THE EFFECTS OF SUCCESSION AND DISTURBANCE ON COLEOPTERAN ABUNDANCE AND DIVERSITY IN THE CENTENNIAL SANDHILLS

by

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APPROVAL

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citation, bibliographic style, and consistency, and is ready for submission to the Division of Graduate Education.

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May 2010

DEDICATION

This thesis is dedicated to the memory of my grandmother, Joanne Hall Winton, who first showed me the beauty of the natural world and all of its “far out” creatures. Deus est regit qui omnia.

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ABSTRACT

Sandhill habitats, and management strategies aimed at maintaining these habitats, were studied for beetles inhabiting the different successional stages in the Centennial Sandhills of southwestern Montana. The effects of the fire treatment on the distribution, abundance, and diversity were studied using pitfall trapping over the course of two field seasons: one before the fire, and one after. Sampling occurred in plots representing three successional stages found in the sandhills, as well as in the unique microhabitat features commonly associated with sandhills and dunes. Specimens were determined to species or morpho-species. A mixed-model was used to assess differences in abundance among treatments and successional stages, for each species and for the coleopteran assemblage as a whole. The controlled burn treatment had no significant effect on overall beetle abundance, but several individual species were affected and species richness decreased significantly after treatment in burned plots. Associations with successional stages and microhabitat were detected for eighteen species. The distributions and habitat associations of seven tiger beetle species are discussed, as along with potential treatment effects and recommendations for increasing the habitat of each species in the Centennial Sandhills.

CHAPTER 1

INTRODUCTION

Vegetation Succession in Sand-Dominated Ecosystems

Vegetation succession is one of the main drivers in the creation of habitat mosaics and insect species diversity. The progression of successional stages in a landscape over time is characterized by several stages or seres. These seres are defined by the vegetation community that dominates the landscape (Clements 1916, 1928; Whittaker 1978). In dynamic sand-dominated systems as with many others, succession constantly changes not only the floral communities, but also populations of the local fauna that have evolved with them. Because a wide range of habitats in different stages of succession are often present at any time, the heterogeneous landscape can potentially maintain a great diversity of species.

The effects of succession on vegetation assemblages are well studied (Laska 2001). However, little work has been done on the relationship between managed disturbance and its effectiveness in restoring not only early seral plant communities, but the insect populations that co-exist with them. Many restoration attempts have been made to re-establish late seral habitat in disturbed areas, with the eventual goal of stabilizing the mature plants on the later end of the successional spectrum (Wilkes 2007, Xiao et al. 2003). My study differed, in that it examined the effects of human-implemented fire disturbance in the reversal of succession, specifically on sandhills' Coleoptera. The dynamic nature of sand ecosystems and the succession involved has been studied by many of the pioneers in landscape ecology, and has heavily influenced the development of modern successional hypotheses (Warming 1895; Clements 1904; Cowles 1899; Cowles 1911). Warming (1895) and Clements (1904) first described the changes in dune-plant communities over time and the environmental conditions that had to be present for new species to colonize and give way to the next sere. Cowles (1899; 1911) demonstrated to the scientific community that sand ecosystems change rapidly and that the study of these systems might lead to a swift increase in the understanding of the underlying principles of vegetation succession in other systems. Succession in sand environments was first described after observations were made by Cowles in the late 1890's in the dunes systems on the eastern shore of Lake Michigan. Cowles noted that as sand was deposited by wind, plant species adapted to the open loose substrate, colonized the area, and began to slowly limit the movement of sand and increase the organic matter content of the soil. As organic matter increased, other species were able to take advantage of the more suitable conditions and began to flourish (Cowles 1911; Olson 1958).

The relationship between the soil compositional change over time and the vegetation communities driving those changes, were more clearly outlined by Clements in 1916. Clements' work was probably the first to provide a summary of the causes and effects of succession, including the first use of the term "sere" to describe the passing from one floral community to another. While there may be distinct plant communities at each stage of succession, Clements admitted that no "sharp line" may be drawn between each sere, due to the unpredictability of the migration of some plant species into an area.

During the late 1960's and early 1970's, several new theories arose that differed from Clements' facilitation model of succession. These theories focused on concepts involving the tolerance of early seral species to their specific environment and also their inhibition of the growth of new potentially colonizing species (Connell & Slatyer 1977). These authors theorized that early colonizing species do not necessarily modify their habitat to inhibit the growth of later species. This concept was defined by Connell & Slatyer (1977) as the inhibition model of succession. The alternative tolerance model of succession, also outlined by Connell & Slatyer (1977), focused on the ability of early colonist species to modify their environment to limit the establishment of later colonist and early seral specialist species. These mechanisms underlying the competitive nature of successional dynamics followed many of the species-competition models in plant ecology popular at the time (Colinvaux 1973; Drury & Nisbet 1973; Horn 1974). All successional models of this era agreed that there may be an evolved mechanism behind the ability of certain colonizer species to be more successful at migrating to newly available habitat. Many of these early theorists differed in their view of the relationship between early and late successional species and the transitional mechanism leading to a later sere (Connell & Slatyer 1977). Pickens et al. (1987) expanded on the models outlined by Connell & Slatyer (1977), but was able to give more clarity to the specific factors increasing or limiting the rates of succession and the species capable of tolerating each seres' specific conditions. Pickens et al. (1987) was able to use investigations by Olson (1958) in the sand dunes of Lake Michigan to demonstrate that multiple successional paths may be taken in any system and that no single model of succession fits absolutely.

Sandhill Dynamics and the Reversal of Succession

The successional ecology models most often associated with sand-dominated ecosystems, such as sandhills or dunes, generally follow the path first outlined by Clements in 1916. The persistence of early successional species in these habitats often facilitates the arrival of intermediate successional associates when disturbance is absent. The slow buildup of soil organic matter encourages the colonization or increased success of intermediate and some late successional species. This is not to say that inhibition and tolerance by early seral associates does not occur in some systems to a degree. In sand-dominated ecosystems with persistent disturbance such as wind, which redistributes sand to and from various locations, early successional associates are often aided in their continued survival. To naturally maintain many sandhill habitats and their associated species, several modes of disturbance must work in unison to allow a diverse mosaic of habitats to exist simultaneously.

When disturbances are allowed to occur at a natural rate, there will often be a spatial mosaic of successional seres across a landscape, varying between one another by the length of time since their most recent disturbance. The new habitats made available by a particular disturbance encourage colonization by a wider array of plant and animal species specializing in, or associated with, a sere. This habitat mosaic also allows for the persistence of each species at some location in the landscape (Denslow 1985; Duncan 1993). The limiting factor for species persistence in a consistently disturbed landscape is the perpetual turnover of habitats throughout the successional cycle and the continued creation of seres required by each species.

With changes in land use practices, and with the continual introduction of non-native species, succession in many sand ecosystems has become unidirectional and the disturbances that once created such dynamic systems have ceased. The elimination of disturbances such as fire and the seeding of soil fixing plant species has led to the stabilization of many of North Americas inland sand ecosystems (Chadwick & Dalke 1965; Wolf 1973; Pfeiffer & Steuter 1994; Lessica & Cooper 1999). The effect of this stabilization has had adverse effects on native communities and many researchers have suggested methods to reverse the effects through a variety of human interventions (Olson 1958; Chadwick & Dalke 1965; Potvin & Harrison 1984; Pfeiffer & Steuter 1994; Lessica & Cooper 1999; Volesky & Cannot 2000; White 1979; Pickett & White 1985a; Loucks et al. 1985; Steuter et al. 1990; Laska 2001).

The most commonly recommended and implemented method of succession reversal is the use of controlled burns (Swengel 2001). Wildfire has played a strong natural role in the maintenance of sand ecosystems by removing a large amount of the organic matter and vegetation, exposing the sand to the influences of wind and other forces. In situations where stabilization has been in place for an extended period of time, extensive buildup of organic matter may not be removed by fire alone. In cases such as these, the literature often suggests the use of livestock to continually place pressure on late-seral grasses and forbs and work the soil through hoof-treading (Arno & Gruell 1986; Bragg 1978; Potvin & Harrison 1984; Pfeiffer & Steuter 1994). There is, however, no evidence that cattle alone increase the frequency of early successional habitat across the landscape in sandhills (Shassberger 1988).

In extreme circumstances, herbicides have been used to remove many persistent invasive plant species. This method is not always completely successful, as some herbicides also have the potential to kill native species. Many dune complexes have also relied on the tilling or disking of small tracks of land, but the method often is not effective for larger expanses of habitat. In addition, both spraying and tilling can be cost and time restrictive in their large scale implementation.

One natural alternative suggested by some authors is to increase the populations of small burrowing mammals such as pocket gophers (Lesica & Cooper 1999; Spencer et al. 1985). In some systems burrowing mammals are capable of tunneling through approximately 25% of soils each year (Spencer et al. 1985; Lesica and Cooper 1999). This tunneling moves subsurface sand to the surface and reduces the organic matter available to most plants (Spencer et al. 1985; Huntley & Inyouye 1988; Lesica and Cooper 1999).

Although many of these methods have been shown to be effective in certain systems, it is ultimately the driving force of wind that moves the sand from previously stabilized areas to new areas and creates early-seral habitat. Without this continued method of disturbance, the responses often seen following a burn or grazing event would disappear in a few years' time. The maintenance of sand-dominated ecosystems requires the use of multiple human-implemented disturbances in the absence or reduction of natural disturbances. Disturbance models for sandhills habitat maintenance were outlined by Lesica & Cooper (1999), where they recommended the utilization of controlled burns to impact late successional habitats, followed by grazing and gopher activity to return those areas to mid or early succession. These models have yet to be tested in the field, but the individual disturbance components have been observed to be effective to the extent predicted by Lesica & Cooper (1999) in increasing species diversity and restoring habitat mosaics.

Insect Responses to Human-Implemented Methods of Succession Reversal

Past research on the effect of disturbance on arthropods has covered a wide variety of disturbance types and taxa. Although many groups of arthropods occupy sandhill habitats, many are not easy to sample. The literature arachnids in sandhills is quite extensive, but they sometimes difficult to determine to species (Pearce and Venier 2006; Buddle et al. 2006; Niwa and Peck 2002). The Lepidoptera and their responses to disturbance have been studied on a few occasions, but most studies have focused on a particular species of conservation concern, rather than species assemblages (Swengle 1998; Mollenbeck et al. 2009). The most extensively studied arthropod group, with regards to its response to disturbance is the Coleoptera (Saint-Germain et al. 2004; Anderson et al. 1989; Dennis et al. 2002; Gibson et al. 2002; Kruess & Tscharntke 2002; Van Dam and Van Dam 2007).

The Coleoptera, specifically the ground-dwelling beetles, are heavily studied because of the ease of sampling and frequency of taxonomic updates. They also have a close biologic tie to a wide variety of habitats (Negro et al. 2007; Vanbergen et al. 2005) and successional stages (de Silva et al. 2008; Eyre & Cuff 2004; Eyre et al. 2003; Khavin 2001; Mayr et al. 2007; Dennis et al. 2002) and have high species richness in a variety of habitats. Responses to disturbance by ground beetles (Carabidae) have been monitored following a wide variety of disturbance types, making them ideal when examining the effects of multiple simultaneous disturbances. Carabid responses to wildfire and prescribed burns have been widely documented in a many habitats. These investigations have had differing results pertaining to the extent and timing of their responses. Larsen and Work (2003) observed that carabid diversity was usually higher in non-burned portions of tallgrass prairie, while several authors found results to the contrary (Van Amburg et al. 1981; Harris & Whitcomb 1974; Holliday 1991). Rickard (1974) observed that there were no significant changes in the abundance of carabids following burns.

Although there have been a wide range of results in these studies, several suggestions have been made to account for them. Warren et al. (1987) and McCullough et al. (1998) suggested that the microhabitat changes that occur following burns, such as increased soil temperature, decreased soil moisture and vegetation litter and cover, could be factors in the relocation of species to microhabitats more suitable to their survival and decrease their population sizes in burned areas. It has also been suggested that the elapsed time since burn will also change the assemblage of beetles in a habitat following fire. This is partially due to mortality as a result to direct contact with flames or extreme temperatures. The biology of different beetles will often protect some species while adversely affecting others. For example, a beetle that is associated with leaf litter will have higher mortality as a result of a low intensity burn, than those inhabiting large decaying logs during the same burn. Winged and flightless beetles also have been observed to have different responses over time and their distributions over the landscape may take longer to observe (Bundle et al. 2006; Holliday 1991; Holliday 1992).

The effects of grazing on Coleoptera are documented somewhat less in the literature. The results of grazing studies as with those on fire are less clear than one would hope. The general consensus from previous studies is that habitat associated beetles are seen in higher numbers in ungrazed habitats (Kruess and Tscharntke 2002; Debano 2006). The literature is lacking studies specifically examining the effects of grazing on ground beetles, but studies on other taxonomic groups have had varying results. Joern (2005) observed a significant increase in Orthopteran species abundance and richness following bison grazing. Although studies conducted by O'Neill et al. (2003), Welch et al (1991), observed significantly higher grasshopper abundances in ungrazed plots, Gibson et al. (1992) observed little to no change in species richness and abundance in several insect orders.

Based on the complex disturbance response effects suggested in the literature, my study will place particular emphasis on the microhabitat and successional associations of trophically pertinent beetle species and the changes to these associations following treatments. The effects of the implemented disturbances will also be observed within the general coleopteran assemblages present in the sandhill habitat.

CHAPTER 2

EFFECTS OF DISTURBANCE ON COLEOPTERAN DIVERSITY IN THE CENTENNIAL SANDHILLS

Abstract

Disturbances such as fire and grazing are effective in restoring early- and mid-successional sandhill habitats, benefiting the plant and vertebrate communities commonly associated with them. However, little research has been conducted to effectively characterize the degree to which these disturbances impact insect populations in sandhill environments. Beetle species were sampled in differing successional seres and unique dune microhabitats over the course of two field seasons. One fall season involved the collection of species abundance data as a baseline count before conducting a single controlled burn. This was then followed by one fall season of data collection post-treatment. The data were analyzed using a repeated measures mixed model to determine if significant changes in species abundance occurred as a result of the treatment. Changes in the habitat associations of the coleopteran community assemblage and species level were also examined. Controlled burns had no significant effect on sandhill Coleoptera, but several individual species were affected.

Introduction

Study Area

Before the formation of the Red Rock Lakes in approximately 8,000 B.C., several seismic and volcanic events isolated the Centennial Valley from other environments in southwest Montana and the Great Basin (Giles 2006; Sonderegger et al. 1982). Three separate mountain ranges border the valley on three sides: the Snowcrest Range to the north, the Gravelly Range to the northeast, and the Centennials to the south (Fig. 1). The Centennial Range also encompasses the Continental Divide and the ultimate source of the Missouri River (Brower 1896).

The Centennial Sandhills of southwest Montana is a unique ecosystem in a region dominated by sagebrush. Formed from the drifting shoreline sands of the once-larger Red Rock Lakes (Giles 2006; Sonderegger et al. 1982), the sandhills have developed into a large, seventeen square kilometer complex of semi-stabilized parabolic dunes. Approximately 10,000 years ago, due to increasing temperatures and drier conditions, the Red Rock Lakes shrunk and exposed a large amount of sediment and sand which were blown by the dominant southwesterly winds into the north-eastern corner of the Centennial Valley (Giles 2006; Sonderegger et al. 1982) (Fig. 1).

The Centennial Sandhills, located approximately 50 kilometers west of West Yellowstone, MT, are considered to be a part of the Greater Yellowstone Ecosystem (GYE). The portions of the sandhills observed in this analysis cover 17 square kilometers (44°42.297'-44°40.576'N., 111°46.380'-111°50.818'W.), with an elevation

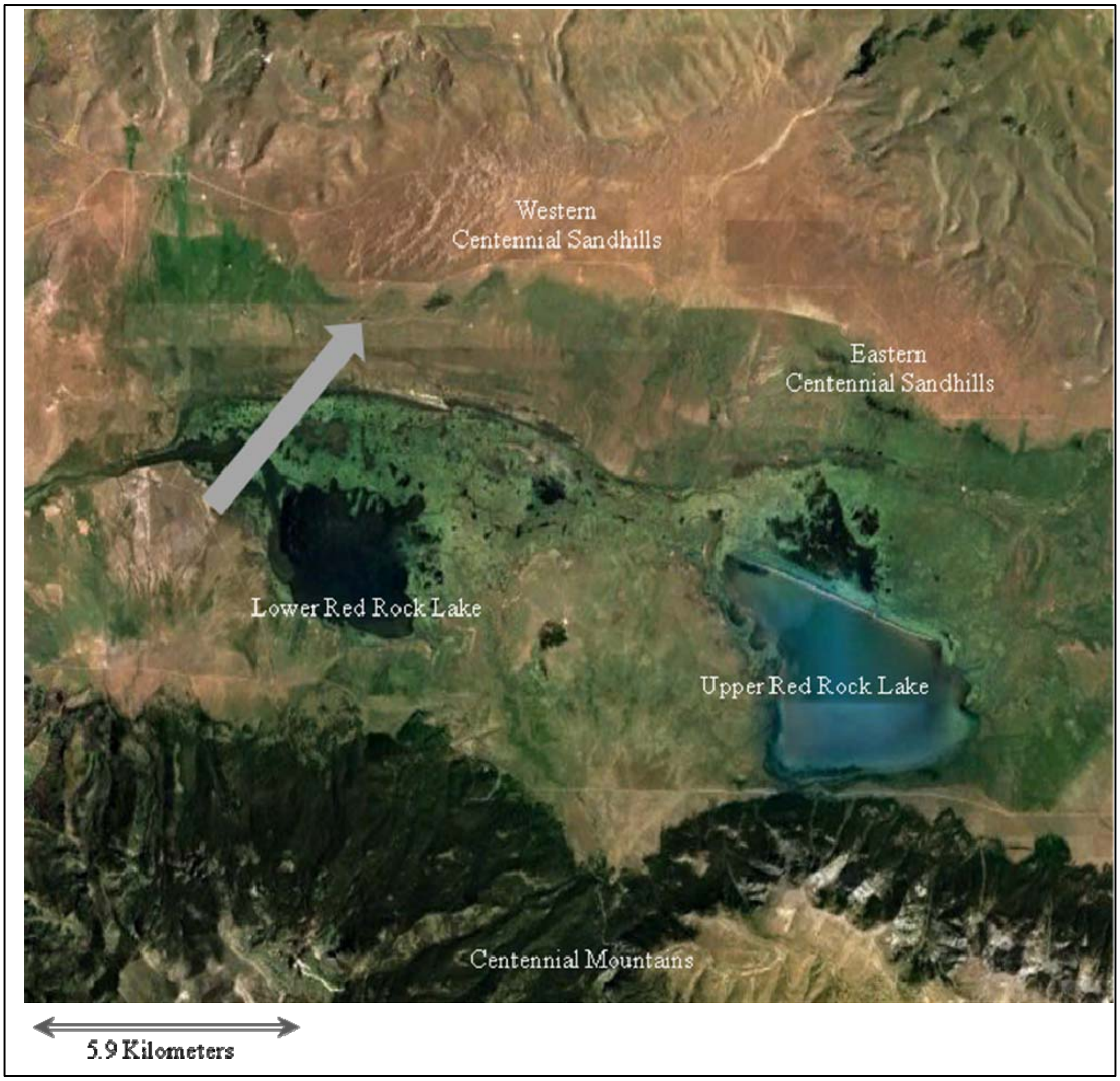

Figure 1. Map of the Eastern Centennial Valley and the Centennial Sandhills (West and East). Arrow indicates the direction of the dominant winds from the remnant shorelines of Lower Red Rock Lake toward the Western Sandhills (WS).

range of 2028m to 2085m. Average precipitation in the Centennial Sandhills is between 22 and 50cm, with 10% of that being in the form of snow.Temperatures range from a mean -13.6°C in January to 13.9°C in July (Hendricks & Roedel 2001; Shassberger 1988). Snow and frost have been documented during every month of the year.

