with the idea of competition under conditions of resource limitation. When a resource is limiting, there should be a tight link between the abundance and diversity of resources and consumers, as consumers should be continually adjusting to changes in the resource base (MacArthur 1972; Tepedino and Stanton 1981). That there were fewer bees in 2005 and more floral resources suggests that if competition for floral resources exists in this community, it would have been more likely to occur in 2006. However, this effect may have been exaggerated by the way in which floral resource availability was measured in this study. Given that variation in floral

displays and nectar production rates vary among plant species, and due to various other factors, counting individual flowering stems likely overestimated actual resource availability for some plant species while underestimated these resources for others. For the purposes of this study, the initial assumption was that these two biases would balance out at a community level. However, seasonal changes in the overall composition of the floral community may have moderated this.   In other habitats, as well as in this study, the contribution of plants in the Asteraceae to community composition increases over the course of the summer (Zimmerman and Pleasants 1981). As such, there would have been an increased trend toward underestimation of resources relative to the visual stimulus provided by flowering plants (Zimmerman and Pleasants 1981). This may have contributed to the disconnection in the relationship between sweep-netting catch frequencies and flowering stem availability in the latter part of 2005 (Figures 6 and 32). This would also account for the late-season peak detected in bee bowls.   In 2006, the dry conditions contributed to the termination of flowering activity by early August, and none of the late season asters bloomed in appreciable numbers. The lack of flowers likely rendered bee bowls very attractive to foraging bees.

There was no evidence that bee bowls were any more or less effective than sweep-netting at representing species among the nesting guilds or pollen specialization classes. No effect of sampling method was detected on the species frequencies among the nesting guilds. While the overall proportion of specialist taxa among non-parasitic bees was higher within the sweep-net sample (23% versus 17% in bowls), this difference was not significant.   Taxa that are missed by either method are randomly drawn from the various nesting guilds identified in my study. That there was no

difference between the methods in the frequency of pollen specialists differs from the finding of Cane *et al.* (2001), in which only two of eight sampled specialists of *Larrea tridentata* were captured in bowls. This difference may be because they sampled only one day at one site at the height of the *Larrea* bloom. Sampling in this study occurred on a weekly basis at three sites, which may have increased the probability for specialists to be collected in bowls if they were present outside of the spatial or temporal window of their hosts' bloom.

Overall, the biases identified herein emphasize the need for careful consideration of the objectives of a sampling program when selecting a sampling method. Bee bowls can contribute important information in sampling programs designed simply to survey the fauna or to study bees in low-resource conditions such as following a disturbance (Cane *et al.* 2000). Also, bee bowls may be helpful for collecting specimens of targeted taxa that are captured more frequently in bowls, such as the *Lasioglossum* or *Osmia* species. Alternatively, sweep-netting may provide greater insights in studies to investigate floral relationships or resource use. However, when the objective is to provide a complete list of the fauna and to monitor changes over large spatial or temporal scales, the use of several methods will provide the most complete representation.

Seasonal turnover in the bee community

In both years, community diversity peaked in the early part of the season and progressively decreased over time (Figure 49). This appears to be the result of a high concentration of species with relatively short temporal distributions appearing early in the season. The cleptoparasites and cavity nesters such as *Osmia* spp. were most

prominent at this time. In 2005, when the early season peaks in N1 values were at their highest, there was a strong representation of *Andrena* species. The early season cleptoparasites, *Nomada* spp., are primarily parasites of *Andrena* spp. While the basic biology of many species is unknown, the early emergence of some species of *Osmia* and *Andrena* has been attributed to their ability to overwinter in the adult stage, whereas other solitary bees that emerge later in the season overwinter in the final larval stage prior to pupation (Donaldson *et al.* 2002; Kemp *et al.* 2004; Krombein 1967; Sheffield *et al.* 1985). Social nesters such as *Bombus* spp. and many *Lasioglossum* spp. overwinter as mated gynes, accounting for the early appearance of some characteristic *Lasioglossum* species in the 2006 ordination. Although social nesters are present all season long, their concentration into the late part of the season in the 2005 ordination likely reflects the concurrent decrease in bee species from other guilds and increase in the abundance of the social nesters when late-summer colonies are strong. This trend towards increasing dominance of social nesters likely accounts for the late season decrease in N1 values observed in both years.

Differences in the generic identities of the characteristic taxa and in nesting guild composition observed in 2006 may be related to reduced resource availability in the latter part of the season. The early spring in 2006 may have given certain early emergent taxa, such as the social *Lasioglossum* spp., a strong start, but as resources depleted, there may not have been enough to allow competitively inferior species to develop strong colonies. As such, they would have achieved peak relative abundance early in the season. The stronger Berger-Parker dominance index values found in 2006 are in agreement with this and may be consistent with a scenario of competition under resource limitation.

Overall, general seasonal composition patterns observed in this study were consistent with other studies in temperate climates (Ginsberg 1983; Oerteli *et al.* 2005; Parrish and Bazzaz 1979). In Swiss alpine meadows sampled by hand-netting, peak catch frequency was achieved in the August and September, while peak species richness occurred in late spring to early summer. Researchers found miners to achieve peak relative abundance of mining species in spring, while *Bombus* spp. were more frequent from July to September (Oerteli *et al.* 2005). However, they found no seasonal affinity of cleptoparasites in their study. The difference between their study and mine may be that their sample was taxonomically and numerically dominated by *Sphecodes* spp., which are primarily associated with halictid hosts (Sick *et al.* 1994), while *Andrena*-associated *Nomada* spp. were more common in my study. In a particularly detailed examination of seasonality, Ginsberg (1983) identified four distinct seasonal assemblages in old fields in New York State. In his study, spring bees were characterized by univoltine *Andrena* spp. and the *Lasioglossum* subgenus *Dialictus*, which would be consistent with the second year of this study. Early summer bees were characterized as the first generation of workers of the social species. *Bombus*, later generation halictids and some late-season andrenids comprised late summer bees. Finally, Ginsberg reserved a class for honey bees, for which abundance grew over the season and peaked in the fall. Ginsberg's system was different in that he had a slightly longer growth season and that it was clearly influenced by the presence of honey bees. As such, the native social nesters in his system peaked toward the middle part of the season rather than the late part of the season when honey bee populations were at their highest. With the exception of an early season peak of honey bees in Section 29, which was adjacent to an over-

wintering site for a local apiarist in 2005, honey bees were not consistently present in appreciable numbers at the YQMGP (Figure 11).

Regarding seasonality of the resource base, there was a tight correspondence in the redundancy analyses between seasonal assemblages of flowering stems and bees in both years. However, the observation that early season bees should be associated with early season plants at a community level is intuitive. It is important to note that this type of analysis does not imply causality, let alone a direction of causality. Seasonal responses of individual species result from a complex interaction of life-history traits, physiological responses to environmental cues such as temperature, precipitation and photoperiod, and to interspecific interactions (Holda 1988). As such, determining causality of the relationship between floral and bee species phenology at the community level is beyond the scope of this study.

Other influential factors

Annual differences

There was an increase in the number of individual bees collected from 2005 to 2006; however, this was not consistent across all components of the bee community. Andrenids, particularly those in Section 28, and apids, including *Bombus ternarius*, decreased in numbers. The increase in the overall bee community was driven by the more common *Lasioglossum* spp. such as *L. succcinipenne*, *L. albipenne*, *L. paraforbessii* because social nesters overall increased despite the decrease in *Bombus* spp.

