ASSESSING THE EFFECT OF HABITAT, LOCATION AND BAIT TREATMENT ON DUNG BEETLE (COLEOPTERA: SCARABAEIDAE) DIVERSITY IN SOUTHERN ALBERTA, CANADA

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ABSTRACT

Dung beetles (Coleoptera: Scarabaeidae) are members of the coprophagous insect community and are important dung degraders in pasture ecosystems. To assess their distribution in North America, I created a checklist of over 300 beetle species known to colonize dung (Chapter 2). To assess the affect of habitat and location on dung beetle diversity, I conducted sampling at Purple Springs Grazing Reserve and Cypress Hills Interprovincial Park (Chapter 3). Each habitat and location was dominated by different species for both sampling years. The affect of bait treatment and age on the attractiveness of the coprophagous insect community was assessed using fresh and frozen dung baits, with frozen baits being more attractive for the first three days (Chapter 4). To expedite sample processing, regression equations were developed for three treatments (wet, air-dried, and oven-dried weight), which allow for counts of individuals to be estimated by their bulk weight (Chapter 5).

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LIST OF ABBREVIATIONS

Symbol	Definition
*	Cow dung
±	Plus or minus
%	Percent
°	Degrees
°C	Degrees Celsius
1-D	Simpson Index
^{A}	Alpaca dung
a.m.	Ante meridiem/before noon
ANOVA	Analysis of variance
^{B}	Bison dung
^{C}	Dog dung
C	Coprophagous
CF1	Cypress Hills forest site one
CF2	Cypress Hills forest site two
CG1	Cypress Hills grassland site one
CG2	Cypress Hills grassland site two
CHIP	Cypress Hills Interprovincial Park
cm	Centimetres
^{D}	Deer dung
DNA	Deoxyribonucleic acid
^{E}	Horse dung
F	Fungivore
^{G}	Chicken dung
^{H}	Human dung
H	Shannon Index
I	Incidental
^{K}	Donkey dung
Kg	Kilogram
Km	Kilometre
L	Litre
Lat	Latitude
Long	Longitude
^{M}	Moose dung
mL	Millilitre
m	Metre
m^2	Metres squared
n	Sample size
^{P}	Pig dung
P	P value
Pa	Parasitoid
Pr	Predator
PS1	Purple Springs site one
PS2	Purple Springs site two

PSGR	Purple Springs Grazing Reserve
Q	Porcupine dung
R^2	Coefficient of determination
S	Sheep dung
SE	Standard error of the mean
sp.	Species
T	Turkey dung
μg/kg	Microgram per kilogram

CHAPTER 1: GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1 Objectives

Coprophagous (i.e., dung-feeding) species of beetles are common in cattle dung and play an important role in pasture ecosystems. This thesis examines the diversity of these beetles in different habitats (i.e., open grassland and forested pasture) in southern Alberta, Canada. It also provides information on the diversity of these beetles in North America, and examines methods to facilitate future research on this group of insects. The specific objectives of this study are to:

1) Create an updated list of the beetle species known to be associated with dung in North America, north of Mexico. The original list by Blume (22) is more than thirty years old in terms of species distribution and taxonomic classifications. This new list compiles old and new information plus several improvements, which provides a starting point for individuals interested in coprophagous beetles.
2) Compare the diversity of dung beetles at different locations and habitat types in southern Alberta. Studies of this nature have not been previously documented in Alberta. This information will provide insight about community composition and species seasonal activity.
3) Compare the attractiveness of baits made from cattle dung of different treatments (fresh or frozen) and age. Information of this nature is scattered throughout the literature with few concrete recommendations suggested. This information will help to optimize pitfall trapping when assessing the dung insect community.
4) Validate the use of a faster alternative method to hand-sorting dung beetles from pitfall trap catches. Wet weight, oven-drying weight and air-drying weight were

used to determine the most accurate method to estimate the number of *Chilothorax distinctus* (Müller) in a sample. This method will reduce the time and money associated with sorting pitfall trap samples.

1.2 Literature Review

This study focuses on dung beetle (Coleoptera: Scarabaeidae) diversity in southern Alberta and some of the factors that are known to affect it such as location and habitat. The attractiveness of bait age and treatment of the dung insect community will also be compared. The literature review will first discuss the dung insect community as a whole as well as its importance to an ecosystem. Second, it will focus on dung beetles, their different nesting guilds, and how each strategy confers beneficial ecosystem services. Third, it will present factors known to affect dung beetle diversity. Finally, methods on how to effectively monitor dung beetle populations will be discussed.