Blowing or drifting sand is the driving force behind the creation of heterogeneous landscapes in sand ecosystems (Loucks et. al. 1985, Steuter et. al. 1990). In natural sandhill ecosystems, disturbances other than wind are also capable of reversing the process of succession. In many sand ecosystems the most common disturbances are those of wildfire and grazing by ungulates (Olson 1958; Chadwick & Dalke 1965; Potvin & Harrison 1984; Pfeiffer & Steuter 1994; Lessica & Cooper 1999; Volesky & Cannot 2000). The pressure placed on late seral vegetation by these two disturbances will, over time, aid in the reduction of organic matter and release of trapped sand. Lesica and Cooper (1999) also observed that burrowing mammals can cycle through significant amounts of substrate while tunneling. This tunneling moves sand from under layers of organic matter and re-deposits it on the surface. Burrowing mammal activity was observed to be limited to the early- and mid-successional habitats with higher slopes. This limits their burrowing effect to current early seres or post-fire disturbed areas. Under the influence of normal disturbances, sandhills will naturally form a diverse mosaic of communities at different seres. It is important to maintain each of these seres and the flora and fauna that are associated with them so that diversity is increased and habitats persist in the long term.

Over the past several decades, the Centennial Sandhills have been utilized for different purposes and the heterogeneity of the system has slowly degraded (Lesica & Cooper 1999, Mantas & Korb 2007). As late-succession habitat begins to dominate the Centennial Sandhills landscape, very little sand is being moved to new locations and creating new early successional blowouts, due to the buildup of organic matter. Cattle grazing has played an influential role in the creation of predominately mid- to late-seral habitats. The suppression of fire has also aided in the dominance of late succession vegetation across the landscape and in turn 80 years of organic matter has accumulated over some portions of the sandhills (Schassberger 1988, Lesica & Cooper 1999). In the last three decades, two agencies have taken over management of most of the Centennial Sandhills. The U.S. Bureau of Land Management (BLM) and The Nature Conservancy (TNC) cooperate in managing most of the sandhills, with a few small areas overseen by the U.S. Fish and Wildlife Service (USFWS) and the State of Montana (Fig. 2). The goal of both managing entities has evolved in an attempt to fuse the traditional pastoral use of the sandhills, while also re-establishing the natural sandhills dynamics.

A cooperative endeavor by the BLM and TNC, with assistance from the USFWS and local residents, began over a decade ago with the goal of establishing a more heterogeneous habitat throughout the western sandhills. Past studies in the Centennial Sandhills have noted that grazing cannot be removed from the area due to the dependence of local ranchers on its continued use (Mantas et al. 2007). For this reason, fire has not been used independently of grazing during any previous studies. It is assumed that bison were present in the Sandhills before European colonization (Haines 1955; Lesica and Cooper 1999). They have been shown to have an important role in the maintenance of other North American sandhill ecosystems (Pfeiffer & Steuter 1994; Fay 2003; Lesica & Cooper 1999).

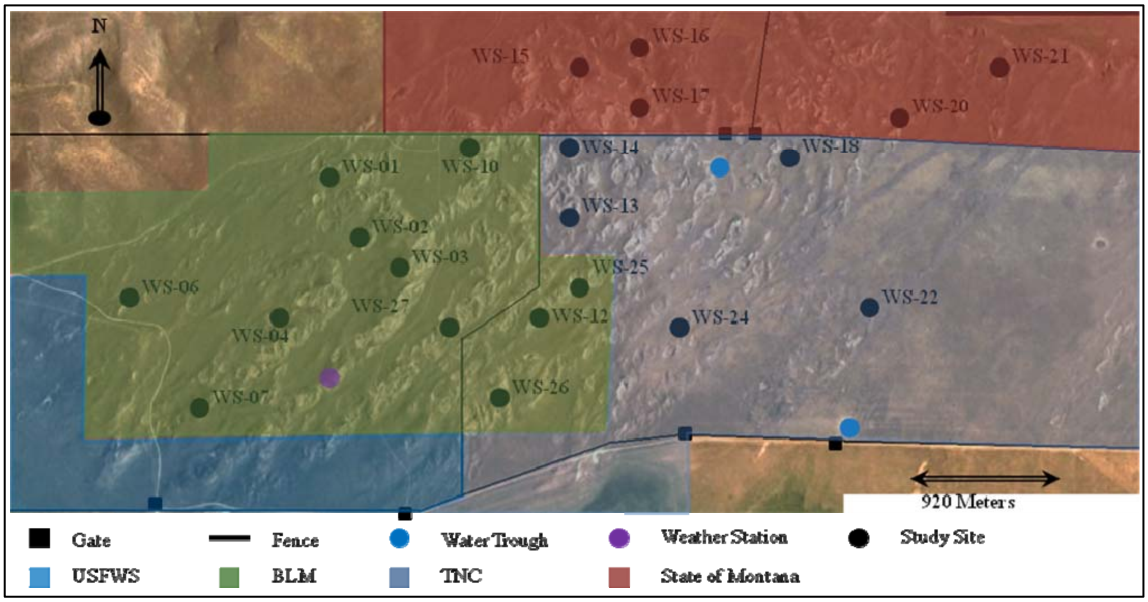

Figure 2. Map of the Centennial Sandhills Land Management areas.

Previous Research and Faunal Surveys in the Centennial Sandhills Ecosystem

In the past several years, baseline surveys have been conducted on the plants and animals that are associated with various stages of succession in the Centennial Sandhills Ecosystem. Multiple projects have been designed to survey and assess the stability of plant populations, and a few projects have involved small mammals (Schassberger 1988, Lesica & Cooper 1999, Hendricks and Roedel 2001, Mantas & Korb 2007). Only in the past few years, have any groups of invertebrates been systematically surveyed in the Centennial Sandhills (Hendricks & Roedel 2001). Tiger beetles (Coleoptera: Carabidae: Cicindelinae) and butterflies (Lepidoptera) have been specifically targeted by two surveys (Hendricks & Roedel 2001, Kippenhan 2007), but these studies did not address the effect of current or future management on their populations.

As previously mentioned, the current management of the Centennial Sandhills includes prescribed burning and grazing in the management plan as suggested by Lesica & Cooper (1990). Before this study, the most recent controlled burn was conducted in 1996. There have been no burning events since their use was recommended by Lesica and Cooper in 1999. The burning of sandhill ecosystems is crucial to endemic fauna as it clears vegetation and encourages the natural movement and deposition of sand, creating new habitats. Pfeiffer & Steuter (1994) noted that fire can often encourage grazers to forage in burned sites in the seasons following a burn due to the increase in forage. The post-fire grazing has also been documented to increase the pressure on stabilizing grasses and forbs. This pressure makes it all the more pressing to determine if grazers are selecting the early-to-mid-successional sites due to the high concentrations of grasses and forbs that exist there. These sites tend to be rarer, and endemics may only be found in these locations.

Because of objectives of the Centennial Sandhills managers in determining the effectiveness of planned treatments on establishing a diverse mosaic of habitats the aim of this study was to determine the effects of the prescribed burning treatment on the abundance and diversity of coleopteran fauna. The primary objective of my study was to determine the effects of prescribed burning on the assemblage of coleopteran species in various successional stages and in the various microhabitats within the sandhills.

Materials and Methods

Coleopteran abundance was sampled in the western portion of the Centennial Sandhills, located approximately 50 kilometers west of West Yellowstone, MT in the Centennial Valley (44°42.297’-44°40.576’N, 111°46.380’-111°50.818’W) at an elevation ranging from 2028 m to 2085 m. Sampling was conducted over the course of two years, the first year serving as a baseline and the second following a controlled-burn treatment conducted by the BLM. The treatment involved a single controlled burn that encompassed approximately 1/3 of the sampling area. Plots were placed near previously selected randomized sites within the treatment and control areas and were sampled during both years. Within each plot a pitfall trap was placed at each of four subplots, three within the primary dune area and one outside, as the plot control. Coleopteran abundances were compared amongst treatments, year, successional stages, and subplots using a repeated measures mixed model.

Treatment Methods

A single controlled burn event initiated by the BLM-Dillon office on 9 September 2008 was lit on the western portions of the sandhills, west of the central road and north of the North Centennial Valley Rd (Figs. 6 & 7). These portions of the sandhills are managed by the USFWS at Red Rock Lakes and the BLM-Dillon Office. The burn was managed by both agencies, in addition to Salt Lake City based fire personnel from the TNC. From first ignition to mop-up, the burned lasted a total of 18 hours and was successful in burning vegetation cover in approximately 95% of the 283 hectare designated area. One flare-up outside of the planned burn unit occurred, but this did not impact any testing localities in the control unit (Nathan Korb, personal communication; Jeremy Bailey, personal communication). Many locations with aspects not in the direct path of the dominant winds at the time of the treatment were incompletely burned. In areas where the fire was allowed to burn, the vegetation was burned to the ground and soil organic matter was thoroughly consumed. In some situations, the wind blew the fire past or over some low lying blowouts and the effects of the burn were reduced in those locations.

Before the second field season in July and August, 385 head of cattle belonging to the J-L Cattle Ranch, were introduced to the sandhills area. The cattle were grazed in the western half of the sandhills from July to early August and the eastern half from late August to early September. The cattle were rotated through different location in the sandhills and in all but the management area owned by the State of Montana in the far north portions of the study area (Fig. 2). Rotations of cattle were conducted to optimize proper forage for the cattle and to ensure that there was consistent grazing over all treated management units. Two watering locations creating during earlier grazing endeavors are present within the sandhills. The first water source was a windmill located just north of North Centennial Valley Road in the southeast corner of the sandhills, and the second was located east of the central road (Fig.3). These limited watering locations may have restricted the dispersal of the cattle to the farthest reaches of the sandhills.

Unfortunately, dewatering of the northern water source meant grazing was not consistent throughout the sandhills. For this reason and due to the difficulties in

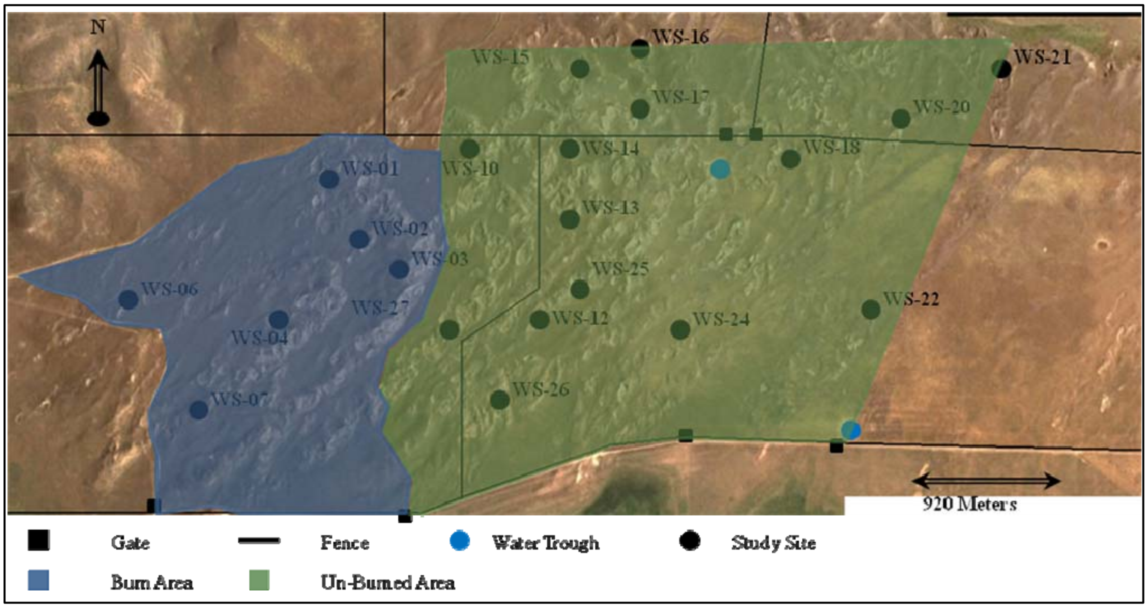

Figure 3. Map of the burn treatment area.

Figure 4. Satellite imagery of treatment and control areas. Image taken in July of 2009, before the commencement of the 2009 field season.

identifying any scale of grazing intensity, the effects of livestock had to be dropped from this study. Attempting to observe any effects could lead to invalid or biased result. These biases could be made while attempting to outline an assumed cattle distribution and level of grazing intensity.

Plot Design

Plots placed in both treatment and control areas were selected using several geographic and vegetation features typical to the sandhills. The first criterion in plot selection was that the slope of the dune face had to be exposed to the dominant southwesterly winds. Second, the average slope of each plot had to be at least 5%. These two selection factors were used because of the higher likelihood that blowout and sand movement would occur or persist if already present. These two factors were also criteria TNC used to form a pool of sites from which they drew a random sample. Third, sets of plots were selected in varying successional stages so that the association of each insect species might be accurately estimated before and after the treatment had been implemented. Succession was determined based on the abundance and density of certain plant species and the soil organic matter at each plot as outlined by Lesica and Cooper (1999). Finally, each plot was selected based on it being no more than 100 m from TNC vegetation inventory sites. This proximity was necessary so that correlations potentially could be made on the relationship between the unique plant communities and insect species present at each plot as well as the randomization method employed by the TNC. In all, 21 plots were selected for this investigation (Fig. 3). Selected plots, their geo-reference data, seral associations, and habitat data are listed in Appendix B.

Investigations into the microhabitat association of insect fauna were conducted by breaking up each plot into four distinct habitats as previously outlined (Shassberger 1988) (Fig. 4). These habitats will be referred to as the dune face (DF), swale (SW), blowout (BO), and dune ridge (DR). The dune ridge will be used to distinguish between the internal and external dune environments. A single pitfall trap was placed in each of the microhabitats (subplots), with the dune ridge pitfall being placed just outside the internal dune area to serve as the plot control. In some cases the topography and vegetation were such that it was difficult to identify where the dune ridge was located. Under these circumstances no control subplot (DR) was established for that plot, and pitfalls were only placed in the other three subplots (DF, SW, BO). Under most conditions (16), four pitfall traps were placed in each microhabitat at each plot. Figure 4 outlines the subplot placement design in each plot.

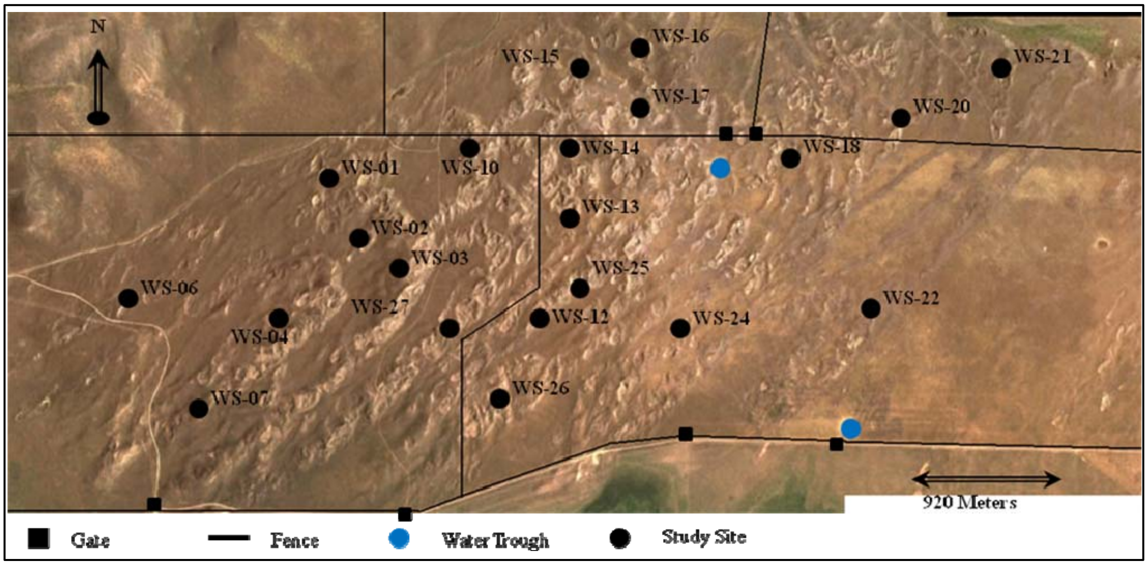

Figure 5. Map of the 21 selected plots included in the study. WS is a site code used by the TNC and designates the sites as being in the Western Sandhills as opposed the Eastern Sandhills.