The extent to which the increase in the overall bee community may be related to climatic conditions is difficult to assess. While abiotic conditions can govern year-to-year variability in other taxa either directly or indirectly by acting on the resource base (Gilbert and Singer 1975), interannual variability in bee abundance is not well understood. Rather, abiotic conditions have been conjured as explanations for spatial patterns of bee abundance at global and altitudinal scales (Devoto *et al.* 2005; Elberling and Olesen 1999) and for temporal patterns on daily or seasonal scales (McCall and Primack 1992; Peat and Goulson 2005). Part of the difficulty in determining relationships between annual abundance and other factors is that rarely are more than two or three years of data published. Even when large data sets are available, researchers have generally failed to detect a relationship. For example, Roubik (2001) tracked patterns in the abundance of euglossine bees (Apidae) in Panama over 17 years, and was not able to detect a relationship between bee abundances and precipitation patterns, even when controlling for other possible explanatory factors.

That the observed increase in bee catch frequency and species richness in my study occurred during a hot, dry year is consistent with global spatial patterns in which bee species richness and abundance peak in warm, xeric climates (Michener 1979, 2000). However, that this increase also occurred in a year that was comparatively poor in terms of floral resource availability suggests that bee abundance from year to year is not linked to resource conditions in that same year. In temperate habitats, Tepedino and Stanton (1981) postulated that bee abundances may reflect conditions and resources levels from the previous year, when cells are being provisioned for the

following year's population of adults. Such an explanation would be consistent with the trend observed in this study; however, studying this community for several more years would be required to substantiate such a hypothesis.

Site differences and leafy spurge

This study detected important differences among the sites in both the floral environment and the bee community. The floral environment in Section 28 was compositionally distinct from the other two sites. Dominated by invasive the exotic invasive plant leafy spurge (*Euphorbia esula*) in both years, Section 28 lacked many of the common species observed at the other two sites including *Monarda fistulosa, Campanula rontundifolia, Chrysopsis villosa* and *Linum lewisii*. The low N1 value found for this site reflects the low diversity of flowering plants. This corresponds with findings by Belcher and Wilson (1989) who found native plant diversity in a nearby mixed-grass prairie remnant in southwestern Manitoba to be negatively correlated to the per cent cover of leafy spurge. Although no statistical difference in the overall density of flowering stems among the sites was found, Section 28 clearly contained the highest density of flowering stems in the early to middle parts of season which correspond to the flowering period of leafy spurge (Figure 7). Late season suppression of floral stem density observed at all sites in 2006 was also apparent in Section 28 in 2006. Leafy spurge may co-opt space and resources from late season forbs, thereby creating a period of late season resource depletion for bees even in climatically favourable years. When looking at the dominant flowering species at each site (Table 5), seven of the ten most common species at Section 28 are primarily early season species, suggesting they may have been taking advantage of the growth conditions prior to the emergence of leafy spurge. Conversely, most of the top ten

species at the other two sites were mid-, mid-late or late season species. This altered seasonal pattern in resource availability was evident in the PCA diagrams (Figures 9 and 10). In 2005, the suppression of characteristic mid-season plants in Section 28 caused the mid-season assemblage from Section 28 to be more closely related to the early season assemblages. In 2006, drought conditions in July curtailed the bloom season of leafy spurge and the subsequent lack of any flowering stems at that site caused the mid-season assemblage to be more closely associated with the depauperate late season assemblages found throughout the YQMGP.

Despite the poor diversity of flowering forbs in Section 28, this site supported a relatively rich bee assemblage. In the bee bowl data, raw species richness among the sites was highest in Section 28, while in the sweep-netting data, values for N1 effective species richness and rarefied species richness were highest at this site. Either leafy spurge is a valuable resource to bees or there are other features of the site that support high bee diversity.

I found no studies in which the quality of leafy spurge as a resource to wild bees was investigated specifically; circumstantial evidence exists. In a comparative study of pollinator visitation rates and pollen transfer in native plants located inside and outside (>100m away) of leafy spurge infestations, Larson *et al.* (2006) indicate that bees made up a smaller proportion of the insect visitors to leafy spurge than to native plants located within infestations. Rather, flies (Diptera) were proportionally more common visitors to leafy spurge. If leafy spurge was very attractive to bees, one might expect them to less frequent visitors to native plant than to leafy spurge.

The reciprocal relationship found in my study between resource availability and sampling method (See Results: *Comparison of methods*) may be of inferential value. Among the sites, bee bowls yielded the greatest number of bees in Section 28 while sweep-netting collected the fewest bees, suggesting that leafy spurge is a poor quality resource. It is possible that low sweep-netting values at this site were the result of poorer sweep-netting efficiency within the dense stand of tall leafy spurge plants. However, this is unlikely, given that no difference in bee catch frequencies was found between the inside and the outside of the grazing exclosure, where vegetation height was lower due to grazing (personal observation).

Therefore, other features of this site likely support high bee diversity. For example, the proximity of a south-sloping, open-faced sand hill may have provided abundant nest sites in a favourable thermal environment early in the season. This may have contributed to the high diversity of early-flying *Andrena* species, which were collected most frequently at this site in 2005. Also, this site was located in close proximity to fairly large tracts of aspen forest relative to the other two sites, which may have provided more diverse nesting and forage opportunities. That the high density of leafy spurge did not impoverish bee diversity at this site may mean that the scale at which many bee species are interacting with the habitat is larger than the size of the infestation. However, this may not apply to specialists. While there was no evidence from either sampling method that the richness of specialist taxa differed among the sites; there were fewer individuals of oligolectic species were captured in bee bowls at this site. Specialists may be less successful in Section 28 and further investigation of the effect of invasive plant species on the success of specialist pollinators is warranted.

Bowl colour

In general, bowl colour was important in determining catch frequencies of bees; however, the taxonomic and ecological groupings did not respond consistently. Megachilids and colletids did not respond to bowl colour overall, nor did three common *Lasioglossum* spp.. When bowl colour was important, blue bowls were generally most effective, yellow bowls were generally least effective, and white bowls varied in effectiveness between the two. Exceptions to this generalized pattern were for *L. perpunctatum* and the cleptoparasites, both of which were captured most frequently in yellow bowls.

Despite the finding of broad colour associations for certain groups overall, significant interactions of bowl colour and site for certain groups and taxa suggest that these associations are not stable. At the group level (e.g. family or ecological class), interactions between site and bowl colour may reflect site differences in the species composition of these groups acting in conjunction with differential species-level responses to the colours. If one species is more strongly associated with a particular bowl colour than other species in its group, and if that species is dominant at only one site, then a significant interaction would be expected. This may explain the significant interaction between bowl colour and site for the cleptoparasites. *Nomada* sp.1, of which two-thirds of the specimens were captured in yellow bowls, was dominant in Section 28 in 2005 (Figure 22). At the other sites, and in 2006, when relative abundances of *Nomada* sp.1 were much lower, the effect of bowl colour on the catch of cleptoparasites was not significant. Unfortunately, this type of explanation does not work as well to explain the interaction observed in the other

groups because some species level responses to bowl colour vary between sites and years.