1.2.1 The Dung Insect Community and Its Importance

In 2016, Alberta contained roughly 42% of all the cattle in Canada, more than double that of its closest counterpart Saskatchewan (204). The proportion of cattle in Alberta accounts for 3.34 million head of beef cattle and 80 thousand head of dairy cattle (204). With the presence of this many animals, there is an equally large amount of faeces that needs to be quickly removed in a cost-effective manner.

Cattle dung is a moist, nutrient-rich, and abundant resource deposited on pastures throughout North America. It is mainly composed of undigested plant material and can have a water content of up to 88% at the time of deposition (136). Its components may also include nitrogen, cellulose and potassium (87), plus bacteria (87), fungi, and different life stages of cattle parasites (e.g., eggs and larvae of roundworms, trematodes, and cestodes) (74).

Although dung is an ephemeral and patchy resource, the rate of accumulation can be high depending on how many animals are present on pasture. On average, one cow can deposit ten dung pats a day, which is roughly equivalent to 25-30 kg of dung in wet weight (13). If there is no overlap, these pats can cover an area of 0.8 m^2 (74). In addition, nitrogen leeching from the dung into the soil alters the taste of adjacent vegetation (74). Cattle avoid this vegetation, which can potentially remove from grazing, an area five times greater than that covered by the pat itself (74). Thus, up to 7.2 hectares of forage may be removed by 100 head of cattle over the course of a 150-day grazing period (74).

If not quickly degraded, these dung pats dry out and become hard piles of nutrient reservoirs that can potentially take years to decompose (63). However, there are hundreds of species of organisms such as arthropods, nematodes, earthworms, and fungi that are capable of utilizing this microhabitat (74, 93, 156). Arthropods are among the most abundant members of the dung community with roughly 300 different dung-associated species present in Canada (74), which is comparable to the 275 species in Britain (198). Numerous studies have focused on the succession (126, 179, 229) and activities of coprophagous insects (75, 165). Without the presence of the dung insect community, the rate of dung pat degradation is slower. In Alberta, Floate & Gill (75) observed no degradation of dung that contained insecticide residues, compared to residue-free dung that was largely degraded within 80 days. In addition, the exclusion of insects within the first two days of dung deposition can greatly affect the rate of degradation (136).

Several factors other than arthropods can accelerate dung degradation and return nutrients to the ecosystem. The presence of organisms such as nematodes, earthworms and fungi (74, 93, 156) are known to accelerate dung degradation. In Denmark, Holter (104) reported that earthworms account for roughly 50% of the pat disappearance through both direct (i.e., feeding) and indirect activity (i.e., stimulating the microbial community). Foraging behaviour of birds such as the western meadowlark (*Sturnella neglecta* Audubon) (7) and the hooded crow (*Corvus cornix* Linnaeus) (107) have been linked to dung pat degradation. Livestock can also increase dung degradation by trampling dung pats especially when stocking rates are high (73, 74). Other key factors that have a role in dung degradation have been outlined by Merritt & Anderson (154), and include pasture type, climate, and time of pat deposition.

Although hundreds of insect species are associated with dung, not all directly contribute to degradation. It is important to make the distinction between incidentals that just happen to be present and those that are 'true' members of the dung insect community. Incidentals do not require fresh dung for breeding or nutritional resources. They are found on or near the dung pat because they have wandered onto it by chance (74, 156), are in search of prey (74), or are using it for shelter. Common incidental species include: springtails (Collembola), ants (Formicidae), spiders (Araneae), bugs (Hemiptera), click beetles (Elateridae), ground beetles (Carabidae) and earwigs (Dermaptera) (74).

The 'true' dung arthropods are members of four main orders: Diptera (flies), Hymenoptera (parasitic wasps), Acarina (mites), and Coleoptera (beetles) (74, 156). Flies such as face flies (*Musca autumnalis* (De Geer)) and horn flies (*Haematobia irritans*

(Linnaeus)) only breed in fresh cattle dung (63) and adult dung beetles feed on the fluids of fresh dung (63).

Most of the flies that are relevant to the dung insect community lay their eggs inside of the dung pat where they develop into adults (92, 133). Flies are the first colonizers to arrive at the dung pat and can be seen within minutes of deposition (74, 92, 133). Some species such as *M. autumnalis* and *H. irritans* are pests of livestock (63) with large numbers being damaging and difficult to reduce. The majority of Hymenoptera species are wasps that mainly parasitize flies (74) and lay their eggs in the eggs, larvae or pupae of flies, killing the host (74). Mites have a phoretic relationship with some flies and beetles (74). They will grab onto legs or bristles of a host and hitch a ride to the dung pat in what is known as phoresy (74). Once on the pat, they are predators of immature insects, other mites and nematodes (74).