Sampling Design

Pitfall trapping was conducted over the course of two fall field seasons. Fall trapping was ideal, as most of the target ground beetles (particularly those of the subfamily Cicindelinae) collected would be post-reproductive members of the population and the catch would not negatively affect future persistence. Pitfall traps are useful and efficient in the study of ground beetles both for population analysis and habitat studies (Greenslade 1964, Luff 1975, Baars 1979). They are also inexpensive and quick and easy to maintain during the field season. The first season began on 30 August 2008 and ended 04 October 2008. The second season commenced on 24 August 2009 and ended 03 October 2009. Seasons began when peak summer heats subsided and late summer or fall conditions became consistent. Seasons ended at either the first snow or at the point that daily average temperatures were consistently non-conducive to insect activity. Pitfall traps were placed at the same plots and subplots during the course of each

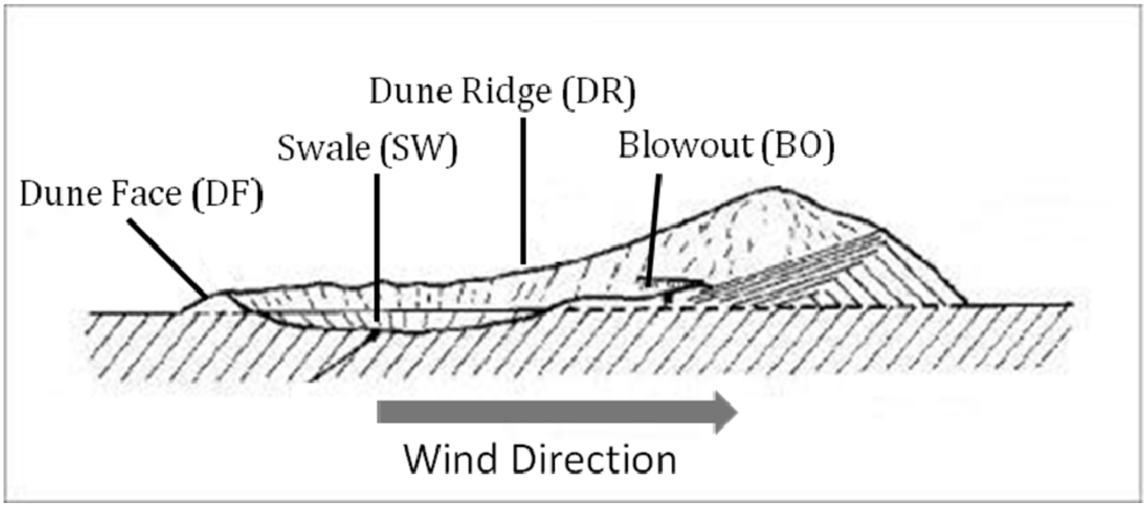

Figure 6. Anatomy of a sand dune with reference to the microhabitats formed by blown and drifting sand. These microhabitats are also the location of the subplots in which pitfalls were placed in each plot.

field season. Plots were marked and relocated in the field with the use of a Garmin™ GPSMAP 60CSx GPS. For easier observation within each plot, each pitfall trap was marked with a pink wire stake flag (Fig. 5).

Pit-fall traps were fashioned from 2-liter soda bottles. The upper portions were cut circumferentially at the point where the bottle's straight sides curve inwards towards the mouth. These top portions were inverted to create funnels that fit snugly within the lower portions. The sampled surface area measured 11 cm in diameter (Sikes 1994). Twelve-ounce Solo® collecting cups were placed within each trap to catch all materials entering

Figure 7. Pitfall placed in the field with lathe guides and pink wire stake flag.

through the funnel opening. The traps were sunk into the ground so that their rims were flush with the substrate. Four, 46 cm sections of wood lathe were arranged in the soil evenly around the perimeter of the trap opening as guides to increase the efficiency of the traps (Fig. 5). The cups within each trap were filled with approximately 150 ml of propylene glycol. The propylene glycol acted as a killing agent and preserved the captured insects. Propylene glycol is an FDA-approved food additive and, if consumed, is harmless to the vertebrate species in the area.

Samples were collected an average of every 14 days over the course of both field seasons (Table 1). Specimens and debris in the samples were removed from the propylene glycol by the use of filter screens. A 15 cm^2 square piece of fabric-netting was placed over a hardware wire frame and the preservative and specimen mixture were poured through the cloth thereby separating the materials from the preservative. The preservative was returned to the traps for reuse unless rain or debris had diluted it, whereupon it was replaced. Each filter cloth and its sample was folded once and placed with a typed sample-specific label into a Whirl-Pac® plastic bag. The use of these bags allowed the removal of most air from the bags, thus maintaining the sample completely in residual preservative. Each trap was inspected and reset if disturbance had occurred to ensure the rim was flush with the substrate. Field notes were made if the trap had been disturbed or was considered ineffective in the previous sampling period.

Sandhill environmental variables were available through MesoWest weather station RRDM8 located in the western portion of the sandhills (44.6833N, -111.8333W) at an elevation of 2039m (see Figure 2 for location). Environmental variables utilized

Table 1. Pitfall Trap Periods in the Centennial Sandhills

Trap Period	Number of Traps	Number of Days in Trap Period	Traps Set	Samples Pulled	Traps Closed
30-Aug-2008	80	0	X		
13-Sept-2008	80	14		X	
4-Oct-2008	80	22		X	X
24-Aug-2009	80	0	X		
5-Sep-2009	80	12		X	X
23-Sep-2009	80	18		X	
3-Oct-09	80	10		X	X
Total Days:	76	Total Trap Days:	6080		

were precipitation (mm) summed per trap cycle, and solar radiation (W/m²) summed per trap cycle. Temperature measurements were also collected and converted into degree days. An average temperature was calculated using daily activity minimum and maximum temperatures of two species of Coleoptera, *Cicindela hybrida* (with an activity temperature range of 19-42°C) and *Eleodes sp.* (12-28°C) (Bolwig 1957; Kramm & Kramm 1972; Holm 1973; Dreisig 1980). The total number of hours within this range were calculated each day to determine the number of degree days for that date. The degree days were then summed for each trap period. These environmental variables were utilized to determine if a difference in the environmental conditions could account for any difference in coleopteran abundances for the trap cycle and year total. See Appendix C for the raw environmental data.

Constraints

Several constraints were encountered during the implementation of this study in the field. The first being the unevenness in the number of control and treatment plots. Plots were placed in the field based on their proximity to TNC vegetation survey sites, which were randomly selected. The controlled burn was conducted only on the BLM and USFWS managed lands which encompass approximately 1/3 of the total sandhills habitat in the study area. The number of plots within the actual treatment area was not known until the burn had been conducted and most of the baseline data already collected. In addition, the total size of the sandhills sampling area limited the number of potential plots to sample. Second, the timing of the controlled burn affected the baseline sampling period in that the burn was conducted while traps were still placed in the field. Fortunately, the design of the pitfall traps allowed them to seal the sample in an intact state. Lastly, the control trap within each plot was difficult to place in circumstances where there was little to no distinction between the primary dune area and the area outside the dune environment. In this situation the control plot was not placed.

Sample Processing and Data Handling

Following collection in the field, specimens were placed in a freezer until each sample could be sorted. Each sample was removed from the Whirl-Pac® and the filter cloths were rinsed under a gentle water stream in two metal soil sieves (mesh sizes 250 and 1400 µm) to remove dirt and specimens from the cloths. Specimens were then transferred into 90 ml specimen cups with 70% ETOH. The specimens were sorted under a Leica® WildM3C dissecting microscope at 10-40x magnification. Coleoptera and

Hymenoptera were pulled from the samples, mounted and labeled. In addition to the beetles and Hymenoptera, Orthoptera and some sand-associated Hemiptera (Cydnidae) were saved. When multiple specimens of common taxa were encountered, 2-3 individuals of each taxon were mounted as representatives and the rest were set aside in labeled vials.

Following mounting and labeling, specimens were first sorted to order, and in the case of many Coleoptera to family and genus. After which specimens were sorted to morpho-species, and if possible identified to species with the aid of the taxonomic literature. Each time a new morpho-species was encountered, it was compared to specimens of or near determined species held in the MTEC. Following confirmation by keys and comparison to determined specimens, the sandhill specimens were used as vouchers in a reference collection for comparison to specimens examined at a later date.

As specimens were sorted and determined, they were tallied and catalogued in Microsoft Excel with a plot, subplot, and date code for each species or morpho-species. This code references the plot number followed by the subplot letter and finally the date when the sample was pulled from the trap. For example, specimens from plot/subplot 01(A) collected on 5 September 2009 would be designated as 01a0905. As each sample was processed, a tally was created of all of the specimens within that sample. Once a full date series was completed, the specimens were arranged by taxa and tallied again to ensure the accuracy of the data. Each species of beetle was coded using an identification code, abbreviated using the first three letters of the genus and species [e.g. cicare = *Cicindela arenicola* Rump (see Appendix A)]. The data identifying each trap sample was recorded as a heading under which the species/number of individuals would be listed, one species per line. Voucher specimens of all species are deposited in the Montana Entomology Collection (MTEC).

Data Analysis

The abundance of each species was calculated at each plot and subplot as described in the Sample Processing and Data Handling section of the methods. The mean abundance, richness, and Jaccard Index were also calculated for each plot, microhabitat (subplot), and successional stage by treatment. Species richness or alpha diversity (α) is defined as the diversity within a particular area or ecosystem usually expressed by the number of species in that ecosystem (Whittaker 1972; Hunter 2002). In this study, species richness was used to describe the alpha diversity in each treatment area, microhabitat, or successional stage. Richness was calculated using the program Spade for each treatment area (Chao and Shen 2003). Spade was also used to compare the shared number of species within each treatment and year. Sorenson's Quotient of Similarity (QS) was utilized to show the similarity between treatments and years.

$$\text{Sorenson's QS} = (2*j / a + b) * 100$$

The Sorenson's QS is calculated by multiplying the number of species common to both samples of interest (j) by two, dividing that number by the sum of species found in both samples (a + b), and multiplying by 100 to get a percentage of faunal similarity (Sorenson 1948).

A mixed model repeated measures ANOVA ($\alpha = 0.05$) was performed using Statistical Analysis System 9.2 (SAS Institute 2009, Cary, NC, USA) to determine significant differences between sampling dates, treatments, microhabitats, and successional stages. BoxCox transformations were performed on the raw data to determine appropriate transformation. The analysis was conducted for the coleopteran community assemblages as well as on each species to determine the effect of treatments and habitat associations related to the treatment effects. For the analysis of treatment effects, singleton species (species where one individual was observed on one occasion) were removed from the data as they contribute nothing to the effects of treatments and can show no biologically significant association with a particular habitat. In addition, individual species abundances that made up less than 0.05% of the total abundance of beetles were excluded from the analysis due to their rarity (Novotny et al. 2007; Grimbacher and Stork 2009). For beetle species, this threshold abundance was found to be 4.6 and was rounded to 5 individuals. To further limit the inclusion of rare species, only the beetles with an abundance greater than 20 were examined for significance. Collection Date (Date) was treated as a repeated measures effect and the REPEATED statement of the PROC MIXED procedure was used to model the variance-covariance relationship of the response variables among dates.

Estimates of least square means (LSM) and corresponding standard errors were obtained using the LSMEANS statement. Significant interaction terms were further examined using the SLICE option of the LSMEANS statement. Because this type of analysis cannot accommodate values less than 1, a value of 0.5 was added to all abundance values before analysis. The dependent variable of species abundance (ABUND) was analyzed in PROC MIXED (SAS Institute 2009) using Restricted Maximum Likelihood (REML) estimation methods, which is a statistical approach to provide unbiased estimates of variance in unbalanced designs. The following explanatory (independent) variables were analyzed using PROC MIXED: BURN, microhabitat (SPLOT), successional stage (SUCCESS), and their interactions. YEAR was also included in the models because the data were set up in a manner that the difference between year 1 (baseline pre-treatment abundance) and year 2 (post-treatment abundance) were differentiated by year. The definition of each of the covariates used in the analysis can be found in Table 2. Specific emphasis must be placed on the biological significance of species observed to respond significantly to treatments. To attempt to more clearly outline the biological background and significance of each species found to be affected in the analyses, summaries were created to explain their trophic niche in the system and better determine the accuracy of the effects.

The significance of the effect of each environmental variable in relation to the abundance, trap cycle association, and year was analyzed at the community level. This was conducted to determine if any outside variable or the trap collection schedule and timing may have biased the abundances of Coleoptera trapped.

Table 2. Covariates, and respective definitions, used in models to estimate the effect of treatments and habitat characteristics on coleopteran abundances in the Centennial Sandhills, MT.

Covariate	Definition
ABUND	Abundance of species at subplot
BURN	Presence or absence of burn at the site or subplot. Burned sites in the baseline study period (year 1) were also identified as burn.
PLOT	One of the 21 Plots (Figure 3 & Appendix B)
SPLOT	One of four subplots designated to represent the four microhabitats (See Chapter 2 Methods)
SUCCESS	Successional stage or sere associated with the site or subplot (Early, Intermediate, Late)
DATE	Date associated with one trap cycle
YEAR	Year designation to distinguish between the baseline study period (year 1) and the post-treatment period
TIGER	Designated the species as a Tiger Beetle or not
SOLRAD	Solar Radiation of one trap cycle
PRECIP	Precipitation of one trap cycle
DGRDAY	Degree Day of one trap cycle

Results

Environmental Variables

The difference in total accumulated degree days between the sampling years was significantly different ($t = 0.35$, d.f. = 75, $P = 0.75$). Similarly, there was no difference between the sampling periods in either accumulated solar radiation ($t = 1.15$, d.f. = 75, $P = 0.33$) or total precipitation ($t = -0.45$, d.f. = 75, $P = 0.68$). These results suggest that the observed environmental variables cannot be used to explain changes in beetle abundance between sampling years.

Coleopteran Abundance, Richness, and Similarity

A total of 99 beetle species or morpho-species and 7,585 individuals were recorded. Of these, 28 species were only observed as singletons and 33 had were represented by fewer than 5 individuals. No transformation was required as the assumptions of normality and homogeneity were met. The abundances of the 71 species included in the analysis (i.e., all with more than a single individual) are found in Appendix D, along with the statistics associated with the treatment.

Coleopteran abundance in the treatment area did not differ significantly from the abundances found in the control ($F_{1,\,28000} = 0.01$, $P = 0.931$). Beetle abundances were significantly higher in intermediate successional habitats ($F_{1,\,28000} = 2.98$, $P = 0.004$), but there were no significant differences in abundance in any particular microhabitat ($F_{1,\,28000} = 0.95$, $P = 0.482$).

The species richness within the control plots was close to constant from the baseline study (48) to the post-burn (51), while it dropped by almost 50% in the treatment plots (71 vs. 40). However, the Sorenson's similarity indices were nearly identical between control (QS = 0.71 ±0.04) and treatment (QS = 0.72 ± 0.04) plots (Table 3). Species richness in control plots during the baseline year (48) was different from those of the treatment plots (71). Therefore, due to the unevenness of treatment and control, it is difficult to make an accurate comparison of species richness. The species similarity in the baseline year comparison shows that there was a high level of similarity in the species found between baseline plots (QS = 0.81 +/- 0.04). Treatment plot species richness, however, became more like those of the control plots in the post treatment comparison (51, 40), yet decreased in the number of shared species (QS = 0.68 ± 0.04) (Table 4). The number of total individuals collected dropped from the baseline to the post-fire year in both the treatment and control plots (Table 3 & 4). There was a great deal of similarity in the control plots between years, while there was a sharp decline in species richness in the treatment area.

Individual Species Associations and Treatment Effects

A total of 19 species were found in abundances greater than 20. Of these 20 species, 10 were found to have significant changes in their abundances or associations with particular seres or microhabitats (APPENDIX D). Several species found to have significant changes in their abundances are highly associated with vegetation and their life history would lead one to expect a strong influence of burning on their populations with the obvious short term loss of many plant species. Pitfall trapping is also not a

Table 3. Within year species richness and diversity

	Total Individuals	Number of Species
	Baseline	
Control	3897	48
Treatment	1561	71
Shared Species		48
Sorenson's QS (S.E.)		0.81 (0.04)
	Post-Burn	
Control	1612	51
Treatment	558	40
Shared Species		31
Sorenson's QS (S.E.)		0.68 (0.04)

Table 4. Within treatment species richness and diversity

	Total Individuals	Number of Species
	Control	
Baseline	3897	48
Post-Burn	1612	51
Shared Species		35
Sorenson's QS (S.E.)		0 .71 (0.04)
	Treatment	
Baseline	1561	71
Post-Burn	558	40
Shared Species		40
Sorenson's QS (S.E.)		0.72 (0.04)

common method for regularly collecting these plant dependent insects, so the associated results could have some trapping bias associated with them, and should be interpreted cautiously. Individual insect species correlated with the treatments and their distributions are found in Appendix D, E, and F. Descriptions of the 10 significant species observations and their significances at the individual species level are listed below and in Table 5. In addition to the species found to be significant, descriptions are also provided for the 9 other species with abundances greater than 20.

To accurately assess the biological significance of each species, we must first consider the trophic role it plays. Of the 10 species found to be significant, close to half were predators of insects or seeds as either an adult or larva (Table 5). Four species exhibited detritivorous or omnivorous feeding behavior, while the remaining two species were herbivores or fungivores (Table 5). Of all 99 species collected in the Centennial Sandhills, 23 were predators and 33 were either detritivores or omnivores. There seemed to be some consistency in the proportion of each in both the entire coleopteran assemblage and at the individual species level. There was also a great deal of similarity in the number of herbivores found to be significant and the number of total herbivores collected. Thirteen species of 99 were herbivores in the beetle assemblage while 1 of the 10 was found to be significant.

Amara quenseli Schönherr is a xerophilous species commonly occupying exposed sandy soils with sparse vegetation. This species is wing-dimorphic in that individuals within this species can be observed to have both fully and partially formed flight wings (Lindroth 1968a; Darlington 1936b). This species is assumed to be a carnivore, although

Table 5. Trophic levels of 10 species (n > 20) and their significance (actual significance levels can be found in the Appendices).

	Trophic Level		Associations and Treatment Effects			
Species	Adults	Larvae	Fire	Year	Sere	Microhabitat
Eleodes cordatus	D/O	D/O	y	n	y	y
Amara confusa	P/S	P/S	n	y	y	n
Harpalus fraternis	P	P	y	n	y	n
Cryptophagus histricus	F	F	n	y	n	n
Lebia vittata	P	PT	y	y	y	n
Anthicus lutulentus	D/O	D/O	y	y	y	y
Disonycha latrifons	H	H	y	y	y	y
Anthicus tobias	D/O	D/O	y	y	y	y
Eleodes extricatus	D/O	D/O	y	y	y	y
Amara quenseli	P/S	P/S	n	y	y	n

P – Predator, S – Seed Predator, PT – Parasatoid, D – Detritivore, O – Omnivore, F – Fungivore, H - Herbivore

there has been no documentation to confirm this. Some literature cites many species of *Amara* as being both insect and seed predators as adults (Lindroth 1968a). The analysis concluded that, although this species was not significantly affected by fire treatments ($F_{1, 396} = 3.02$, $P = 0.08$), its abundances showed a swift decline from year one to year two, and was not affected by the burn. This species was the most abundant and widespread beetle in the sandhills, yet was significantly restricted to intermediate succession ($F_{2, 394} = 6.75$, $P = 0.0013$) and the swale microhabitat ($F_{3, 392} = 3.22$, $P = 0.02$).