Possible alternative explanations for species level interactions involving bowl colour include differential responses of the sexes to bowl colour (Leong and Thorp 1999) or changing floral context. In vernal pools in California, Leong and Thorp (1999) captured females of oligolectic *Andrena limnanthis* Timberlake significantly more often in white and blue bowls while males tended to be caught in white bowls. Such an effect could drive site-colour interactions at the species level if high numbers of males and females were collected at different sites; however, in my study, colour-site interactions tended to occur in the more common social nesting species including *L. succinipenne, L. albipenne, L. paraforbesii* and *Bombus ternarius*. As such, females made up the bulk of the samples of these species, likely rendering any differences among the sexes inconsequential. Therefore, it seems possible that floral context may affect certain species responses at different sites.

Results from other studies in which different coloured bowls or pan traps were incorporated allude to the importance of floral context at the habitat level, as there appears to be no consistent trend in the most and least effective bowl colours among habitats. For example, Cane and others (2000) found blue bowls to be more effective than yellow bowls for capturing oligolectic species at a site in Arizona dominated by yellow-flowered *Larrea tridentata*. In a survey of the bee fauna of a forest reserve in New York State, yellow bowls were most effective and blue bowls were least effective (Giles and Ascher 2006). In a Louisiana long-leaf pine savanna, Bartholomew (2005) found white bowls to be significantly less effective than yellow

and blue bowls in terms of the number of bees and species. In the west Sonoran desert, Toler and colleagues (2005) found no effect of bowl colour on the total number of individuals or species captured; however, they detected colour preferences at the species level. While differences in the shades of blue and yellow or other bowl features among studies may have also affected such results, these inconsistencies are worth exploring. For example, is it possible that some relationship exists between bowl colour preference and the dominant floral colour in that habitat? Toler *et al.* (2005) provide the only examination of this question in the literature, and they found no effect of the prevailing bloom colour at the time of sampling on bowl colour associations of taxa or individuals at the community level. However, insights regarding the extent to which colour associations are robust across sites, floral contexts and habitats may best be gained by working at the species level. Until such questions are addressed, sampling protocols that are developed with the intention of sampling across habitats should retain several bowl colours, in spite of recommendations to the contrary (e.g. Bartholomew 2001).

Grazing effects

Investigating the effect of grazing was not an explicit object of this study; however, it was included because I thought that it might explain some of the variability observed. Indeed, the density of flowering stems was greater in the grazed areas outside of the exclosure than on the inside, although this was only significant in 2005. Whereas flowering was probably universally limited for climatic reasons in 2006, in 2005, a grazing effect could have occurred due to such mechanisms as exclusion of competitively dominant graminoids, removal of detritus to allow underlying plants

better access to solar radiation, or by triggering increased resource allocation at the plant level to reproduction (Collins and Barber 1985; Coupland 1992a; Kerley *et al.* 1993; Knapp *et al.* 1999; Wissman 2006). There were significant within-subjects effect of week (Table 4); so perhaps the effect of grazing was stronger in some weeks than in others, likely corresponding to the presence of grazers and seasonal effects.

Despite the difference observed inside and outside of the grazing exclosures on resource availability, there were no differences in sweep-netting catch frequencies. This should not be taken as an indication that grazing does not impact bees, as the spatial scale and design of this study was not appropriate to address this question adequately. Foraging ranges of even small bees were likely greater than the distance between the grazing exclosures and the adjacent grazed areas where sweep-netting occurred in this study (Gathmann and Tscharntke 2002). Bees would have been able to move freely between the grazed areas and the ungrazed areas located inside the 1-ha exclosures. As such, some form of facilitation may have been occurring among flowering stems located inside the grazing exclosure where floral densities were generally lower. This could have increased the bee to flower ratio inside the exclosure relative to outside of the exclosure. Alternatively, greater competition for pollinators among more densely co-occurring flowering stems outside of the grazing exclosure may have reduced the bee to flower ratio relative to the ungrazed areas. Either scenario could have resulted in similar number of bees being collected on either side of the exclosure fence.

Time of day

In general, sweep-netting catch frequency was highest in the morning and subsequently decreased over the course of the day; however, at the community level, this was only significant in 2006. It is possible that this general pattern in catch frequency corresponds with daily community-level patterns in nectar and/or pollen availability; however such data were not collected. That the greater catch frequencies observed in the morning were significant only in 2006 when drought conditions prevailed is suggestive of a resource basis to this trend. Water stress can reduce the volume and/or concentration of nectar produced by plants (Carroll *et al.* 2001; Villareal and Freeman 1990); however, there is little information about how weather or drought conditions affect daily patterns of nectar secretion or pollen presentation at a community level (Peat and Goulson 2005). Without such information it is difficult to relate daily floral resource patterns to patterns in sweep-net catch frequency. However, with more bees and fewer flowers in 2006, it is conceivable that bees may have been forced to forage early in the day to access resources before they were depleted by other foragers.

This same pattern was observed for different groups of bees, but significance varied. When a significant time-of-day effect was found in only one year, it tended to occur in 2006 rather than 2005. This was the case for the social nesters, the colletids and *L. albipenne* and the potential reasons for this would be similar to those discussed for the community level. Groups for which the time-of day effect was significant in both years showed longer periods of peak catch frequencies in 2006. For example, miners were caught significantly more often in the morning sweeps versus the afternoon and evening in 2005; however in 2006, the difference in catch frequency between morning

and afternoon was not significant. In 2006, reduced availability of floral resources may have forced the bees that are already early foragers to forage for longer periods of time to meet their requirements.

While sweep-net catches are highest prior to noon for several groups, bee bowl catches peaked somewhat later, between late morning and mid-afternoon (Figure 17). If indeed the daily pattern in sweep-net catches corresponds to daily patterns in floral resource availability, then the later peak in bee bowl catches may provide further evidence on a temporal scale of competition between flowers and bowls. For example, if nectar and pollen resources decrease from the morning onwards, then bowls may become more attractive as floral resources are depleted. Further studies on daily patterns of nectar and pollen availability in mixed-grass prairie would allow for more explicit examination of this possibility.

While bees could continue to be collected into the evening with both methods, there were no species that would have been missed had sampling not included evening collections. Evening collections were initially included because of the relatively high latitude at which this study was conducted. Given the long hours of daylight in the mid-season, it seemed reasonable that certain taxa might take advantage of this temporal niche. Particular efforts were made to collect evening primrose (*Oenothera* spp., Onagraceaea) specialists, *Lasioglossum* (*Sphecodagastra*) spp., as these tend to be crepuscular or nocturnal. However, despite targeted placement of bowls in patches of *Oenothera* spp. and two attempts of late night net-sampling, none of these taxa were encountered. Therefore, if targeted efforts are made to collect potential

crepuscular taxa, foregoing evening sampling in northern prairie habitats should not

adversely affect estimates of species richness.

SUMMARY AND CONCLUSIONS

Sampling at three sites within the Yellow Quill Mixed-grass Prairie Preserve over two years yielded 100 species of wild bee; however, this number was deemed to be an incomplete representation of the local fauna. The YQMGP bee fauna was primarily eastern in affinity; though there were several representatives with central and western distributions. Fifteen taxa were newly recorded for Manitoba. Social nesters from the genera *Lasioglossum* and *Bombus* dominated the community in terms of the number of individuals, while mining species from the genus *Andrena* represented the greatest species richness. The proportions of pollen specialists, social nesting and mining species were within expected ranges compared to other studies; however, the proportions of cavity nesters and parasitic taxa collected over the course of this study were lower than expected. In the case of cavity nesters, this was attributed to low habitat heterogeneity in a prairie environment. The low number of parasitic taxa was likely due to sampling and taxonomic limitations. This study greatly improved our knowledge of mixed-grass prairie bee species in southwestern Manitoba.

