Effects of Cattle Grazing on the Food Abundance of Prairie Bird Species in Grasslands National Park, Saskatchewan

By

Allison Selinger

A Thesis
Submitted to the Faculty of Graduate Studies
In Partial Fulfillment of the Requirements
For the Degree of

Master of Natural Resources
Management

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FACULTY OF GRADUATE STUDIES
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Abstract

Grassland bird species have experienced dramatic declines since 1966. This rapid decline can be linked to changes in land use practices, such as grazing. Livestock grazing is a commonly used management tool; its impact on grasslands birds has been studied, however, its impact on the invertebrate food sources of grassland birds is less well-known. I examined the effects of cattle grazing on the abundance, richness, and diversity of invertebrates on the mixed grass prairie, and measured whether this influenced the abundance and diversity of prairie bird species.

I examined the effect of food abundance on birds by testing a prediction of the More Individuals Hypothesis (MIH): that the more resources available in a system, the greater number of individuals that system can support at higher trophic levels. The study was conducted in Grasslands National Park of Canada (GNPC) in Saskatchewan. Thirteen pastures, each containing 10 plots, were sampled. In 2006 and 2007, 9 of the pastures were ungrazed and 4 were grazed. In the spring of 2008, cattle were placed in 6 of the 9 previously ungrazed pastures, leaving 3 ungrazed pastures. Point counts were used to sample richness and relative abundance of birds. I sampled two groups of invertebrates: grasshoppers and carabid beetles. In addition, vegetation height and above ground biomass were measured to assess the intensity of grazing. I used two-sided *t*-tests, correlations and linear regression models to test for relationships. I found that (1) grasshopper abundance, richness and diversity was higher in grazed pastures than in ungrazed areas; (2) in contrast, carabid abundance, richness and diversity showed mixed responses to grazing; (3) there were few statistically significant relationships between structure, composition and richness of vegetation and abundance, relative to richness and diversity of invertebrates; and (4) bird abundance was correlated with carabid abundance, thus supporting the assumptions of the MIH; and finally (5) the strength of the correlation between invertebrates and birds seems to be independent of the birds' reliance on invertebrates as a food source (6) Evenness of carabids seems to have an effect on bird abundance. Overall, my results indicate that grazing can be beneficial for both birds and their invertebrate prey in southern Saskatchewan mixed-grass prairies

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Section 1.0: Introduction

1.1 Background

Grassland birds have experienced a faster rate of population decline than any other group of North American birds (Fondell & Ball 2004). More than 50% of grassland bird species have experienced dramatic declines since 1966 (Herkert 1995). Because of these declines, conservation of these species has become a priority. While there are a number of factors contributing to this decline the principal reason in temperate ecosystems seem to be a lack of suitable habitat (Powell 2006).

There are two main factors contributing to the reduction of grassland bird habitat: the conversion of grasslands to agricultural lands (Powell 2006) and changes in grassland management (Atkinson et al. 2005, Fleischner 1994, Powell 2006). In the 19th and 20th centuries the conversion of prairie to agricultural lands resulted in a loss of over 95% of the native grasslands in North America and the world (Powell 2006). Prior to this conversion, there were over 162 million hectares of native grasslands in North America (Davis 2004). This loss of habitat can also be seen in Saskatchewan, where 20% of the original native grassland remains (Davis 2004). More recently, declines in suitable habitat seem to be a result of changes in land use practices, such as grazing (Powell 2006; Atkinson et al. 2005). There is growing evidence that the rapid decline in prairie bird populations over the last 40 years can be linked to the changes in farm management (Atkinson et al. 2005; Soderstrom et al. 2001; Powell 2006; Fuhlendorf & Engle 2001; Ottvall & Smith 2006; Tichit et al. 2005). It is well documented that birds are affected by changes in vegetation structure (Fondell & Ball 2004, Vickery et al. 2001, and Buckland et al. 2006), however, the underlying mechanisms such as the effect of farm management on invertebrates remain poorly understood (Atkinson et al. 2005).

Grazing is thought to be important for the maintenance of prairie ecosystems (Madden et al. 1999; Olff & Richie 1998). However, current grazing regimes using cattle are very different than past cattle grazing patterns and unrecognizable when compared to pre-contact grazing disturbances applied by bison, elk, deer and antelope. There has been a major shift in modern range management practices over the last 60 years including the conversion of rangeland to cropland (Isacch et al. 2005), the intensification of grazing regimes (Soderstrom et al. 2001; Powell 2006; Fuhlendorf & Engle 2001; Ottvall & Smith 2006; Tichit et al. 2005), and the halting of grazing activity (Luoto et al. 2003). All of these changes have had a profound effect on the structure and composition of grassland ecosystems.

When looked at from a landscape perspective, grazing by livestock is the most common land management technique utilized in western North America (Fleischner 1994), and therefore has profound impacts on prairie ecosystems and their inhabitants (Fleischner 1994). Despite its widespread use, (Fondell & Ball 2004) its impact on the invertebrate prey of grassland birds is uncertain (Debano 2006). Due to the scarcity of suitable habitat remaining, identifying sound range management techniques is critically important to the conservation of prairie bird species (Davis 2005), and must sustain the resources required by birds, such as adequate habitat structure and food sources.

There is much debate over which biophysical characteristics of grasslands have the greatest influence on bird populations (Fondell & Ball 2004, Vickery et al. 2001, Buckland et al. 2006, Davis 2004, Tichit et al. 2005; Brotons et al. 2005). Birds respond to a variety of direct and indirect effects of grazing such as vegetation composition (Isacch et al. 2005), vegetation structure (Fondell & Ball 2004, Vickery et al. 2001, Buckingham et al. 2006, Davis 2004), heterogeneity (Tichit et al. 2005; Brotons et al. 2005), and food availability (Fondell & Ball

2004, Vickery et al. 2001). Some scientists have found the most influential of these factors is vegetation structure (Fondell & Ball 2004, Vickery et al. 2001, and Buckland et al. 2006). A study by Fondell and Ball (2001) found that vegetation structure was the best predictor of nest density for 9 of the 10 species examined. A review of studies by Chapman et al. (2004); Fondell & Ball (2004); Sutter & Bringham (1998); and Knopf (1996), in Henderson (2006) found that depending on the study, anywhere from 10 to 15 common mixed prairie species abundances were correlated to vegetation structure. However, vegetation is not the only factor involved in habitat selection (Isacch et al. 2005, Tichit et al. 2005; Brotons et al. 2005, Fondell & Ball 2004, Vickery et al. 2001).

Structural changes in grasslands can lead to other changes to the grassland that will have an effect on grassland birds. One reason that structural changes in vegetation are thought to affect grassland birds is that it may lead to changes in invertebrate populations (Atkinson et al. 2005; Vickery et al. 2001, Buckingham & Morris 2004; McCracken & Tallowin 2004); however, few studies have been able to determine whether birds are responding to preferences in vegetation structure or prey abundance when selecting habitats (Buckingham et al. 2006). Nevertheless, some studies have found that food abundance is the principal factor in habitat choice for birds (Atkinson et al. 2005; Robinson & Sutherland 1999; Brickle et al. 2000; Moorcroft et al. 2002; Stephens et al. 2003). These studies have also demonstrated links between the abundance of invertebrate prey and management activities, vegetation structure and composition (Atkinson et al. 2005; Vickery et al. 2001, Buckingham & Morris 2004; McCracken & Tallowin 2004)

1.2 The More Individuals Hypothesis

The More Individuals Hypothesis (MIH) proposes that there is a direct relationship between the energy available in a system and species richness. The main predictions of the hypothesis are (1) areas with more abundant food resources will support a greater number of individuals, and (2) communities with a greater number of individuals are able to support a greater number of species with populations above a minimum viable size (Hurlbert 2004; Evans et al. 2006). With respect to this study the predictions are (1) areas with a greater number of invertebrates will support a greater abundance of birds, and (2) areas with a greater number of birds will have higher richness and diversity. However, this hypothesis is relatively new and there have been few real tests; in fact, the MIH has never been tested in a mixed grass prairie ecosystem (Bonn et al. 2004, Hurlbert 2004; Evans et al. 2006). I examined the effects of cattle grazing on prairie birds and their invertebrate prey in Grasslands National Park of Canada (GNPC) and tested the predictions of the More Individuals Hypothesis.

1.3 Research Questions

I investigated the following questions:

1) Do the structural changes in vegetation that are caused by cattle grazing influence food abundance for prairie bird species?
2) Does abundance and diversity of food influence abundance and diversity of grassland birds?
3) Do 1) and 2) support the More Individuals Hypothesis in a mixed grass prairie ecosystem?

Section 2.0: Literature Review

2.1: The use of grazing as a tool in prairie ecosystem management

Livestock grazing is one of the preeminent grasslands management tools (Fondell & Ball 2004). Grassland ecosystems have evolved under a complex disturbance regime (Collins 2000) and grazing by cattle is a historical practice that has largely replaced bison grazing as an important process in the maintenance of prairie ecosystems (Madden et al. 1999; Olff & Richie 1998). In addition, disturbances such as fire, insect and small mammal grazing were once more influential in grassland habitats than they are today (Madden et al. 1999; Fuhlendorf & Engle 2001; Knapp et al. 1999). Periodic disturbance can be essential in prairie maintenance, but it has also been shown that disturbance is important in the maintenance and enhancement of heterogeneity (Fuhlendorf & Engle 2001) and therefore biodiversity (Madden et al. 1999; Olff & Ritchie 1999) on the prairies. Under this model, disturbances arrest succession and maintain the habitat at an early seral stage. This promotes the dominance of grass species and stops the establishment of woody vegetation (Collins 2000), although the establishment of woody vegetation is not as much of a problem in the northern mixed grass prairies due to the arid climate.

However, current grazing regimes are very different from those historically practiced. Intensity and frequency of grazing has increased dramatically in many places. This has led to the homogenization of prairie landscapes, which in turn has led to a dramatic decrease in diversity, particularly in prairie bird populations (Soderstrom et al. 2001; Powell 2006; Fuhlendorf & Engle 2001; Ottvall & Smith 2006; Tichit et al. 2005). Although the effects of these intense grazing regimes are well established, there are still gaps in our knowledge about the direct and indirect effects of less intense, moderate grazing regimes.

2.2 Literature Gaps

2.2.1 The effects of grazing on invertebrates

Invertebrates are a very important component of many ecosystems including the grassland ecosystem, and make up the majority of the animal biodiversity and biomass of animals on the prairies (Debano 2006). They are an essential part of the prairie food web and a key player in many ecosystem functions such as decomposition, pollination, seed dispersal, and nutrient cycling. Despite their pivotal role in these ecosystems, there have been relatively few studies looking at the effects of grazing on invertebrates in North America (Debano 2006). The effect of grazing on invertebrate populations has been widely studied in Europe (Morris 1967; Morris 1968; Morris 1969a; Morris 1969b; Dennis et al. 1997; Kruess & Tscharntke 2002), Studies that have been conducted in North America tend to focus on the effects of grazing on grasshoppers only (Jepson-Innes & Bock 1989).

There has been debate in the literature over the effects of grazing on invertebrates. Some studies concluded that grazing decreases insect diversity and abundance (Fahrig & Jonsen 1998; Dawes-Gromadzki 2005) and others claim that diversity and abundance increase with grazing (Wettstein & Schmid 1999, Cagnolo et al. 2002). These conflicts seem to arise from the fact that different species of invertebrates will respond differently to grazing depending on their resource needs (Debano 2006). This is supported by the literature from Europe, which shows some invertebrate species are more sensitive to the impacts of grazing than others (Debano 2006).

Invertebrates respond to changes in both vegetation structure and composition caused by grazing. Some herbivorous species such as ground carabids (Coleoptera: Carabidae) respond to changes in vegetation composition, whereas other invertebrate groups such as spiders (Arachnida: Araneae), leaf hoppers (Homoptera), Hemiptera and grasshoppers (Orthoptera:

Acrididae) seem to respond more strongly to changes in vegetation structure (Cagnolo et al. 2002). In addition to vegetation changes, there are also direct impacts of grazing on invertebrates such as mortality of larvae by trampling and burial under dung (Ehrlich & Murphy 1987 in Henderson 2006), and soil compaction. The severity of the impact of these effects on invertebrates depends on their life-history strategies (Cagnolo et al. 2002).

Morris (1967) found that uniform, intensive grazing causes decreases in invertebrate abundance and biodiversity. He concluded that a heterogeneous habitat created by rotational grazing was the best way to maximize invertebrate biodiversity. A review of the literature by Buchanan et al. (2006) supported this finding. Buchanan found that heterogeneity in vegetation composition and structure resulted in increased abundance of invertebrates. Therefore, to maximize biodiversity of invertebrates, grazing regimes that create heterogeneity across the landscape are recommended (Capinera & Sechrist 1982, Sugden 1985, and Schlicht & Orwig 1992 in Henderson 2006).

2.2.2 The effects of invertebrate abundance on bird populations

Invertebrates are a very important part of prairie songbirds' diets. A study by Wiens and Rotenberry (1979) showed that invertebrates make up about 76% of grassland songbird diets during the breeding season, over half (53%) of which consists of Orthoptera and Coleoptera. For some species, such as with Sprague's pipits (Robbins & Dale 1999), chestnut-collared longspurs (Hill & Gould 1997), western meadowlarks (Lanyon 1994) and grasshopper sparrows (Vickery 1996), invertebrates make up more than half of their diet. This is particularly true in the breeding season when the diet of Sprague's pipits can be as much as 94% invertebrates (Robbins & Dale 1999)

Understanding how grazing affects bird abundance is vital in the development of conservation strategies (Buckingham et al. 2004). However, little is known about the relationship between habitat selection by birds, agricultural management practices, and the abundance of food resources (Atkinson et al. 2005; Buckingham et al. 2004). There are very few studies that have examined the relationship between grassland birds and their food resources (Atkinson et al. 2005). The majority of the studies on the subject have been conducted in Europe (Brickle et al. 2000; Moorcroft et al. 2002; Tucker 1992; Atkinson et al. 2005; Buckingham et al. 2006; Whittingham et al. 2006; Hoi et al. 2004; Buckingham et al. 2004), with very few studies in North America (Miller et al. 1994; Martin et al. 2000; Martin et al. 1998). The studies that have been conducted have often yielded conflicting results and it is apparent that more research is required (Brickle et al. 2000; Moorcroft et al. 2002; Tucker 1992; Atkinson et al. 2005; Buckingham et al. 2006; Whittingham et al. 2006; Hoi et al. 2004; Buckingham et al. 2004; Miller et al. 1994; Martin et al. 2000; Martin et al. 1998).

2.2.3 The More Individuals Hypothesis

Scientists have found a strong correlation between the energy availability and species richness within a community (Algar et al. 2007, Allen et al. 2006, Bonn et al. 2004, Currie et al. 2004, Evans et al. 2005). There are a number of theories that have been proposed in an attempt to explain this phenomenon. One of the major differences between these theories is how they define energy availability (Evans et al. 2005). The two most common definitions of energy availability can be classified into two main categories: (1) richness linked to ambient energy, and (2) richness based on net primary productivity (NPP) (Algar et al. 2007, Allen et al. 2006). Ambient energy is essentially a measure of climatic conditions such as temperature or actual and potential evapotranspiration (Algar et al. 2007). Net primary productivity is a measure of the amount of light energy that has been converted to chemical energy by plants minus the energy used for respiration (Campbell et al. 1999).

The foremost explanation of this phenomenon is the More Individuals Hypothesis or the MIH (Algar et al. 2007). The More Individuals Hypothesis (MIH) or the Species-energy Theory, as it is also known was first proposed by Wright (1983) and was derived from the Theory of Island Biogeography (TIB: MacArthur & Wilson 1963, 1967). The MIH simply replaces the variable area in TIB with available energy. Therefore, the hypothesis states that the greater the energy available through food availability in a system the greater the number of individuals the system can support (Wright 1983).

The hypothesis proposes that there is a direct relationship between the food energy available in a system and the species richness. The main predictions of the hypothesis are (1) areas with more abundant food resources will support a greater number of individuals, and (2) communities with a greater number of individuals are able to support a greater number of species with populations above a minimum viable size (Hurlbert 2004; Evans et al. 2006). In addition, the hypothesis predicts that there will be fewer species extinctions in areas of high energy than in areas with less energy, because areas of higher energy can maintain a greater number of species above a minimal viable size (Bonn et al. 2004).

This hypothesis, however, is limited by scale and generally does not hold true at very broad spatial scales. For instance, on the global scale we are finding higher extinction rates in areas of high energy such as the tropics than in areas of lower energy availability (Gaston 2000).

Contrary to the more individuals hypothesis is the “Specialization” hypothesis (Bonn et al. 2004). The specialization hypothesis predicts that higher energy levels can actually lead to decreased species abundance through increased resource specialization. This decrease is thought to be the result of reductions in niche breadth and/or higher diversity or greater heterogeneity of resources (Bonn et al. 2004). The hypothesis assumes that higher energy levels causes species to become increasingly specialized and therefore increasing dependent on a particular resource or habitat characteristic. If this resource disappears, or the habitat changes, the species will no longer be able to survive in the area. It also predicts that areas of higher energy will have higher rates of species turnover than areas of lower energy availability (Bonn et al. 2004).

According to the MIH, we should find a greater abundance of birds in areas with a greater abundance of invertebrate prey species and greater prey abundance, as was found in the study by Hurlbert (2004). A study by Bonn et al. (2004) also found that species richness increased as energy availability increased, which supports the MIH. However, they also found a decrease in local densities with an increase in energy, which supports the "Specialization" hypothesis (Bonn et al. 2004). This finding may be a result of the scale at which the study was conducted at. Researchers compared avian species richness of South Africa and Lesotho to energy availability. A study by Evans et al. (2005) also found that species richness increased with increased energy availability. However, this study also found that this relationship is much stronger in common species than it is with less common species, which is contrary to the MIH. The study found that rarer species were more strongly influenced by factors other than energy availability.