Amara confusa LeConte is a xerophilous beetle often collected in dry habitats with sparse vegetation. Species of *Amara* have been observed to be carnivorous and granivorous predators (Lindroth 1968a). Although the feeding behavior of this species has not been documented, it is assumed to be a carnivorous species. Most of the captures of this species were made during the baseline sampling in year one (16 of 21). There was no significant effect of fire treatments ($F_{1, 396} = 1.53$, $P = 0.22$) as most of the individuals were collected in the control plots. There was a significant association with intermediate succession for this species ($F_{2, 394} = 3.33$, $P = 0.04$).

Harpalus fraternis LeConte is a xerophilous species often found in sandy, dry, open habitats with little to no vegetation. Many species of *Harpalus* are known insect predators (Lindroth 1968b). There was a significant positive response to burning by this species ($F_{2, 394} = 11.53$, $P = 0.0008$) with treatment site abundances nearly tripling post-treatment. There was, however, no significant association with particular successional habitats ($F_{2, 394} = 0.45$, $P = 0.64$) or microhabitat ($F_{3, 392} = 0.07$, $P = 0.97$).

Lebia vittata Fabricius is a widespread species of carabid that is commonly associated with vegetation, as the larvae are thought to be parasitoids of chrysomelids particularly of the genus *Disonycha* (Lindroth 1968b). This species had a strong negative response to burn treatments ($F_{1, 396} = 10.27$, $P = 0.0015$), most likely due to its dependence on vegetation and the insects associated with them to complete its lifecycle. There did not seem to be a significant difference in the habitat or seral preference of this beetle species ($F_{3, 392} = 0.93$, $P = 0.42$; $F_{2, 394} = 2.44$, $P = 0.09$).

Cymindis planipennis LeConte is often associated with the dry sand prairies of the North American west (Lindroth 1968b). This species was not observed to have any significant changes in its abundance as a result of burn treatments ($F_{1, 396} = 0.25$, $p = 0.61$), and was also not significantly associated with any sere or microhabitat ($F_{2, 394} = 1.81$, $p = 0.08$; $F_{3, 392} = 0.64$, $p = 0.78$).

Cicindela decemnotata Say and *Cicindela formosa* Say are typically restricted to bare, sandy soil throughout their range. These species are predators that stalk their insect prey during the daylight hours. *Cicindela formosa* was the second most collected beetle and most collected tiger beetle, while *C. decemnotata* was the second most collected tiger beetle. Neither species were significantly impacted by fire ($F_{1, 396} = 0.92$, $P = 0.34$; $F_{1, 396} = 3.27$, $P = 0.07$) or had any association with a particular microhabitat ($F_{3, 392} = 0.80$, $P = 0.63$; $F_{3, 392} = 1.10$, $P = 0.36$) or sere ($F_{2, 394} = 1.57$, $P = 0.14$; $F_{2, 394} = 0.91$, $P = 0.50$).

Eleodes (E.)extricatus Say is a common species, often associated with grassy or sparsely vegetated habitats. Like most *Eleodes*, *Eleodes extricates* exhibits both omnivorous and detritivorous feeding behavior (Arnett et al. 2002). In the Centennial Sandhills, this species is widespread, yet shows no significant association with a particular habitat or sere ($F_{3, 392} = 0.26$, $P = 0.86$; $F_{2, 394} = 0.47$, $P = 0.63$). There was, however, a complex yet significant response to burn treatments. Overall, this species showed a negative response to burn ($F_{1, 396} = 24.12$, $p < 0.0001$). Its abundances dropped in treatment plots, yet oddly its population increased in control plots. An explanation could be that the sandhills' population would have had an overall increase across the landscape but was limited in the burned areas due to the treatment, but this cannot be demonstrated in the data. It is also possible, due to their mobility and longevity, that individuals may have moved out of the treatment areas following the burn and been captured in higher numbers in the control plots.

Eleodes cordatus Eschscholtz belongs to a subgenus that is highly confused taxonomically and is difficult to determine to species due to the unavailability of accurate keys. It is believed that all individuals encountered in pitfall traps are of the same species, so for the purposes of the analysis all individuals were defined by the species *E. cordatus*. Questions relating to the taxonomic status of these individuals should be made by consulting voucher specimens. This species is restricted to western North America, but little of their biology is known. It is assumed to be a detritivore and omnivore (Arnett et al 2002). It is a flightless beetle with limited mobility, so the significant effects of burn ($F_{1, 396} = 4.66$, $P = 0.0315$) on this species group are not surprising.

Eleodes nigrinus LeConte is a very common Tenebrionid species in North America and is a known detritivore and omnivore. This species was widespread across the sandhills and showed no association to a particular sere ($F_{2, 394} = 0.50$, $P = 0.83$) or microhabitat ($F_{3, 392} = 0.67$, $P = 0.75$). This species was also not affected by the burn treatment ($F_{1, 396} = 0.11$, $P = 0.74$).

Hyperaspidius mimus Casey feeds predominantly on aphids, so naturally it has a close association with vegetation communities. Strangely there was no effect of the burn on this species ($F_{1, 396} = 2.21$, $P = 0.14$). This species also showed no significantly associated with early seral habitat ($F_{2, 394} = 0.55$, $P = 0.80$) and no significant association to any particular microhabitat ($F_{3, 392} = 0.48$, $P = 0.91$).

Dysonycha latrifrons Schaeffer is herbivorous both in its larval and adult forms. As was mentioned previously, this species is the host of the carabid *Lebia vittata*. As with that species, *D. latrifrons* was highly impacted by fire ($F_{1, 396} = 12.14$, $P = 0.0005$) and showed a strong associated with intermediate succession ($F_{2, 394} = 5.93$, $P = 0.0029$).

Lebia vittata did not have a significant association with intermediate association but it was found in higher abundance in early to intermediate seres.

Otiorhynchus ovatus LeConte is a non-native species introduced to North America from Europe. This species commonly feeds on the roots and foliage of herbaceous plants. Despite having close life history ties to vegetation this species underwent no significant changes in abundance as a result of the burn treatment ($F_{1, 396} = 0.01$, $P = 0.94$) and was not associated with any sere or microhabitat $F_{2, 394} = 1.37$, $P = 0.22$; $F_{3, 392} = 1.27$, $P = 0.25$).

Anthicus tobias Marseul and *Anthicus lutulentus* Casey, as with many other Anthicids, are associated with flowers and foliage. Though they are associated with vegetation they are thought to be detritivores and omnivores (Werner 1964). As this association would imply, fire had a negative impact on their abundance ($F_{1, 396} = 15.81$, $p < 0.0001$; $F_{1, 396} = 18.40$, $p < 0.0001$). There were no significant seral or microhabitat associations for either species.

Cryptophagus histricus Casey is not well documented biologically in the literature but many species in the genus have been collected feeding on fungi or living in animal nests (most likely feeding on cryptic varieties of fungi) (Bousquet 1989). Due to the dry conditions in the sandhills, not many fungi were observed and there is no information in the literature on what type of animal nests they are associated with, so it is not known what might be driving their abundance. There was a significant difference in the abundance of this species in control sites but not in treatment sites ($F_{1, 396} = 3.63$, $P = 0.0574$), so there was no effect of burn. However, there was a distinct decline in the populations of *C. histricus* following the treatment (46 vs. 16). There were no observed associations with any habitat type or sere ($F_{3,\,392} = 0.37$, $P = 0.7751$; $F_{2,\,394} = 1.10$, $P = 0.3339$, respectively).

Nicrophorus hybridus Hatch & Angell and *Nicrophorus guttula* Mutschulsky are both carrion feeders that were found in abundance in pitfall traps containing small mammals. Due to the attraction to carrion no statistical associations can be drawn as habitat characteristics would not directly influence the availability of carrion.

Onthophagus nuchicornis LeConte is a dung beetle that was seen almost exclusively in the second field season most likely due to the presence of cattle. While grazing was excluded from this study, the presence of this species is most likely influences by the availability of fresh dung. No statistical associations were observed.

Discussion

Burning did not seem to have a significant effect on the abundance of most coleopteran species. The few exceptions were species that either had a strong life history association with vegetation (*Dysonycha latrifrons*, *Lebia vittata* and two species of *Anthicus*), or seemed to have a general landscape-wide population fluctuation (*Cryptophagus histricus*). Five species showed effects of burning and are known to be dependent on specific habitat types or are more susceptible to fire in the short-term. These species belonged to the beetle families Carabidae (*Amara confusa*, *Amara quenseli*, and *Harpalus fraternis*) and Tenebrionidae (*Eleodes cordatus,* and *Eleodes extricatus*). While responding to the burn, populations of these five species fluctuated in different directions. Both tenebrionid species responded negatively to the treatment, while *Harpallus fraternis* showed a significant increase in abundance and *Amara confusa* and *Amara quenseli* showed no change. Although this study was only observing the short-term effects of the controlled burns, a long-term study would most likely see a swift rebound in the abundances of species negatively affected. Findings also showed that it is necessary to determine specimens to the species level to ensure greater sensitivity and to understand the biological and ecological limitations of certain species observations.

It was interesting to see that most significant species associations to a particular sere were to intermediate succession. Of the nine species shown to have a significant association to one successional stage, six of them were associated with intermediate succession. It was expected, based on the unique associations of many sandhill floral species, that the beetle species found to be significantly associated with a sere would similarly be to early succession. Most of these intermediate associates were also strongly tied to the vegetation communities in that sere.

Great differences in the species richness of Coleoptera in burned and non-burned plots were not unlike the results seen in other short-term effects studies. It makes intuitive sense that there will be immediate effects on the number of invertebrate species. As shown in the discussion of individual species' biology, several of the species have strong life history associations with vegetation, and were all but completely removed from the habitat by burning. Situations such as these greatly influence the number of species observed by a short-term study. The effects of newly created habitats may not be seen for a several years post-burn, and the animal species richnesses may not increase until the producer and prey species associated with them have time to colonize. Insect species richness is therefore supported directly by increasing the populations of associated plants in these newly created early and intermediate seres.

In conclusion, no immediate change in coleopteran abundance was observed, but a decrease in beetle species richness followed the burning treatment. With respect to habitat management and biological conservation, no conclusions can be made from this study regarding the long-term impacts of controlled burning on beetle abundance and richness in the Centennial Sandhills. The strong short-term association of several coleopteran species to intermediate succession suggests that disturbance is necessary to maintain those habitats. It may be that the dispersal capabilities of many early successional associates are limited in the short term and their re-colonization may not be immediately observed. This underlines the importance of maintaining a mosaic of seral habitats across the Centennial Sandhills landscape.

CHAPTER 3

DISTRIBUTION AND HABITAT ASSOCIATIONS OF CENTENNIAL SANDHILL TIGER BEETLE POPULATIONS

Abstract

The habitat associations of seven species in Montana's Centennial Valley were observed over the course of two field seasons, with an emphasis on the distribution of tiger beetles across the Centennial Sandhills landscape. Two tiger beetles were recorded for the first time in the Centennial Sandhills, one being a new state record and a species of conservation concern in its previously known Idaho habitats. There were no statistically significant habitat associations of any of the tiger beetles observed, primarily due to several species being encountered in small numbers.

Introduction

Sandhill/dune stabilization is widespread in North America, and its effect on endemic species has been tremendous. Dozens of sand obligate species have been listed as federally threatened or endangered due to degraded and stabilized sandhills and dunes (USFWS 2008). Among the many species affected by stabilization, invertebrates are some of the most overlooked, because of their size diversity and inability to captivate the public. Many species of the genus *Cicindela* (tiger beetles) are extremely dependent on the mosaic of successional stages that exist in a functional sandhill/dune ecosystem (Willis 1967, Knisley 1984, Knisley & Hill 1992). While many species are not limited to just one stage of succession, some are greatly affected by the loss of the open drifting sand associated with early-/mid-succession.

Open, drifting sand is of vital importance to the reproductive success of many tiger beetle species. Due to the developmental requirements of larval tiger beetles and their burrowing behavior, ovipositing females select sites with a unique consistency in soil composition, in addition to moisture content and soil depth (Hamilton 1925; Shelford 1908; Pearson 1988). Tiger beetle larvae of sandhill species require sites with some open-loose or packed sand in which to build their burrows, from which they prey on wandering insects (Shelford 1908; Pearson & Vogler 2001). In each of their three stages, *Cicindela* larvae select different burrow depths and tunnel angles due to their changing predation strategy (Shelford 1908; Pearson & Vogler 2001; Pearson et al. 2006). Larvae will spend 2-3 years feeding from small subterranean borrows and are highly vulnerable to disturbances in soils. These specific habitat requirements have made tiger beetles and many other sand-associated insects excellent indicators of the health and stability of the ecosystems which they inhabit (Pearson & Cassola 1992, Carroll & Pearson 1998, McGeoch 1998, Rodriguez et. al. 1998, Rainio & Niemela 2003).

Significant changes in the landscape of the Centennial Sandhills over the last several decades has led the current managers to attempt to restore a more natural habitat mosaic that will increase species numbers and diversity of both flora and fauna. Based on research in other sand ecosystems, the use of prescribed burns (Pfeiffer & Steuter 1994, Volesky & Cannot 2000, Niwa & Peck 2002, Fay 2003, Joern 2005, Knight & Holt 2005) and cattle grazing (Potvin & Harrison 1984, Pfeiffer & Steuter 1994, Joern 2005) were implemented to increase pressure on mid-to-late succession plant species, in the hope that Aeolian processes will be restored to portions of the sandhills. The variation in habitat preference among species of tiger beetle and the specificity of each species to a particular stage of succession makes their study invaluable when attempting to make observations on the diversity of habitats within an ecosystem.

Tiger beetle species occupy a wide variety of habitats across North America and they occupy them because of the very specific physico-chemical makeup of the substrate and the amount of vegetation cover (Schultz 1989, Knisley 1992, Pearson & Vogler 2001, Romey & Knisley 2002, Satoh & Hori 2005). The variations in habitat selection by tiger beetle populations can be useful to researchers who are attempting to gain a better understanding of the health and stability of a specific habitat. This practice can be taken a step further by examining multiple species in one ecosystem and estimating their relative abundances to determine if there are a wide variety of habitats sufficient enough to accommodate each population. Endemic species of tiger beetles have been used for this purpose across the globe by either looking at the diversity of species in each habitat (Pearson & Cassola 1992, Carroll & Pearson 1998, McGeoch 1998, Rodriguez et. al. 1998, Rainio & Niemela 2003), or the relative abundances of individual sensitive species (Niemela et. al. 1993, Greenberg and McGrane 1996). As managers in the Centennial implement both prescribed burns and some cattle grazing in their attempts to restore habitat, it is necessary to have multiple methods for determining the treatment's success.

Formal presence/absence surveys for tiger beetle species were conducted in 1999 and 2007, and plans for intensive sandhill-wide surveying have been suggested by the Nature

Conservancy before the implementation of fire and grazing prescriptions (Hendricks & Roedel 2001; Mantas & Korb 2007). Surveys conducted in 1999 discovered four species of the genus *Cicindela* in the Centennial Sandhills: *Cicindela decemnotata, Cicindela formosa, Cicindela longilabris, and Cicindela tranquebarica*. Four field days spent at the sandhills by Mike Kippenhan in the summer of 2007 observed these same four species and two additional species which were not observed in 1999 (*Cicindela nebraskana* and *Cicindela purpurea)*. Kippenhan's surveys were primarily limited to roadside locations due to limited time and the inability to navigate rough terrain that required a four-wheel drive vehicle (Kippenhan, personal communication).

Past surveys of tiger beetles have suffered from very short sampling periods and limited sampling locations. These are not expected to accurately represent the species present, or habitat preferences over the entire landscape. Many of the past surveys have allotted only 3-5 days per field season (March – September) and only a few minutes at each site. Due to the very small required habitat size of many cicindelines, it is impossible to survey every possible site in all of the sandhills, but more time could be allotted to cover all major habitat types. A second concern raised by previous surveys was the locations surveyed. Most sites where pitfall traps or roadside transects were used were adjacent to roads, which limits the surveys to easy access sites. While surveys in proximity to roads do allow for easy sampling, results are limited to the microhabitats created by roads, and road cutouts and do not sample portions of the population unaffected by edge effects.

The objectives of this investigation are two-fold: first to survey the populations of *Cicindela* in the Centennial Sandhills and for each species determine presence, relative abundance, and habitat preference, and second, to determine the effect, if any, of controlled burns on populations of tiger beetles in differing successional stages.

Materials and Methods

Tiger beetles were collected by pitfall trap utilizing the methods outlined in Chapter 2. In addition to pitfall sampling, each site was surveyed for tiger beetles using hand nets and visual observations of behavior. If larvae were observed, a small sample from each site was collected for identification. Larvae were preserved using the methods described by Maser (1971). Notes were also made on the approximate percentage of each larval instar observed during each trap cycle at each site. Statistical methods also followed those in Chapter 2.

Results

Tiger Beetle Species Observed

Seven tiger beetle species were observed over the course of two field seasons. All previously recorded species were found during this study except *C. longilabris* Say. Two additional species were collected from the sandhills *Cicindela punctulata* Olivier and *Cicindela arenicola* Rumpp. Both of these new detections were limited to one site, and their distribution is assumed to be limited. Species also encountered in small numbers were *C. tranquebarica* Herbst, *C. purpurea* Olivier and *C. nebraskana* Casey.

Conversely, *C. formosa* Dejean and *C. decemnotata* Say were collected throughout the sandhills in large numbers.

Descriptions and Associations of Centennial Sandhills Tiger Beetles

Cicindela formosa Dejean, The Big Sand Tiger Beetle: *Cicindela formosa* prefers dry sandy areas with little or no vegetation. This species is widespread in the eastern U.S. and southern Canada and can be persistent in suitable habitat well into the Rocky Mountain region. In the western parts of its range, it is limited to sandy areas such as dunes and blowouts. There are several recognized subspecies of *C. formosa* (Pearson et al. 2006), and the exact subspecies occurring in the Centennial is not known. The maculation that purportedly distinguishes *C. formosa gibsoni* Brown from the “manitoba” morph of *C. formosa generosa* Dejean are not consistent among the individuals in the Centennial population. The current series of almost 2,000 specimens contains individuals with broad ivory maculation to very narrow ivory maculation (Fig. 9). The metallic ventral coloration is also quite diverse in this population, varying from metallic green to blue and even purple. The Centennial Valley population is considered to be disjunct from other populations of the species. The closest reported population to the south and east is located in Moffat County, Colorado and to the north specimens have been collected near Logan, Gallatin County, Montana (Catherine E. Seibert Collection). The species is not found to the south into Idaho even though suitable habitat exists approximately 40 km away at St. Anthony Dunes.