While the proportions of bee species distributed among the nesting guild were stable between methods, bee assemblages collected through sweep-netting were more diverse and had lower dominance values than those collected through bee bowls. Due to differential effectiveness of each of the methods for capturing certain taxa, species composition was more similar between years and sites than among sampling methods. Although bee bowls are typically viewed as more efficient in the field, the greater species accumulation rate achieved through sweep-netting may reduce processing

time in the laboratory. Bee bowls were most effective during periods of low resource availability and may compete with flowers for bees; whereas sweep-netting may be more appropriate for detecting patterns associated with floral resource availability. As such, consideration of a sampling protocol should reflect the objectives of the study. When the objective is to compile a species list or to characterize the fauna at a particular site, bee bowls should not be used to the exclusion of sweep-netting or other means of collection.

Wild bee diversity in the YQMGP peaked in the early part of the season with a subsequent decline over the course of the season. While there was a strong association between seasonal turnover in the composition of the bee community and that of the flowering stem community, causality of this relationship could not be established. Rather, this approach allowed early season peaks in bee diversity to be identified as being associated with a rich assemblage of univoltine, *Andrena* mining bees, *Osmia* cavity nesters and *Nomada* cleptoparasites. A generically rich mid-season community was followed in 2005 by a strong late-season contingent of social *Bombus* spp. and *Lasioglossum* spp. Higher bee catches combined with lower resource availability in the 2006 likely created conditions of resource limitation, which modified the seasonal association of social nesters in the second year. Therefore, seasonal trends in diversity and taxonomic and ecological composition of the wild bee community were apparent, but likely modified by annual climatic factors and related changes in the resource base.

The most notable site differences occurred between Section 28 and the other two sites, and this was deemed to be the result of an infestation of the exotic invasive, leafy

spurge (*Euphorbia esula*) at that the former site. High densities of *E. esula* in Section 28 were associated with reduced floral resource diversity, an altered seasonal pattern in resource availability and reduced frequencies of oligolectic bees. However, lack of replication of leafy spurge-infested sites renders these effects circumstantial.

Bowl colour affected the catch frequency of wild bees. In general, blue bowls were most effective, while yellow bowls were least effective; however, these results were not consistent among taxa or sites. Combining evidence from this study and other studies, the relative effectiveness of bowl colours may be subject to the floral context among habitats, and further modified by temporal and spatial changes at a local level. While grazing was an important source of variation in the floral community in 2006, this was not an important source of variation in the bee community collected by sweep-netting. However, the scale of this study was likely inadequate for detecting such changes. In general, sweep-netting catch frequency was highest in the morning and subsequently decreased over the course of a day; however, at the community level, these changes were only significant in 2006. As there were no species that were collected exclusively in the evening, studies conducted with the objective of compiling a species list in northern mixed grass-prairie site will likely not severely compromise results by restricting sampling periods to the day time.

SUGGESTED FUTURE STUDIES

This discussion, along with synthesis of the pertinent literature (Chapter 1), has given rise to the following recommendations for research that needs to be undertaken to improve knowledge of prairie bees and to better inform resource managers.

1) Continued sampling of the YQMGP should be undertaken to complete the local species list, with particular focus on sampling in early spring (i.e. April) and in wooded and riparian areas and with a focus towards parasitic species. The use of additional sampling techniques, such as malaise traps or trap nests, could be incorporated to potentially target additional taxa.

2) The genetic and distributional relationship of *Lasioglossum* (*Dialictus*) *succinipenne* and *L.* (*D.*) *pilosus* should be examined.

3) The status of *Bombus terricola* in Manitoba should be assessed given its decline in other regions and apparent decrease from historical records.

4) Directed studies of the host association of the pollen specialist, *Dufourea maura*, should be undertaken at the YQMGP and elsewhere throughout its range with the preliminary focus being directed towards *Campanula rotundifolia* and *Monarda fistulosa*.

5) Studies investigating the extent to which possible central-ranging specialists such as *Colletes robertsonii*, *C. susannae*, *C. andrewsii*, *Pseudopanugus simulans*, *P. renimaculatus* and *D. maura* are dependent on prairie remnants will be important in guiding prairie management and pollinator conservation efforts.

6) *Euphorbia esula* appeared to affect the diversity and seasonality of the floral resource base and possibly the success of oligolectic bees at one single site; however, replicated studies need to be conducted to substantiate these findings.

7) To better support prairie management activities, the effects of *Euphorbia esula* at should be examined at different spatial scales.

8) Studies to investigate the relationship between bowl colour effectiveness and dominant floral colour across habitat types would support large-scale monitoring efforts. For example, bowl colour preferences of selected species of wide-ranging, common bees with fairly general habitat requirements could be compared to the dominant floral colour at different temporal and spatial scales across habitats and geographic location.

9) Experimental studies designed to investigate the effect of prairie-specific management practices, such as grazing and fire, are needed to better inform managers of impacts on prairie bees.

10) Long-term studies on wild bees in mixed-grass prairie habitat are needed to provide a substantial basis upon which impacts of habitat loss and anthropogenic effects can be evaluated.

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Appendix A. Dates during which 153 grazing cattle (75 calf/cow pairs and three bulls) were present within three gazing paddocks at the Yellowquill Mixed-grass Prairie Preserve, near Treesbank Manitoba.

Year	Site	Period 1	Period 2
2005	Section 27	June 11 - June 25	August 18 - September 20
	Section 28	June 1 - June 11	July 16 - August 18
	Section 29	July 25 - July 16	September 20 - October 31
2006	Section 27	June 30 - July 15	September 21 - October 15
	Section 28	Jun 15 - June 30	August 30 - September 21
	Section 29	June 1 - June 15	July 15 - August 30

Appendix B. Total number of specimens of bee species collected by sampling week and year at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba. Weekly samples were taken at three sites by a total of 90 bee bowls and 3 - 4.5 hours of sweep-netting.

		Sampling week																						Total*		
		May		Jun.						Jul.				Aug.					Sep.							
	Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	♀**	♂	Overall
Andrenidae																										
Andrena (Andrena) thaspii Graenicher	2005	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	2006		0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1
A. (Euandrena) geranii Robertson	2005	118	19	33	4	11	10	13	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	107	112	219
	2006		5	17	12	18	12	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	60	8	68
A. (Gonandrena) persimulata Viereck	2005	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2	2
	2006		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. (Leucandrena) barbilabris (Kirby)	2005	1	0	27	6	0	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	23	40
	2006		0	12	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	8	17
A. (Melandrena) carlini Cockerell	2005	0	0	0	0	0	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	7
	2006		0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
A. (Melandrena) dunningi Cockerell	2005	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	2
	2006		0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	3
A. (Melandrena) nivalis Smith	2005	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3
	2006		0	2	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	5	0	5
A. (Melandrena) regularis Malloch	2005	0	0	0	0	0	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	5
	2006		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
A. (Melandrena) vicina Smith	2005	2	0	8	14	0	25	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34	18	52
	2006		0	14	0	1	1	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	9	21
A. (Parandrena) wellesleyana Robertson	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
A. (Rhacandrena) robertsonii Dalla Torre	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
A. (Scaphandrena) arabis Robertson	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1
	2006		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. (Scrapteropsis) imitatrix Cresson	2005	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	4
	2006		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. (Thysandrena) medionitens Cockerell	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	1
A. (Trachandrena) ceanothi Viereck	2005	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1
	2006		0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3