2.3 Hypothesis

If moderate levels of grazing increases invertebrate food abundance of prairie bird species through changes in vegetation structure and through the creation of a more heterogeneous environment, and if the More Individuals Hypothesis is true, then there will be a greater abundance of prairie birds in moderately grazed and structurally heterogeneous areas than in ungrazed areas. In addition, species that are more insectivorous would be more likely to choose habitats with increased invertebrate abundance compared with less insectivorous species and that I would therefore observe a stronger relationship between more insectivorous bird abundance and invertebrate abundance than between less insectivorous bird abundance and invertebrate abundance.

Section 3.0: Methods

3.1 Study Area

Grasslands National Park of Canada (GNPC) lies in the northern mixed-grass prairie (Coupland 1950). The park is made up of two geographically isolated blocks; east and west. With in the East Block, there are three distinct sub-habitats: riparian shrublands, upland grasslands, and valley grasslands (Michalsky & Ellis 1994). The riparian shrublands are dominated by prairie shrub species, such as western snowberry (*Symphoricarpos occidentalis*), prairie rose (*Rosa acicularis*) and sage brush (*Artemisia cana*) (Michalsky & Ellis 1994). Due to the richness of nutrients and high soil moisture levels in this area, the herbaceous layer is characterized by Canada goldenrod (*Solidago canadensis*), wild licorice (*Glycrrhizae lepidota*), and bluegrass (*Poa compressa*) (Michalsky & Ellis 1994).

The upland grassland areas are dominated by grass species such as speargrass (*Stipa comata*), northern wheatgrass (*Elymus lanceolatus*), blue grama (*Bouteloua gracilis*), June grass (*Koeleria macrantha*), and western wheatgrass (*Pascopyrum smithii*) (Henderson 2006). In addition to these grasses, the upland vegetation also includes numerous forb species (Henderson 2006). Some of the species found in the uplands are pasture sage (*Artemisia frigida*), moss phlox (*Phlox hoodii*), and scarlet globe mallow (*Sphaeralcea coccinea*). There is considerable variation in the relative abundance of speargrass (*S. comata*) and wheatgrass (*E. lanceolatus*) within the upland area. Speargrass (*S. comata*) is more dominant on hill crests and shoulder slopes where the soil is drier. Wheatgrass (*E. lanceolatus*) is more abundant on the slopes and swales where soil moisture level is higher (Henderson 2006).

Vegetation cover in the valley grasslands is much patchier than in the other 2 areas. This is primarily due to a wide range of soil salinity levels and microtopography (Henderson 2006). The areas that are elevated and relatively saline support vegetation like cacti (*Opuntia* spp.), shrubs, and grasses (Henderson 2006). Some of the shrubs that can be found in this area include sage brush (*Artemisia cana*), saltbrush (*Atriplex* spp.), rabbit brush (*Chrysothamnus nauseosus*), and greasewood (*Sarcobatus vermiculatus*) (Henderson 2006). The area also supports species of wheatgrass, bluegrass (*Poa sandbergii*, *Poa compressa*) and salt grass (*Distichlis stricta, Puccinella nuttallii*). Shallow areas that have less saline soils have vegetation similar to the upland areas (Henderson 2006).

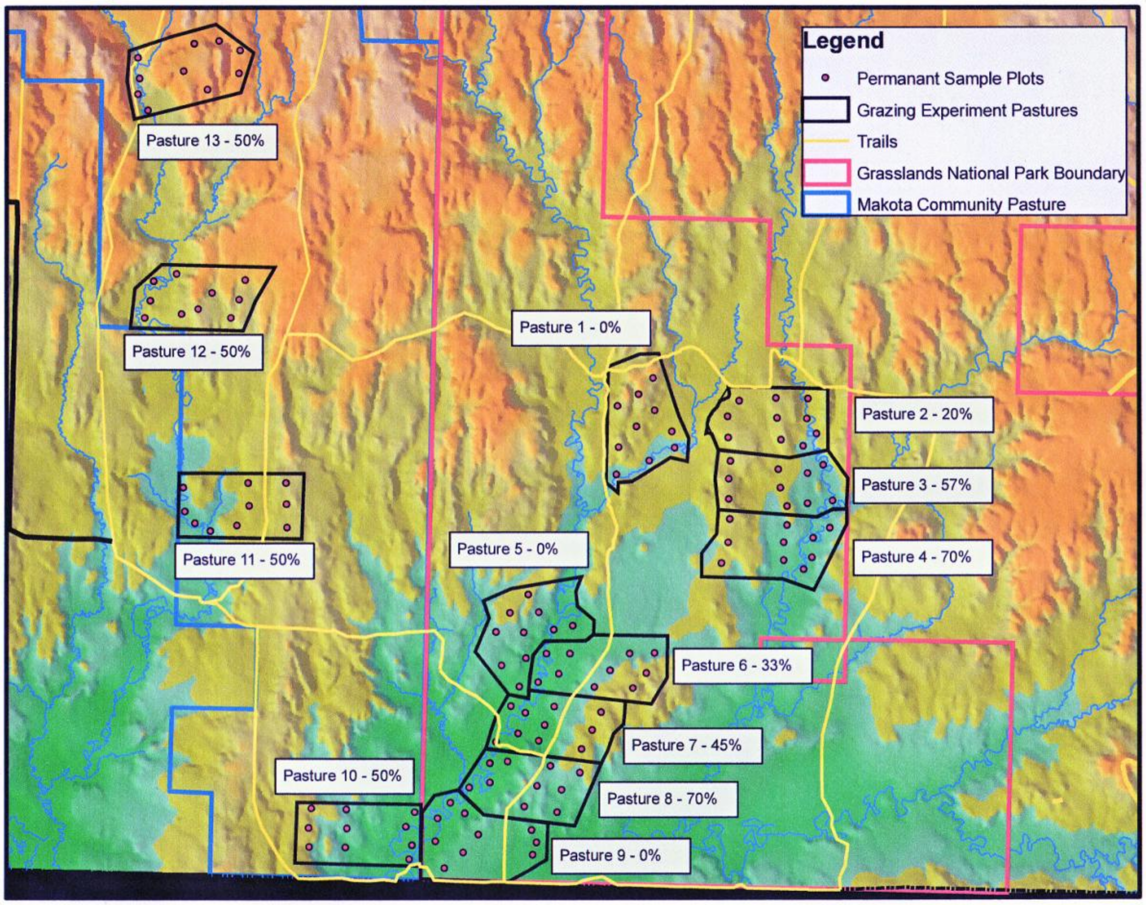

Figure 1: Map of pasture and plot layout, including cattle stocking rates in Grasslands Nation Park of Canada.

The study area consists of nine, 300-ha pastures located in the East Block of GNPC and four grazed community pastures adjacent to GNPC(Figure 1) (Henderson 2006). These nine pastures had previously been ungrazed for more than fifteen years. The grazing history of the four grazed pastures is unknown, but have been grazed annually or almost annually for a number of years (Henderson 2006).

Fences were constructed around 9 of the previously ungrazed pastures in the third year of the study, spring of 2008. Cattle were placed in 6 (2, 3, 4, 6, 7, 8) of the 9 pastures in June 2008 at different grazing intensities (0, 25, 39, 57, 0.71, 0.82, 0.83 AUM/ha; estimated to result in 20, 57, 70, 33, 45, 70% biomass removal, respectively). Data from these grazed pastures were then compared to data from the ungrazed pastures to assess the effect of grazing on food abundance of prairie birds. The community pastures (10, 11, 12, and 13) remained at the same grazing intensities as in previous years (approximately 50% biomass removal)

3.2 Invertebrate Sampling

Two families of insects were sampled: grasshoppers (Orthoptera: Acrididae) and ground carabids (Coleoptera: Carabidae). These families were chosen because they are some of the main food sources for the birds we are interested in their breeding grounds (Wiens & Rotenberry, 1979).

3.2.1 Grasshopper sampling

Grasshopper richness and density were estimated using two sampling techniques (Onsanger & Henry 1977 in Henderson 2006). I estimated grasshopper density using counts from 0.1-m^2 diameter rings made of galvanized steel wire. They were placed at 5 m intervals along three 50m north-south transects within each plot. A total of 33 rings were placed in each plot, 11 along each of the three transects (Koper et al. 2006). The start of the central transect was located 25 m north of the center of the experimental plot and ran 50 m north. The other two transects were located 25 m east and west of the central transect and also ran 50m north. Observers walked along the transects and recorded the number of grasshoppers that flushed from within the rings.

Two years of ring count data were included in the study: 2006 and 2008. In each year, one round of ring count data was collected. In 2006, data were collected on July 24 and July 27. In 2008, data were collected between July 19 and July 21. Two rounds of ring counts were attempted in 2007. A full round was completed on May 17, 2007 but was not included because no grasshoppers were observed. A second partial round of ring counts was conducted by researchers from outside the University of Manitoba but was not completed and therefore was not included in this study.

Proportional abundance of each species was estimated using sweep nets that were dragged through the vegetation. Sweeps were conducted along the three 50m north-south transects within each plot that were also used for ring counts. During sweeps we walked the three transects, sweeping nets 180 degrees over the grass to capture grasshoppers. The method of sweeping varied slightly over the three years of collection. In 2006, each transect was swept 50 times (Koper et al. 2007). In 2007, observers walked along transects and swept until they reached 100 sweeps. The insects caught were placed in plastic freezer bags labeled with the date, the experimental site number and “100 sweeps”. Additional sweeps were usually needed to complete all three transects. The samples collected from the additional sweeps were placed in a separate bag labeled with the date, the experimental plot number and “Extra sweeps”. In 2008, observers swept all three transects without counting the number of sweeps. All the insects captured were place in one bag. Bags were placed in the freezer until they could be sorted and weighed.

Sampling was conducted between late July and early August to ensure the maximum number of species could be captured (Cushing et al. 2000 in Henderson 2006). In 2006, only one round of sweeps was completed on July 21 and between July 27 and July 30 (Koper et al. 2007). In 2007, two rounds of sweeps were completed; one between May 25 and May 26, and the second on July 28. Because few samples were obtained from the first round of sweeps in 2007, we only conducted one round of sweeps in 2008 between July 29 and July 30. Only one year (2008) of grasshopper sweeps data is included in the study, because the density of grasshoppers in May was too low for us to sample. Only one year of data was used because the previous years of data were collected by another researcher and we do not have access to the information.

Whenever possible, sampling was conducted on warm, dry, sunny, and calm days in mid afternoon. This helped increase the detectability of individuals and improve the visual estimates in the rings (Berry et al. 2000 in Henderson 2006).

3.2.2 Carabid sampling

Pitfall traps were used to estimate richness and relative abundance of carabids (Coleoptera: Carabidae). There is some debate over the number of traps that should be used and how they should be positioned; a study by Spence & Niemela (1994) suggests placing the traps in a circle. We placed 5 traps in a 10 m diameter circle at each of the 130 plots for a total of 650 traps, at 0°, 72°, 144°, 216°, and 288° around the circle (Koper et al. 2006). The center of the carabid trapping area was located 25 meters west of the center of the plot.

Traps consisted of two plastic containers placed one inside the other. Holes were punched in the bottom of the containers to allow water to drain out of them. The containers were placed in holes in the ground, ensuring that the edges of the containers were level with the ground. When the traps were not being used for sampling they were sealed with plastic lids (Koper et al. 2006).

During the sampling period (early June, and in mid-August) traps were opened and left for three days. After three days, insects caught in the traps were collected, labeled and frozen. The samples were separated into carabids and non-carabids and weighed, and sent to David Larson (Maple Creek, Saskatchewan), an insect taxonomist be identified to species (Koper et al. 2006). Three years of carabid data were included in this study: 2006, 2007, and 2008. In all three years two rounds of trapping were completed. In 2006, round 1 was conducted between June 7 and June 11, and round 2 was completed between August 12 and August 16. In 2007, round 1 was completed between June 1 and June 5 and round 2 was completed between August 11 and August 15. In 2008, round 1 was completed between June 4 and June 8, round 2 was completed between August 7 and August 11.

3.3 Point Counts

Point counts were used to sample richness and relative abundance of birds (Koper et al. 2006), and the data were used to assess the effect that food abundance and vegetation structure had on bird populations. Every bird detected visually or aurally within a 100-m radius of the point count stations was recorded (Buckland, 2006). The distance of the individual to the observer was also recorded, as was flight activity, behavior and sex (Koper et al. 2006). Sampling was conducted during the breeding season, from late May to late June. Each point count round consisted of 130 point counts: 10 point counts at each of the 13 pastures. The number of point count rounds varied by year, but most years each point count was surveyed 3 times. On average observers completed 15 point counts daily.

Point counts were conducted within the first 4 hours after sunrise when songbird activity was at its peak. Point counts were not collected on days with excessive winds (>16 kph), and during fog or rain (Koper et al. 2006).

Three years of point count data were included in the study: 2006, 2007, and 2008. Length of point count intervals and number of rounds vary slightly among years. In 2006, 5-minute point count intervals were used. In 2007 and 2008, 6 minute intervals were used (2, 2 minute intervals and 2-1 minute intervals). However, for analysis purposes only the first 3 intervals were used (2-2 minute intervals and 1- 1 minute interval), so 5-minute samples were analyzed for all 3 years.

In 2006, three rounds of point counts were completed between May 25 and June 19 (Koper, 2006). In 2007, three rounds of point counts were completed between May 25 and June

16. In 2008, a total of 4 full rounds and 1 partial round of point counts were completed; 2 full and 1 partial (Pastures 1, 5, 9, 10, 11, 12, 13) round before the cows were put in the pastures (May 25 to June 10) and 2 rounds after the cows were put in the pastures (June 16 to June 24). The study is intended to continue for a total of ten years to assess the long term affects of cattle grazing on biodiversity.

Plot count plots were already chosen we I began my study in 2007. They were chosen to ensure that four plots fell within a lowland area of the pasture and six plots fell within an upland area of the pasture. Special attention was also taken to ensure that plots were a minimum of 250m away from adjacent plot centers to decrease the likelihood of double counting individuals.

Where ever possible, stations were sampled by a different observer from the previous round, to minimize bias (Koper et al. 2006). In addition, the order in which point count stations were sampled was reversed between each round to reduce bias associated with time of observation (Koper et al. 2006). I was only interested in looking at the effects of grazing on songbirds so any other species encountered were omitted prior to analysis. Unidentified individuals were also omitted from the data set (ie. Sparrow, blackbird, songbird).

3.4 Vegetation Sampling

A number of vegetation structural components (vegetation height, vegetation density, litter depth, litter cover and bare cover) were measured to determine if and how vegetation structure influences invertebrate abundance and diversity.

3.4.1 Vegetation Height

Vegetation height was measured within 1000-m^2 (50 m X 20 m) modified Whittaker plots that were set up at each study site. Vegetation height was estimated by measuring the height of the maximum height of the plants with in the plot with a meter stick. The Whittaker plot was situated 25 m south of the center of each plot. Ten measurements were taken from 0.5 m X 1 m subplots within the Whittaker plot. Upland vegetation was sampled between late June and early July. Lowland vegetation was sampled between mid-July and early August (Koper et al. 2006).

3.4.2 Vegetation Density

We measured vegetation density using a Robel pole at a distance of 4 m from the pole, 1m above the ground. Observers recorded the maximum height class (0 = 0 - 5cm, 1 = 5 - 10cm, etc.) in which vegetation partially obscures the view onto the Robel pole (Henderson 2006). Vegetation density was measured within the same 10 subplots in which we sampled vegetation height. The value was then converted into centimeters for analysis by taking an average of the upper and lower values of the height class (0 = 2.5cm, 1 = 7.5cm, etc.)

3.4.3 Vegetation structure

We also measured litter depth, litter cover and bare ground cover. Litter depth - the height of the dead plant matter lying on the ground - was measured with a meter stick within the 10 subplots. Bare ground cover and litter cover were visually estimated within a 0.5m X 1m frame in the same 10 subplots (Koper et al. 2007). It was assigned a value from 0 to 9 which corresponds to a percentage cover class (0 = absent; 1 = >0 to 0.1%; 2 = 0.1 to 1 %; 3 = 1 to 3%; 4 = 3 to 10%; 5 = 10 to 25%; 6 = 25 to 50%; 7 = 50 to 75%; 8 = 75 to 95%; 9 = 95 to 100%). I converted cover classes to percentages by taking the average of the upper and lower cover class percentages.

3.4.4 Vegetation composition

Vegetation richness was sampled at each experimental plot from within the Modified Whittaker plot by completing a walk-through survey of the entire plot and identifying all of the vascular plant species present. Further identification of species was also completed by identifying all species found with in the Whittaker plot.

3.5 Statistical Analysis

Abundance, richness, and diversity (Simpson's) for each year, as well as average abundance, richness and diversity for all three years, were calculated in Excel 2003 (version 11). Prior to completing formal statistical analyses, exploratory graphical analysis was conducted to determine the distribution of the data, to check for outliers, and to identify appropriate analyses.

To determine if there was a difference between invertebrate abundance, richness and diversity in grazed and ungrazed plots, I conducted a Welch Modified Two-Sample *t*-test in S+ version 8.0.4 (2009) (Table 1 & Table 2), using an alpha of 0.05.

The second goal of my research was to determine if there was a relationship between invertebrate abundance, diversity and richness on the one hand, and bird abundance, diversity and richness on the other hand. To test these relationships, I used correlations and linear regressions.

In the linear regressions bird abundance, bird richness and bird diversity were the dependent variables and carabid abundance, carabid richness and carabid diversity were the independent variables. All three years of data were combined to one analysis, but sampling rounds 1 (Table 3) and 2 (Table 4) were analyzed separately. The grasshopper data were not included in the analyses because I did not have data for all three years. I chose to combine the three years of data because I was more interested in the overall trend in the data rather than the differences among years. However, I also performed the analysis on all three years of data separately and have included the results in the appendix of the manuscript. Caution must be taken when making conclusions based data from round 2 because round 2 data was collected after the bird data collection was already complete.

I realized that there are factors other than prey availability that influence bird richness and diversity, such as habitat, bird species, time of day, and time of year. To determine if and how these factors influenced bird-invertebrate relationships I did some addition analyses:

Habitat preferences could influence bird populations in some habitats. Some species may be specialists and are therefore restricted by habitat availability and may not be able to move into areas of higher energy (Evans et al. 2005). To determine if habitat type had an effect on these relationships, I evaluated the relationship between bird abundance, richness and diversity and carabid and grasshopper abundance, richness and diversity in upland habitats (Table 5) and lowland (Table 6) separately. In this case, I only used data from 2008 because it is the only year for which I had a complete data set.