There are five main families of beetles that are commonly associated with dung: Scarabaeidae (scarab beetles), Geotrupidae (earth-boring beetles), Histeridae (clown and hister beetles), Hydrophilidae (water scavenger beetles) and Staphylinidae (rove beetles). Many Histeridae in Canada are classified as saprophagous, and are mainly predators of fly larvae (31, 162). Most species of interest belong to the genera *Hister*, *Atholus* and *Margarinotus*, plus genera within the subfamily Saprininae (31). Hydrophilidae are dung feeders and predators (74, 133) usually of fly larvae (156). Species of *Sphaeridium* and *Cercyon* are common in dung (133). Staphylinidae beetles are mainly classified as predators (74, 133) of adult (133, 236) and larval (133) dung beetles as well as flies (162). However, depending on the species, they can also be fungivores or parasitoids (74). Other beetle species of interest are in Families Clambidae (fringe-winged beetles), Cryptophagidae (silken fungus beetles), and Ptiliidae (feather-winged beetles). These latter groups typically feed on fungi present in the dung pats during later states of decomposition (72, 74).

1.2.2 Dung Beetle Guilds

The term "dung beetle" refers to coprophagous species of Families Scarabaeidae (scarab beetles; subfamilies Aphodiinae, Scarabaeinae) and Geotrupidae (earth-boring beetles). They are the focus of many studies due to their dominance in terms of numerical abundance and biomass on cattle dung. These beetles are found in various environments throughout North America with several commonly collected species (e.g., *Chilothorax distinctus* (Müller) and *Otophorus haemorrhoidalis* (Linnaeus)) being of European origin (16, 39, 75, 122, 141). Each beetle exhibits a specific nesting and reproductive strategy, which can be divided into five guilds: telecoprids (rollers), paracoprids (tunnellers), endocoprids (dwellers), detritivores and kleptoparasites (50, 93). Each strategy is unique in the way it degrades the pats thus providing different ecosystem services, with a combination of representatives from the first three guilds being ideal for the health of an ecosystem.

Rollers (Scarabaeidae: Scarabaeinae: Tribe Canthonini), sometimes referred to as tumble bugs, break off a piece of the dung pat and roll it into a ball (90, 93). This activity is often done in partners, with the male and female rolling the ball with their hind legs a distance away from the dung pat to be buried (90, 93). This ball then becomes one of two things; a brood ball if a single egg is laid inside (90, 151) or a food ball if no egg is laid (63). The brood ball becomes a food reserve and pupation chamber for the developing egg (90, 151). In Alberta, there are two native species of rollers; *Canthon praticola* LeConte and *Canthon pilularius* (Linnaeus), the latter being the largest of all Albertan dung beetles (122). The size, distance moved and burial depth of the brood ball is species-dependant (93), with *C. pilularius* averaging a rolling distance of 4 m and a burial depth of 10 cm (151).

Tunnellers (Geotrupidae; Scarabaeidae: Scarabaeinae) bury dung in tunnels beneath the pat (63). Similar to the rollers, this dung either becomes a brood ball if an egg is laid, and if not, the ball is consumed (63). In Alberta there are two species of tunnellers, *Colobopterus erraticus* (Linnaeus) (184) and *Onthophagus nuchicornis* (Linnaeus), which are both of European origin (122). There has been an attempt to establish *Onthophagus taurus* (Schreber) in Alberta, with no success (78). However, this study did indicate the most plausible areas where this species could establish (78). Tunnel depth has been shown to vary with species, soil type and soil depth (65), with *Phanaeus vindex* MacLeay averaging 13 cm (32).

Dwellers are comprised of the Aphodiinae (Scarabaeidae) subfamily (68) and develop from egg to adult inside of the pat (93) or close to the soil surface (160). Dung degradation occurs mainly due to the feeding activity of the developing larvae (74). They transform the dung into a dry, granular consistency that is easily dispersed (74). Species belonging to this guild are the most common in Alberta, although they are the least effective dung degraders. Some dwellers found in Alberta, are *Teuchestes fossor* (Linnaeus), *Aphodius pedellus* (De Geer), *and Otophorus haemorrhoidalis* (Linnaeus), which are all of European origin (122). Native dwellers of Canada include *Pseudagolius coloradensis* (Horn) and *Planolinellus vittatus* (Say) (122).