			Sampling week																					Total*		
		May				Jun.				Jul.				Aug.					Sep.							
	Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	♀**	♂	Overall
Andrenidae (cont'd)																										
A. (Trachandrena) cyanophila Cockerell	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	1	0	6	6	0	1	0	0	0	0	0	0	0	0	0	0	0	0	14	0	14
A. (Trachandrena) forbesii Robertson	2005	0	0	1	1	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	5
	2006		0	6	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	3	9
A. (Trachandrena) mariae Robertson	2005	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
	2006		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. (Trachandrena) miranda Smith	2005	0	0	0	0	0	0	1	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	5	0	5
	2006		0	0	0	2	0	2	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	4	3	7
A. (Trachandrena) sigmundi Cockerell	2005	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3
	2006		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. (Tylandrena) erythrogaster (Ashmead)	2005	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
	2006		0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Andrena sp. 1	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1
Andrena sp. 2	2005	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	1
	2006		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calliopsis (Calliopsis) andreniformis Smith	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1
Pseudopanurgus (Heterosarus) nebrascensis (Crawford)	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2	0	2
	2006		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
P. (Heterosarus) renimaculatus (Cockerell)	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1
	2006		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. (Heterosarus) simulans (Swenk and Cockerell)	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1
	2006		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Apidae																										
Anthophora (Clisodon) terminalis Cresson	2005	0	0	0	0	0	0	0	0	0	4	2	2	1	1	0	1	0	0	0	0	0	0	11	0	11
	2006		0	0	0	0	1	1	3	7	1	0	0	0	0	0	0	0	0	0	0	0	0	12	1	13
Bombus (Bombias) nevadensis Cresson	2005	0	0	1	4	4	0	2	2	0	0	3	1	3	1	0	1	0	1	0	0	0	0	-	-	23
	2006		0	0	1	4	0	1	3	1	0	1	1	2	1	0	0	0	0	0	0	0	0	11q/3w	1	15
B. (Bombus) terricola Kirby	2005	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	0	0	0	4q	0	4
	2006		0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	0	0	0	0	0	2q/2w	0	4

		May				Jun.				Jul.				Aug.					Sep.					Total*		
	Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	♀**	♂	Overall
Apidae (cont'd)																										
B. (Cullumanobombus) rufocinctus Cresson	2005	0	0	0	1	1	10	11	8	4	0	0	0	1	0	8	24	26	32	28	35	8	0	-	-	197
	2006		0	1	3	4	4	3	2	2	2	1	11	3	8	6	10	5	18	20	11	0	0	38q/68w	8	114
B. (Fervidobombus) fervidus (Fabricius)	2005	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0	0	0	0	0	0	-	-	4
	2006		0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1q/1w	0	2
B. (Pyrobombus) bimaculatus Cresson	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0
	2006		0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1q/1w	0	2
B. (Pyrobombus) sandersoni Franklin	2005	1	0	0	0	0	3	0	1	0	1	1	0	0	1	0	4	1	0	1	4	1	0	6q/13w	0	19
	2006		0	0	1	1	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	4q/4w	0	8
B. (Pyrobombus) ternarius Say	2005	40	1	81	34	7	16	1	4	1	2	1	3	3	2	2	25	16	11	12	15	6	1	-	-	284
	2006		0	4	8	9	4	2	1	8	8	19	48	20	3	11	23	3	6	3	2	0	0	36q/144w	2	182
B. (Pyrobombus) vagans Smith	2005	0	0	0	1	3	1	0	0	0	1	8	0	0	6	4	13	5	4	3	2	0	0	-	-	51
	2006		0	3	4	1	1	0	0	2	4	1	8	3	2	0	4	4	3	3	1	0	0	17q/44w	0	44
B. (Separatobombus) griseocollis (DeGeer)	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	8	0	2	2	1	0	0	-	-	16
	2006		0	0	0	2	1	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	4q/2w	0	6
B. (Subterraneobombus) borealis Kirby	2005	0	0	0	1	3	6	9	5	1	1	2	2	8	19	6	34	27	11	5	7	4	0	-	-	151
	2006		0	3	3	3	7	4	8	14	5	2	29	4	5	7	14	4	8	5	5	0	0	44q/73w	13	130
Epeolus (Epeolus) ainsliei Crawford	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1
Epeolus sp. 1	2005	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	2006		0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1
Melissodes (Eumelissodes) agilis Cresson	2005	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1
	2006		0	0	0	0	0	0	0	2	0	4	6	6	2	1	0	0	2	1	0	0	0	12	12	24
M. (Eumelissodes) druriella (Kirby)	2005	0	0	0	0	0	0	0	0	0	0	0	2	5	7	0	2	3	10	0	1	0	0	30	0	30
	2006		0	0	0	0	0	0	0	1	1	1	3	4	3	17	6	2	2	0	0	0	0	40	0	40
M. (Eumelissodes) menuachus Cresson	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
M. (Eumelissodes) rustica (Say)	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
	2006		0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	2	0	2
Melissodes sp. 1	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1
Nomada (Nomada) cressonii Robertson	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1

	Year	May 1	2	3	4	Jun. 5	6	7	8	Jul. 9	10	11	12	Aug. 13	14	15	16	17	Sep. 18	19	20	21	22	Total* ♀**	♂	Overall
Apidae (cont'd)																										
N. (Nomada) cuneata (Robertson)	2005	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
	2006		0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3
N. (Nomada) maculata Cresson	2005	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	2006		0	8	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	1	10
N. (Nomada) pygmaea Cresson	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	1
Nomanda sp. 1	2005	21	3	5	2	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	18	36
	2006		0	14	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	2	17
Nomada sp. 2	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Colletidae																										
Colletes andrewsi Cockerell	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
C. brevicornis Robertson	2005	0	0	0	0	0	0	0	0	4	7	8	0	1	1	1	0	0	0	0	0	0	0	9	13	22
	2006		0	0	0	0	0	0	4	6	4	1	0	0	0	0	0	0	0	0	0	0	0	11	4	15
C. kincaidii Cockerell	2005	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	3	0	3
	2006		0	0	0	0	0	0	1	0	1	0	5	0	3	0	0	0	0	0	0	0	0	8	2	10
C. robertsonii Dalla Torre	2005	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	2
	2006		0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
C. susannae Swenk	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1
	2006		0	0	0	0	0	0	1	1	0	1	2	1	1	0	0	0	0	0	0	0	0	4	3	7
C. willistoni Robertson	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Hylaeus (Hylaeus) mesillae (Cockerell)	2005	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	4	0	4
	2006		0	0	0	1	3	3	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	11	0	11
Halictidae																										
Agapostemon (Agapostemon) sericeus (Förster)	2005	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	2	3
	2006		0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	2	1	3
A. (Agapostemon) splendens (Lepeletier)	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1