To determine whether different species were affected differently by invertebrate abundance, richness and diversity I used generalized linear modes. I looked at a number of species: Brown-headed cowbird (BHCO), Baird’s sparrow (BAIS), Brewer’s sparrow (BRSP), Chestnut-collared longspur (CCLO), Clay colored sparrow (CCSP), Common yellowthroat (COYE), Eastern kingbird (EAKI), Grasshopper sparrows (GRSP), Horned Larks (HOLA), Lark bunting (LARB), McCown’s longspur (MCLO), Red-winged blackbird (RWBL), Savannah sparrow (SAVS), Sprague’s pipit (SPPI), Vesper sparrow (VESP) and Western meadowlark (WEME). These species range in their reliance on invertebrates as a food source. I compared the species dependence on invertebrates as food sources, to the relationship between the species and invertebrate populations (Table 7). Due to the timing of invertebrate sampling I could only use data from the first round of carabid sampling for 2008 (June 4 - 8). Round 2 of carabid sampling and grasshopper sampling were completed later in the year (August 7-11 and July 29-30 respectively) and I do not have bird abundance data from this time because singing activity tends to decline after July 1.In addition, invertebrates are much more important to birds during the breeding season because all passerine young are fed invertebrates.

To determine if avian dependence on invertebrates as food sources vary with times during the season, I looked at the relationship between bird abundance, richness and diversity, and grasshopper abundance, richness and diversity in the first and second round (Table 8) of beetle trapping separately.

I was interested if the changes in vegetation structure, which in turn is influenced by cattle grazing, influences invertebrate abundance richness and diversity. For this analysis I used a linear regression model in S+, with an alpha of 0.05 to minimize the risk of Type II error (Table 9, 10, 11).

Finally, I was also interested if weather (temperature, precipitation) had any effect on invertebrate populations. I graphed total rainfall amounts (Figure 11) and mean temperature (Figure 12) for May, June, July and August in 2006, 2007, and 2008. I was also interested in the daily average temperature for the five days of carabid trapping in round 1 (Figure 13) and round 2 (Figure 14) for 2006, 2007, 2008. Weather data were taken from the Environment Canada website (http://www.weatheroffice.gc.ca/canada_e.html).

My statistical analysis assumed that each point-count plot was independent of other plots. This assumption is valid in 2006 and 2007 because there were no cows in the pastures and no fence lines to fragment the prairie; therefore, the issue of closer plots being more similar because they were exposed to the same grazing intensity is not there. However, this may not be true in 2008, when fences were built and cattle were introduced to the pastures at a range of varying grazing intensities. Plots that are close to one another may be more similar than plots that are farther apart. Including northing in the analyses helped to control for this potential lack of independence, as it allowed for plots to vary spatially. Further, ensuring that the centres of point-count plots were at least 400m apart in most cases also helped to reduce the likelihood that nearby plots are particularly similar, and prevented us from double-counting individuals. However, if this assumption was inadvertently violated, the likelihood of Type I error would be inflated. Previous analyses on birds in this area showed that including random variables to allow for point counts within the same pastures to be more similar than point counts in different pastures did not change statistical results. As my study used the same plots, it is therefore likely that including pasture as a random variable is not necessary to control for similarity among plots within pastures.

4.0 Results

4.1 Effects of grazing on invertebrates

4.1.1 Carabids

Table 1 shows the effect of grazing treatment (grazed/ungrazed) on carabid abundance, richness and diversity, it shows that grazing had no consistent effect on carabid abundance and richness (Table 1). In 2006, carabid abundance and richness were twice as high in grazed than ungrazed plots, and diversity was higher in grazed than ungrazed plots. In contrast, in 2007 mean abundance and diversity of carabids was lower in grazed than ungrazed pastures (Table 1). In 2008, before cows were introduced to the pastures, mean diversity of carabids was again higher in ungrazed areas, whereas there was no effect of grazing on richness or abundance. Finally, in 2008 (after cows) none of the three measures differed significantly among management types.

Table 1: Influence of grazing treatment on carabid abundance, richness and diversity at Grasslands National Park in 2006, 2007 and 2008 before and after cows. Species diversity values were calculated using the Simpson's Diversity Index (*1/D*). β = intercept, SE = standard error and *p* = p-value and α = 0.05

Year		*Mean (grazed)*	*Mean (ungrazed)*	*t-statistic*	*p-value*
2006	Carabid abundance	3.863	1.861	5.401	< **0.001**
	Carabid richness	4.600	2.389	6.296	< **0.001**
	Carabid diversity	3.566	2.040	5.641	< **0.001**
2007	Carabid abundance	2.975	4.650	-2.562	**0.012**
	Carabid richness	3.525	4.033	-1.332	0.1858
	Carabid diversity	3.007	2.930	2.429	**0.0167**
2008 Before Cows	Carabid abundance	3.975	2.967	1.347	0.1835
	Carabid richness	1.525	1.767	-0.961	0.340
	Carabid diversity	1.178	1.622	-2.271	**0.017**
2008 After Cows	Carabid abundance	2.541	2.767	-0.292	0.772
	Carabid richness	1.653	1.467	0.616	0.5409
	Carabid diversity	1.504	1.248	1.164	0.2498

4.1.2 Effect of grazing on grasshoppers

Table 2 shows the effect of grazing treatment (grazed/ungrazed) on grasshopper abundance, richness and diversity. Although grasshopper abundance was independent of grazing in 2006, in 2008, mean abundance, richness and diversity was significantly higher in grazed than in ungrazed pastures. In fact, grasshopper abundance was three times higher and richness was two times as high in grazed pastures (Table 2).

Table 2: Influence of grazing treatment on grasshopper abundance, richness and diversity at Grasslands National Park in 2006 and 2008 before and after cows. Species diversity values were calculated using the Simpson's Diversity Index (*1/D*). β = intercept, SE = standard error, *p* = p-value and α = 0.05

Year		*Grazed (mean)*	*Ungrazed (mean)*	*t-statistic*	*p-value*
2006	Grasshopper abundance	12.579	10.089	1.210	0.232
2008	Grasshopper abundance	13.150	4.300	5.082	**<0.001**
	Grasshopper richness	6.800	2.867	5.347	**<0.001**
	Grasshopper diversity	5.759	3.090	4.830	**<0.001**

4.2 *Relationship between invertebrates and birds*

I used correlations and linear regression to determine the relationship between birds and invertebrates. With the correlations, I found no evidence that bird richness, abundance and diversity was influenced by carabid richness, abundance and diversity, or grasshopper richness, abundance and diversity, in any of the three years of data. The strongest correlation was between bird abundance and carabid abundance in 2007 (*r* = 0.3347).

Table 3: Multiple linear regression between bird abundance, richness and diversity and carabid abundance, carabid richness, and carabid diversity for round 1 (June) in 2006, 2007 and 2008 at Grasslands National Park. Species diversity values were calculated using the Simpson's Diversity Index (*1/D*). β = intercept, SE = standard error, *p* = p-value and α = 0.05

	Parameter	*Carabid Abundance*	*Carabid Richness*	*Carabid Diversity*	*Year* (2007)	*Year* (2008)
Bird Abundance	β	0.0326	0.0530	-0.0180	-1.4078	-1.6391
	SE	0.0157	0.0568	0.0691	0.2158	0.2089
	p	**0.0379**	0.3518	0.7951	**<0.001**	**<0.001**
Bird Richness	β	0.0139	-0.0670	-0.1449	-1.3683	-1.6031
	SE	0.0187	0.0668	0.0806	0.2188	0.2131
	p	0.4564	0.3167	0.0703	**<0.001**	**<0.001**
Bird Diversity	β	0.0153	-0.0382	-0.0899	-1.2955	-1.6183
	SE	0.0138	0.0492	0.0595	0.2167	0.2142
	p	0.2671	0.4375	0.1314	**<0.001**	**<0.001**

Table 3 shows the relationship between birds and carabids in round 1 using linear regressions. In round 1, the only significant correlation among the variables of interest was a positive one between carabid abundance and bird abundance (Table 3). I also found that this relationship was significant in round 2. Year was also often significant, but was included only as a nuisance variable, and will not be discussed in detail here or below (Table 3). Figure 2 shows the only significant relationship, the one between bird abundance and carabid abundance. This model has an R^2 value of 0.1972. This means that just under 20% of the variation in the models was explained by the variables that were included (Figure 2).

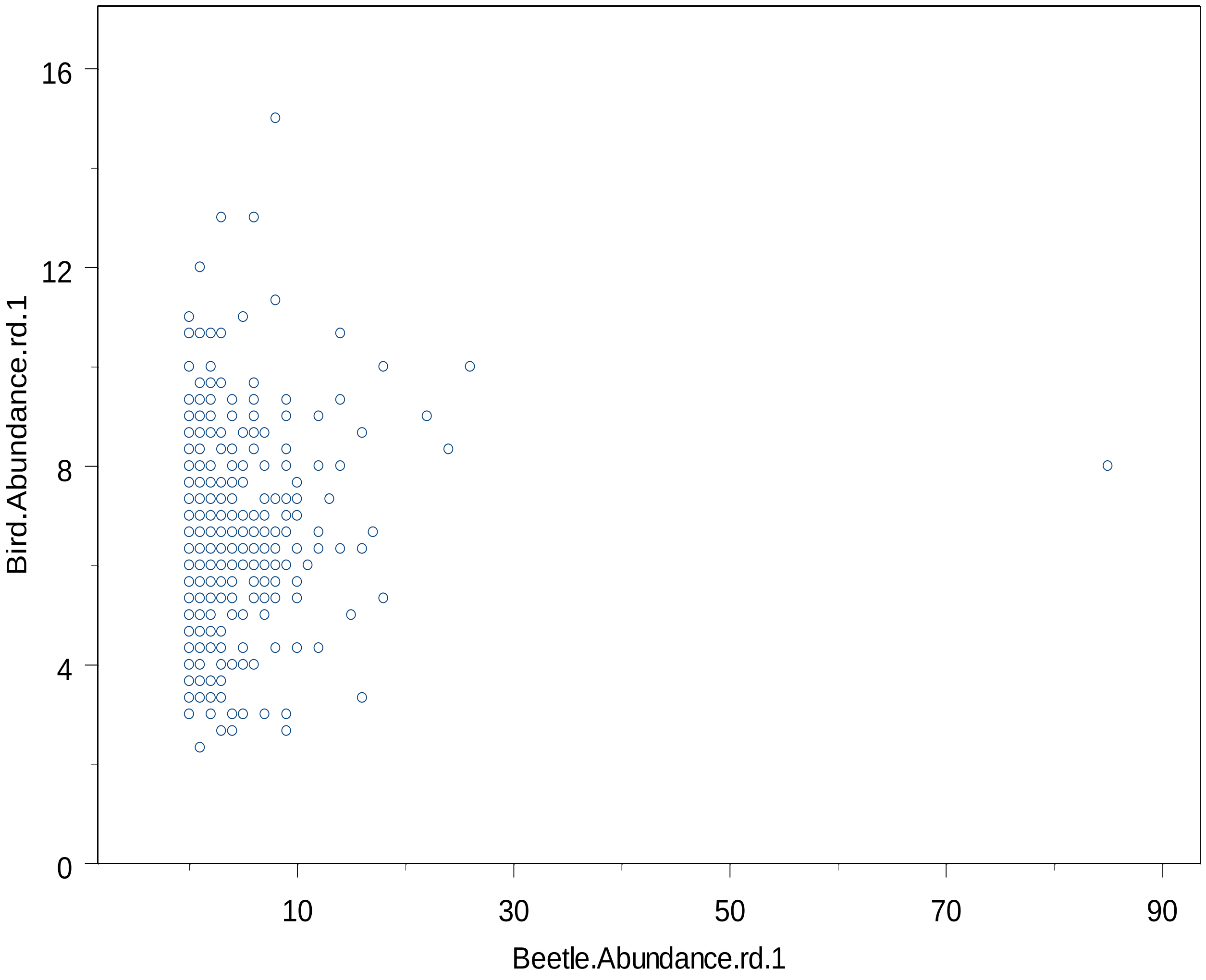

Figure 2: Scatter plot showing the relationship between bird abundance and carabid abundance in round 1 (June) in 2006, 2007, and 2008 at Grasslands National Park

Table 4: Multiple linear regression between bird abundance, richness and diversity and carabid abundance, carabid richness, and carabid diversity for round 2 (August) in 2006, 2007 and 2008 at Grasslands National Park. Species diversity values were calculated using the Simpson's Diversity Index (*1/D*). β = intercept, SE = standard error, *p* = p-value and α = 0.05

	Parameter	*Carabid Abundance*	*Carabid Richness*	*Carabid Diversity*	*Year (2007)*	*Year (2008)*
Bird Abundance	β	0.0733	0.0724	0.0713	-1.4324	0.5729
	SE	0.0278	0.0570	0.0673	0.1959	0.1897
	p	**0.0087**	0.2054	0.2899	**<0.001**	**0.0027**
Bird Richness	β	0.0348	0.0290	-0.3062	-1.1863	-1.3197
	SE	0.0343	0.0699	0.2226	0.2418	0.2341
	p	0.3110	0.6784	0.1698	**<0.001**	**<0.001**
Bird Diversity	β	-0.0023	-0.0013	0.0123	0.0425	0.0387
	SE	0.0014	0.0029	0.0644	0.0102	0.0099
	p	0.1203	0.6521	0.8486	**<0.001**	**0.0001**

Table 4 shows the relationship between birds and carabids in round 2 using linear regressions Similarly, in round 2, there was a significant positive relationship between carabid abundance and bird abundance. The R^2 value for the second model was higher than the R^2 value for round 1. Approximately 25% of the variation in the models was explained by the variables that were included compared to 19% in the round 1 model (Figure 2). Both R^2 values fairly high especially for biological data. This suggests that food availability, and more specifically invertebrate availability, is an important factor in habitat selection and use for birds. Figure 3 shows the relationship graphically and further demonstrates the strength of the relationship.

In addition to these analyses, I also looked at the relationship between bird abundance, richness and diversity, and invertebrate (carabid and grasshopper) abundance and diversity for 2006, 2007 and 2008 separately (Appendix 1). There were no significant relationships in 2006 and 2008 before and after cows. In 2007 there were significant relationships between bird abundance, richness and diversity and carabid abundance.

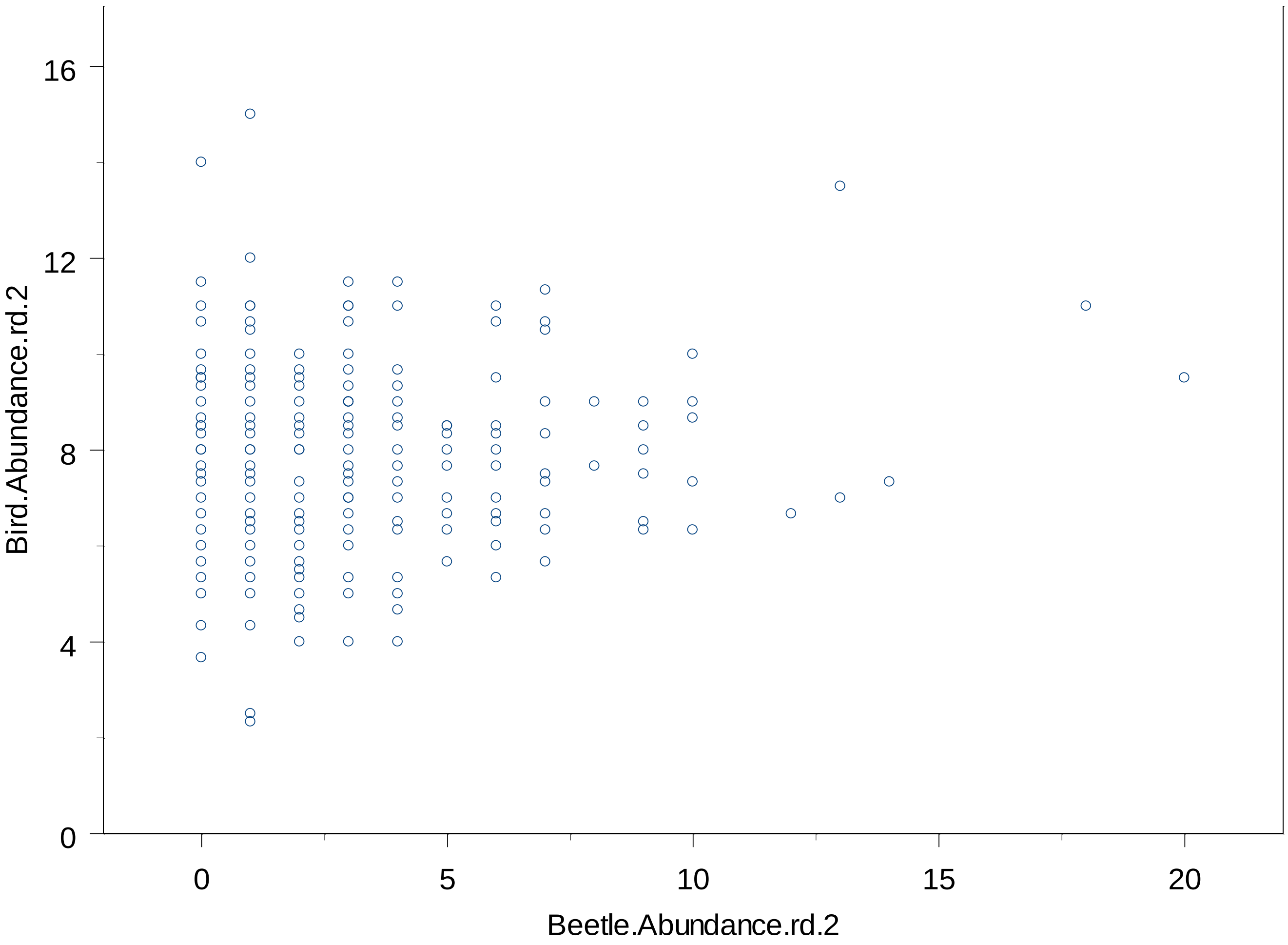

Figure 3: Scatter plot showing the relationship between bird abundance and carabid abundance in round 1 (June) in 2006, 2007, and 2008 at Grasslands National Park

Table 5: Multiple linear regression between bird abundance, richness and diversity (dependent) and carabid and grasshopper abundance, richness, and diversity in uplands plots only in 2008 at Grasslands National Park. Species diversity values were calculated using the Simpson's Diversity Index (*1/D*). β = intercept, SE = standard error, *p* = p-value and α = 0.05

	Parameter	*Carabid abundance*	*Carabid Richness*	*Carabid diversity*	*Grasshopper abundance*	*Grasshopper richness*	*Grasshopper diversity*
Bird abundance	β	0.0070	1.2093	-1.5785	0.0818	-0.5430	0.4659
	SE	0.1153	0.8993	0.8859	0.0723	0.4340	0.4289
	p	0.9515	0.1830	0.0790	0.2613	0.2150	0.2810
Bird richness	β	-0.1586	0.9534	-1.0956	0.0072	-0.1273	0.1027
	SE	0.0999	0.7794	0.7677	0.0626	0.3761	0.3717
	p	0.1169	0.2253	0.1579	0.9088	0.7361	0.7831
Bird diversity	β	-0.1423	0.6405	-0.6578	-0.0054	0.0714	-0.0906
	SE	0.0654	0.5105	0.5028	0.0410	0.2463	0.2434
	p	**0.0330**	0.2137	0.1950	0.8949	0.7727	0.7110

Table 5 shows the relationship between bird abundance, richness and diversity and carabid and grasshopper abundance, richness, and diversity in uplands plots. I found that in upland habitats, bird diversity was negatively correlated with carabid abundance (Table 5).