The majority of species in the fourth guild, the detritivores, do not use dung for breeding. It is usually the adults who feed on manure and the larvae tend to feed on organic rich soils, rotting organic matter, or manure that is under the ground (122, 193). Species of detritivores in Alberta are *Chilothorax distinctus* (Müller) (85, 178), *Calamosterus granarius* (Linneaus) (85, 122), and *Melinopterus prodromus* (Brahm) (85, 133).

A fifth guild, the kleptoparasites, is more common in tropical habitats, whereas dwellers are least common in these areas (93). This guild parasitizes the work of other species by claiming brood balls and tunnels as their own (93).

1.2.3 Importance of Dung Beetles to the Ecosystem

In addition to dung degradation, dung beetles are considered to be beneficial to an ecosystem because of their role as a bioindicator as well as the ecosystem services they provide. Dung beetles are bioindicators of environmental change (194) because the biology, behaviour and guild structure of most species is well studied, and they are easily captured (91). In Brazil, dung beetle communities near rivers can be indicators of riparian zones (215). In Indonesia, some dung beetle species could indicate different habitat types (i.e., shaded and unshaded) (194). The beneficial ecosystem services provided by dung beetles include the reduction of pest populations and accelerated nutrient cycling (162). Several fly species that are pests of livestock breed in dung; e.g., bush flies (*M. vetustissma*), face flies (*M. autumnalis*) and horn flies (*H. irritans*) (63). Dung beetle activity reduces available breeding sites for these pests and damages eggs that are present (162). Populations of helminth species that are pests of livestock are reduced in a similar fashion. Burial of dung by tunnellers and rollers returns nutrients to the soil to promote plant growth and the formation of tunnels increases soil aeration and water porosity (162).

The benefits of dung beetles has been capitalized with the introduction of African dung beetles into Australia (116). Native dung beetles in Australia evolved to degrade marsupial dung and had trouble adapting to cattle dung (74). Introduced species such as *Euoniticellus intermedius* Reiche helped to degrade dung pats and reduced the abundance of the Australian bush fly (*M. vetustissima*) (116, 201).

1.2.4 Factors Affecting Dung Beetle Activity

There are various abiotic and biotic factors that can affect dung beetle activity. Parasiticides are a veterinary product used to treat livestock for internal and external parasites (74, 214). Studies have shown that faecal residues can have detrimental effects on members of the dung insect community. Ivermectin is one of several commonly used parasiticides that has been extensively studied (100, 164, 202). Overall findings show that parasiticide residues can be detected in dung days or weeks after treatment. Iwasa et al. (121) were able to detect ivermectin 21 days post-treatment. However, the concentration decline is dependant on the formula and method of administration. Injectable or topical formulas may persist for four to six weeks (77) and the slow-release bolus can be detected 147 days post treatment (54). It has been reported that parasiticides containing macrocyclic lactone compounds (i.e., ivermectin) are excreted with little breakdown (77). These residues kill insects in dung or delay their development. In Alberta, fecal residues affected a wide array of taxa with emergence being delayed for *Sepsis* flies (twelve weeks post-treatment) and *Planolinellus vittatus* (Say) (four weeks post-treatment) (72). Because the emergence of dung insects is delayed, this inherently affects dung degradation (72).

Lower doses of ivermectin (100 μg/kg compared to 500 μg/kg) have been shown to affect the sensory responses and locomotion of some species of adult dung beetles (214).

Soil type has been shown to affect the species and diversity of dung beetles. In Texas, clay soils have been found to be less species rich than sandy soils, presumably because of the denser texture (159). Harder soils could make it difficult for some species to bury brood balls (159) or create tunnels. Vegetation can also make it difficult for brood balls to be rolled or dung pats to be located (159). However, soil type was found to be more important than the vegetation to determine segregation of species (13, 159). Vegetative cover, specifically forests have also been linked to harbouring different dung beetle species (64, 106, 177). In addition, the effect of clear-cutting (147) and forest fragmentation (8) have also been studied to determine their effects on the dung beetle community. Clear-cutting in the Missouri Ozark forest reduced dung beetle abundance and diversity (147). Forest fragmentation areas contains dung beetles with a smeller average body size compared to continuous forested areas (8). This inherently decreased dung removal and seed dispersal rates (8).

1.2.5 Monitoring Dung Beetle Populations

Although dung is a temporary resource it is renewable, which permits most dung beetles to be opportunistic and generalists when choosing dung (56). Some species prefer one type with the typical favourite being omnivore dung (224). Studies comparing the attractiveness of different dung have found that the number and abundance of dung beetles species are affected by dung type (i.e., cattle vs. swine) (13, 66, 113, 224).