Behavior: *Cicindela formosa* is an active daylight predator and was usually the first tiger beetles to be observed in the early morning hours, sitting just outside the previous night's burrow. This also could be due to its great abundance across the Sandhills and its greater tendency to fly when disturbed, making a loud buzzing sound. The behavior of this species was the most diverse of any in the area when it became affected by temperature extremes. During both low and high temperatures, *C. formosa* would appear very lethargic and would not avoid the mid-day heat as often as other species. This made this species very easy to capture in these situations, even by hand, with very little effort.

Seasonality: While the sampling of this study was limited to the fall seasons, *C. formosa* is a known spring/fall occurring species often appearing in the Centennial as early as late April in warm, dry years and can been found well into mid-October.

Larval Biology: Larvae of this species were found quite frequently in the early succession habitats of the Centennial Valley. At some locations, burrows occurred every 16-20 centimeters across open sandy areas. The larval burrows are easily identifiable by the borrow pit with an overhanging tunnel for grabbing prey.

Centennial Valley Habitat Associations and Treatment Response: *Cicindela formosa* was more abundant in intermediate succession habitats particularly in the swale and blowout portions of the sandhills. This species was the most abundant of any tiger beetle species, occupying every site sampled (Fig. 10). There was no statistically significant association of *C. formosa* to a particular sere or dune microhabitat and there was no significant effect of controlled burning treatment. This species was observed by

Figure 8. Variation in the maculation of *Cicindela formosa* in the Centennial Valley.

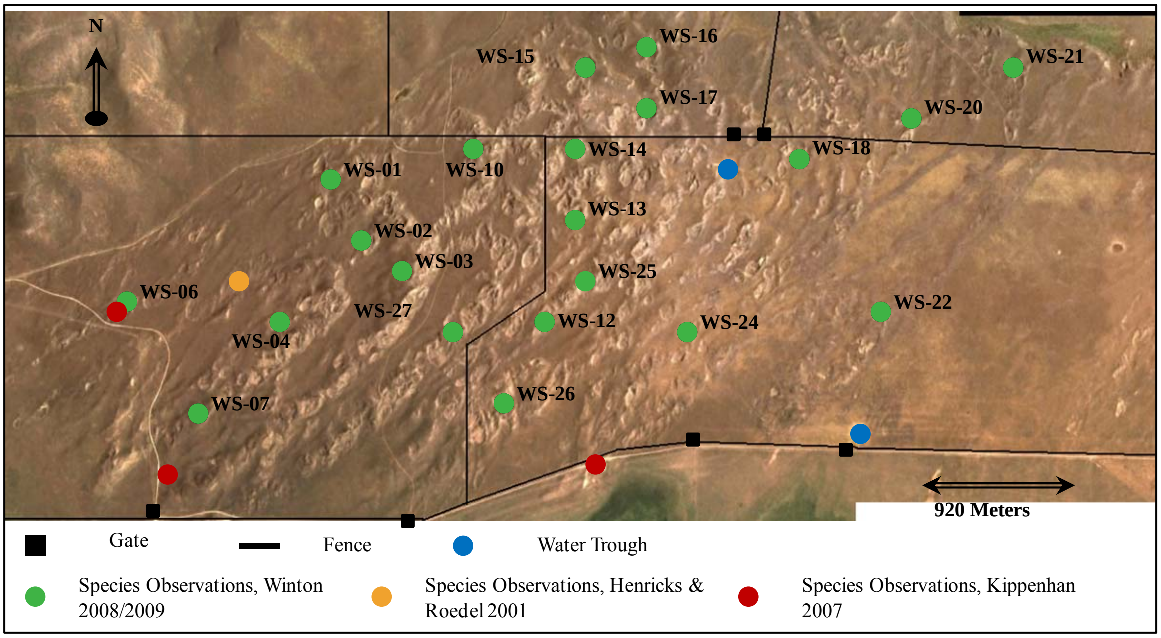

Figure 9. The observations and distribution of *Cicindela formosa* in the Centennial Sandhills.

all previous studies in large numbers. Pearson and Roedel (2001) collected consistent numbers at a single site and made numerous other observations throughout the sandhills including the Eastern Sandhills. Peter Lesica observed this species in the late 1990's and was the first to document it in the sandhills. Kippenhan also found *C. formosa* in large numbers three sites in the western sandhills and two in the eastern (Kippenhan 2007).

*Cicindela decemnotata* Say, Badlands Tiger Beetle: *Cicindela decemnotata* is commonly found in open areas with sparse vegetation. This species is widespread in the Rocky Mountain region and has quite diverse external characters. In the northern parts of its range, it is commonly found near sagebrush and other small shrubs. In the Centennial, the species can be a coppery-brown to a dull sage green with a small degree of variety in the maculation (Fig. 11).

Behavior: This species is quick to fly and when it does take flight it is capable of flying long distances. In most localities where this beetle persisted, it was often present in small numbers.

Seasonality: This species has been collected in the Centennial as early as May, but it could emerge earlier depending on seasonal conditions. It has been collected into early October. *C. decemnotata* is a known spring/fall active species.

Larval Biology: No larvae of this species were encountered in the Centennial Sandhills and its larval biology has not been documented.

Centennial Valley Habitat Associations & Treatment Response: *C. decemnotata* was observed in most habitats in the Centennial, even in some of the completely stabilized areas outside the wind influenced portions of the dune. In other portions of its

Figure 10. Variations of *Cicindela decemnotata* in the Centennial Sandhills.

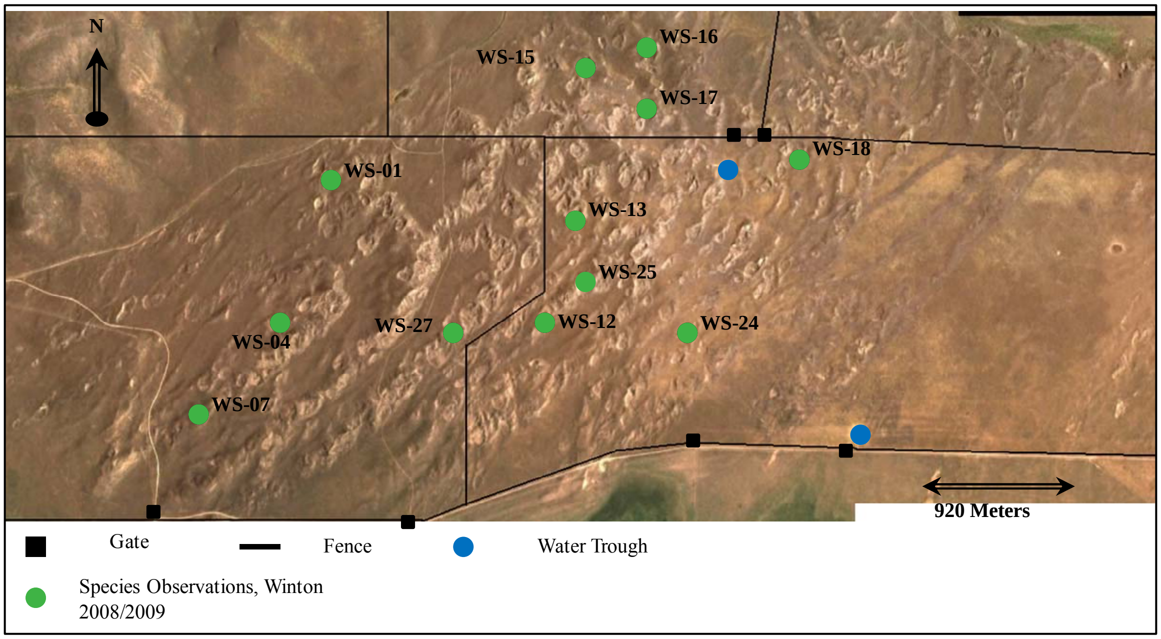

Figure 11. The observation of *Cicindela decemnotata* in the Centennial Sandhills.

range, this species is commonly associated with soils other than sand (Pearson et al. 2006), but in the sandhills it seems to tolerate and persists in virtually all habitat types, particularly those with more organic matter. This species was observed and collected by both the MTNHP surveying in the Eastern Sandhills in 2001 and Kippenhan in 2007.

Cicindela tranquebarica Herbst, Oblique-lined Tiger Beetle: *Cicindela tranquebarica* is not often associated with dry, sandy habitats. This species is typically found in areas near water or with significant amounts of moisture. It was collected only twice in the West Sandhills but was found to be quite common by Hendricks & Roedel in the expanses of older sandhills between the Eastern and Western Sandhills, most likely due to the proximity of Teepee Creek.

Behavior: Not Documented

Seasonality: This species is fairly tolerant of season conditions and could be encountered in the Centennial when the area is free of snow and the danger of hard frosts has passed (this is typically from late April to late October).

Larval Biology: Oviposition of this species often occurs in close proximity to water. The potential ovipositional habitat in the sandhills is most likely near Teepee Creek. Most individuals encountered were likely transients.

Centennial Valley Habitat Associations and Treatment Response: Due to the low number of individuals collected in the sandhills, there were no observable associations to any of the common habitats. Kippenhan noted this species preference towards the hard-packed sand and soil in areas near the eastern sandhills and in the vicinity of Teepee Creek.

Figure 12. *Cicindela tranquebarica*

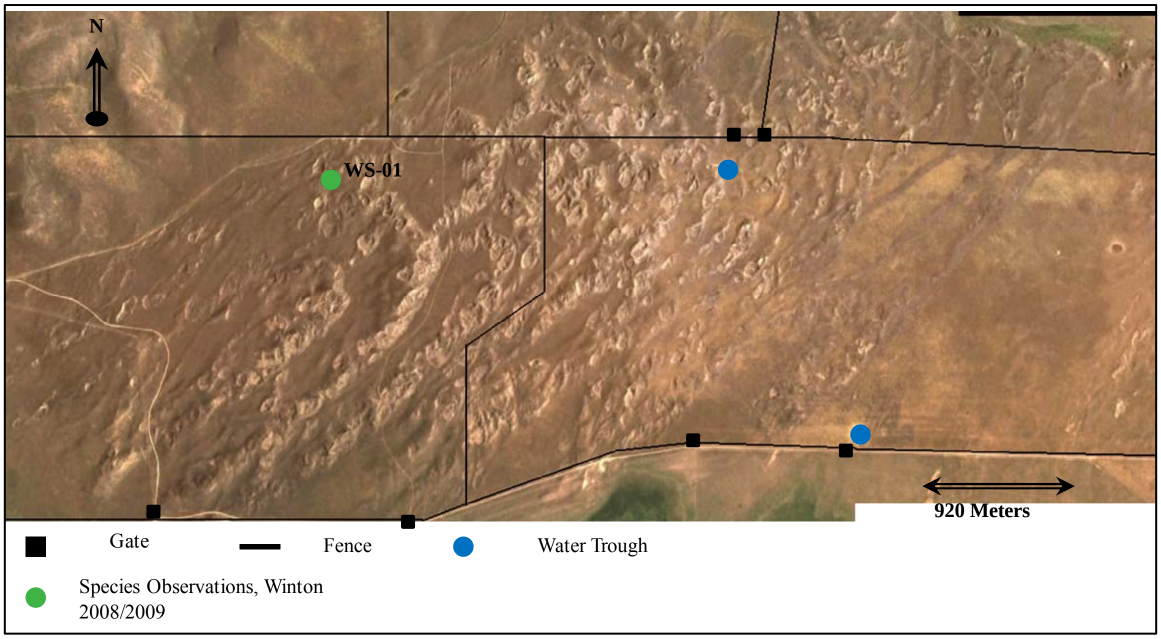

Figure 13. The observation of *Cicindela tranquebarica* in the Centennial Sandhills.

Cicindela purpurea Olivier, Cow Path Tiger Beetle: *Cicindela purpurea* is a widespread North American tiger beetle that prefers grassy habitats with some exposed soils. In the Centennial it is often a dull green color with a significantly reduced rear maculation (Fig. 15).

Behavior: Not Observed

Seasonality: *Cicindela purpurea* is a spring/fall emerging species and can be seen in the Centennial from April until late September.

Larval Biology: None Observed

Centennial Valley Habitat Associations and Treatment Response: Despite its common name, this species was collected in higher number in areas void of the influences of cattle. Four specimens of *C. purpurea* were collected on four separate occasions: one by hand and three by pitfall trap. The distribution of sites where it was collected were located on the proximal edges of the sandhills leading one to believe it does not prefer the fine sands found in the core dunes. Based on its preference for mixed sand/clay substrates, it may be targeting the areas where sand and the outlying soils have mixed. This species showed no significant population reduction as a result of sandhill treatments, most likely due to it being observed on so few occasions.

Figure 14. Centennial Sandhills representative of the species *Cicindela purpurea*.

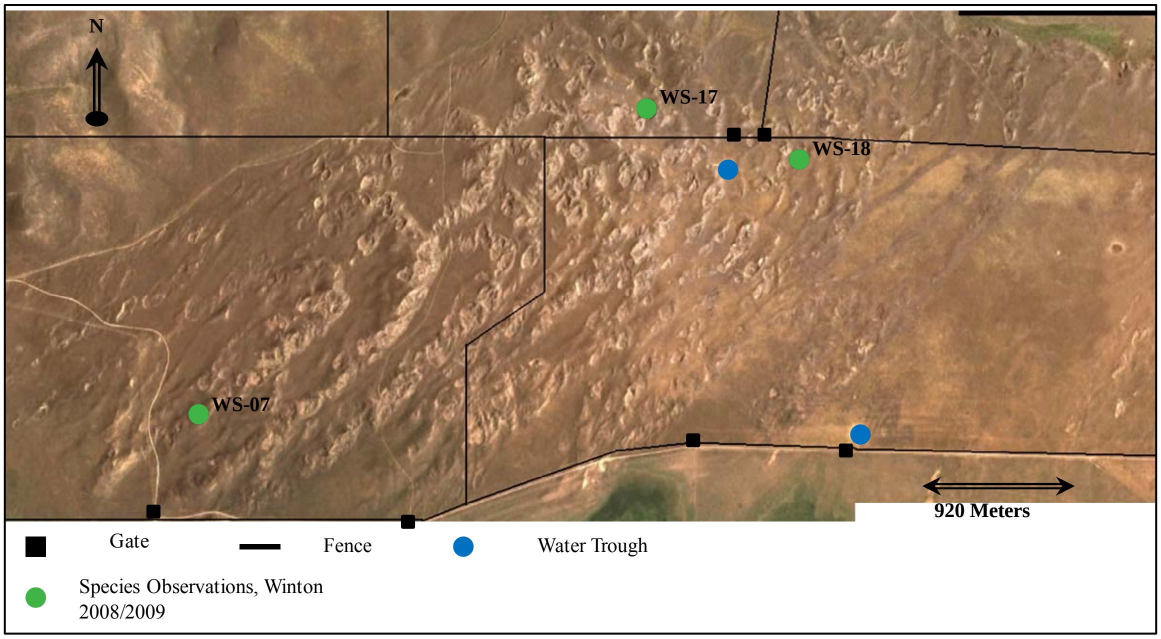

Figure 15. The observations of *Cicindela purpurea* in the Centennial Sandhills.

Cicindela nebraskana Casey, Prairie Long-lipped Tiger Beetle: This species was surprising to see in the sandhills, as it is typically found in areas having darker soils, as a result of this association its elytra are a dark black (Fig. 17). The areas where it was observed had high amounts of organic matter in the soil or small dense areas of grasses and forbs. It was often quick to fly when disturbed and flew long distances to find safety.

Behavior: See Habitat Associations.

Seasonality: This species was most often observed and collected in the August and September months.

Larval Biology: None Observed

Centennial Valley Habitat Associations and Treatment Response: This species was observed much more frequently in the second year of sampling following the burn. In pitfall traps it was collected almost exclusively in the burned areas following treatment, but visual observations were more often in non-burned areas. There was a significant association to the swale portion of dunes, but these results are based on the distribution of five specimens and should be interpreted with care. That this species was observed more frequently in the second field season may be the result of normal population fluctuations.

Figure 16. Representative of the Centennial Sandhills population of *Cicindela nebraskana.*

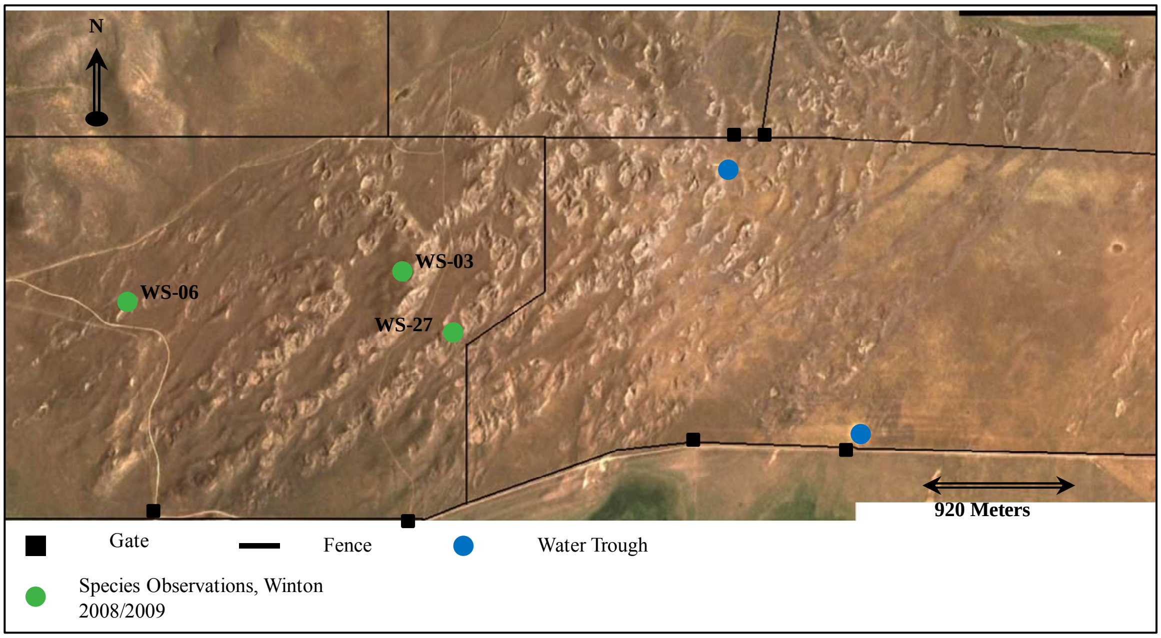

Figure 17. The observations of *Cicindela nebraskana* in the Centennial Sandhills.