Table 6 shows the relationship between bird abundance, richness and diversity and invertebrate abundance, richness and diversity in lowland plots. In contrast to the upland results, I found no significant effect of carabid diversity on bird diversity in previous models. In addition, I found no significant correlation between bird abundance, richness, or diversity and carabid richness and diversity in lowland habitats (Table 6). R^2 value was quite low at 0.06486, so the model explains only a small amount of variation in the data.

Table 6: Multiple linear regression between bird abundance, richness and diversity (dependent) and carabid and grasshopper abundance, richness, and diversity in lowland plots only in 2008 at Grasslands National Park. Species diversity values were calculated using the Simpson's Diversity Index (*1/D*). β = intercept, SE = standard error, *p* = p-value and α = 0.05

	Parameter	*Carabid abundance*	*Carabid Richness*	*Carabid diversity*	*Grasshopper abundance*	*Grasshopper richness*	*Grasshopper diversity*
Bird abundance	β	-0.3875	1.4326	-1.0339	0.0069	-0.2623	0.5293
	SE	0.3107	1.5911	1.4243	0.0495	0.3635	0.4033
	p	0.2188	0.3727	0.4716	0.8896	0.4743	0.1960
Bird richness	β	-0.1670	0.2124	-0.0146	-0.0143	-0.0972	0.4780
	SE	0.2933	1.5016	1.3442	0.0467	0.3430	0.3806
	p	0.5719	0.8881	0.9914	0.7604	0.7781	0.2157
Bird diversity	β	-0.0645	-0.5816	0.5196	0.0067	-0.0882	0.3233
	SE	0.2189	1.1208	1.0033	0.0349	0.2560	0.2841
	p	0.7695	0.6064	0.6071	0.8476	0.7322	0.2611

Table 7 shows the relationship between bird species abundance and carabid abundance, richness, and diversity. I ran this analysis because different avian species have different levels of reliance on invertebrates as a food source (Lanyon 1994, Yasukawa & Searcy 1995, Jones & Cornely 2002, Murphy 1996)(Table 7). Chestnut collared longspur (Figure 5) and McCown's longspur (Figure 8) abundances increased significantly with the abundance of carabid beetles. Although this result was statistically significant, the R^2 values were only 0.1325 and 0.1853 respectively, demonstrating that a large amount of the variability in the distribution of these species is influenced by factors other than invertebrate availability. I also found that three species were negatively correlated with carabid abundance; Brown headed-cowbirds (Figure 4), Savannah sparrows (Figure 9) and Clay-colored sparrows (Figure 6). Clay-colored sparrows (Figure 7) and Savannah sparrows (Figure10) were also negatively correlated with carabid richness.

Table 7: Multiple linear regression between bird species abundance (dependent) and carabid abundance, richness, and diversity at Grasslands National Park in 2008. Species diversity values were calculated using the Simpson's Diversity Index (*1/D*). β = intercept, SE = standard error, *p* = p-value and α = 0.05. N/A = no quantitative studies available, IBS = Invertebrates in breeding season.

		% Invertebrate in diet	*Carabid abundance*	*Carabid richness*	*Carabid diversity*
BHCO abundance	β	N/A, IBS	-0.0579	-0.0232	-0.0100
	SE		0.0291	0.0775	0.0902
	p		**0.0490**	0.7653	0.9123
BAIS abundance	β	N/A, IBS	-0.0127	-0.0105	0.0149
	SE		0.0197	0.0518	0.0603
	p		0.5228	0.8349	0.8054
BRSP abundance	β	N/A	-0.0039	0.0341	0.0408
	SE		0.0095	0.0249	0.0289
	p		0.6840	0.1723	0.1609
CCLO abundance	β	72	0.1204	0.0965	0.0097
	SE		0.0272	0.0761	0.0891
	p		**<0.0001**	0.2072	0.9139
CCSP abundance	β	Mainly vegetable matter	-0.0600	-0.1048	-0.0982
	SE		0.0194	0.0520	0.0608
	p		**0.0025**	**0.0459**	0.1088
COYE abundance	β	N/A	-0.0045	0.0083	0.0198
	SE		0.0087	0.0227	0.0264
	p		0.6041	0.7163	0.4552
EAKI abundance	β	85	-0.0121	0.0061	0.0033
	SE		0.0132	0.0347	0.0404
	p		0.3620	0.8598	0.9353
GRSP abundance	β	61	0.0080	0.0078	0.0051
	SE		0.0072	0.0189	0.0219
	p		0.2664	0.6810	0.8155
HOLA abundance	β	4 – 56	-0.0105	-0.0145	-0.0469
	SE		0.0191	0.0501	0.0582
	p		0.5842	0.7723	0.4214
LARB abundance	β	N/A	-0.0105	-0.0098	-0.0022
	SE		0.0119	0.0312	0.0363
	p		0.3760	0.7540	0.9519
MCLO abundance	β	72	0.0489	0.0355	0.0081
	SE		0.0091	0.0261	0.0306
	p		**<0.0001**	0.1767	0.7926
RWBL abundance	β	70	-0.0219	-0.0298	-0.0170
	SE		0.0180	0.0474	0.0533
	p		0.2263	0.5312	0.7595
SAVS abundance	β	N/A	-0.0461	-0.0921	-0.0937
	SE		0.0172	0.0456	0.0533
	p		**0.0084**	**0.0457**	0.0812
SPPI abundance	β	94	0.0221	0.0149	0.0235
	SE		0.0191	0.502	0.0584
	p		0.2489	0.7678	0.6885
VESP abundance	β	51	-0.0266	-0.0545	-0.0601
	SE		0.0175	0.0460	0.0536
	p		0.1318	0.2387	0.2643
WEME abundance	β	63.3	-0.0347	-0.0517	-0.0346
	SE		0.0179	0.0475	0.0554
	p		0.0549	0.2777	0.5339

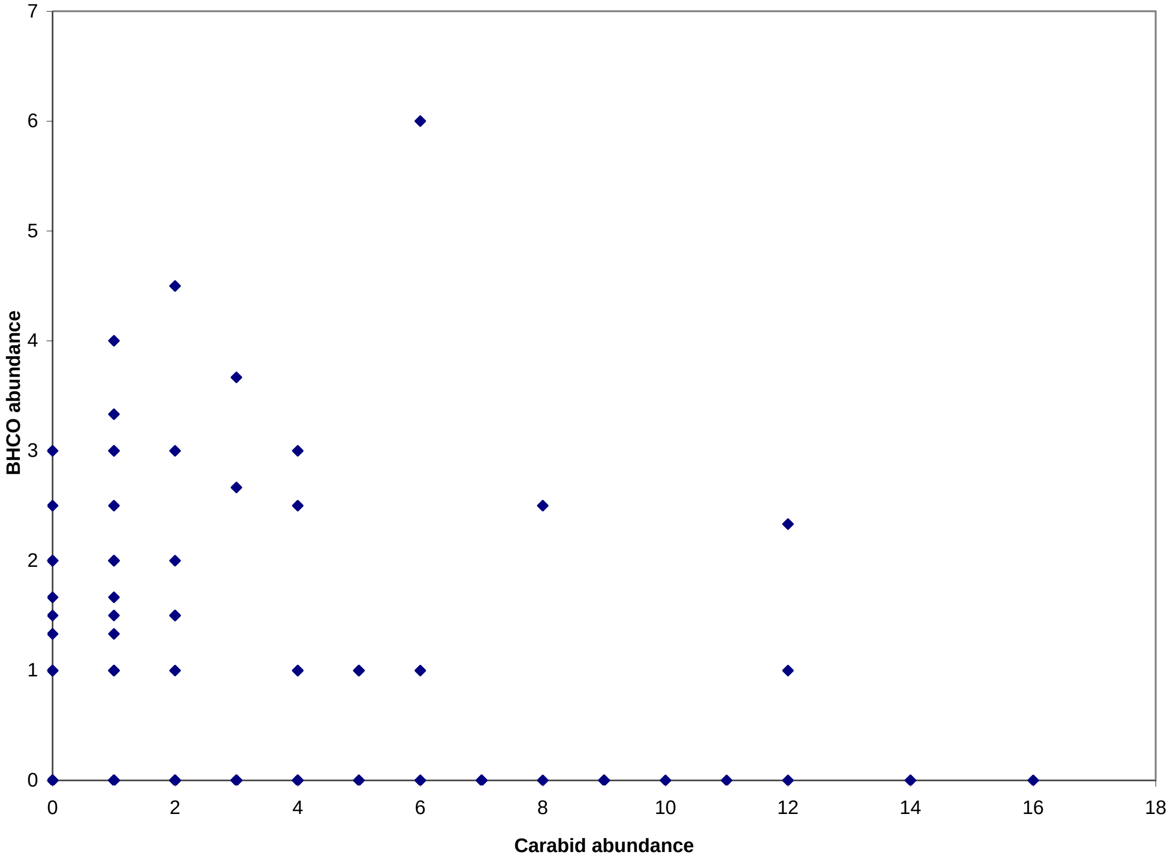

Figure 4: Scatter plot showing the relationship between Brown-headed cowbird abundance and carabid abundance in round 1 in 2008 at Grasslands National Park

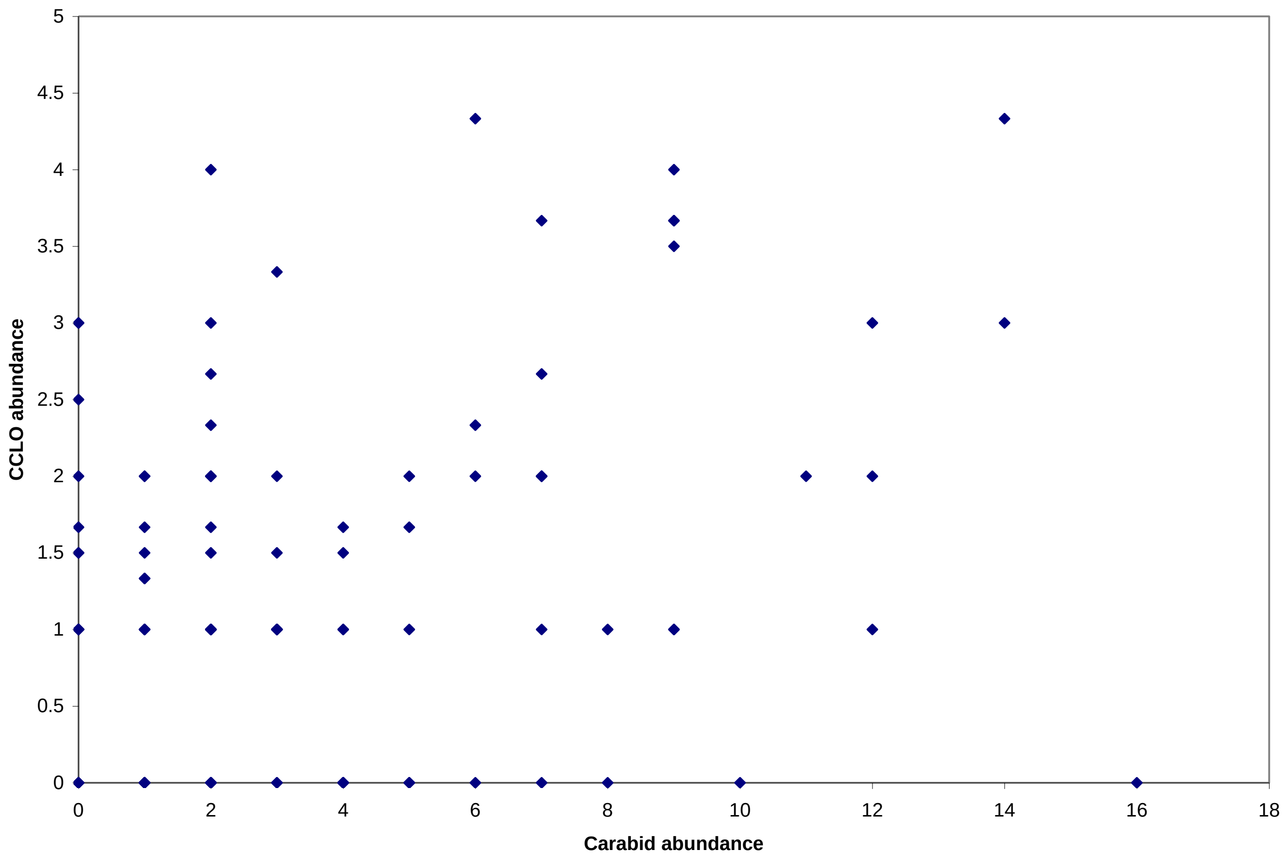

Figure 5: Scatter plot showing the relationship between Chestnut-collared longspur abundance and carabid abundance in round 1 in 2008 at Grasslands National Park

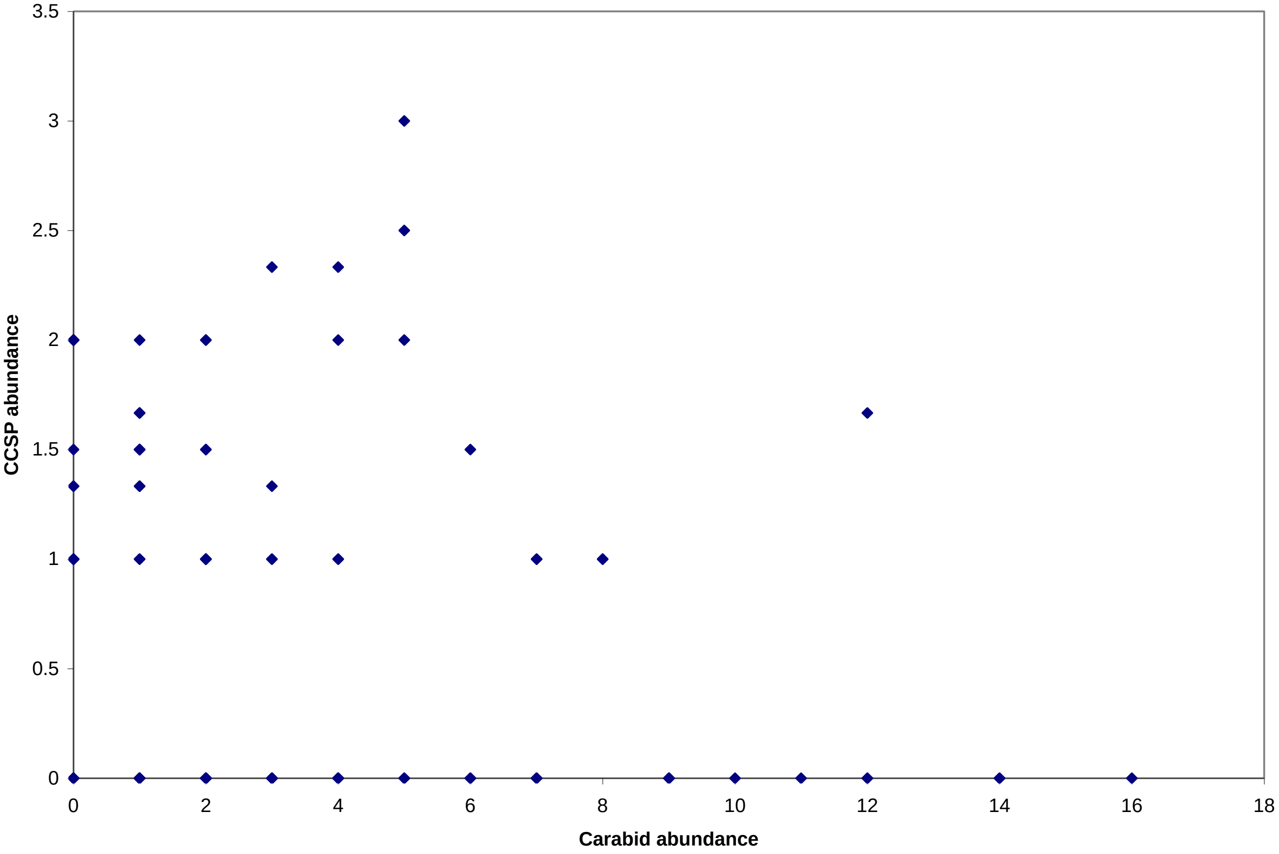

Figure 6: Scatter plot showing the relationship between Clay-colored sparrow abundance and carabid abundance in round 1 in 2008 at Grasslands National Park