Pitfall trapping is the most common method to monitor the dung insect community (80, 113, 122) as it is quick, cost effective and has a high capture rate. The trap consists of two nested buckets buried flush with the soil surface, which permits both flying and epigeal insects to be caught. The bait is suspended over the top bucket, which contains a few inches of a killing agent such as non-toxic antifreeze or soapy water. Traps are usually emptied and rebaited at specific intervals. However, rebaiting time is inconsistent throughout the literature with studies using rebaiting times of one (14, 66), two (134, 187), three (13), five (113) or seven days (39, 55, 59, 76). Few studies have directly compared rebaiting times (10, 95, 113), but all have found attractiveness to decrease over time.

Treatment of dung baits is also inconsistent with some studies freezing the dung prior to use (69, 71, 146), and others using fresh (174, 187). Little investigation has been done to determine what effect freezing has on the attractiveness of the dung. Pimsler (170) compared the two treatments and found frozen dung to collect more insects over a 24-hour period.

1.3 Structure of Thesis

CHAPTER 2: AN UPDATED CHECKLIST AND DISTRIBUTIONAL RECORD OF THE COLEOPTERA ASSOCIATED WITH LIVESTOCK DUNG IN NORTH AMERICA NORTH OF MEXICO

This chapter provides an updated checklist of beetles known to be associated with livestock dung in North America, north of Mexico. Beetles included in this list belong to six families; Geotrupidae (earth-boring beetles), Histeridae (clown and hister beetles), Hydrophilidae (water scavenger beetles), Scarabaeidae (scarab beetles), Staphylinidae (rove beetles) and Trogidae (hide beetles). This list expands previous information compiled by Blume (22). As well as the addition of new species and distributions, the correct taxonomic classifications have also been included.

CHAPTER 3: DUNG BEETLE (COLEOPTERA: SCARABAEIDAE) DIVERSITY IN DIFFERENT HABITATS AND LOCATIONS IN SOUTHERN ALBERTA, CANADA

This chapter compares the effect of location and habitat on dung beetle diversity in southern Alberta. Cattle dung baited pitfall traps were set up at Cypress Hills Interprovincial Park and Purple Springs Grazing Reserve from May to October in 2016 and 2017. The effect of location was examined using dung beetles collected from both locations as they contain native rangeland pastures. The effect of habitat was only examined at Cypress Hills Interprovincial Park, which has native fescue grassland and forest encroachment areas within the same vicinity.

CHAPTER 4: THE ATTRACTIVENESS OF FRESH AND FROZEN CATTLE DUNG ON THE COPROPHAGOUS INSECT COMMUNITY

This chapter compares rebaiting time and dung treatment on the attractiveness to members of the dung insect community. Dung-baited pitfall traps were set up in pairs with one fresh and one frozen bait (n = 20). Collections were made every 24-hours for seven days. These data indicate at what point attractiveness beings to decrease and whether fresh or frozen dung is more effective for trapping. Information of this nature is scattered or missing throughout the literature. These results indicate the most effective pitfall trapping techniques.

CHAPTER 5: USING WEIGHT TO ESTIMATE THE NUMBER OF *Chilothorax distinctus* (MÜLLER) CAPTURED IN DUNG BAITED PITFALL TRAPS

This chapter validates the use of faster and cheaper alternative methods to hand-counting *Chilothorax distinctus* (Müller) collected from pitfall traps. Wet weight, and two methods to obtain dry weight, oven-drying, and air-drying, were all tested to determine the most accurate method. The current literature provides few recommendations of this nature with none pertaining to Scarabaeidae.

CHAPTER 6: GENERAL DISCUSSION AND CONCLUSIONS

The final chapter summarizes the findings from all chapters and provides conclusions that synthesize the research. It highlights the findings and also provides recommendations and suggestions for future research.

CHAPTER 2: AN UPDATED CHECKLIST AND DISTRIBUTIONAL RECORD OF THE COLEOPTERA ASSOCIATED WITH LIVESTOCK DUNG IN NORTH AMERICA NORTH OF MEXICO

2.1 Abstract

Most distributional lists are limited to geographical areas such as states or provinces and often include information regarding smaller subsets of coprophagous insects. This checklist builds on the data previously compiled from R. R. Blume in 1985 and adds several improvements to make it more robust and applicable to a modern audience. These improvements include information regarding only coprophagous species, their current distributional records in North America, the different types of livestock dung they are attracted to, and taxonomic changes. For added convenience, an electronic excel file has been created to permit the reader to generate a specific checklist of coprophagous beetles for any state or province in North America north of Mexico or dung type of interest.