| | | Sampling week | | | | | | | | | | | | | | | | | | | | | | Total* | | |
| | | May | | | | Jun. | | | | Jul. | | | Aug. | | | | | Sep. | | | | | | | | |
	Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	♀**	♂	Overall
Halictidae (cont'd)																										
A. (Agapostemon) texanus Cresson	2005	0	0	0	5	0	6	0	5	0	0	0	0	0	0	1	1	2	0	0	1	0	0	21	0	21
	2006		0	6	7	3	4	10	0	1	0	0	0	0	0	5	6	0	2	1	5	0	0	43	7	50
Augochlorella (Augochlorella) aurata (Smith)	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3
Dufourea (Halictoides) maura (Cresson)	2005	0	0	0	0	0	0	0	0	10	21	1	0	0	0	0	0	0	0	0	0	0	0	8	24	32
	2006		0	0	0	0	0	1	16	11	1	0	0	0	0	0	0	0	0	0	0	0	0	9	20	29
Halictus (Nealictus) parallelus Say	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1
	2006		0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	2
H. (Protohalictus) rubicundus (Christ)	2005	0	0	2	6	2	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	12	1	13
	2006		0	4	6	1	4	0	1	1	1	1	3	2	1	0	0	0	0	0	0	0	0	21	4	25
H. (Seladonia) confusus Smith	2005	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	2006		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3	0	3
Lasioglossum (Dialictus) albipenne (Robertson)	2005	0	0	2	2	2	3	6	12	7	11	5	7	6	13	16	30	6	14	2	0	3	0	108	39	147
	2006		0	1	5	16	39	86	32	18	13	15	28	63	56	17	93	16	33	46	74	0	0	517	134	651
L. (Dialictus) perpunctatum (Ellis)	2005	0	0	3	5	2	7	11	9	0	11	3	40	25	0	2	4	2	9	13	1	0	0	146	1	147
	2006		0	25	22	17	58	32	3	1	4	2	0	1	1	3	1	2	7	2	4	0	0	185	0	185
L. (Dialictus) pruinosiforme (Crawford)	2005	0	0	0	0	0	0	0	0	0	1	1	2	2	1	1	1	0	1	0	9	6	21	45	1	46
	2006		0	0	0	0	0	1	0	0	0	0	0	2	1	2	5	3	5	1	1	0	0	14	7	21
L. (Dialictus) pruinosum (Robertson)	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	2	0	2
	2006		0	12	19	0	5	6	0	0	4	2	0	3	3	2	12	6	4	8	10	0	0	86	10	96
L. (Dialictus) sp. 1	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	4	2	0	0	9	0	9
L. (Dialictus) sp. 2	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	-	-	3
L. (Dialictus) succinipenne (Ellis)	2005	0	0	36	115	33	12	14	19	0	33	70	75	26	11	50	119	98	90	30	18	28	5	775	107	882
	2006		0	279	157	23	47	46	14	44	89	73	37	59	139	107	181	57	58	146	172	0	0	1412	316	1728
L. (Dialictus) vierecki (Crawford)	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	3	0	3
	2006		0	1	2	0	0	0	0	0	0	1	0	0	0	0	3	0	1	1	0	0	0	9	0	9
L.(Dialictus) pectoraloides (Cockerell)	2005	0	0	0	0	0	0	2	1	0	1	0	1	0	2	0	1	0	0	0	0	0	0	8	0	8
	2006		0	1	0	1	10	7	1	0	0	0	3	1	0	0	0	0	1	0	0	0	0	5	2	25
L.(Dialictus) pictum (Crawford)	2005	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	10	0	0	2	0	2	0	17	0	17
	2006		0	5	0	1	3	1	1	0	0	0	1	0	0	0	2	0	2	12	4	0	0	32	0	32

| | | Sampling week | | | | | | | | | | | | | | | | | | | | | | Total* | | |
| | | May | | Jun. | | | | | | Jul. | | | | Aug. | | | | Sep. | | | | | | | | |
	Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	♀**	♂	Overall
Halictidae (cont'd)																										
L. (Lasioglossum) athabascense	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1
(Sandhouse)	2006		0	2	16	0	2	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	22	0	22
L. (Lasioglossum) coriaceum (Smith)	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	0	0	0	0	0	0	0	1	0	5	0	0	1	2	0	0		3	6	9
L. (Lasioglossum) leuzoconium	2005	0	0	0	0	0	0	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	1	5	0	5
(Schrank)	2006		0	0	0	2	1	0	1	1	0	0	0	1	1	1	1	0	2	0	1	0	0	12	0	12
L.(Lasioglossum) paraforbesii	2005	0	0	4	8	10	10	20	19	1	0	0	0	0	4	10	20	16	10	0	1	1	0	115	19	134
McGinley	2006		0	7	2	3	13	21	4	1	1	0	0	4	4	16	19	12	20	17	48	0	0	170	22	192
L.(Lasioglossum) zonulum (Smith)	2005	0	0	1	2	0	1	5	8	1	0	0	0	1	1	2	10	4	0	0	1	1	0	27	11	38
	2006		0	3	5	0	8	9	2	1	1	0	0	0	1	0	1	2	2	2	3	0	0	40	0	40
Sphecodes sp.1	2005	0	0	1	1	1	1	3	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	-	-	9
	2006		0	2	2	0	2	2	0	0	0	6	2	0	0	0	0	0	0	0	0	0	0	-	-	16
Sphecodes sp. 2	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1
Megachilidae																										
Anthidium (Anthidium) clypeodentatum	2005	0	0	0	0	0	2	0	3	0	13	7	1	1	1	1	0	0	0	0	0	0	0	18	11	29
Swenk	2006		0	0	0	1	0	1	2	7	4	0	0	0	0	0	0	0	0	0	0	0	0	11	4	15
Hoplitis (Alcidamea) pilosifrons	2005	0	0	0	0	2	12	8	0	0	2	2	1	0	0	0	0	0	0	0	0	0	0	8	19	27
(Cresson)	2006		0	0	12	6	6	5	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	30	32
H. (Androicus) cylindrica (Cresson)	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
H. (Monumetha) albifrons (Kirby)	2005	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	2
	2006		0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Megachile (Litomegachile) brevis Say	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	4	3	0	0	0	0	10	1	11
	2006		0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	4	0	4
M. (Megachile) inermis Provancher	2005	0	0	0	0	0	0	1	0	0	1	1	2	0	1	0	1	0	1	0	0	0	0	7	1	8
	2006		0	0	0	0	0	0	1	1	2	1	0	0	0	0	0	0	0	0	0	0	0	3	2	5
M. (Megachile) relativa Cresson	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	0	0	0	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	4
M. (Xanthosarus) frigida Smith	2005	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	2	1	3
	2006		0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2