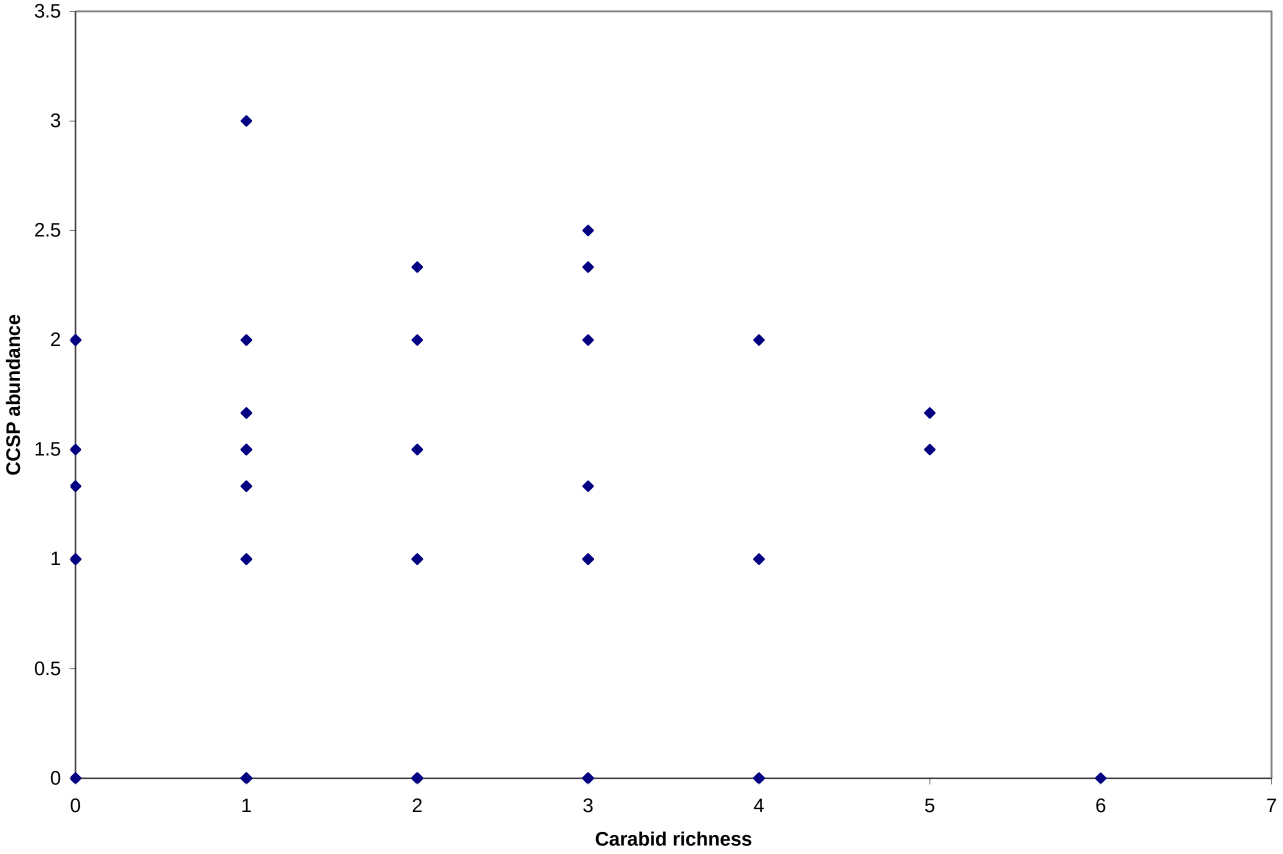

Figure 7: Scatter plot showing the relationship between Clay-colored sparrow abundance and carabid richness in round 1 in 2008 at Grasslands National Park

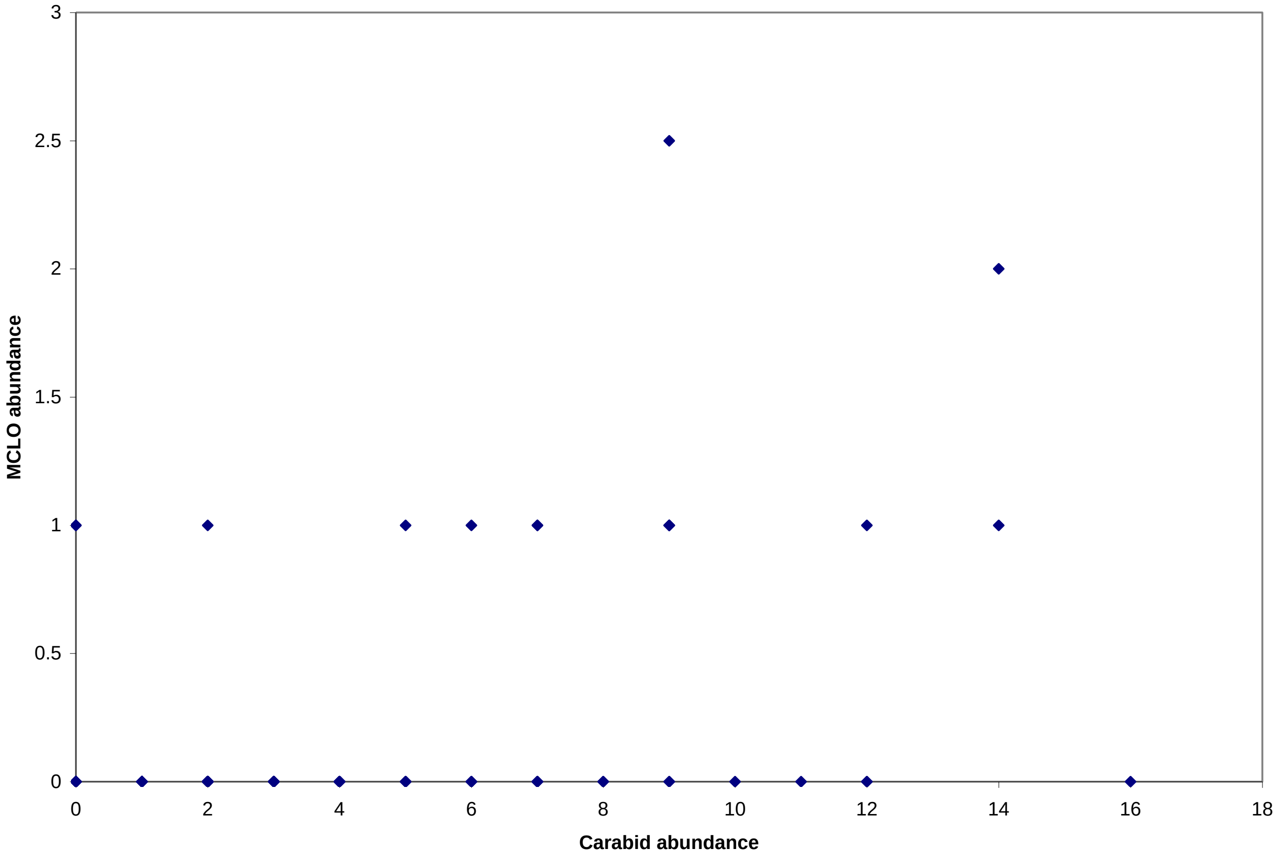

Figure 8: Scatter plot showing the relationship between McCown's longspur abundance and carabid abundance in round 1 in 2008 at Grasslands National Park

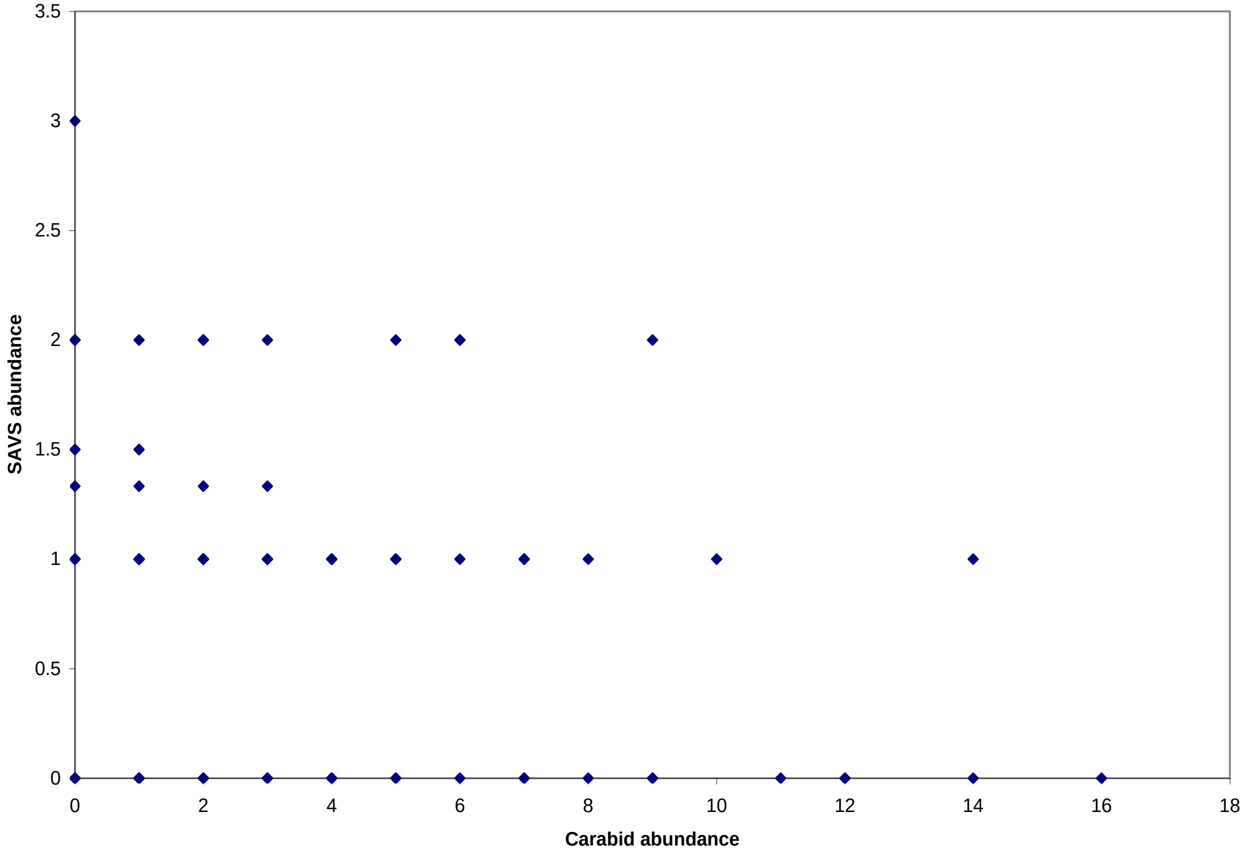

Figure 9: Scatter plot showing the relationship between Savannah sparrow abundance and carabid abundance in round 1 in 2008 at Grasslands National Park

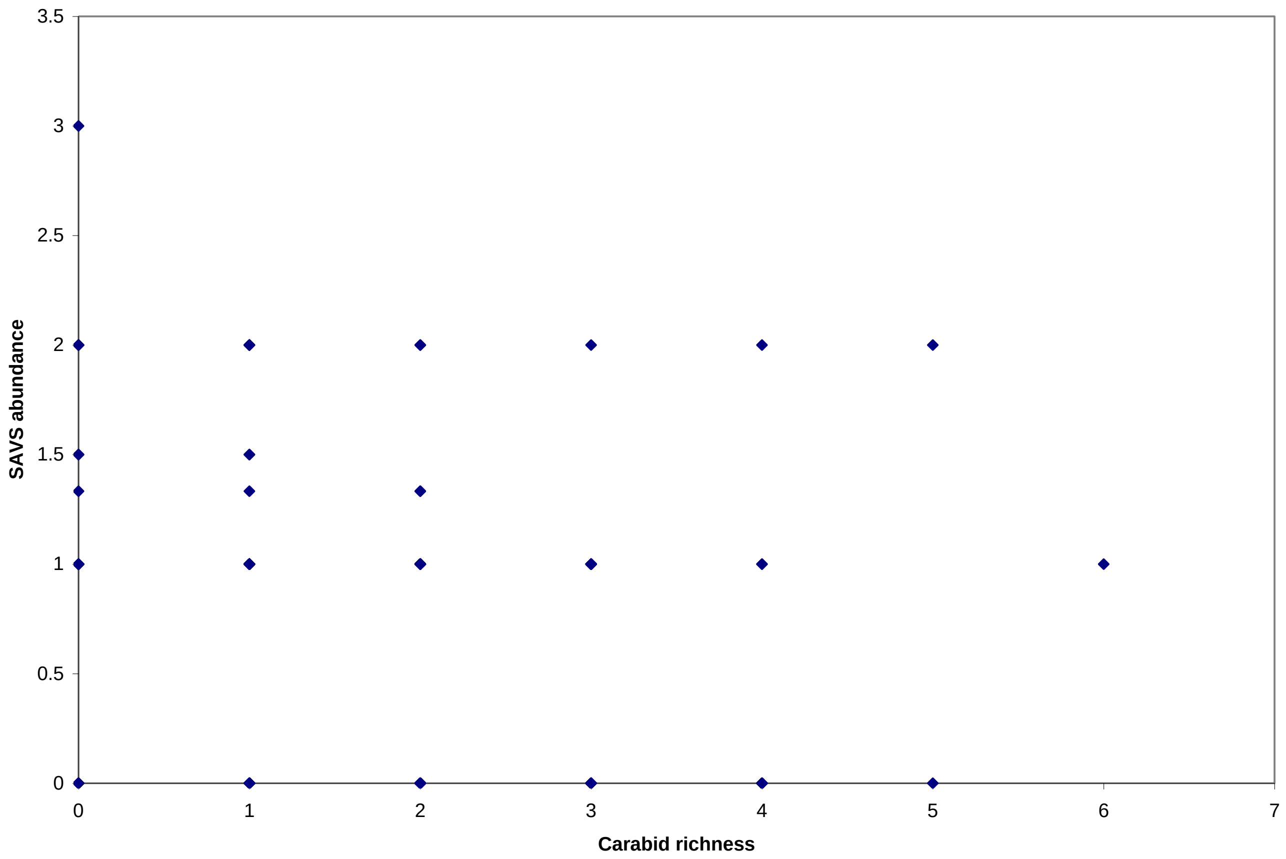

Figure 10: Scatter plot showing the relationship between Savannah sparrow abundance and carabid richness in round 1 in 2008 at Grasslands National Park

Birds may be more dependent on invertebrates as food sources during the breeding season (Lanyon 1994, Yasukawa & Searcy 1995, Jones & Cornely 2002, Murphy 1996). To determine if timing has an effect on these relationships I looked at the relationship between bird abundance, richness and diversity and grasshopper abundance, richness and diversity in the first (Table 8) and second round (Table 9) of beetle trapping separately.

Table 8: Multiple linear regression between bird abundance, richness and diversity and carabid and abundance, richness, and diversity in round 1 and 2 separately at Grasslands National Park in 2008. Species diversity values were calculated using the Simpson's Diversity Index (*1/D*). β = intercept, SE = standard error, *p* = p-value and α = 0.05.

			Carabid abundance	*Carabid richness*	*Carabid diversity*
Round 1	Bird abundance	β	0.0082	0.5235	-0.5909
		SE	0.0239	0.2135	0.2289
		p	0.7314	**0.0147**	**0.0102**
	Bird richness	β	0.0141	0.2504	-0.4335
		SE	0.0281	0.2509	0.2689
		p	0.6156	0.3189	0.1078
	Bird diversity	β	0.0216	0.0729	-0.1949
		SE	0.0207	0.1851	0.1984
		p	0.2975	0.6940	0.3265
Round 2	Bird abundance	β	0.1415	-0.0896	-0.0567
		SE	0.0515	0.2138	0.2049
		p	**0.0063**	0.6753	0.7820
	Bird richness	β	0.1142	-0.2337	0.0817
		SE	0.0632	0.2632	0.2513
		p	0.0716	0.3735	0.7454
	Bird diversity	β	0.1166	-0.3555	0.2069
		SE	0.0495	0.2053	0.1967
		p	**0.0189**	0.0841	0.2935

Bird abundance was significantly influenced by richness and diversity of carabids in round 1 (June 4-8). The relationship between bird abundance and carabid richness was positive but the relationship between bird abundance and carabid diversity is negative. Bird abundance was significantly related to carabid abundance in round 2 (August) and bird diversity was significantly related to carabid abundance and carabid richness.

4.3 Effect of vegetation structure on invertebrates

Figures 9, 10, and 11 show the relationship between vegetation structure and composition and invertebrate abundance, richness and diversity. In 2006, the number of grasshoppers decreased with increasing litter depth (Table 9). Relationships between carabid abundance and carabid diversity, and vegetation richness, were all positive. This means that as vegetation richness increased, the number and diversity of carabids also increased. Although these results were statistically significant, the R^2 values were 0.08337 and 0.06355 for carabid abundance and carabid diversity respectively. This means that only approximately 8 % and 6 % of the variation in the models were explained by the variables that were included (Table 9).

Table 9: Linear regression showing the effect of vegetation structure (vegetation density, bare cover and litter depth) and vegetation richness on abundance and diversity of invertebrates for 2006 at Grasslands National Park. Species diversity values were calculated using the Simpson's Diversity Index (*1/D*). β = intercept, SE = standard error, *p* = p-value and α = 0.05.

	Parameter	*Grasshopper abundance*	*Carabid abundance*	*Carabid diversity*
Vegetation density	β	-0.0377	0.0140	-0.0152
	SE	0.1032	0.0244	0.0187
	p	0.7155	0.5671	0.4187
Bare cover	β	-0.1683	-0.0185	-0.0280
	SE	0.0919	0.0219	0.0168
	p	0.0695	0.3995	0.0974
Litter depth	β	-0.0966	-0.0024	-0.0047
	SE	0.0445	0.0106	0.0082
	p	**0.0318**	0.8205	0.5622
Vegetation richness	β	0.1517	0.0693	0.0412
	SE	0.0903	0.0215	0.0165
	p	0.0955	**0.0016**	**0.0138**

Table 10: Linear regression showing the effect of vegetation structure (vegetation density, vegetation height, bare cover and litter depth) and vegetation richness on abundance and diversity of invertebrates for 2007 at Grasslands National Park. Species diversity values were calculated using the Simpson's Diversity Index (*1/D*). β = intercept, SE = standard error, *p* = p-value and α = 0.05.