2.2 Dung Insect Community: An Overview

Arthropods are dominant members of the dung community with numerous studies having focused on the succession (126, 179, 229) and activities of coprophagous insects (75, 165). Without the presence of the dung insect community, the rate of dung pat degradation can be reduced. In comparisons of dung pats with and without insecticide residues, essentially no degradation was observed if residues were present (75). More recently, Lee & Wall (136) found that excluding insects within the first two days of dung deposition greatly affected the rate of degradation.

Although hundreds of insect species have been associated with dung pats, it is important to make the distinction between incidental species that just happen to be present and species that are ‘true’ members of the dung insect community. Incidentals do not require fresh dung for breeding or nutritional resources. In most cases, they have walked onto it by chance (74, 156), are in search of prey (74), or are using it for shelter. Some of the commonly recorded incidental species include: springtails (Collembola), ants (Formicidae), spiders (Araneae), bugs (Hemiptera), click beetles (Elateridae), ground beetles (Carabidae) and earwigs (Dermaptera) (74).

The dung insect community is mainly composed of species of beetles (Coleoptera), flies (Diptera), and wasps (Hymenoptera). Roughly 300 different species have been reported from pastures in Canada (74), which is comparable to the 275 species reported from Britain (198). Given their dominance in terms of numerical abundance and biomass on cattle dung, many studies have reported on species of coprophilous beetles. Common species in dung include members of Families Histeridae (clown and hister beetles), Hydrophilidae (water scavenger beetles) and Staphylinidae (rove beetles). Many Histeridae in Canada are classified as saprophagous, and are mainly predators of fly larvae (31, 162). Most species of interest belong to the genera *Hister*, *Atholus*, *Margarinotus* as well as many groups within the subfamily Saprininae (31). Hydrophilidae are dung feeders and predators (74, 133) usually of fly larvae (156). The most common species associated with dung pats are in the genera *Sphaeridium* and *Cercyon* (133). Staphylinidae beetles are mainly classified as predators (74, 133) of adult (133, 236) and larval (133) dung beetles as well as flies (162). However, depending on the species, they can also be fungivores or parasitoids (74). Other beetle species of interest are in Families Clambidae (fringe winged beetles), Cryptophagidae (silken fungus beetles), and Ptiliidae (feather-winged beetles). These latter groups typically feed on fungi present in the dung pats during later states of decomposition (72, 74).

The majority of studies, however, have focused on dung beetles, the common term reserved for coprophagous species of Families Scarabaeidae (scarab beetles; subfamilies Aphodiinae, Scarabaeinae) and Geotrupidae (earth-boring beetles). These beetles are found in various environments throughout North America with several commonly collected species such as, *Chilothorax distinctus* and *Otophorus haemorrhoidalis*, being of European origin (16, 39, 75, 122, 141). The specific nesting and reproductive strategies of dung beetles are what make them important to an ecosystem. These strategies can be classified into three guilds; rollers (telecoprids), tunnellers (paracoprids) and dwellers (endocoprids) (50, 93). Each strategy is unique in the way it degrades the pats thus providing different ecosystem services, with a combination of representatives from the first three guilds being ideal for the health of an ecosystem.

2.3 Benefits of the Dung Insect Community

The nesting strategies employed by dung beetles help to break down dung pats, but also provides additional ecosystem services. Nichols et al. (162) outlines nine important ecological functions that dung beetles provide in addition to pat degradation. One benefit is the reduction of available breeding area for livestock pest flies including bush flies (*Musca vetustissma* Walker), face flies (*Musca autumnalis* De Geer) and horn flies (*Haematobia irritans* Linnaeus). Dung beetle activity not only breaks up the pat, which causes rapid drying of the dung and reduces available breeding area, they can also damage any eggs present in the dung (162). High densities of *Onthophagus gazella* Fabricius (= *Digitonthophagus gazella* (Fabricius)) have been shown to relocate enough dung in 24-hours that maggots died of starvation (27). In addition, some species of phoretic mites found on beetles prey on fly eggs and larvae (162). Pest flies can have detrimental effects on cattle. Specifically, biting stable flies (*Stomoxys calcitrans* (Linnaeus)) are known to reduce productivity of livestock and cause pain and suffering to the animals (207). In Australia, dung beetles were introduced to reduce populations of bush fly (182, 183).