Appendix B. continued

		Sampling week																							Total*		
		May		Jun.						Jul.				Aug.					Sep.								
	Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	♀**	♂	Overall
M. (Xanthosarus) latimanus Say	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1
	2006		0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2	0	2
M. (Xanthosarus) melanophaea Smith	2005	0	0	0	0	0	0	0	2	0	2	1	0	0	0	0	0	0	0	0	0	0	0	3	2	5
	2006		0	0	0	1	1	1	7	2	0	0	0	0	0	0	0	0	0	0	0	0	0	3	8	12
M. (Xanthosarus) perihirta Cockerell	2005	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	2006		0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2	0	2
Osmia (Melanosmia) bucephala Cresson	2005	1	0	0	6	3	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	4	16
	2006		0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
O. (Melanosmia) distincta Cresson	2005	0	0	0	4	3	2	2	0	0	4	1	0	0	0	0	0	0	0	0	0	0	0	6	10	16
	2006		0	15	9	2	15	4	0	7	4	0	0	0	0	0	0	0	0	0	0	0	0	29	27	56
O.(Melanosmia) atriventris Cresson	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
O. (Melanosmia) simillima Smith	2005	0	0	0	3	1	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	6	8
	2006		0	8	4	1	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	10	17
Osmia (Chenosmia) sp. 1	2005	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	2006		0	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4
Stelis (Stelis) lateralis Cresson	2005	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	2006		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total individuals	2005	189	23	208	228	92	150	137	115	33	121	122	144	86	78	110	327	210	200	101	98	62	28	-	-	2862
Total individuals	2006		5	463	311	129	267	270	126	155	163	130	193	180	244	202	390	119	178	279	348	0	0	-	-	4152
Grand total		189	28	671	539	221	417	407	241	188	284	252	337	266	322	312	717	329	378	380	446	62	28	-	-	7014
Total taxa	2005	12	3	17	24	19	27	34	20	11	22	22	18	16	22	17	29	13	15	12	15	12	4	-	-	76
Total taxa	2006	0	1	33	30	30	37	38	33	33	28	18	23	18	22	19	21	14	20	20	19	0	0	-	-	90
Grand total		12	3	35	34	33	45	49	38	34	34	31	34	24	32	26	33	17	24	23	23	12	4	-	-	100

* the symbol '-' in a cell indicates that information on the sex of the specimens is incomplete.

** For females of *Bombus* spp. 'q' refers to queens and 'w' refers to workers.

Appendix C. Number of flowering stems counted per species in 46 permanent 1m X 1m quadrats at the Yellow Quill Mixed-grass Prairie Preserve near Treesbank, Manitoba by sampling week and year.

| | | Sampling week | | | | | | | | | | | | | | | | | | | | | | |
| | | May | | | | Jun. | | | | Jul. | | | | Aug. | | | | Sep. | | | | | | |
	Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	Total
Asteraceae																								
Achillea millefolium L.	2005	0	0	0	0	0	0	2	6	17	27	24	12	16	6	4	0	1	0	0	0	0	0	115
	2006	0	0	0	0	12	14	28	41	57	24	2	0	0	0	0	0	0	0	0	0	0	0	178
Agoseris glauca (Pursh) Raf.	2005	0	0	0	0	0	1	0	0	20	6	1	0	0	0	0	0	0	0	0	0	0	0	28
	2006	0	0	0	0	0	1	7	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	9
Antennaria neodioica Greene	2005	0	0	0	0	108	90	92	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	294
	2006	0	7	10	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	42
Aster ericoides L.	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	10	26	24	58	28	0	0	151
	2006	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2
A. ptarmicoides (Nees) Torr. & Gray	2005	0	0	0	0	0	0	0	0	0	0	0	0	3	24	18	21	6	4	0	0	0	0	76
	2006	0	0	0	0	0	0	0	0	0	0	0	7	5	0	0	0	0	0	0	0	0	0	12
Chrysopsis villosa (Pursh) Nutt.	2005	0	0	0	0	0	0	0	0	0	2	8	7	5	6	12	26	20	13	15	7	0	0	121
	2006	0	0	0	0	0	0	3	4	12	15	12	8	4	1	2	2	2	1	0	0	0	0	66
Echinacea angustifolia DC	2005	0	0	0	0	0	0	0	0	0	0	0	2	3	1	0	0	0	0	0	0	0	0	6
	2006	0	0	0	0	0	0	0	0	1	1	3	0	0	0	0	0	0	0	0	0	0	0	5
Erigeron glabellus Nutt.	2005	0	0	0	0	0	0	2	6	2	1	0	0	3	1	3	0	0	0	0	0	0	0	18
	2006	0	0	0	0	2	2	16	3	0	0	2	3	0	0	0	0	0	0	0	0	0	0	28
Erigeron sp. 1	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006	0	0	0	0	0	0	0	15	17	13	0	0	0	0	0	0	0	0	0	0	0	0	45
Erigeron sp. 2	2005	0	0	0	0	0	0	0	0	0	13	16	11	17	12	2	4	3	0	0	1	0	0	79
	2006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Erigeron sp. 3	2005	0	0	0	0	0	0	0	0	0	0	0	0	2	14	20	0	0	0	0	0	0	0	36
	2006	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3
Gaillardia arista Pursh	2005	0	0	0	0	0	0	0	1	11	9	5	1	0	2	0	0	0	0	0	0	0	0	29
	2006	0	0	0	0	0	1	13	6	11	3	0	0	0	0	0	0	0	0	0	0	0	0	34
Helianthes laetiflorus Pers.	2005	0	0	0	0	0	0	0	0	0	0	0	1	2	9	12	21	1	0	0	0	0	0	46
	2006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lactuca pulchella (Pursh)	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	2	0	0	0	6
	2006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Liatris punctata Hook.	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	2	4	2	1	1	0	0	0	0	10
	2006	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1

		Sampling week																						
		May				Jun.				Jul.				Aug.					Sep.					
	Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	Total
Asteraceae (cont'd)																								
Senecio plattensis Nutt.	2005	0	0	0	0	0	5	5	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	16
	2006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Solidago missouriensis Nutt.	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	12
Solidago nemoralis Ait.	2005	0	0	0	0	0	0	0	0	0	0	1	11	21	18	18	27	21	10	9	0	0	0	136
	2006	0	0	0	0	0	0	0	0	0	0	0	0	0	4	9	4	3	2	1	0	0	0	23
Solidago sp. 1	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	4
	2006	0	0	0	0	0	0	0	0	0	0	3	11	6	0	0	0	0	0	0	0	0	0	20
Taraxacum officinale G.H. Webber ex Wiggers	2005	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	2006	0	4	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
Tragopogon dubius Scop.	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2006	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Boraginaceae																								
Lithospermum canescens (Michx.) Lehm	2005	0	0	0	2	31	63	71	18	1	0	0	0	0	0	0	0	0	0	0	0	0	0	186
	2006	0	2	43	74	48	33	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	203
L. incisum Lehm	2005	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
	2006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onosmodium hispidissimum MacKenzie	2005	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2
	2006	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Brassicaceae																								
Arabis holboellii var. collinsii (Fern.) Rollins	2005	0	0	0	0	4	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
	2006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arabis sp.	2005	0	0	0	3	0	7	23	6	1	1	0	0	0	0	0	0	0	0	0	0	0	0	41
	2006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brassica sp. 1	2005	0	0	0	0	0	0	0	0	0	5	0	2	4	1	0	0	0	0	0	0	0	0	12
	2006	0	0	0	0	0	1	7	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	9
Erysimum asperum (Nutt.) DC.	2005	0	0	0	0	0	1	3	1	5	5	5	2	2	1	1	0	0	0	0	0	0	0	26
	2006	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2