	Parameter	*Carabid abundance*	*Carabid diversity*
Bare cover	β	-0.0611	-0.0211
	SE	0.0472	0.0157
	p	0.1971	0.1824
Vegetation density	β	0.2083	-0.0565
	SE	0.1341	0.0448
	p	0.1229	**0.02089**
Vegetation height	β	-0.0485	0.0741
	SE	0.1297	0.0433
	p	0.7090	0.0894
Litter depth	β	-0.0940	0.0187
	SE	0.1985	0.0633
	p	0.6367	0.7787
Vegetation richness	β	-0.0174	-0.0031
	SE	0.0446	0.0149
	p	0.6969	0.8334

Table 11: Linear regression showing the effect of vegetation structure (vegetation density, vegetation height, bare cover and litter depth), vegetation richness, and northing on abundance and diversity of invertebrates for 2008 at Grasslands National Park. Species diversity values were calculated using the Simpson's Diversity Index (*1/D*). β = intercept, SE = standard error, *p* = p-value and α = 0.05.

	Parameter	*Grasshopper abundance*	*Grasshopper diversity*	*Carabid abundance*	*Carabid diversity*
Vegetation density	β	0.4807	0.0916	0.08355	0.1297
	SE	0.4041	0.1011	0.08260	0.1491
	p	0.2366	0.3670	0.3138	0.3927
Vegetation height	β	-0.6522	-0.1801	-0.0868	-0.1366
	SE	0.4142	0.1042	0.0847	0.1528
	p	0.1179	0.0868	0.3074	0.3732
Litter depth	β	0.3790	0.3164	-0.3587	-0.4342
	SE	1.0168	0.2476	0.2078	0.3752
	p	0.7100	0.2041	0.0869	0.2493
Bare cover	β	0.0867	0.0629	-0.0021	0.0264
	SE	0.1090	0.0269	0.0223	0.0402
	p	0.4278	**0.0213**	0.9263	0.5132
Richness	β	0.3178	0.0259	-0.0133	-0.0122
	SE	0.1055	0.0265	0.0216	0.0389
	p	**0.0031**	0.3304	0.5376	0.7552
Northing	β	0.0005	0.0001	-0.0001	-0.0002
	SE	0.0003	0.0001	0.0001	0.0001
	p	0.0634	0.0818	**0.0152**	0.0627

There was only one significant correlation between vegetation structure and the invertebrate community in 2007 (Figure 10). As the vegetation became denser, the diversity of carabids decreased. The result was statistically significant but the R^2 value was only 0.07417, indicating that only about 7 percent of the variation in the models was explained by the variables that were included.

In 2008, there was more evidence of a significant effect of vegetation structure on the invertebrate community (Figure 11). There was a significant negative relationship between carabid abundance and northing. The relationships between grasshopper diversity and bare cover, and grasshopper abundance and richness, were positive. The R^2 values were only 0.1348, 0.1436, 0.0945, for grasshopper abundance, grasshopper diversity, and carabid abundance, respectively. This means that about 14, 14, and 10% of the variation in the models was explained by the variables that were included.

4.4 Weather data

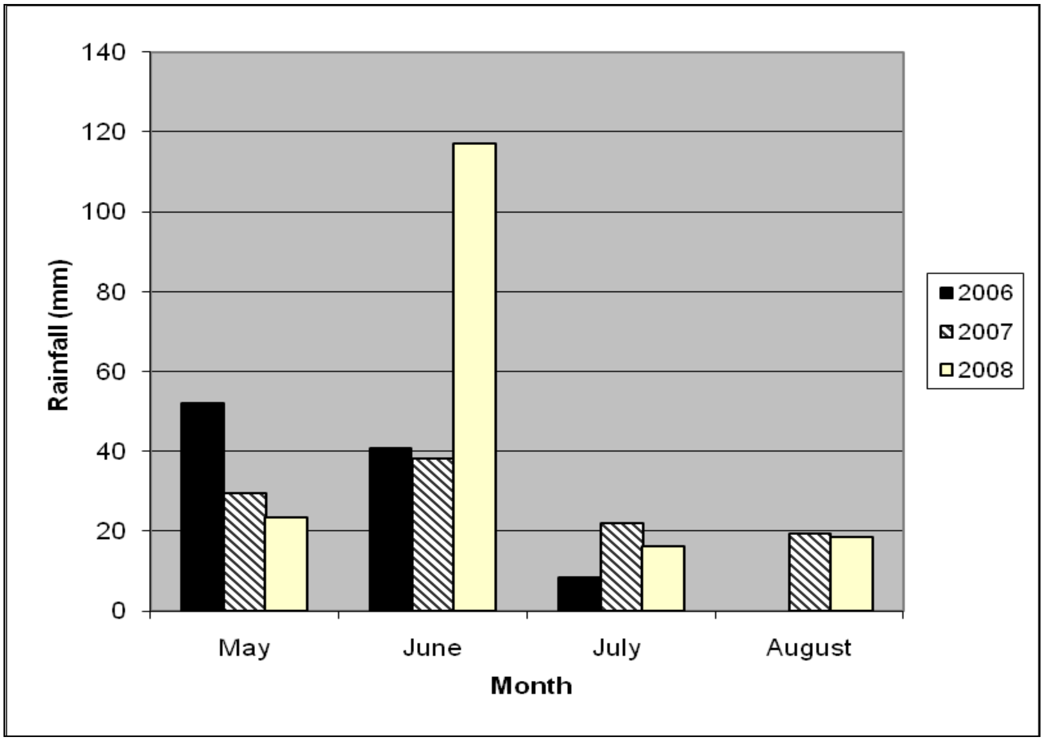

Figure 11: Total rainfall (mm) in May, June, July, and August in 2006, 2007, and 2008 in Grasslands National Park.

Figure 11 shows the total rainfall in May, June, July and August of 2006, 2007, and 2008. 2008 (175mm) had the highest rainfall amounts, followed by 2007 (109.6mm) , 2006 (101.2mm). It is interesting to note that rainfall was very high in June of 2008, which is when the first round of carabid trapping occurred and there was no precipitation in August of 2006 when the second round of carabid trapping took place.

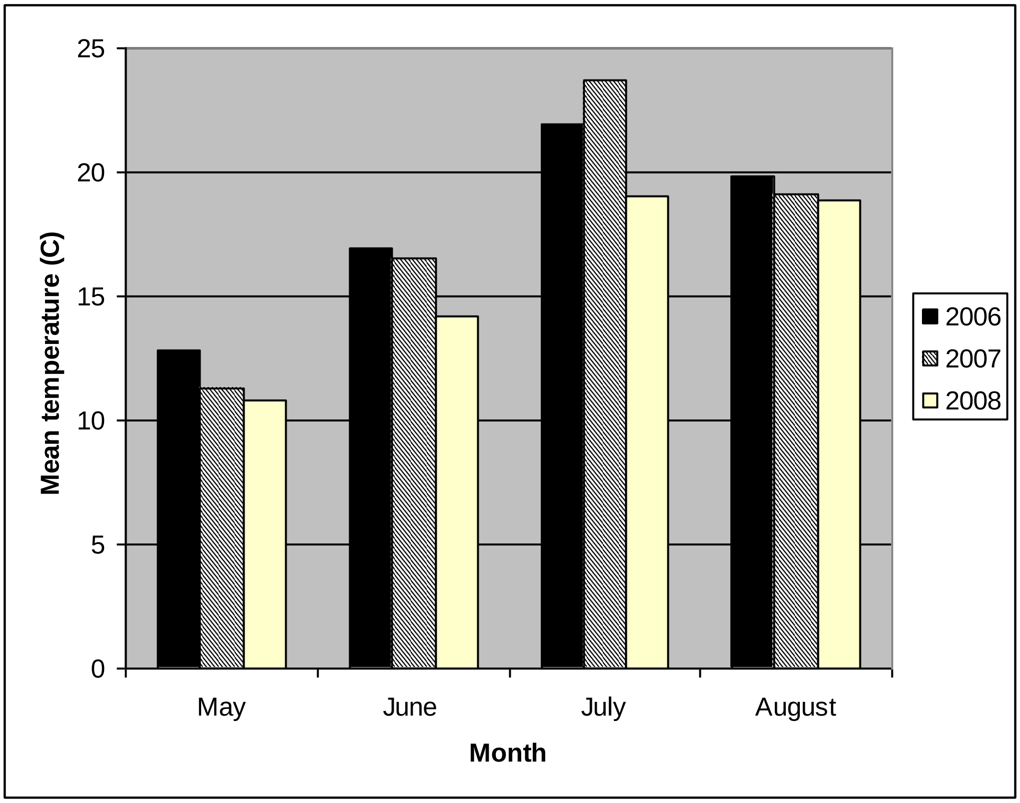

Table 12: Mean temperature (ºC) in May, June, July, and August in 2006, 2007, and 2008 in Grasslands National Park.

Figure 12 shows the mean temperature in May, June, July and August of 2006, 2007, and 2008. The mean monthly temperature were all very close, overall 2008 was slightly cooler than 2006 and 2007.

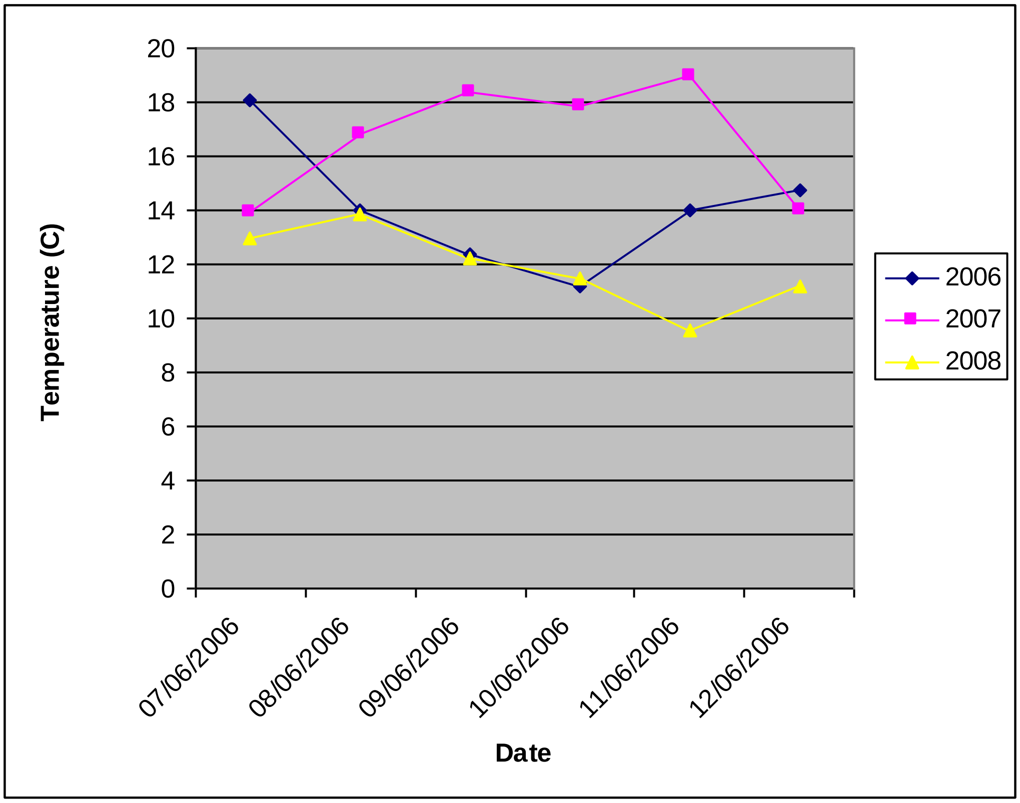

Table 13: Daily mean temperature (ºC) during round 1 of carabid trapping: June 7-11, 2006, June 1-5, 2007, and June 4-8, 2008 in Grasslands National Park.

Figure 13 shows the mean daily temperature over the five days of carabid trapping in round 1 in 2006, 2007 and 2008. The average temperature over the five days of carabid trapping was the highest in 2007 (16.7 ºC), followed by 2006 (14.1 ºC) and 2008 (11.9 ºC).

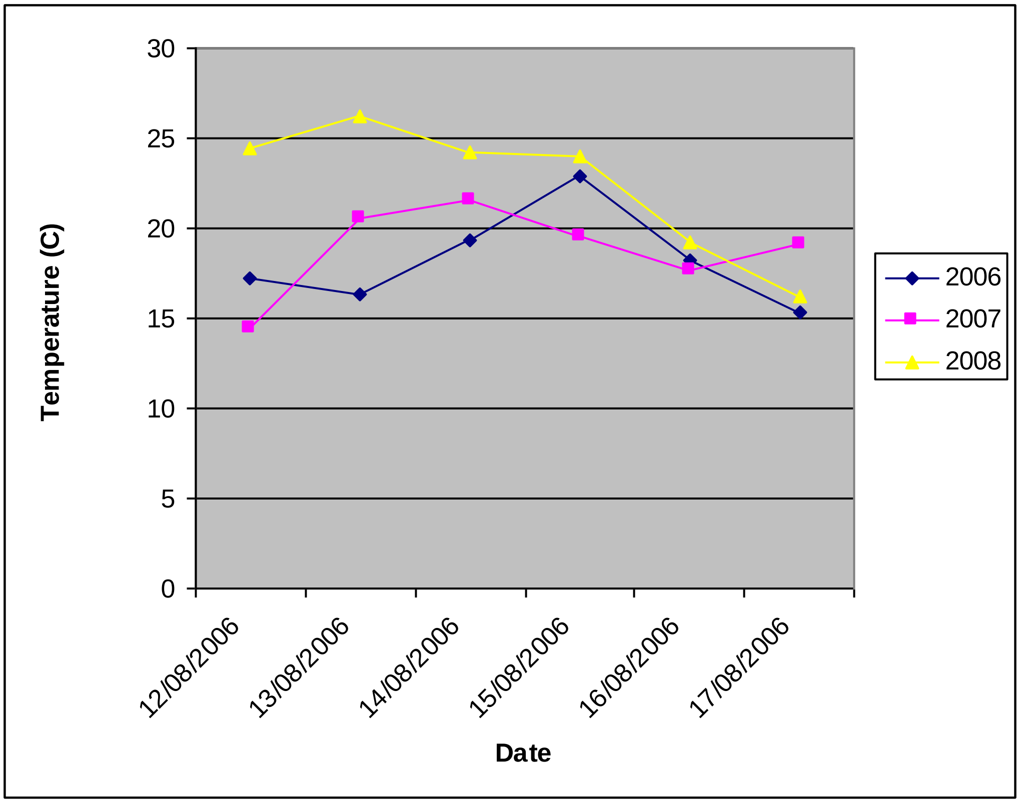

Table 14: Daily mean temperature (ºC) during round 2 of carabid trapping: August 12-16, 2006, August 11-15, 2007, and August 7-11, 2008 in Grasslands National Park.

Figure 14 shows the mean daily temperature over the five days of carabid trapping in round 2 in 2006, 2007 and 2008The average temperature over the five days of carabid trapping was the highest in 2008 (22.4 ºC), followed by 2007 (18.8 ºC) and followed closely by 2006 (18.2 ºC).

4.5 Results Summary

Tables 12 through 15 are summaries of results. Table 12 is a summary of the results from the t-tests showing the effect of grazing treatments on carabid and grasshopper abundance, richness and diversity. Table 13 is a summary of the linear regression results showing the relationship between bird abundance, richness and diversity and invertebrate abundance, richness and diversity. Table 14 is a summary of the relationships between bird species and invertebrate abundance, richness and diversity.

Table 15 is a summary of the relationship between vegetation structure and composition and invertebrate abundance, richness and diversity.

Table 12: Summary of *t*-test results in Grassland National Park in 2006, 2007, and 2008. (+) denotes a positive relationship between carabid or grasshopper abundance, richness or diversity and grazing regime and (-) denotes a negative relationship. Shaded cells denote no significant relationships.

	Variable	**2006**	**2007**	**2008 (before cows)**	**2008 (after cows)**
t-test	Grazed	Carabid abundance (+) Carabid richness (+) Carabid diversity (+)	Carabid diversity (+)	Grasshopper abundance (+) Grasshopper richness (+) Grasshopper diversity (+)	▨
	Ungrazed		Carabid abundance (-)	Carabid diversity (-)	▨

Table 13: Summary of linear regression results between carabid abundance, richness, and diversity and bird abundance, richness and diversity in Grassland National Park in round 1 and round 2. 2006, 2007, and 2008 are combined for analysis purposes. (+) denotes a positive relationship and (-) denotes a negative relationship.

	Round 1	**Round 2**
Linear Regressions	Carabid abundance & Bird abundance (+)	Carabid abundance & Bird abundance (+)

Table 14: Summary of linear regression results between carabid abundance, richness, and diversity and individual bird species abundance in Grassland National Park in 2008. (+) denotes a positive relationship and (-) denotes a negative relationship. The following codes are used for avian species: BHCO – brown-headed cowbird, CCLO – Chestnut-collared longspur, CCSP – clay-colored sparrow, MCLO – McCown's longspur, SAVS – Savannah sparrow. Shaded cells denote no significant relationships.

Linear Regressions	Carabid abundance	BHCO (-) CCLO (+) CCSP (-) MCLO (+) SAVS (-)
	Carabid richness	CCSP (-) SAVS (-)
	Carabid diversity	▨

Table 15: Summary of linear regression results between grasshopper and carabid abundance, richness, and diversity and vegetation density, bare cover, litter depth, vegetation richness, vegetation height, and northing in Grassland National Park in 2008. (+) denotes a positive relationship and (-) denotes a negative relationship. A grey square indicates the variable was not measured in that year.

		2006	2007	2008
Linear Regressions	Vegetation density		Carabid diversity (-)	
	Bare cover			Grasshopper diversity (+)
	Litter depth	Grasshopper abundance (-)		
	Vegetation richness	Carabid abundance (+) Carabid diversity (+)		Grasshopper abundance (+)
	Vegetation height	▨		
	Northing	▨	▨	Carabid abundance (-)

5.0 Discussion

My research suggested the following: (1) carabid abundance, richness and diversity did not differ consistently between grazed and ungrazed pastures, (2) grasshopper abundance, richness, and diversity were higher in grazed pastures, (3) there were few consistent relationships throughout the years between vegetation structure and composition, and invertebrate abundance, richness, and diversity; however, increased vegetation richness did lead to increased abundance and diversity of invertebrates (4) in some cases there was a correlation between bird abundance and carabid abundance, providing some evidence in support of the MIH (5) the strength of the correlation between carabid abundance and bird abundance seems to be independent of the species reliance on invertebrates as a food source and finally (6) evenness of carabid populations may have an effect on bird populations.