Other benefits of dung beetles are nutrient cycling and seed dispersal (162). Species belonging to the roller and tunneller guilds help accelerate this process due the relocation of dung below the soil surface (162). Tunnelling could also facilitate an increase of soil aeration and water porosity, which may enhance plant growth (162). Bang et al. (12) were able to show that an increase in air permeability of the soil was linked to the presence of a tunneler *Copris ochus* (Motschulsky), presumably because of its large body size. They also found that beetle presence only increases air permeability at a maximum depth of 10 cm (12).

Due to the many benefits that the dung insect community offers, many studies have compiled lists of coprophilous arthropods associated with different geographical regions. Most of these lists are limited to subsets of dung-dwelling insects or to individual states or provinces; e.g., Québec (149), British Columbia (141), Alberta (74), North Dakota (98), Minnesota (39), New York (213), and North Carolina (16). Blume (22) provides the most comprehensive record for all taxa reported in association with cattle dung on pastures in North America north of Mexico. However, this list is now more than thirty years old and has a specific focus on bovine droppings.

2.4 Improvements Offered in this Update

To facilitate future research on coprophilous beetles in North America, I updated Blume's list (22) with a number of significant improvements. First, I only included species of beetles that are known to be coprophagous; Geotrupidae (earth-boring beetles), Histeridae (clown and hister beetles), Hydrophilidae (water scavenger beetles), Scarabaeidae (scarab beetles), Staphylinidae (rove beetles) and Troginidae (hide beetles). Blume (22) also included Cicindelidae (tiger beetles) and Carabidae (ground beetles), which are excluded in my list because they are considered incidental species, not dung-dwelling species. The exclusion of incidental species avoids confusing researchers who are new to the studies of coprophagous beetles. Because of time limitations, I did not include the many non-beetle species of insects that were included in the original list by Blume (22).

The second improvement is the inclusion of current references. These were used in conjunction with those provided by Blume (22) to update information for beetle species present in the original list and to include additional species that Blume (22) did not include. Any species known to colonize dung was included even if the citation did not use dung as a trapping method. Some references used carrion or light traps as an attractant whereas others were just a list of species known to be present in an area.

The third improvement that this update offers is the inclusion of insects recovered using dung from other common livestock and wildlife. The type of animal dung can influence both the type and the number of dung beetle species. Although some species are specialists in which dung they select, many are generalists and will use a variety of dung for breeding and nutritional purposes. Some studies have directly compared the effects of different animal dung to the species of dung beetles caught (66, 224). A legend of the included animals and the letter associated with them can be found in Table 2.1. This system is included as superscript letters at the end of the species name and with the associated reference. For clarity, only the animals that I felt were most common and of most value were included. Few papers have extensively compared the attractiveness of various types of dung and those that have, are scattered throughout the literature. Including various types of dung creates a more complete data set and provides more comprehensive information to the reader.

The final and possibly most valuable improvement of this update is the inclusion of current taxonomic information. In Blume's list (22), there were 34 different species of *Aphodius*. Because of current taxonomic revisions, only two species of *Aphodius* are now recognized as occurring in North America (85, 155). As well, the associated authority name that correspond with each species are included. This information was acquired using published literature. Some articles fail to include the proper authorities or the authority is abbreviated, which can be confusing if someone is unfamiliar with the names. The electronic taxonomic database Integrated Taxonomic Information System (ITIS) was used as a starting point to determine the proper classifications and authorities (120).

In recent years, publications have surfaced which have reclassified the species belonging to the genus *Aphodius*. Gordon & Skelley (85) proposed; 20 new genera, 179 new combinations, 38 new species and 28 new synonyms. Their goal was to combine various references in regards to the Aphodiinae subfamily for ease of use and uniform classification. More recently however, a publication by Dellacasa et al. (45) reclassified those species belonging to the genera *Alloblackburneus* Bordat and *Blackburneus*

Schmidt. I followed the suggestions present in both publications to reclassify the species belonging to the *Aphodius* genus. Updated taxonomic information for Histeridae and Staphylinidae (*Aleochara*) was derived from Bousquet & Laplante (31) and Klimaszewski (128), respectively.

To help alleviate confusion between the old and new classifications, the name given in Blume and the previous classification have been included under what is now believed to be the currently accepted classification. Synonyms of the species were not included in this update as they have been sufficiently documented in the publications listed above, as well as in Smith (200).