				May			Jun.				Jul.				Aug.				Sep.						
	Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	Total
Brassicaceae (cont'd)																								
Erysimum inconspicum (Watson) McMill.	2005	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3
	2006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campanulaceae																								
Campanula rotundifolia L.	2005	0	0	0	0	0	0	0	0	7	49	72	44	47	12	23	10	0	0	1	0	0	0	265
	2006	0	0	0	0	0	2	9	23	61	40	13	2	2	0	0	0	0	0	0	0	0	0	152
Caprifoliaceae																								
Symphoricarpos occidentalis Hook.	2005	0	0	0	0	0	0	0	0	0	1	3	3	6	2	1	0	0	0	0	0	0	0	16
	2006	0	0	0	0	0	0	0	2	3	2	0	0	0	0	0	0	0	0	0	0	0	0	7
Caryophyllaceae																								
Cerastium arvense L.	2005	0	0	0	18	374	337	108	20	6	2	0	0	0	0	0	0	0	0	0	0	0	0	865
	2006	8	41	344	217	41	13	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	665
Euphorbiaceae																								
Euphorbia esula L.	2005	0	0	0	0	17	45	75	33	44	73	97	93	92	81	29	15	3	0	0	0	0	0	697
	2006	0	0	28	87	179	214	89	81	106	84	24	2	0	0	0	0	0	0	0	0	0	0	894
Fabaceae																								
Astragalus crassicarpus Nutt.	2005	0	0	0	0	0	0	3	11	5	2	3	1	1	1	0	0	0	0	0	0	0	0	27
	2006	0	0	1	1	12	10	7	4	6	2	0	0	0	0	0	0	0	0	0	0	0	0	43
Dalea candida Michx. Ex Willd.	2005	0	0	0	0	0	0	0	0	0	0	3	6	5	8	8	6	0	0	0	0	0	0	36
	2006	0	0	0	0	0	0	0	0	14	57	62	24	0	0	0	0	0	0	0	0	0	0	157
D. purpurea Vent.	2005	0	0	0	0	0	0	0	0	0	0	0	16	23	29	34	53	27	15	3	0	0	0	200
	2006	0	0	0	0	0	0	0	0	1	45	124	71	3	0	0	0	0	0	0	0	0	0	244
Medicago lupulina L.	2005	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2
	2006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Medicago sativa L.	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	3
	2006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

		Sampling week																						
		May				Jun.				Jul.				Aug.				Sep.						
	Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	Total
Fabaceae (cont'd)																								
Oxytropis splendens Dougl. ex Hook.	2005	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	2006	0	0	0	0	6	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
Psoralea esculenta Pursh	2005	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	2006	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Vicia americana Mull. ex Willd.	2005	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	2006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Iridaceae																								
Sisyrinchium montanum Greene	2005	0	0	0	0	3	6	5	6	0	4	1	0	0	0	0	0	0	0	0	0	0	0	25
	2006	0	0	0	23	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	27
Lamiaceae																								
Monarda fistulosa L.	2005	0	0	0	0	0	0	0	0	0	0	8	63	57	6	1	0	0	0	0	0	0	0	135
	2006	0	0	0	0	2	0	0	0	13	99	37	0	0	0	0	0	0	0	0	0	0	0	151
Liliaceae																								
Allium textile Nels. And Macbr.	2005	0	0	0	0	0	0	0	0	0	0	0	0	0	4	3	3	1	0	0	0	0	0	11
	2006	0	0	0	0	0	0	0	0	0	0	11	5	2	0	0	0	0	0	0	0	0	0	18
Lilium philadelphicum L.	2005	0	0	0	0	0	0	0	0	2	5	0	0	0	0	0	0	0	0	0	0	0	0	7
	2006	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Linaceae																								
Linum lewisii Pursh	2005	0	0	0	0	0	0	4	13	22	6	1	0	2	0	0	0	0	0	0	0	0	0	48
	2006	0	0	0	0	8	8	43	5	19	0	0	0	0	0	0	0	0	0	0	0	0	0	83
Onagraceae																								
Oenothera nuttallii Sweet	2005	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2
	2006	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2

| | | Sampling week | | | | | | | | | | | | | | | | | | | | | |
| | | May | | | | Jun. | | | | Jul. | | | | Aug. | | | | | Sep. | | | | |
	Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	Total
Onagraceae (cont'd)																								
O. serrulata Nutt.	2005	0	0	0	0	0	0	0	0	0	2	3	5	3	2	3	2	0	0	0	0	0	0	20
	2006	0	0	0	0	0	0	0	1	4	2	1	1	0	0	0	0	0	0	0	0	0	0	9
Primulaceae																								
Androsace septentrionalis L.	2005	0	0	66	27	338	225	181	44	13	0	0	0	0	0	0	0	0	0	0	0	0	0	894
	2006	17	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23
Ranunculaceae																								
Anemone cylindrica Gray	2005	1	0	0	0	0	0	0	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	5
	2006	0	0	0	0	0	0	5	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
Ranunculus rhomboideus Goldie	2005	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
	2006	8	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
Rosaceae																								
Potentilla argentea L.	2005	0	0	0	0	0	0	0	0	1	10	14	4	6	1	0	0	0	0	0	0	0	0	36
	2006	0	0	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Rosaceae (cont'd)																								
P. arguta Pursh	2005	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	4
	2006	0	0	0	0	5	0	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
Prunus pumila L.	2005	0	0	0	13	12	8	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	35
	2006	6	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29
Rosa arkansana Porter	2005	0	0	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	4
	2006	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	4
Geum triflorum Pursh	2005	0	0	0	1	40	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
	2006	15	22	14	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	60
Rubiaceae																								
Galium boreale L.	2005	0	0	0	0	0	0	1	1	23	33	21	6	9	11	3	3	0	0	0	0	0	0	111
	2006	0	0	0	0	0	42	110	101	37	4	0	0	0	0	0	0	0	0	0	0	0	0	294

		Sampling week																					
		May				**Jun.**				**Jul.**				**Aug.**				**Sep.**					
	Year	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**Total**
Rubiaceae (cont'd)																								
Houstonia longifolia Gaertn.	2005	0	0	0	0	0	19	20	13	10	5	0	0	0	0	0	0	0	0	0	0	0	0	67
	2006	0	0	0	22	112	231	37	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	404
Santalaceae																								
Comandra umbellata (L.) Nutt.	2005	0	0	0	0	1	37	16	4	7	0	0	0	0	0	0	0	0	0	0	0	0	0	65
	2006	0	0	1	12	7	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25
Saxifragaceae																								
Heuchera richardsonii R. Br.	2005	0	0	0	0	0	0	3	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	7
	2006	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Scrophulariaceae																								
Orthocarpus luteus Nutt.	2005	0	0	0	0	0	0	0	0	0	0	0	4	2	10	11	13	3	0	0	0	0	0	43
	2006	0	0	0	0	0	0	0	0	3	22	14	6	2	0	0	0	0	0	0	0	0	0	47
Penstemon gracilis Nutt.	2005	0	0	0	0	0	0	0	3	12	14	4	1	0	0	0	0	0	0	0	0	0	0	34
	2006	0	0	0	0	0	3	17	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25
Violaceae																								
Viola pedatifida G. Don	2005	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
	2006	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Total stems	2005	1	0	66	64	932	858	617	201	215	284	293	298	333	265	216	217	121	67	88	36	0	0	5172
Total stems	2006	61	106	443	464	439	582	406	307	374	415	308	140	42	5	11	6	5	3	1	0	0	0	4118
Total taxa	2005	1	0	1	6	13	19	19	21	24	26	22	24	25	26	22	16	15	6	6	3	0	0	60
Total taxa	2006	6	8	9	10	14	17	21	20	24	17	13	11	11	2	2	2	2	2	1	0	0	0	52
Grand total taxa		7	8	10	13	22	29	32	31	38	33	28	28	30	26	22	16	15	6	6	3	0	0	63