5.1 The effect of grazing on invertebrates

Overall, the effects of grazing on carabids were variable and the results were unpredictable. In contrast, the grasshopper data support my prediction that grazing increases invertebrate abundance. This result is consistent with other studies (e.g., Wettstein & Schmid 1999, Cagnolo et al. 2002). However, this prediction was not consistent with my carabid results. Studies by Fahrig and Jonsen (1998) and Dawes-Gromadzki (2005) also showed that grazing decreases insect diversity and abundance.

These conflicting results appear to relate to the different life-history strategies of these two different families of invertebrates, each of which has different resource needs (Cagnolo et al. 2002). Some invertebrate species are more sensitive to the impacts of grazing than others (Debano 2006). For example, some invertebrates respond to changes in vegetation structure, some respond to changes in vegetation composition, and some respond to the combination of the two. Ground carabids will respond to changes in vegetation composition, whereas other invertebrate groups such as spiders (Arachnida:

Araneae), leafhoppers (Homoptera), Hemiptera and grasshoppers (Orthoptera: Acrididae) will respond to changes in vegetation structure (Cagnolo et al. 2002).

Grasshopper populations may respond quickly to grazing because they respond to both vegetation structure and composition; changes in vegetation structure are more immediate than changes in vegetation composition (Persons et al. 2003). A study by Person et al. (2003) found that there is a time lag between the onset of grazing and changes to vegetation composition, and therefore a lag in responses of invertebrates to those composition changes. There is some evidence of this in my data. In 2006, carabid abundance and diversity were all higher in grazed pastures. This finding is in contrast to my findings in 2007, 2008(before cows) and 2008 (after cows); which are inconsistent. It is possible that grazing has caused changes in vegetation composition that are just beginning to effect carabid populations leading to more consistent results for 2006 than in 2007 and 2008.

In addition to vegetation changes, there are also direct impacts of grazing on invertebrates such as mortality of larvae by trampling and burial under dung (Ehrlich & Murphy 1987 in Henderson 2006), and soil compaction (Dennis 2003). Again the severity of the impact of these effects on invertebrates will depend on their life-history strategies (Cagnolo et al. 2002). A study by Dennis (2003) found that carabids were found at higher population densities in sheep grazed plots than in sheep and cattle grazed plots. *Carabus* spp. use cracks in the soil to escape from the heat and predators. Soil compaction caused by cattle can reduce these cracks and leave carabids vulnerable to predation and desiccation (Dennis 2003). There is evidence to support this in my data; 2007 was the warmest year of the study and I found that carabid richness and carabid abundance decreased with grazing in this year. This could be the result of increased soil compaction due to cattle, causing increased carabid mortality due to desiccation.

Data from 2008 differ from previous years because sampling was done before and after cows were put into the previously ungrazed pastures 2, 3, 4, 6, 7, and 8. In addition, 2008 was unique because pastures were not grazed at constant intensities. In 2008, before the cows went in abundance was higher in grazed pastures and richness and diversity were higher in ungrazed pastures. These results contrast with results after cows were introduced, at which point abundance was higher in ungrazed pastures and richness and diversity were higher in grazed pastures. This may suggest that the increased grazing intensity in some pastures had an effect on carabid populations. A study by Morris (1967) and a review by Buchanan et al. (2006) also found that more intensive grazing causes decreases in invertebrate abundance and biodiversity. Abundance was higher in ungrazed pastures after the cows went in but richness and diversity were lower in ungrazed areas. This means that there are fewer individuals in grazed areas but more species and greater evenness amongst those species (Hurlbert 1971). It is possible that an abundant species was very sensitive to grazing, and removal of this species from the community through grazing reduced competition and allowed other species to move in (Berryman & Pienaar 1973).

Despite the debate over the direction of change, the literature does agree that invertebrate populations can be affected by grazing, generally through the effect of grazing on vegetation composition and structure (Fahrig & Jonsen 1998; Dawes-Gromadzki 2005; Wettstein & Schmid 1999; Cagnolo et al. 2002; Debano 2006). To better answer the question, we need more information on how the vegetation is influenced by grazing.

5.2 The effect of grazing on vegetation

I found vegetation structure and composition had few consistent effects on invertebrate diversity or abundance among years. My results were not consistent with my prediction that grasshoppers would respond to vegetation structure and carabids would respond to vegetation composition. In 2006, carabid abundance and diversity did show a significant positive relationship with vegetation richness but showed no significant relationship in 2007 or 2008. Grasshoppers only showed one significant relationship with any of the vegetation structure variables; that relationship was a positive one between grasshopper diversity and bare cover in 2008. Therefore, in southern Saskatchewan, grasshoppers did not consistently respond to vegetation structure, and carabids did not consistently respond to vegetation composition. This result is surprising because most of the studies found some consistent effect, whether positive (Wettstein & Schmid 1999; Cagnolo et al. 2002) or negative (Fahrig & Jonsen 1998; Dawes-Gromadzki 2005), of grazing on invertebrate populations. It could be possible that it is too soon to see a measurable affect of vegetation changes on invertebrates. In, addition some of the studies were also collecting data other families of invertebrates, such as butterflies (Wettstein & Schmid 1999). Nonetheless, my study showed that invertebrate populations can be affected by grazing, generally through the effect of grazing on vegetation composition and structure (Debano 2006), but in Saskatchewan grazing did not seem to have a strong effect on the carabid and grasshopper communities.

5.3 The effect of prey availability on bird abundance

I also hypothesized that there will be a greater abundance of prairie birds in areas with higher invertebrate abundance and diversity. I based this assumption on the More Individuals Hypothesis (Wright 1983). My correlation analyses did not support the More Individuals Hypothesis; I found no significant relationship between carabid or grasshopper abundance, richness, and diversity and bird abundance, richness and diversity.

However, the linear regressions I performed did suggest a positive relationship between carabid abundance and bird abundance, which supports one of the assumptions of the More Individuals Hypothesis (Wright 1983). In the combined-years analysis I found a positive relationship between carabid abundance and bird abundance in both rounds 1 and 2. The relationship between carabid abundance and bird abundance was also positive in 2007 but not in any of the other years when the years were analyzed separately. In the combined-years analysis the R^2 were actually quite high at 20 and 25% for rounds 1 and 2 respectively. These results provided support for the More Individuals

Hypothesis. Studies by Hurlbert (2004); Nocera et al. (2007); Buckingham et al. (2004) and Whittingham et al. (2006) also found and increases in abundance with an increase in resource availability. Conversely, studies by Bonn et al. (2004), Miller et al. (1994), Martin et al. (2000), Martin et al. (1998), and Hoi et al. (2004) found that increased food availability does not lead to increased bird abundance.

The second assumption of the hypothesis, that communities with a greater number of individuals are able to support a greater number of species above a minimum viable size, was not satisfied (Hurlbert 2004; Evans et al. 2006). I found no increase in bird richness and diversity despite an increase in bird abundance. A study by Nocera et al. (2007) also found an increase in the abundance of birds with increased food availability, but that increase did not lead to an increase in richness or diversity. This result means that there are more birds but fewer species and less evenness amongst those species (Hurlbert 1971, Belovsky & Slade 1993). This may be a result of increased competition in areas of high invertebrate abundance. A study by Belovsky and Slade (1993) also found that competition lead to increased abundance of grasshoppers but a decrease in richness and diversity. The birds could be experiencing increased competition in areas of high invertebrate abundance.

The study by Belovsky and Slade (1993) is also interesting because it provides an example of birds suppressing or controlling invertebrate populations. The study found an increase in the abundance of grasshoppers in an area with birds as compared to an area where birds were excluded. They found a decrease in the amount of large-bodied grasshoppers due to the birds’ dietary preference and an increase in the abundance of medium-bodied grasshoppers, most likely due to the decrease in competition (Belovsky & Slade 1993). I also found some evidence in my data that the avian community was suppressing the diversity of carabids. I found that increased bird abundance lead to a decrease in carabid diversity. This result is interesting because it is contrary to our other results and the More Individuals Hypothesis (MIH). The MIH suggests that increased energy availability will lead to an increase in the abundance of individuals or a bottom up regulation of populations. Our result and the study by Belovsky and Slade (1993) suggest a top down regulation of populations. However, while this result is interesting, it is impossible for me to make any conclusions about the direction of regulation with the data I have because my study was correlative and not experimental.

Another interesting result that arose from this analysis was that the relationship between bird abundance and carabid richness was positive, but the relationship between bird abundance and carabid diversity was negative. This suggests that the evenness of invertebrate populations is having an effect on the relationship between birds and carabids. This suggests that birds may be preferentially selecting a certain species of carabid.

5.4 Other factors that may affect bird populations

Habitat, avian species present, and time of year can also have an effect on the relationship between invertebrate abundance, richness, and diversity and bird abundance, richness and diversity. Species habitat preferences have an effect on bird populations in some habitats. Some species may be specialists, and thus only use a specific type of habitat. These species may be restricted by habitat availability and may not be able to move into areas of higher energy (Evans et al. 2005). This hypothesis led me to explore the relationship between invertebrates and birds in lowland and upland habitat separately. I found no significant relationship between birds and invertebrates in lowland habitats, although there were some significant correlations in upland habitats. This suggests that lowland species are specialists and are bound by habitat and not by energy availability (Evans et al. 2005).

5.4.1 Habitat

In upland communities I found a negative relationship between bird diversity and carabid abundance. This suggests that birds could be regulating invertebrate populations. A study by Belovsky and Slade (1993) found that birds did have an effect on grasshopper populations, decreasing the amount of large bodied individuals through selective consumption; however, in their study this lead to an increase in overall grasshopper populations. Another study by Sipura (1999) showed that the inclusion of birds in a system decreased insect-caused damage to trees by decreasing invertebrate populations. However, many studies (Hurlbert 2004; Nocera et al. 2007; Buckingham et al. 2004 and Whittingham et al. 2006) have found that increases in invertebrate populations are causing increased bird populations, leading us to believe that in other ecosystems, invertebrate populations are in fact regulating bird populations.

Although I did find a significant negative correlation between bird diversity and carabid abundance this does not necessarily mean that birds are regulating invertebrate populations. It is possible that this result occurred due to chance rather than due to a causal relationship between the two. The rest of my data and many literature sources suggest that invertebrate populations are determining bird populations, not the other way around. To conclude that bird populations are regulating invertebrate populations we would need more evidence.

5.4.2 Seasonal dependence on invertebrates

Timing is another factor that may affect the relationship between birds and invertebrates. The amount of invertebrates in a birds’ diet varies throughout the year. Invertebrates seem to be most vital to birds during the breeding season. To test this I looked at the relationship between birds and invertebrates early in the breeding season (May) and later in the breeding season (June). There was an interesting difference between the results in round 1 and the results in round 2. In round 1 there were two significant relationships; the relationship between bird abundance and carabid richness and the relationship between bird abundance and carabid diversity. In round 2, there was just one significant relationship, the one between carabid abundance and bird abundance. This result suggests that invertebrate abundance, richness and diversity are important factors in habitat selection by some bird species during the breeding season, depending whether it is early or late in the breeding season. However, it also suggests that invertebrate richness and diversity are more important early in the breeding season when parents are establishing territories, and that invertebrate abundance may be more important late in the breeding season when adults are feeding larger young. Parents may be more selective in their choice of food early in the breeding season when feeding young then therefore richness and diversity of invertebrates becomes the most important factor in habitat selection.

5.4.3 Species composition

Another way that species composition can affect the relationship between bird abundance and invertebrate abundance is through birds' dietary preferences. Some species, such as the Sprague's pipit (Robbins & Dale 1999) are much more reliant on invertebrates as a food source compared with other species, such as Baird's Sparrows (Green et al. 2002). Therefore, I predicted that pipits would be more likely to choose habitats with increased invertebrate abundance compared with less insectivorous species such as Baird's sparrows, and would therefore observe a stronger relationship between Sprague's pipit abundance and invertebrate abundance than between Baird's sparrow abundance and invertebrate abundance. This prediction was not supported, as I did not find a consistent relationship between more insectivorous birds and invertebrate populations. However, we must consider that I have not included grasshopper abundance in the model, due to a lack of data. This is important to remember especially in the case of Sprague's pipits. Studies (Robbins & Dale 1999) have shown that grasshoppers may account for as much as 84% the pipits' diet. It is possible the birds that we might expect to have higher abundances in areas with greater invertebrate abundance are more reliant on grasshopper populations than carabids and that is why I am not seeing the correlation that I expected.

However, if birds were truly influenced by invertebrate abundance as I and the More Individuals Hypothesis predict then I would have expected to find a stronger relationship between the birds' diets and invertebrate abundance. These data demonstrate that there are factors other than food abundance affecting birds' selection of habitat. Whereas my data suggest that food abundance may be a factor that influences avian habitat selection, there are other processes that have a cumulatively large effect on songbird populations.

5.4.4 Weather conditions

Weather conditions can have an effect on invertebrate populations. A study by White (1984) found that certain changes in weather patterns can cause outbreaks of invertebrates as plants under stress increase the amount of nitrogen available in their tissues. Weather can also have an effect on the mobility of invertebrates; if the weather is too cold or too hot invertebrates are less mobile (Dennis 2003). I found this to be true in this study. All of the round 1 trapping numbers were higher than all of the round 2 trapping numbers despite the fact that the temperature was always higher in round 2. This suggests that there is an optimal temperature for invertebrate mobility.

6.0 Conclusions

Although I found some evidence both that some grassland birds might benefit from higher invertebrate abundance, and that birds might suppress some invertebrate communities, it is important to remember that this study was only based on three years of data. In addition, most of the trends in my data were not strong. In addition, round 2 invertebrate data was collected after bird data collection was already complete. Furthermore, this study was based on moderate grazing regimes; higher intensity grazing would definitely have a different impact on birds and invertebrates. My study does suggest that grazing could be beneficial to several groups of species, especially grasshoppers and birds, but further investigation would be beneficial to find out the longer term impacts of grazing, as well as optimal grazing intensities.

Did this study validate the More Individuals Hypothesis? Yes and No. I did find a relationship between invertebrate abundance and bird abundance but there was no relationship between invertebrate abundance and bird richness and diversity as was predicted in the hypothesis. In addition, I did not find a strong relationship between invertebrate abundance and bird species that are more reliant on invertebrates as a food source. I therefore conclude that food abundance may have an effect on bird abundance but there are other population regulators that are also important factors.

7.0 Management implications

My results indicate that grazing can be beneficial for both birds and their invertebrate prey in southern Saskatchewan mixed-grass prairies. However, I would caution managers as effects of grazing vary greatly depending on a number of factors such as the species of invertebrates present, the species of birds present, and the habitat. Therefore no one solution will work in every situation. In addition, a longer term study on the impacts of grazing on invertebrate food sources for birds would be useful, so we can evaluate the longer-term impacts of grazing on both invertebrates and birds.

8.0 Literature Cited

Algar, A.C., Kerr, J.T. and Currie, D.J. 2007. A test of Metabolic Theory as a mechanism underlying broad-scale species-richness gradients. Global Ecology an Biogeography. 16: 170-178.

Allen, A.P., Gillooly, J.F., and Brown, J.H. 2006. Recasting the species-energy hypothesis: the different roles of kinetic and potential energy in regulating biodiversity.

Atkinson, P.W., Buckingham, D., and Morris, A.J. 2004. What factors determine where invertebrate-feeding birds forage in dry agricultural grasslands? Ibis. 146(Suppl. 2): 99-107.

Atkinson, P.W., Fuller, R.J., Vickery, J.A., Conway, G.J., Tallowin, J.R.B., Smith, R.E.N., Haysom, K.A., Ings, T.C., Asteraki, E.J., and Brown, V.K. 2005. Influence of agricultureal management, sward structure and food resources on grassland field use by birds in lowland England. Journal of Applied Ecology. 42: 932-942.

Belovksy, G.E. & Slade, J.B. 1993. The role of vertebrate and invertebrate predators in a grasshopper community. Oikos. 68: 193-201.

Berry, J.S., Onsanger, J.A., Kemp, W.P., McNary, T., Larsen, J., Legg, D., Lockwood, J.A., and Foster, R.N. 2000. Assessing rangeland grasshopper populations. Section VI.10 is Cunningham, G.L., Sampson, M.W. (eds). 2000. Grasshopper integrated pest management user handbook. USDA, Animal and Plant Health Inspection Service. Technical Bulletin No. 1809. Washington D.C.

Berryman, A.A., and Pienaar, L.V. 1973. Simulation of intraspecific competition and survival of *Scolytus ventralis* broods (Coleoptera; Scolytidae)

Brickle, N.W., Harper, D.G.C., Aebischer, N.J., Cockayne, S.H. 2000. Effects of agricultural intensification on the breeding success of Corn Buntings (Miliaria calandra). The Journal of Applied Ecology. 37 (5): 742-755.

Brotons, L., Wolfe, A., Paulus, G. and Martin, J. 2005. Effect of adjacent agriculture habitat on the distribution of passerines in natural grasslands. Biological Conservation. 124: 407-414.

Bonn, A., Storch, D. and Gaston, K.J. 2004. Structure of the species-energy relationship. The Royal Society. 271: 1685-1691.

Buchanan, G.M., Grant, M.C., Sanderson, R.A., and Pearce-Higgins, J.W. 2006. The contribution of invertebrate taxa to moorland birds diets and the potential implications of land-use management. Ibis. 148: 615-628.

Buckingham, D.L., Peach, W.J., and Fox, D.S. 2006. Effects of agriculture management on the use of lowland grasslands by foraging birds. Agriculture, Ecosystems and Environment. 112: 21-40.

Buckingham, D.L., Atkinson, P.W., and Rock, A.J. 2004. Testing solutions in grass-dominated landscapes: a review of current research. Ibis. 146: 163-170.