Cicindela punctulata Olivier, Punctured Tiger Beetle: This species is widespread across North America and occupies a wide variety of habitats throughout its range. It is typically associated with moist areas with packed soils, such as trails and dirt roads. It was encountered in the middle of some of largest areas of open sand in the sandhills, and far from water and the moisture typical of its preferred habitat.

Behavior: Not Observed

Seasonality: This species is known to emerge in the spring and fall, and is typically seen in the middle of summer. This seasonality could suggest reasons why this species was not encountered more frequently.

Larval Biology: Not Observed

Centennial Valley Habitat Associations and Treatment Response: The presence of this species in the sandhills is a new record for the area. Although common throughout its range and expected to be found in the Centennial Valley, it was surprising to find it in the sandhills, as it is often associated with riparian areas. Only one specimen of this species was collected so there is no way of estimating the effects of treatments or the habitat associations of this species, likely due to it being a transient.

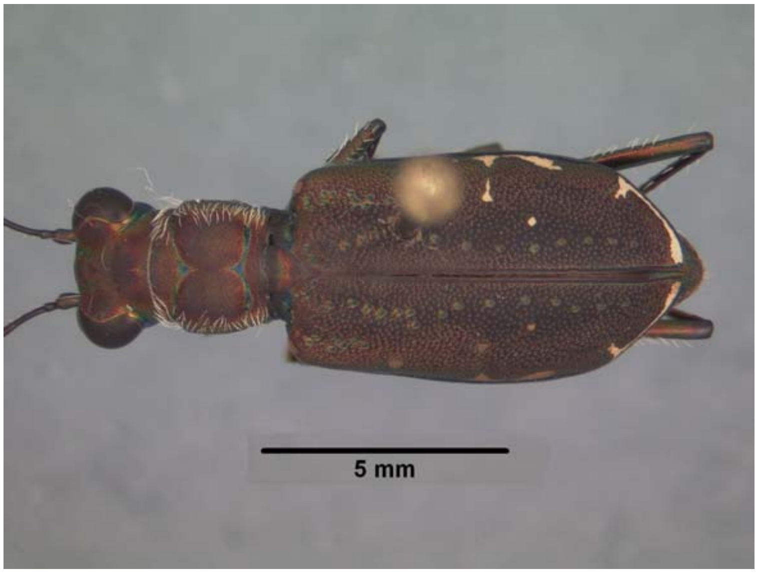

Figure 18. *Cicindela punctulata* from the Centennial Sandhills.

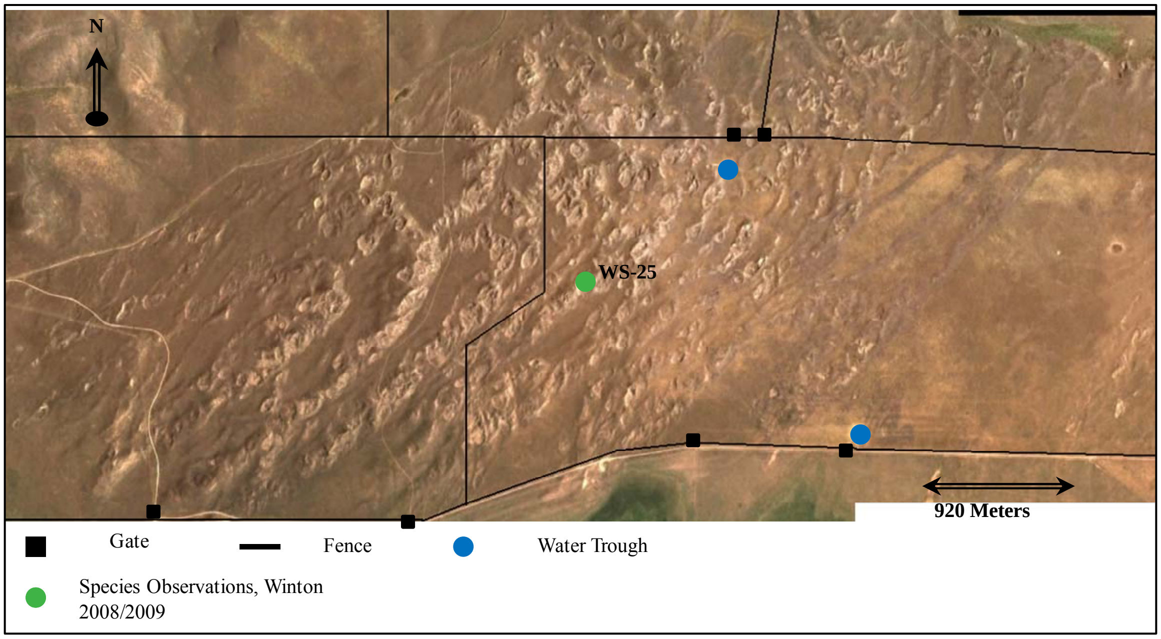

Figure 19. The observations of *Cicindela punctulata* in the Centennial Sandhills.

Cicindela arenicola Rumpp, St. Anthony Dune Tiger Beetle: *Cicindela arenicola* is native to the Snake River Plain of southern Idaho and was previously thought to be limited to that area. This species was either observed or collected on four separate occasions over the course of two year. Observations were made at only one small location in the Centennial Sandhills. Other suitable habitat throughout the sandhills was surveyed, but it appears the populations of this species are extremely limited. In addition to being a new state and Atlantic Drainage record, this species is also significant due to its listing in Idaho as a species of conservation concern. Due to its limited distribution and known sensitivity in Idaho, this population should be watched and managed closely (Winton et al. 2010).

Behavior: Adults and larvae were limited to windswept areas of open sand, particularly to the swale area and just below the blowout. There was little to no vegetation in the area where it was observed and small bit of random substrate mixed with the sand.

Seasonality: In its Idaho range, this species can be observed in early March and well into late fall. The Centennial populations were observed from May to September.

Larval Biology: First, second, and third instars were collected, and attempts are being made to rear adults and describe their larval biology.

Centennial Valley Habitat Associations and Treatment Response: This Centennial population is unique and the early seral wind-swept habitats associated with it need to be managed effectively. It has been locally extirpated in parts of its Idaho range due to vegetation succession. There has been a great deal of work on this species by several entomologists at Boise State and Idaho State University (Anderson 1989; Baker et al. 1997, 1997; Bauer 1991). The biology and population dynamics of this species are well studied. There is currently a molecular analysis being run at University of Idaho to determine the relatedness of the Montana population to those in Idaho.

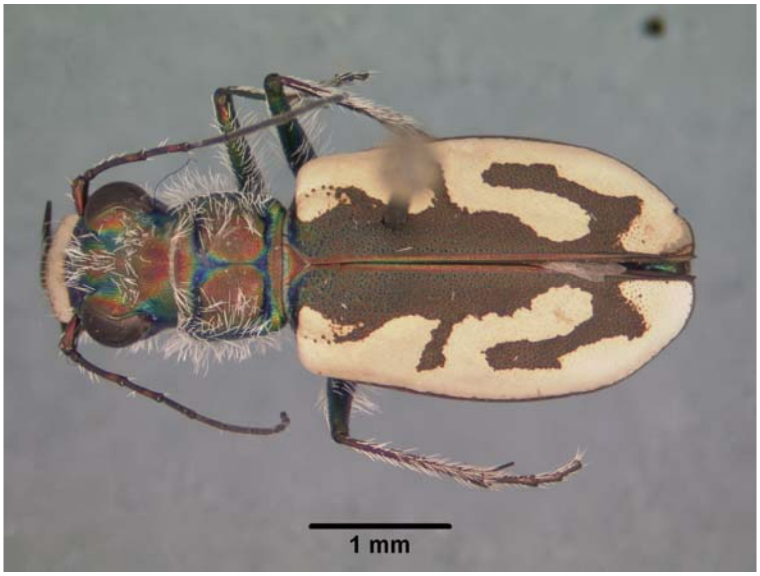

Figure 20. *Cicindela arenicola* from the Centennial Sandhills.

Discussion

Previous tiger beetle surveys in the Centennial Sandhills were expected to observe a greater number of species due to their common associations with a variety of sand-dominated habitats. Hendricks and Roedel expected to encounter *C. arenicola* due to the Centennial Valley's proximity to populations at the St. Anthony Dunes in Idaho (Hendricks & Roedel 2001). Although this species was not observed during their survey, they were correct in their prediction that it could possibly exist at some locations in the valley. Kippenhan, a highly experienced collector and observer of tiger beetles, expected that both *Cicindela lengi* and *Cicindela scutellaris* would occur in the Centennial Sandhills due to their common association with *C. formosa*. These species have not been encountered by any sampling efforts, but may only occur in a few localities. The Eastern Sandhills still require a great deal of attention and sampling to better understand the full extent of tiger beetle distribution in the Centennial. The only species not encountered in the West Sandhills that has been documented in the east, *C. longilabris*, was observed with *C. decemnotata,* and may occupy similar habitat in the Eastern sandhills. As with this circumstance, there may still be other species occurring in the East Sandhills not observed in the west. Only further sampling will fully expose the distributions of all tiger beetles over the entire Centennial sandhills landscape.

The distribution of several encountered tiger beetles in the Centennial Valley leaves questions to be answered. How are species such as *C. arenicola* able to cross the continental divide and persist in such small numbers and yet *C. formosa* is not present in Idaho habitats it would be more successful in? Why are *C. lengi* and *C. scuttelaris* not found in the Centennial when their distributions overlap that of *C. formosa* through much of its range and they prefer much the same habitat? The answers to questions such as these will require a more thorough investigation. There is also a great deal of work needing to be done in the state of Montana on the distributions of tiger beetle and other coleopteran species. When viewing a distribution map, of all but the common Rocky Mountain species, there often appears to be a large gap coincidently around Montana’s border. Further research into the phylo-geography of these species is also needed so that we can better understand how related species have been distributed through time and space.

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APPENDICES

APPENDIX A

FAMILY AND SPECIES LIST

Appendix A. Family and species list of all species collected by pitfall trap in the Centennial Sandhills during both seasons. All species listed were incorporated into the dataset. Species are listed with their corresponding alphabetical and numeric codes as described in the methods section of Chapter 2. Family classification is according to Arnett et al. (2002).

COLEOPTERA
ADEPHAGA

CARABOIDEA

CARABIDAE

amacon	8	*Amara confusa* Leconte
amaobe	9	*Amara obesa* Say
harfra	10	*Harpalus fraternis* LeConte
harbas	11	*Harpalellus basilaris* Kirby
haramp	12	*Harpalus amputatus* Say
pioset	13	*Piosoma setosum* LeConte
callux	14	*Calosoma luxatum* Say
pteads	15	*Pterostichus adstrictus* Eschscholtz
eurgro	16	*Euryderus grossus* Say
cympla	17	*Cymindis planipennis* LeConte
calvir	18	*Calleida viridis* Dejean
cartae	19	*Carabus taedatus* Fabricius
lebvit	20	*Lebia vittata* Fabricius
syname	21	*Syntomus americanus* Dejean
carsp1	22	Carabidae sp.1
carsp2	23	Carabidae sp.2
carsp3	24	Carabidae sp.3

CICINDELINAE

cicfor	1	*Cicindela formosa* Say
cicdec	2	*Cicindela decemnotata* Say
cictra	3	*Cicindela tranquebarica* Herbst
cicpur	4	*Cicindela purpurea* Olivier
cicneb	5	*Cicindela nebraskana* Casey
cicpun	6	*Cicindela punctulata* Olivier

POLYPHAGA

HYDROPHILOIDEA

HISTERIDAE

xeraci	73	*Xerosaprinus acilinea* Marseul
xerlub	74	*Xerosaprinus lubricus* LeConte
haetri	75	*Haeterius tristriatus* Horn

STAPHYLINOIDEA

PTILIIDAE

ptisp1	95	Ptiliidae sp.1

AGYRTIDAE

aptten	98	*Apteroloma tenuicorne* LeConte

LEIODIDAE

hydsp1	69	*Hydnobius* sp.
ptosp1	70	*Ptomaphagus* sp.
leisp1	71	Leiodidae sp.

SILPHIDAE

nichyb	77	*Nicrophorus hybridus* Hatch & Angell
nicgut	78	*Nicrophorus guttula* Mutschulsky
thalap	79	*Thanatophilus lapponicus* Herbst

STAPHYLINIDAE

stasp1	47	Staph. sp.1
stasp2	48	Staph. sp.2
stasp3	49	Staph. sp.3
stasp4	50	Staph. sp.4
stasp5	51	Staph. sp.5
stasp6	52	Staph. sp.6
stasp7	53	Staph. sp.7
stasp8	54	Staph. sp.8
stasp9	55	Staph. sp.9
stasp10	56	Staph. sp.10

stasp11	57	Staph. sp.11
stasp12	58	Staph. sp.12
stasp13	59	Staph. sp.13

SCARABOIDEA

SCARABIDAE

aphgra	83	*Aphodius granarius* Linnaeus
ontnuc	84	*Onthophagus nuchicornis* LeConte
cansim	85	*Canthon simplex* LeConte
aphnsp	86	*Aphodius n.sp. nr. perfimbriatus* Gordon
aphsp1	87	*Aphodius* sp.1

GLARESIDAE

glansp	88	*Glaresis* n.sp.

BYRRHOIDEA

BYRRHIDAE

byrame	72	*Byrrhus americanus* LeConte

HETEROCERIDAE

laptri	89	*Lapsus tristris* Mannerheim

BOSTRICHOIDEA

DERMESTIDAE

dertal	80	*Dermestes talpinus* Mann.
dermar	81	*Dermestes marmoratus* Say

CLEROIDEA

MELYRIDAE

trisp1	90	*Trichochrous* sp.1

CUCUJOIDEA

MONOTOMIDAE

rhidim	82	*Rhizophagus dimiatus* Mannerheim

PHALACRIDAE

phasp1	96	*Phalacrus* sp.1
phasp2	97	*Olibrus* sp.1

CRYPTOPHAGIDAE

cryhis	76	*Cryptophagus histricus* Casey

COCCINELIDAE

gnansp	33	*Gnathoweisea n.sp.*
coctra	34	*Coccinella transversoguttata richardsoni* Brown
brusep	35	*Brumoides septentrionis septentrionis* Weiser
hypmim	36	*Hyperaspidius mimus* Casey
hypher	37	*Hyperaspidius hercules* Belicek
hyplat	38	*Hyperaspus lateralis* Mulsant
hipmoe	39	*Hippodamia moesta bowditchi* Johnson
hipsin	40	*Hippodamia sinuata* Mulsant

LATHRIDIIDAE

melame	99	*Melanopthalma americana* Mannerheim

TENEBRIONOIDEA

MORDELLIDAE

morsp1	91	Mordellidae

TENEBRIONIDAE

eleext	25	*Eleodes extricatus* Say
elenig	26	*Eleodes nigrinus* LeConte
elecor	27	*Eleodes cordatus* Eschscholtz
eleten	28	*Eleodes tenebrosa* Horn
conobe	29	*Coniontis obesa* Leconte
conova	30	*Coniontis ovalis* LeConte
blapim	31	*Blapstinus pimalis* Casey
helcon	32	*Helops convexulus* LeConte

ANTHICIDAE

notser	66	*Notoxus serratus* LeConte
anttob	67	*Anthicus tobias* Marseul

antlut	68	*Anthicus lutulentus* Casey

CRYSOMELOIDEA

CRYSOMELIDAE

gransp	41	*Graphops n.sp.*
dislat	42	*Disonycha latrifons* Schaeffer
galrud	43	*Galeruca rudis* LeConte
pachep	44	*Pachybrachis sp. nr. hepaticus*
dibsp1	45	*Dibolia* sp. 1
monsp1	46	*Monoxia* sp.

CURCULIONOIDEA

CURCULIONIDAE

otiova	60	*Otiorhynchus ovatus* LeConte
cursp1	61	Curculionid. sp.1
cursp2	62	Curculionid. sp.2
cursp3	63	Curculionid. sp.3
cursp4	64	Curculionid. sp.4
cursp5	65	Curculionid. sp.5

APPENDIX B

SITE DESCRIPTIONS

Appendix B. Description and distribution of sites and subplots in Centennial Sandhills as well as their treatment and seral association.

Plot Number	Subplot	Burn Treatment	Successional Stage	Latitude	Longitude
01	A	Burned	Intermediate	44° 41.576'N	111° 49.587'W
01	B	Burned	Intermediate	44° 41.576'N	111° 49.575'W
01	C	Burned	Intermediate	44° 41.576'N	111° 49.563'W
01	D	Burned	Intermediate	44° 41.583'N	111° 49.575'W
02	A	Burned	Intermediate	44° 41.365'N	111° 49.402'W
02	B	Burned	Intermediate	44° 41.374'N	111° 49.396'W
02	C	Burned	Intermediate	44° 41.384'N	111° 49.389'W
02	D	Burned	Intermediate	44° 41.382'N	111° 49.382'W
03	A	Burned	Early	44° 41.302'N	111° 49.259'W
03	B	Burned	Early	44° 41.296'N	111° 49.251'W
03	C	Burned	Early	44° 41.294'N	111° 49.234'W
03	D	Burned	Early	44° 41.306'N	111° 49.265'W
04	A	Burned	Early	44° 41.144'N	111° 49.757'W
04	B	Burned	Early	44° 41.148'N	111° 49.743'W
04	C	Burned	Early	44° 41.152'N	111° 49.735'W
04	D	Burned	Early	44° 41.155'N	111° 49.747'W
06	A	Burned	Intermediate	44° 41.196'N	111° 50.383'W
06	B	Burned	Intermediate	44° 41.195'N	111° 50.376'W
06	C	Burned	Intermediate	44° 41.196'N	111° 50.368'W
07	A	Burned	Early	44° 40.886'N	111° 50.104'W
07	B	Burned	Early	44° 40.893'N	111° 50.085'W
07	C	Burned	Early	44° 40.893'N	111° 50.104'W
07	D	Burned	Early	44° 40.893'N	111° 50.085'W
10	A	Control	Late	44° 41.681'N	111° 49.035'W
10	B	Control	Late	44° 41.682'N	111° 49.025'W
10	C	Control	Late	44° 41.683'N	111° 49.016'W
10	D	Control	Late	44° 41.678'N	111° 49.028'W
12	A	Control	Early	44° 41.134'N	111° 48.826'W
12	B	Control	Early	44° 41.143'N	111° 48.826'W
12	C	Control	Early	44° 41.152'N	111° 48.825'W
13	A	Control	Intermediate	44° 41.462'N	111° 48.590'W
13	B	Control	Intermediate	44° 41.470'N	111° 48.576'W
13	C	Control	Intermediate	44° 41.475'N	111° 48.561'W
13	D	Control	Intermediate	44° 41.484'N	111° 48.587'W
14	A	Control	Intermediate	44° 41.640'N	111° 48.588'W
14	B	Control	Intermediate	44° 41.652'N	111° 48.579'W
14	C	Control	Intermediate	44° 41.663'N	111° 48.577'W
14	D	Control	Intermediate	44° 41.653'N	111° 48.607'W
15	A	Control	Late	44° 41.878'N	111° 48.558'W

Appendix B cont.