Buckland, S.T. 2006. Point-transect surveys for songbirds: Robust methodologies. The Auk. 123(2): 345-357.

Cagnolo, L., Molina, S.I., and Valladares, G.R. 2002. Diversity and guild structure of insect assemblages under grazing and exclusion regimes in a montane grassland from Central Argentina. Biodiversity and Conservation. 11: 407-420.

Capinera, J.L. & Sechrist T.S. 1982. Grasshopper (Acrididae) - host plant associations: Response of grasshopper populations to cattle grazing intensity. Canadian Entomologist. 114: 1055-1062.

Chapman, R.N., Engle, D.M., Masters, R.E., and Leslie, D.M. 2004. Grassland vegetation and bird communities in the southern Great Plains of North America. Agriculture, Ecosystems and Environment. 104: 577-585.

Collins, S.L. 2000. Disturbance frequency and community stability in native tallgrass prairie. The American Naturalist. 155(3): 311-325.

Coupland R.T. 1950 Ecology of mixed prairie in Canada. Ecological Monographs 20:271-315.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guegan, J., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E., and Turner, J.R.G. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness.

Cushing, W.J., Foster, R.N., Reuter, K.C., and Hirsch, D. 2000. Seasonal occurrence of common western North Dakota Grasshoppers. Section VI.8 in Cunningham, G.L., Sampson, M.W. (eds). 2000. Grasshopper integrated pest management user handbook. USDA, Animal and Plant Health Inspection Service. Technical Bulletin No. 1809. Washington D.C.

Davis, S.K. 2004. Area sensitivity in grassland passerines: effects of patch size, patch shape and vegetation structure on bird abundance and occurrence in southern Saskatchewan. The Auk. 121(4):1130–1145.

Davis, S.K. 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. The Condor. 107: 605-616.

Dawes-Gromadzki, T.Z. 2005. Bugs beneath the surface: the functional significance of soil macroinvertebrates to landscape health in Australia's tropical savannas. Insect Science. 12: 307-312.

Debano, S.J. 2006. Effects of livestock grazing on aboveground insect communities in semi-arid grasslands of south eastern Arizona. Biodiversity and Conservation. 15: 2547-2564.

Dennis, P. 2003. Sensitivity of upland arthropod diversity to livestock grazing, vegetation structure and landform. Food, Agriculture & Environment. 1(2): 301-307.

Dennis, P., Young; M. R., Howard, C. L., and Gordon, I. J. 1997. The response of epigeal beetles (Col.: Carabidae, Staphylinidae) to varied grazing regimes on upland *Nardus stricta* Grasslands. The Journal of Applied Ecology. 34(2): 433-443.

Ehrlich, P.R. & Murphy, D.D. 1987. Conservation lessons from long-term studies of checkerspot butterflies. Conservation Biology 1:122-131

Evans, K.L., Greenwwod, J.J.D., and Gaston, K.J. 2005. Dissecting the species-energy relationship. Proceedings of the Royal Society. 272: 2155-2163.

Evans, K.L., James, N.A., and Gaston, K.J. 2006. Abundance, species richness and energy availability in the North American avifauna. Global Ecology and Biogeography. 15: 372-385.

Fahrig, L., and Jonsen, I. 1998. Effects of habitat patch characteristics on abundance and diversity of insects in an agricultural landscape. Ecosystems. 1: 197-205.

Fleischner, T.L. 1994. Ecological costs of livestock grazing in western North America. Conservation Biology. 8(3): 629-644.

Fondell, T.F., and Ball, I.J. 2004. Density and success of bird nests relative to grazing on western Montana grasslands. Biological Conservation. 117: 203-213.

Fuhlendorf, S.D., and Engle, D.M. 2001. Restoring heterogeneity on rangelands: Ecosystem management based on evolutionary grazing patterns. BioScience. 51(8): 625-632.

Gaston, K.J. 2000. Global patterns in biodiversity. Nature. 405(11): 220-227.

Green, M.T., Lowthers, P.E., Jones, S.L., Davis, S.K., and Dale, B.C. 2002. Baird’s Sparrow. The Birds of North America. 638.

Henderson, D. C. 2006. Restoring grazing-induced heterogeneity in Grasslands National Park of Canada: Landscape-scale experiment and long-term monitoring plan, March 9, 2006. Parks Canada Agency, Western and Northern Service Center, Winnipeg, Manitoba, Canada.

Herkert, J. R. 1995. An analysis of Midwestern breeding bird population trends: 1966-1993. American Midland Naturalist. 134:41-50.

Hill, P.H. & Gould, L.K. 1997. Chestnut-collared Longspur. The Birds of North America. 288

Hoi, H., Kristin, A, Valera, F., and Hoi, C. Clutch enlargement in lesser gray shrikes (*Lanius minor*) in Slovakia when food is superabundant: A maladaptive response? 2004. The Auk. 121(2): 557-564.

Hurlbert, A. 2004. Species-energy relationships and habitat complexity in bird communities. Ecology Letters. 7: 714-720.

Hurlbert, S. 1971. The nonconcept of species diversity; a critique and alternative parameters. Ecology. 52(4): 577-586.

Isacch, J.P., Maceira, N.O., Bo, M.S., Demaria, and M.R., Peluc, S. 2005. Bird-habitat relationship in semi-arid natural grasslands and exotic pastures in the west pampas of Argentina. Journal of Arid Environments. 62: 267-283.

Jepson-Innes, K.J., and Bock, C.E. 1989. Response of grasshoppers (Orthoptera: Acrididae) to livestock grazing in southeastern Arizona: differences between season and subfamiles. Oecologia 78: 430-431.

Jones, S.L. & Cornely, J.E. 2002. Vesper Sparrow. The Birds of North America. 624.

Knapp, A.K., Blair, J.M., Briggs, J.M., Collins, S.L., Hartnett, D.C., Johnson, L.C., Towne, E.G. 1999. The keystone role of Bison in North American tallgrass prairie. BioSceince. 49(1): 39-50.

Knopf, F.L. 1996. Prairie legacies-birds. Pp. 135-148 In: Samson, F.B. and Knopf, F.L. (eds). Prairie Conservation: Preserving North America’s most endangered ecosystem. Island Press. Covelo CA.

Koper, N., Ash, D., Lusk, J., and Teetaert, T. 2006. Preliminary report on east block grazing experiment field sampling, May – September 2006. 2006. Natural Resources Institute.

Kruess, A. & Tscharntke, T. 2002. Contrasting responses of plant and insect diversity to variation in grazing intensity. Biological Conservation. 106: 293-302

Lanyon, W.E. 1994. Western Meadowlark. The Birds of North America. 104:

Luoto, M., Pykala, J., and Kuussaari, M. 2003. Decline of landscape-scale habitat and species diversity after the end of cattle grazing. Journal of Nature Conseration. 11: 171-178.

MacArthur, R.H. & Wilson, E.O. 1963. An equilibrium theory of insular zoogeography. Evolution. 17: 373-387.

MacArthur, R.H. & Wilson, E.O. 1967. The theory of island biogeography. p. 203. Princeton University Press. Princeton, New Jersey.

Madden E.M., Hansen, A.J., and Murphy, R.K. 1999. Influence of prescribed fire history on habitat and abundance of passerine birds in northern mixed-grass prairie. Canadian Field Naturalist. 113 (4): 627-640.

Martin, P.A., Johnson, D.L., Forsyth, D.J., and Hill, B.D. 1998. Indirect effects of the pyrethroid insecticide deltamethrin on reproductive success of chestnut-collared longspurs. Ecotoxicology. 7: 89-97.

Martin, P.A., Johnson, D.L., Forsyth, D.J., and Hill, B.D. 2000. Effects of two grasshopper control insecticides on food resources and reproductive success of two species of grassland songbird. Environmental Toxicology and Chemistry. 19(12): 2987-2996.

McCracken, D.I. and Tallowin, J.R. 2004. Swards and structure: the interactions between farming practices and bird food resources in lowland grasslands. Ibis. 146(Suppl.2): 108-114.

Michalsky, S.J., and Ellis, R.A. 1994. Vegetation of Grasslands National Park. D.A. Westworth and Associates Ltd. Calgary AB.

Milchunas, D.G., Sala, O.E., and Lauenroth, W.K. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. The American Naturalist. 132(1): 87-106.

Miller, C.K., Knight, R.L., McEwen, L.C., and George, T.L. 1994. Responses of nesting savannah sparrows to fluctuations in grasshopper densities in interior Alaska. The Auk. 111(4): 962-969.

Moorcroft, D., Whittinham, M.J., Bradbury, R.B., and Wilson, J.D. 2002. The selection of stubble fields by wintering granivorous birds reflects vegetation cover and food abundance. The Journal of Applied Ecology. 39 (3): 535-547.

Morris, M.G. 1967. Differences between the invertebrate faunas of grazed and ungrazed chalk grassland. I. Responses of some phytophagous insects to cessation of grazing. The Journal of Applied Ecology. 4(2): 459-474.

Morris, M.G. 1968. Differences between the invertebrate faunas of grazed and ungrazed chalk grassland. II. The faunas of sample turves. The Journal of Applied Ecology. 5(3): 601-611.

Morris, M.G. 1969a. Differences between the invertebrate faunas of grazed and ungrazed chalk grassland III. The heteropterous fauna. The Journal of Applied Ecology. 6(3): 475-487.

Morris, M.G. 1969b. Populations of Invertebrate Animals and the Management of Chalk Grassland in Britain. Biological Conservation. 1: 225-231.

Murphy, M.T. 1996. Eastern Kingbird. The Birds of North America. 253.

Nocera, J.J., Forbes, G., and Milton, R. 2007. Habitat relationships of three grassland breeding bird species: broadscale comparisons and hayfield management implications. Avian Conservation and Ecology. 2(1): 7

Olff, H. & Ritchie, M.E. 1998. Effects of herbivores on grassland plant diversity. Tree. 13(7): 261-265.

Onsanger, J.A., and Henry, J.E. 1977. A method for estimating the density of rangeland grasshoppers (Orthoptera: Acrididae) in experimental plots. Acrida 6: 231-237.

Ottvall, R., and Smith, H.G. 2006. Effects of an agri-environment scheme on wader populations of coastal meadows of southern Sweden. Agriculture, Ecosystems and Environment. 113:264-271.

Parks Canada Website. 2002. http://www.pc.gc.ca/pn-np/sk/grasslands/visit/visit1_e.asp

Persons, B.T., Herzog, M.P., Ruess, R.W., Sedinger, J.S., Anthony, R.M., and Babcock, C.A. 2003. Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. Oecologia. 135: 583:592.

Powell, A.F.L.A. 2006. Effects of prescribed burns and Bison (*Bos bison*) grazing on breeding bird abundances in tallgrass prairie. The Auk. 123(1): 183-197.

Quinn, G.P. and Keough, M.J. 2002. Experimental design and data analysis for biologists. University Press. Cambridge, United Kingdom.

Robbins, M.R. & Dale, B.C. 1999. Sprague's Pipit. The Birds of North America. 439: 1-13.

Schlicht, D.W. & Orwig, T. T. 1992. Sequential use of niche by prairie obligate skipper butterflies (Lepidoptera: Hesperiidae) with implications for management. pp137-139 in Smith, D. D. and C. A. Jacobs, eds. Proceedings of the Twelfth North American Prairie Conference. University of Northern Iowa, Cedar Falls, IA

Sipura, M. 1999. Trophic interactions: willows, herbivorous insects and insectivorous birds. Oecologia. 121(4): 537-545.

Soderstrom, B., Part, T., and Linnarsson, E. 2001. Grazing effects on between-year variation of farmland bird communities. Ecological Applications. 11(4): 1141-1150.

Spence, J.R., and Niemela, J.K. 1994. Sampling carabid assemblages with pitfall traps- the madness and the method. Canadian Entomologist. 126: 881-894.

Stephens, P.A., Freckleton, R.P., Watkinson, A.R. and Sutherland, W.J. 2003. Predicting the response of farmland bird populations to changing food supplies. Journal of Applied Ecology. 40: 970-983.

Stohlgren, T.J., Bull, K.A., and Otuski, Y. 1998. Comparison of rangeland vegetation sampling techniques in the central grasslands. Journal of Range Management. 51: 164-172.

Sugden, E A. 1985. Pollinators of *Astragalus monoensis* Barneby (Fabaceae): new host records; potential impact of sheep grazing. Great Basin Naturalist 45 (2):299-312

Sutter, G.C., and Bringham, R.M. 1998. Avifaunal and habitat changes resulting from conversion of native prairie to crested wheat grass: patterns at songbird community and species levels. Canadian Journal of Zoology. 76: 869-875.

Tichit, M., Renault, D., and Potter, T. 2005. Grazing regime as a tool to assess positive side effects of livestock farming systems on wading birds. Livestock Production Science. 96: 109-117.

Tucker, G.M. 1992. Effects of agricultural practices on field use by invertebrate-feeding birds in winter. The Journal of Applied Ecology. 29(3): 779-790.

Vickery, J.A., Tallowin, J.R., Ferber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J., and Brown, V.K. 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. Journal of Applied Ecology. 38: 647-664.

Vickery, P.D. 1996. Grasshopper Sparrow. The Birds of North America. 239.

Vickery, P. D., J. R. Herkert, F. L. Knopf, J. Ruth, and C. E. Keller. 2000. Grassland birds: An overview of threats and recommended management strategies. *In* Strategies for bird conservation: The Partners in Flight planning process; Proceedings of the 3rd Partners in Flight Workshop; 1995 October 1-5; Cape May, NJ. R. Bonney, D. N. Pashley, R. J. Cooper, and L. Niles, eds. Proceedings

RMRS-P-16. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 281 p.

Weins, J.A., and Rotenberry, J.T. 1979. Diet niche relationships among North American grassland and shrubsteppe birds. Oecologia. 42: 253-292.

Wettstein, W., and Schmid, B. 1999. Conservation of arthropod diversity in montane wetlands: effects of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. Journal of Applied Ecology. 36: 363-373.

White, T.C.R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen stressed food plants. Oecologia. 63(1): 90-105.

Whittingham, M.J., Devereux, C.L., Evans, A.D. and Bradbury, R.B. 2006. Altering perceived predation risks and food availability: management prescriptions to benefit farmland birds on stubble fields. Journal of Applied Ecology. 43: 640-650.

Wootton, J.T. 1998. Effects of disturbance on species diversity: A multiple perspective on species diversity. The American Naturalist. 152(6): 803-825.

Wright, D.H. 1983. Species-energy theory: an extension of species-area theory. Oikos. 41: 496-506.

Yasukawa, K. & Searcy, W.A. 1995. Red-winged Blackbird. The Birds of North America. 184.

9.0 Appendices

9.1: Linear regression results for invertebrates and birds in 2006, 2007, and 2008 separately

	Parameter	*Carabid abundance*	*Carabid diversity*	*Grasshopper abundance*
Bird abundance	β	0.0931	0.0497	-0.0069
	SE	0.0961	0.1255	0.0172
	p	0.3345	0.6927	0.6875
Bird richness	β	0.0909	-0.1430	0.0252
	SE	0.1237	0.1616	0.0221
	p	0.4641	0.3778	0.2564
Bird diversity	β	0.0591	-0.0666	0.0255
	SE	0.0912	0.1191	0.0163
	p	0.5181	0.5770	0.1697

Table 16: Multiple linear regression between bird abundance, richness and diversity and carabid abundance, and carabid diversity and grasshopper abundance in 2006 at Grasslands National Park. Species diversity values were calculated using the Simpson's Diversity Index (*1/D*). β = intercept, SE = standard error, *p* = p-value and α = 0.05

	Parameter	*Carabid abundance*	*Carabid diversity*
Bird abundance	β	0.0937	0.0165
	SE	0.0225	0.0670
	p	**0.0001**	0.8058
Bird richness	β	0.0895	-0.1538
	SE	0.0351	0.1043
	p	**0.0120**	0.1438
Bird diversity	β	0.0864	-0.1428
	SE	0.0263	0.0783
	p	**0.0013**	0.0704

Table 17: Multiple linear regression between bird abundance, richness and diversity and carabid abundance and diversity in 2007 at Grasslands National Park. Species diversity values were calculated using the Simpson's Diversity Index (*1/D*). β = intercept, SE = standard error, *p* = p-value and α = 0.05

	Parameter	*Carabid abundance*	*Carabid diversity*	*Grasshopper abundance*	*Grasshopper diversity*
Bird abundance	β	0.0440	0.1249	-0.0085	-0.0081
	SE	0.1560	0.0832	0.0195	0.0855
	p	0.1473	0.1360	0.6621	0.9250
Bird richness	β	-0.0451	0.0259	-0.006	0.0855
	SE	0.1573	0.0539	0.0197	0.0863
	p	0.7749	0.7582	0.7369	0.3220
Bird diversity	β	-0.0885	0.0040	0.0093	0.0480
	SE	0.1126	0.0601	0.0141	0.0618
	p	0.4339	0.9476	0.5123	0.4387

Table 18: Multiple linear regression between bird abundance, richness and diversity and carabid and grasshopper abundance and diversity in 2008 before the cows were put into the pastures at Grasslands National Park. Species diversity values were calculated using the Simpson's Diversity Index (*1/D*). β = intercept, SE = standard error, *p* = p-value and α = 0.05

	Parameter	*Carabid abundance*	*Carabid diversity*	*Grasshopper abundance*	*Grasshopper diversity*
Bird abundance	β	-0.0216	0.0633	0.0040	0.0495
	SE	0.1301	0.0694	0.0163	0.0714
	p	0.2418	0.3636	0.8055	0.4895
Bird richness	β	-0.0623	-0.0191	0.0069	0.1254
	SE	0.1251	0.0667	0.0156	0.0686
	p	0.6194	0.7751	0.6588	0.0703
Bird diversity	β	-0.1292	0.0257	0.0023	0.1012
	SE	0.1113	0.0593	0.0139	0.0610
	p	0.2480	0.6660	0.8698	0.1000

Table 19: Multiple linear regression between bird abundance, richness and diversity and carabid and grasshopper abundance and diversity in 2008 after the cows were put into the pastures at Grasslands National Park. Species diversity values were calculated using the Simpson's Diversity Index (*1/D*). β = intercept, SE = standard error, *p* = p-value and α = 0.05