Plot Number	Subplot	Burn Treatment	Successional Stage	Latitude	Longitude
15	B	Control	Late	44° 41.885'N	111° 48.542'W
15	C	Control	Late	44° 41.895'N	111° 48.530'W
15	D	Control	Late	44° 41.878'N	111° 48.534'W
16	A	Control	Late	44° 41.921'N	111° 48.283'W
16	B	Control	Late	44° 41.940'N	111° 48.285'W
16	C	Control	Late	44° 41.948'N	111° 48.299'W
16	D	Control	Late	44° 41.923'N	111° 48.306'W
17	A	Control	Late	44° 41.776'N	111° 48.314'W
17	B	Control	Late	44° 41.761'N	111° 48.287'W
17	C	Control	Late	44° 41.764'N	111° 48.270'W
17	D	Control	Late	44° 41.747'N	111° 48.284'W
18	A	Control	Intermediate	44° 41.616'N	111° 47.682'W
18	B	Control	Intermediate	44° 41.626'N	111° 47.684'W
18	C	Control	Intermediate	44° 41.645'N	111° 47.684'W
18	D	Control	Intermediate	44° 41.629'N	111° 47.671'W
20	A	Control	Late	44° 41.679'N	111° 47.253'W
20	B	Control	Late	44° 41.693'N	111° 47.244'W
20	C	Control	Late	44° 41.708'N	111° 47.234'W
20	D	Control	Late	44° 41.702'N	111° 47.266'W
21	A	Control	Late	44° 41.838'N	111° 46.797'W
21	B	Control	Late	44° 41.850'N	111° 46.790'W
21	C	Control	Late	44° 41.870'N	111° 46.796'W
21	D	Control	Late	44° 41.860'N	111° 46.772'W
22	A	Control	Late	44° 41.183'N	111° 47.346'W
22	B	Control	Late	44° 41.193'N	111° 47.339'W
22	C	Control	Late	44° 41.202'N	111° 47.335'W
22	D	Control	Late	44° 41.197'N	111° 47.355'W
24	A	Control	Early	44° 41.132'N	111° 48.147'W
24	B	Control	Early	44° 41.126'N	111° 48.137'W
24	C	Control	Early	44° 41.126'N	111° 48.122'W
25	A	Control	Early	44° 41.257'N	111° 48.566'W
25	B	Control	Early	44° 41.253'N	111° 48.550'W
25	C	Control	Early	44° 41.264'N	111° 48.545'W
26	A	Control	Late	44° 40.934'N	111° 48.869'W
26	B	Control	Late	44° 40.933'N	111° 48.856'W
26	C	Control	Late	44° 40.950'N	111° 48.853'W
26	D	Control	Late	44° 40.941'N	111° 48.842'W
27	A	Control	Late	44° 41.121'N	111° 49.054'W
27	B	Control	Late	44° 41.125'N	111° 49.043'W
27	C	Control	Late	44° 41.133'N	111° 49.035'W
27	D	Control	Late	44° 41.116'N	111° 49.036'W

APPENDIX C

ENVIRONMENTAL DATA

Appendix C. Survey date, temperature, degree day, solar radiation and precipitation for the baseline sampling year.

Date	Temperatures (°F)		Degree-days		Average Solar Radiation (W/m^2)	Total Precip (mm)
	Min	Max	Daily	Accumulated		
30-Aug-2008	44	76	2.38	2.38	163.75	0
31-Aug-2008	57	79	4.45	6.83	232.20	0
1-Sep-2008	33	61	0	6.83	84.04	9.4
2-Sep-2008	24	58	0	6.83	245.33	0
3-Sep-2008	38	57	0	6.83	208.5	1.02
4-Sep-2008	35	59	0	6.83	144.79	0
5-Sep-2008	24	55	0	6.83	164.79	0
6-Sep-2008	35	60	0	6.83	193.25	0
7-Sep-2008	34	59	0	6.83	207.33	0
8-Sep-2008	22	69	0.29	7.12	255.79	0
9-Sep-2008	31	77	2.28	9.4	209.21	0
10-Sep-2008	37	71	0.78	10.17	156	0
11-Sep-2008	26	62	0	10.17	249.92	0
12-Sep-2008	25	70	0.47	10.65	230.63	0
13-Sep-2008	33	72	0.96	11.61	202	0
14-Sep-2008	26	73	1.11	1.11	244.04	0
15-Sep-2008	32	77	2.3	3.42	242.29	0
16-Sep-2008	35	76	2.09	5.5	239.79	0
17-Sep-2008	34	79	2.99	8.49	238	0
18-Sep-2008	33	77	2.33	10.82	166.83	0
19-Sep-2008	35	75	1.79	12.62	203.38	0
20-Sep-2008	43	73	1.41	14.03	108.54	3.3
21-Sep-2008	40	50	0	14.03	117.63	5.33
22-Sep-2008	37	52	0	14.03	166.17	0
23-Sep-2008	22	55	0	14.03	216.25	0
24-Sep-2008	39	65	0	14.03	202.25	0
25-Sep-2008	43	66	0	14.03	114.25	0
26-Sep-2008	28	67	0.05	14.07	206.75	0
27-Sep-2008	29	72	0.92	14.99	181	0
28-Sep-2008	29	73	1.15	16.14	210.42	0
29-Sep-2008	29	76	1.94	18.09	210.75	0
30-Sep-2008	31	77	2.28	20.36	208.25	0
1-Oct-2008	34	76	2.06	22.42	165.58	0
2-Oct-2008	37	72	1.02	23.44	175.58	0
3-Oct-2008	46	63	0	23.44	175.71	0
4-Oct-2008	45	59	0	23.44	28.67	1.78

Appendix C cont.

Date	Temperatures (°F)		Degree-days		Average Solar Radiation (W/m^2)	Total Precip (mm)
	Min	Max	Daily	Accumulated		
24-Aug-2009	17	50	0	0	281.29	0
25-Aug-2009	16	45	0	0	298.58	0
26-Aug-2009	20	38	0	0	324.79	0
27-Aug-2009	28	48	0	0	327.83	0
28-Aug-2009	49	69	0.45	0.45	286.04	0
29-Aug-2009	29	74	1.4	1.85	184.71	0
30-Aug-2009	39	67	0.06	1.91	242.04	15.24
31-Aug-2009	34	78	2.67	4.58	157	5.33
1-Sep-2009	34	79	2.99	7.57	276.08	1.02
2-Sep-2009	33	82	3.95	11.52	306.83	0
3-Sep-2009	32	80	3.24	14.76	228.42	0
4-Sep-2009	28	74	1.39	1.39	303.75	0
5-Sep-2009	28	60	0	1.39	163.46	0
6-Sep-2009	36	60	0	1.39	210.58	0
7-Sep-2009	41	77	2.59	3.98	249.92	0
8-Sep-2009	40	78	2.89	6.87	317.125	0
9-Sep-2009	39	78	2.85	9.72	302.92	0
10-Sep-2009	41	78	2.93	12.65	279.04	0
11-Sep-2009	36	76	2.11	14.76	295.04	0
12-Sep-2009	47	75	2.17	16.93	298.92	0
13-Sep-2009	31	70	0.51	17.44	235.5	0
14-Sep-2009	30	74	1.42	18.86	209	0
15-Sep-2009	38	74	1.58	20.43	211.17	0
16-Sep-2009	35	76	2.09	22.52	232.33	0
17-Sep-2009	28	75	1.65	24.17	268.67	0
18-Sep-2009	27	64	0	24.17	265.125	0
19-Sep-2009	46	64	0	24.17	257.125	0
20-Sep-2009	52	74	2.05	26.22	274.33	0
21-Sep-2009	44	78	3.07	29.28	280.38	0
22-Sep-2009	41	81	3.98	3.98	266.58	0
23-Sep-2009	44	80	3.79	7.77	264.83	0
24-Sep-2009	41	81	3.98	11.75	264.58	0
25-Sep-2009	40	77	2.56	14.31	253.04	0
26-Sep-2009	47	60	0	14.31	258.42	0
27-Sep-2009	50	78	3.41	17.72	265.55	0
28-Sep-2009	43	78	3.02	20.74	252.5	0
29-Sep-2009	42	83	4.78	25.52	222.625	0
30-Sep-2009	44	81	4.16	29.68	80.41	0
1-Oct-2009	42	79	3.32	33	166.83	0
2-Oct-2009	41	73	1.36	34.36	231.125	0
3-Oct-2009	49	69	0.45	34.81	205.25	1.02

APPENDIX D

ABUNDANCE AND ASSOCIATION OF SPECIES TO TREATMENT

Appendix D. Beetle species included in the analysis and the effect of the prescribed burning treatment on their abundances (the significant change in abundance in burn and control between years). See methods for details.

Species	Total	Baseline		Post-Treatment		F-Value	d.f.	P-Value
		Control	Burn	Control	Burn			
Cicindela formosa	2098	851	357	714	176	0.92	1, 396	0.34
Cicindela decemnotata	31	22	3	4	2	3.27	1, 396	0.07
Cicindela purpurea	4	2	1	0	1	0.21	1, 396	0.65
Cicindela nebraskana	5	0	0	1	4	3.13	1, 396	0.08
Amara quenseli	3648	2505	672	392	79	3.02	1, 396	0.08
Amara confusa	22	16	3	2	0	1.53	1, 396	0.22
Harpalus fraternis	64	11	7	13	33	11.53	1, 396	<0.001
Harpalellus basilaris	6	0	5	1	0	18.74	1, 396	<0.001
Piosoma setosum	7	0	0	7	0	0.49	1, 396	0.49
Pterostichus adstrictus	3	0	0	2	1	0.02	1, 396	0.89
Euryderus grossus	10	3	0	7	0	0.12	1, 396	0.73
Cymindis planipennis	23	12	3	6	2	0.25	1, 396	0.61
Calleida viridis	3	0	2	1	0	6.52	1, 396	0.01
Lebia vittata	97	37	44	14	2	10.27	1, 396	<0.001
Syntomus americanus	3	0	3	0	0	6.89	1, 396	0.01
Carabidae sp.1	2	0	0	2	0	0.27	1, 396	0.61
Carabidae sp.2	3	0	0	2	1	0.02	1, 396	0.89
Eleodes extricatus	340	29	151	66	94	24.12	1, 396	<0.001
Eleodes nigrinus	28	10	4	9	5	0.11	1, 396	0.74
Eleodes cordatus	22	1	14	0	7	4.66	1, 396	0.03

Appendix D cont.

Species	Total	Baseline Control	Baseline Burn	Post-Treatment Control	Post-Treatment Burn	F-Value	d.f.	P-Value
Eleodes tenebrosa	4	0	1	1	2	0.00	1, 396	0.95
Coniontis obesa	14	1	11	1	1	15.11	1, 396	<0.001
Coniontis ovalis	4	0	3	0	1	3.46	1, 396	0.06
Blapstinus pimalis	3	0	2	0	1	2.26	1, 396	0.13
Helops convexulus	3	0	1	1	1	0.45	1, 396	0.50
Coccinella transversoguttata	8	1	0	4	3	0.83	1, 396	0.36
Brumoides septentrionis	3	1	1	1	0	0.93	1, 396	0.34
Hyperaspidius mimus	101	17	0	81	3	2.21	1, 396	0.14
Hyperaspidius hercules	2	0	1	0	1	0.21	1, 396	0.65
Hippodamia moesta	4	3	0	0	1	3.32	1, 396	0.07
Hippodamia sinuata	5	1	4	0	0	7.17	1, 396	0.01
Graphops n.sp.	12	6	1	3	2	1.21	1, 396	0.27
Disonycha latrifons	110	40	36	31	3	12.14	1, 396	<0.001
Galeruca rudis	4	2	0	2	0	0.07	1, 396	0.80
Pachybrachis sp. nr. hepaticus	10	1	0	9	0	1.57	1, 396	0.21
Dibolia sp. 1	6	0	3	1	2	1.78	1, 396	0.18
Staph. sp.1	5	1	1	2	1	0.16	1, 396	0.69
Staph. sp.2	3	3	0	0	0	1.85	1, 396	0.18
Staph. sp.3	5	3	1	0	1	0.58	1, 396	0.45
Staph. sp.4	2	2	0	0	0	1.22	1, 396	0.27
Staph. sp.5	3	2	0	1	0	0.36	1, 396	0.55
Staph. sp.7	3	3	0	0	0	1.85	1, 396	0.18

Appendix D cont.

Species	Total	Baseline		Post-Treatment		F-Value	d.f.	P-Value
		Control	Burn	Control	Burn			
Staph. sp.8	8	1	3	2	2	1.55	1, 396	0.21
Staph. sp.9	4	1	0	2	1	0.26	1, 396	0.61
Staph. sp.10	1	0	1	0	0	3.76	1, 396	0.05
Staph. sp.11	5	2	0	0	3	6.00	1, 396	0.01
Staph. sp.12	3	2	0	1	0	0.36	1, 396	0.55
Otiorhynchus ovatus	172	96	29	43	4	0.01	1, 396	0.94
Curculionid. sp.1	2	1	1	0	0	0.66	1, 396	0.42
Curculionid. sp.2	3	1	1	1	0	0.93	1, 396	0.34
Curculionid. sp.3	2	1	0	1	0	0.03	1, 396	0.85
Notoxus serratus	8	1	7	0	0	7.65	1, 396	0.01
Anthicus tobias	130	25	48	35	22	15.81	1, 396	<0.001
Anthicus lutulentus	100	27	45	21	7	18.40	1, 396	<0.001
Ptomaphagus sp.	2	0	0	2	0	0.54	1, 396	0.46
Byrrhus americanus	13	2	11	0	0	20.85	1, 396	<0.001
Xerosaprinus acilinea	19	9	0	7	3	0.96	1, 396	0.33
Xerosaprinus lubricus	2	1	0	1	0	0.03	1, 396	0.85
Haeterius tristriatus	3	1	0	2	0	0.01	1, 396	0.91
Cryptophagus histricus	67	46	3	16	2	3.63	1, 396	0.06
Nicrophorus hybridus	131	53	0	44	34	1.98	1, 396	0.16
Nicrophorus guttula	95	35	0	38	22	1.17	1, 396	0.28
Thanatophilus lapponicus	4	3	0	1	0	0.33	1, 396	0.57
Dermestes talpinus	3	3	0	0	0	1.10	1, 396	0.30

Appendix D cont.

Species	Total	Baseline		Post-Treatment		F-Value	d.f.	P-Value
		Control	Burn	Control	Burn			
Aphodius granarius	2	0	2	0	0	7.69	1, 396	0.01
Onthophagus nuchicornis	24	0	1	0	23	2.53	1, 396	0.11
Canthon simplex	6	0	0	2	4	1.71	1, 396	0.19
*Aphodius sp.*1	2	0	0	1	1	0.29	1, 396	0.59
Mordellidae sp.	8	0	0	8	0	1.09	1, 396	0.30
*Phalacrus sp.*1	4	0	3	1	0	6.78	1, 396	0.01
Apteroloma tenuicorne	2	0	0	2	0	0.54	1, 396	0.46

APPENDIX E

ABUNDANCE AND ASSOCIATION OF SPECIES TO SERE

Appendix E. Beetle species included in the analysis and the effect of the prescribed burn treatment on their abundance and successional association (the significant change in abundance in treatment, control, and sere between years). See methods for details.

		Pre-Treatment						Post-Treatment								
		Control			Treatment			Control			Treatment					
Species	Abundance	Early	Intermediate	Late	Early	Intermediate	Late	Early	Intermediate	Late	Early	Intermediate	Late	F-Value	d.f.	P-Value
Cicindela formosa	2098	240	423	188	46	257	54	189	369	156	17	130	29	1.57	2, 394	0.14
Cicindela decemnotata	31	5	10	7	2	1	0	2	0	2	2	0	0	0.91	2, 394	0.50
Cicindela purpurea	4	0	1	1	1	0	0	0	0	0	1	0	0	1.02	2, 394	0.42
Cicindela nebraskana	5	0	0	0	0	0	0	0	1	0	0	2	2	2.14	2, 394	0.04
Amara quenseli	3648	835	1147	523	172	358	142	208	51	133	23	39	17	5.32	2, 394	<0.001
Amara confusa	21	6	8	2	1	1	1	0	0	2	0	0	0	2.41	2, 394	0.02
Harpalus fraternis	64	6	3	2	1	6	0	7	3	3	13	17	3	2.63	2, 394	0.01
Harpalellus basilaris	6	0	0	0	2	3	0	1	0	0	0	0	0	3.86	2, 394	<0.001
Piosoma setosum	7	0	0	0	0	0	0	6	0	1	0	0	0	0.91	2, 394	0.50
Pterostichus adstrictus	3	0	0	0	0	0	0	0	0	2	1	0	0	0.82	2, 394	0.58
Euryderus grossus	10	2	1	0	0	0	0	5	2	0	0	0	0	0.72	2, 394	0.65
Cymindis planipennis	23	3	9	0	1	1	1	4	1	1	1	0	1	1.81	2, 394	0.08
Calleida viridis	3	0	0	0	2	0	0	1	0	0	0	0	0	3.54	2, 394	<0.001
Lebia vittata	97	25	9	3	6	30	8	6	4	4	0	2	0	5.05	2, 394	<0.001
Syntomus americanus	3	0	0	0	3	0	0	0	0	0	0	0	0	4.98	2, 394	<0.001
Carabidae sp.1	2	0	0	0	0	0	0	0	0	2	0	0	0	0.27	2, 394	0.97
Carabidae sp.2	3	0	0	0	0	0	0	2	0	0	0	1	0	1.41	2, 394	0.20
Eleodes extricatus	340	9	14	6	72	61	18	25	24	17	51	42	1	5.30	2, 394	<0.001

Appendix E cont.

		Pre-Treatment						Post-Treatment								
		Control			Treatment			Control			Treatment					
Species	Abundance	Early	Intermediate	Late	Early	Intermediate	Late	Early	Intermediate	Late	Early	Intermediate	Late	F-Value	d.f.	P-Value
Eleodes nigrinus	28	3	3	4	2	2	0	5	2	2	1	3	1	0.50	2, 394	0.83
Eleodes cordatus	22	0	0	1	11	3	0	0	0	0	3	4	0	3.81	2, 394	<0.001
Eleodes tenebrosa	4	0	0	0	0	1	0	0	0	1	0	2	0	1.02	2, 394	0.42
Coniontis obesa	14	0	1	0	4	4	3	0	0	1	1	0	0	2.69	2, 394	0.01
Coniontis ovalis	4	0	0	0	3	0	0	0	0	0	0	1	0	4.09	2, 394	<0.001
Blapstinus pimalis	3	0	0	0	2	0	0	0	0	0	0	1	0	3.73	2, 394	<0.001
Helops convexulus	3	0	0	0	1	0	0	0	0	1	1	0	0	1.09	2, 394	0.37
Coccinella transversoguttata	8	0	1	0	0	0	0	2	1	1	1	1	1	0.63	2, 394	0.73
Brumoides septentrionis	3	0	1	0	0	1	0	0	1	0	0	0	0	0.43	2, 394	0.89
Hyperaspidius mimus	101	2	1	14	0	0	0	16	16	49	1	0	2	0.55	2, 394	0.80
Hyperaspidius hercules	2	0	0	0	0	0	1	0	0	0	0	0	1	4.37	2, 394	<0.001
Hippodamia moesta	4	1	1	1	0	0	0	0	0	0	0	1	0	0.73	2, 394	0.65
Hippodamia sinuata	5	0	0	1	4	0	0	0	0	0	0	0	0	6.46	2, 394	<0.001
Graphops n.sp.	12	3	2	1	1	0	0	1	2	0	0	1	1	1.21	2, 394	0.30
Disonycha latrifons	110	16	20	4	8	19	9	9	5	17	0	0	3	4.53	2, 394	<0.001
Galeruca rudis	4	0	1	1	0	0	0	0	0	2	0	0	0	0.30	2, 394	0.95
Pachybrachis sp. nr. hepaticus	10	0	0	1	0	0	0	1	1	7	0	0	0	0.79	2, 394	0.60
Dibolia sp. 1	6	0	0	0	1	2	0	0	0	1	0	2	0	0.98	2, 394	0.44
Staph. sp.1	5	0	1	0	0	1	0	1	0	1	0	1	0	0.72	2, 394	0.65

Appendix E cont.

		Pre-Treatment						Post-Treatment								
		Control			Treatment			Control			Treatment					
Species	Abundance	Early	Intermediate	Late	Early	Intermediate	Late	Early	Intermediate	Late	Early	Intermediate	Late	F-Value	d.f.	P-Value
Staph. sp.2	3	1	0	2	0	0	0	0	0	0	0	0	0	0.85	2, 394	0.55
Staph. sp.3	5	1	0	2	0	1	0	0	0	0	1	0	0	1.04	2, 394	0.41
Staph. sp.4	2	0	0	2	0	0	0	0	0	0	0	0	0	1.12	2, 394	0.35
Staph. sp.5	3	2	0	0	0	0	0	0	1	0	0	0	0	2.02	2, 394	0.05
Staph. sp.7	3	3	0	0	0	0	0	0	0	0	0	0	0	4.38	2, 394	<0.001
Staph. sp.8	8	0	1	0	0	3	0	0	1	1	0	2	0	1.37	2, 394	0.22
Staph. sp.9	4	1	0	0	0	0	0	0	1	1	0	1	0	0.74	2, 394	0.63
Staph. sp.11	5	1	0	1	0	0	0	0	0	0	1	2	0	1.47	2, 394	0.18
Staph. sp.12	3	0	2	0	0	0	0	0	1	0	0	0	0	0.72	2, 394	0.66
Otiorhynchus ovatus	172	8	22	66	10	13	6	4	5	34	3	1	0	1.37	2, 394	0.22
Curculionid. sp.1	2	0	0	1	0	1	0	0	0	0	0	0	0	0.99	2, 394	0.44
Curculionid. sp.2	3	1	0	0	1	0	0	0	0	1	0	0	0	1.21	2, 394	0.30
Curculionid. sp.3	2	0	1	0	0	0	0	0	0	1	0	0	0	0.61	2, 394	0.75
Notoxus serratus	8	0	1	0	0	7	0	0	0	0	0	0	0	3.86	2, 394	<0.001
Anthicus tobias	130	4	4	17	18	19	11	7	4	24	20	1	1	4.23	2, 394	<0.001
Anthicus lutulentus	100	2	7	18	23	19	3	2	4	15	5	2	0	4.70	2, 394	<0.001
Ptomaphagus sp.	2	0	0	0	0	0	0	0	2	0	0	0	0	0.79	2, 394	0.59
Byrrhus americanus	13	2	0	0	4	7	0	0	0	0	0	0	0	4.99	2, 394	<0.001
Xerosaprinus acilinea	19	0	4	5	0	0	0	1	6	0	0	0	3	0.32	2, 394	0.32

Appendix E cont.

		Pre-Treatment						Post-Treatment								
		Control			Treatment			Control			Treatment					
Species	Abundance	Early	Intermediate	Late	Early	Intermediate	Late	Early	Intermediate	Late	Early	Intermediate	Late	F-Value	d.f.	P-Value
Xerosaprinus lubricus	2	0	1	0	0	0	0	0	1	0	0	0	0	0.97	2, 394	0.97
Haeterius tristriatus	3	0	0	1	0	0	0	0	0	2	0	0	0	1.00	2, 394	1.00
Cryptophagus histricus	67	12	11	23	0	3	0	9	4	3	0	1	1	0.32	2, 394	0.32
Nicrophorus hybridus	131	2	14	37	0	0	0	33	8	3	12	0	22	0.11	2, 394	0.11
Nicrophorus guttula	95	0	9	26	0	0	0	34	2	2	12	0	10	0.16	2, 394	0.16
Thanatophilus lapponicus	4	0	0	3	0	0	0	1	0	0	0	0	0	0.73	2, 394	0.73
Dermestes talpinus	3	0	0	3	0	0	0	0	0	0	0	0	0	0.43	2, 394	0.43
Aphodius granarius	2	0	0	0	0	1	1	0	0	0	0	0	0	0.00	2, 394	<0.001
Onthophagus nuchicornis	24	0	0	0	0	1	0	0	0	0	16	0	7	0.18	2, 394	0.18
Canthon simplex	6	0	0	0	0	0	0	2	0	0	0	1	3	0.00	2, 394	<0.001
*Aphodius sp.*1	2	0	0	0	0	0	0	0	1	0	1	0	0	0.44	2, 394	0.44
Mordellidae sp.	8	0	0	0	0	0	0	0	4	4	0	0	0	0.90	2, 394	0.90
*Phalacrus sp.*1	4	0	0	0	2	1	0	0	1	0	0	0	0	0.06	2, 394	0.06
Apteroloma tenuicorne	2	0	0	0	2	1	0	0	1	0	0	0	0	0.80	2, 394	0.80

APPENDIX F

ABUNDANCE AND ASSOCIATIONS OF SPECIES TO MICROHABITAT

Appendix F. Beetle species included in the analysis and the effect of the prescribed burn treatment on their abundance and subplot associations (the significant change in abundance in burn, control, and microhabitat between years). See methods for details.

		Pre-Treatment								Post-Treatment										
		Control				Treatment				Control				Treatment						
Species	Abundance	Dune Face	Swale	Blowout	Control	Dune Face	Swale	Blowout	Control	Dune Face	Swale	Blowout	Control	Dune Face	Swale	Blowout	Control	F-Value	d.f.	P-Value
Cicindela formosa	2098	182	349	238	82	110	146	85	16	120	282	276	36	43	68	43	22	0.80	3, 392	0.63
Cicindela decemnotata	31	6	9	3	4	2	0	0	1	0	2	2	0	1	0	1	0	1.10	3, 392	0.36
Cicindela purpurea	4	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1.55	3, 392	0.12
Cicindela nebraskana	5	0	0	0	0	0	0	0	0	0	0	0	1	0	3	1	0	2.12	3, 392	0.02
Amara quenseli	3648	608	965	528	404	155	222	202	93	100	125	95	72	31	15	16	17	1.57	3, 392	0.11
Amara confusa	21	4	3	5	4	1	2	0	0	0	1	0	1	0	0	0	0	0.77	3, 392	0.66
Harpalus fraternis	64	1	4	2	4	2	1	2	2	2	4	4	3	8	7	9	9	1.37	3, 392	0.19
Harpalellus basilaris	6	0	0	0	0	1	1	3	0	1	0	0	0	0	0	0	0	4.58	3, 392	<0.001
Piosoma setosum	7	0	0	0	0	0	0	0	0	5	1	0	1	0	0	0	0	0.31	3, 392	0.98
Pterostichus adstrictus	3	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0.79	3, 392	0.64
Euryderus grossus	10	0	3	0	0	0	0	0	0	3	3	1	0	0	0	0	0	0.50	3, 392	0.89
Cymindis planipennis	23	2	1	4	5	2	0	1	0	2	1	2	1	1	0	0	1	0.64	3, 392	0.78
Calleida viridis	3	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	4.14	3, 392	<0.001
Lebia vittata	97	6	15	15	1	10	11	15	8	0	2	8	4	0	1	0	1	1.41	3, 392	0.17
Syntomus americanus	3	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	2.87	3, 392	<0.001
Carabidae sp.1	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0.52	3, 392	0.87
Carabidae sp.2	3	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0.49	3, 392	0.90
Eleodes extricatus	340	4	9	12	4	39	45	33	34	19	18	25	4	28	32	21	13	2.76	3, 392	<0.001
Eleodes nigrinus	28	3	3	3	1	0	1	2	1	2	2	2	3	0	2	3	0	0.67	3, 392	0.75

Appendix F cont.

		Pre-Treatment								Post-Treatment									
		Control				Treatment				Control				Treatment					
Species	Abundance	Dune Face	Swale	Blowout	Control	Dune Face	Swale	Blowout	Control	Dune Face	Swale	Blowout	Control	Dune Face	Swale	Blowout	Control	F-Value	d.f.
Eleodes cordatus	22	1	0	0	0	1	8	3	2	0	0	0	0	2	3	0	2	1.89	3, 392
Eleodes tenebrosa	4	0	0	0	0	0	0	1	0	1	0	0	0	2	0	0	0	1.95	3, 392
Coniontis obesa	14	1	0	0	0	2	5	2	2	0	1	0	0	0	1	0	0	2.20	3, 392
Coniontis ovalis	4	0	0	0	0	0	2	1	0	0	0	0	0	0	1	0	0	1.78	3, 392
Blapstinus pimalis	3	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1.95	3, 392
Helops convexulus	3	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1.31	3, 392
Coccinella transversoguttata	8	1	0	0	0	0	0	0	0	1	1	0	2	1	2	0	0	0.98	3, 392
Brumoides septentrionis	3	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1.44	3, 392
Hyperaspidius mimus	101	11	2	3	1	0	0	0	0	24	25	16	16	0	2	0	1	0.48	3, 392
Hyperaspidius hercules	2	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1.95	3, 392
Hippodamia moesta	4	2	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1.47	3, 392
Hippodamia sinuata	5	1	0	0	0	2	1	1	0	0	0	0	0	0	0	0	0	1.51	3, 392
Graphops n.sp.	12	0	1	4	1	0	1	0	0	1	0	2	0	0	1	0	1	1.34	3, 392
Disonycha latrifons	110	16	9	6	9	3	20	11	2	10	7	7	7	1	1	1	0	4.78	3, 392
Galeruca rudis	4	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0.36	3, 392
Pachybrachis sp. nr. hepaticus	10	1	0	0	0	0	0	0	0	2	2	4	1	0	0	0	0	0.46	3, 392
Dibolia sp. 1	6	0	0	0	0	3	0	0	0	0	0	0	1	1	1	0	0	3.13	3, 392
Staph. sp.1	5	1	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0.89	3, 392
Staph. sp.2	3	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1.38	3, 392
Staph. sp.3	5	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0.96	3, 392

Appendix F cont.

		Pre-Treatment								Post-Treatment										
		Control				Treatment				Control				Treatment						
Species	Abundance	Dune Face	Swale	Blowout	Control	Dune Face	Swale	Blowout	Control	Dune Face	Swale	Blowout	Control	Dune Face	Swale	Blowout	Control	F-Value	d.f.	P-Value
Staph. sp.4	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.57	3, 392	0.84
Staph. sp.5	3	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0.59	3, 392	0.82
Staph. sp.7	3	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.38	3, 392	0.96
Staph. sp.8	8	0	0	1	0	0	0	2	1	0	1	1	0	0	0	2	0	1.44	3, 392	0.16
Staph. sp.9	4	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0.75	3, 392	0.68
Staph. sp.11	5	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0.95	3, 392	0.49
Staph. sp.12	3	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0.34	3, 392	0.97
Otiorhynchus ovatus	172	33	27	8	28	8	3	7	11	7	23	3	10	2	1	1	0	1.27	3, 392	0.25
Curculionid. sp.1	2	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1.64	3, 392	0.09
Curculionid. sp.2	3	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1.13	3, 392	0.34
Curculionid. sp.3	2	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0.70	3, 392	0.73
Notoxus serratus	8	0	0	1	0	0	2	5	0	0	0	0	0	0	0	0	0	3.06	3, 392	<0.001
Anthicus tobias	130	3	7	7	8	13	11	12	12	12	9	2	12	10	5	3	4	1.99	3, 392	0.03
Anthicus lutulentus	100	4	11	5	7	3	13	13	16	5	5	4	7	3	2	1	1	3.40	3, 392	<0.001
Ptomaphagus sp.	2	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0.29	3, 392	0.98
Byrrhus americanus	13	0	1	1	0	3	5	3	0	0	0	0	0	0	0	0	0	3.96	3, 392	<0.001
Xerosaprinus acilinea	19	0	0	8	1	0	0	0	0	5	0	2	0	0	0	0	3	1.45	3, 392	0.16
Xerosaprinus lubricus	2	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0.63	3, 392	0.78
Haeterius tristriatus	3	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0.21	3, 392	1.00
Cryptophagus histricus	67	14	6	14	12	0	1	1	1	7	1	3	5	1	1	0	0	0.67	3, 392	0.76

Appendix F cont.

Species	Abundance	Pre-Treatment								Post-Treatment								F-Value	d.f.	P-Value
		Control				Treatment				Control				Treatment						
		Dune Face	Swale	Blowout	Control	Dune Face	Swale	Blowout	Control	Dune Face	Swale	Blowout	Control	Dune Face	Swale	Blowout	Control			
Nicrophorus hybridus	131	18	1	31	3	0	0	0	0	1	7	36	0	0	0	12	22	0.87	3, 392	0.56
Nicrophorus guttula	95	13	0	20	2	0	0	0	0	5	2	30	1	0	0	12	10	0.45	3, 392	0.92
Thanatophilus lapponicus	4	0	0	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0.76	3, 392	0.67
Dermestes talpinus	3	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0.61	3, 392	0.81
Aphodius granarius	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2.26	3, 392	0.01
Onthophagus nuchicornis	24	0	0	0	0	0	0	1	0	0	0	0	0	0	0	16	7	1.32	3, 392	0.22
Canthon simplex	6	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	3	1.42	3, 392	0.17
*Aphodius sp.*1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1.07	3, 392	0.39
Mordellidae sp.	8	0	0	0	0	0	0	0	0	1	2	3	2	0	0	0	0	0.17	3, 392	1.00
*Phalacrus sp.*1	4	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	4.51	3, 392	<0.001
Apteroloma tenuicorne	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0.29	3, 392	0.98

APPENDIX G

NOTES ON SPECIES OF SPECIAL INTEREST

Microweiseiini n. sp.:

Undescribed new Genus and species in the Family Coccinellidae, Tribe Microweiseiini. This species belongs to a group of rare beetles that have been collected on very few occasions. The biology is unknown. Only one male specimen was collected over two field seasons.

Figure 21. *Microweiseiini n. sp* dorsal and ventral habitus.

Graphops n. sp.:

Species in the genus *Graphops* are often collected on vegetation in sandy habitats. The species found in the Centennial Sandhills closely resembles the species *Graphops tenuis* and *G. nebulosa*, yet differs slightly in color and is much smaller than the descriptions of both species. It is likely that the Centennial specimens are a color variant of one of these two species. The genus *Graphops* is in great need of revision, and accurate determinations of the Centennial species will most likely remain unknown until one occurs. Many *Graphops* species are associated with primrose species in the genus *Oenothera*. Two species of Oenothera exist in the Centennial one of which is a species of concern in Montana and known only from Centennial Sandhills localities (*Oenothera pallida ssp. pallid*). Three males and nine females were collected by pitfall over the course of this study. An overlay of the distributions of both *Graphops* and Pale Evening-Primrose (*Oenothera pallida ssp. pallid*) show a great deal of similarity in sites sampled for both rare plants and Coleoptera (n=3).

Figure 22. *Graphops n. sp.* lateral habitus.

***Glaresis* n. sp.**: Very little is known of the biology of species in the genus *Glaresis*, but most are commonly associated with very sandy areas and are assumed to be detritivores. One female was collected from the Centennial Sandhills. Most individuals are collected at lights and more specimens may be collected in the future if this collecting method is employed.

Figure 23. Dorsal and lateral habitus of *Glaresis n. sp*.

***Aphodius (Flaviellus) n.sp. nr. perfimbriatus* Gordon**: *Aphodius perfimbriatus* Gordon is a species known from sand dunes in Colorado, Wyoming, and Idaho. One female specimen from the Centennial Sandhills closely resembles individuals collected from the Saint Anthony Dunes in Idaho. Variations in the scutellum and the margins of the pronotum and clypeus in addition to the teeth of the protibia seem to make this individual unique from the Idaho population. Revisions of the genus *Aphodius* have moved these species into their own genus (*Flaviellus*), and are often described as sand loving detritivores.

Figure 24. Dorsal and lateral habitus of *Aphodius n. sp. nr. perfimriatus* Gordon.

APPENDIX H

RAW DATA

(SEE CD IN LIBRARY)