This updated list includes 305 species (plus 8 subspecies) of beetles, including 153 species not listed by Blume; i.e., 8 species (4 not in Blume) and 2 subspecies (2 not in Blume) of Geotrupidae, 54 species of Histeridae (34 not in Blume), 24 species of Hydrophilidae (9 not in Blume), 148 species (51 not in Blume) and 6 subspecies (6 not in Blume) of Scarabaeidae, 63 species of Staphylinidae (39 not in Blume), 8 species of Trogidae (8 not in Blume). All species are arranged alphabetically by genera in their respective families. The species present in the original list by Blume (22) have been denoted with bolded text. Those that are not bolded represent species that Blume did not include, but are known to be associated with dung.

To conclude, this update, although comprehensive, is by no means exhaustive. I encourage the reader to use this update as a starting point. For added convenience, an excel file has been created to allow the reader to focus on the location, species or dung type of interest. For example, using this excel file can quickly generate a list of coprophagous beetles reported for any province or state in North America north of Mexico. Any blank cells in the excel file indicates that I did not find any published data for that area. The last column of the excel file is a notes section with added information that could not easily be placed into one of the existing columns. I would like to note that when the word 'Present' is written, that simply means that the trapping method used was either not specified, did not use dung, or the reference was simply a list of the beetle species known to be present in a certain area. The associated references for each cell have been included in square brackets with the entire reference list being included in a separate sheet. It is hoped that the availability of this updated and expanded list will facilitate future research on coprophilous beetles and further increase appreciation for the diverse community of insects in dung.

Table 2.1. Checklist of coprophilous beetle species associated with dung of livestock and other animals on pastures in America north of Mexico. Dung sources include: Cow (*), Pig (P), Horse (E), Human (H), Sheep (S), Deer (D), Chicken (G), Dog (C), Alpaca (A), Moose (M), Donkey (K), Bison (B), Turkey (T), and Porcupine (Q). Bolded text indicates species present in Blume's list (22) and underlined text indicates synonyms that were common in the literature. The associated reference is also underlined.

Family Geotrupidae Latreille, 1802 (Earth-boring scarab beetles)	
Geotrupes balyi Jekel [E]	Massachusetts (124)[E] (82), Manitoba (30), New Brunswick (30) (220), Nova Scotia (30), Ontario (30), Québec (30)
***Geotrupes blackburnii* (Fabricius) *[EHP]**	Indiana (17), Maryland (179)[EH] (174)[EH], Massachusetts (124)[E], North Carolina (135)* (15)*, Ohio (196), Oklahoma (34), Texas (26)* (64)[P], east to Massachusetts and south through Virginia to Florida (111)
Geotrupes blackburnii blackburnii (Fabricius) *	Massachusetts (82), North Carolina (16)* (14)*, South Carolina (41)
Geotrupes blackburnii excrementi Say *	Arkansas (59)*
***Geotrupes egeriei* Germar *[EH]**	Florida (123)*, Maryland (179)[EH] (174)[H], Massachusetts (124)[E] (82), Michigan (187)*, South Carolina (41), New Hampshire south to Florida and west to Michigan, Illinois, and Louisiana (111) (233)
Geotrupes hornii Blanchard [E]	Connecticut (197), Illinois (197), Indiana (197), Maine (197), Maryland (197), Massachusetts (124)[E] (82) (197), Michigan (197), New Hampshire (197), New Jersey (197), New York (197), Ohio (197), Pennsylvania (197), Rhode Island (197), District of Columbia (197), Wisconsin (197), Newfoundland (30), Ontario (30), Québec (30), may occur in Nebraska (178)
***Geotrupes opacus* Haldeman *[PH]**	Colorado (111), Indiana (111), Kansas (178), Louisiana (111), Michigan (187)* (111), Missouri (111), Nebraska (178) (43), Ohio (111), Oklahoma (34), South Dakota (178), Texas (20)*, Wisconsin (131)[PH] (111), Colorado to Ohio (178)
Geotrupes semiopacus Jekel *[PHSDC]	Michigan (187)*, Minnesota (39)*, Nebraska (178), New Jersey (172)* (173)[HCS], New York (170)*, North Dakota (98)*[SD], Wisconsin (131)[PH], Manitoba (30), Ontario (30) (178), Québec (30) (178), southeast Canada south to North Carolina and westward to the eastern Dakotas (178), probably occurs in eastern Kansas (178)
***Geotrupes splendidus* (Fabricius) [PEH]**	Louisiana (218), Massachusetts (124)[E], Missouri (148), eastern Nebraska (178), Ohio (196), Wisconsin (131)[PH], Ontario (111) and Quebec (111), south to Georgia and Florida and west to Mississippi, Arkansas, Oklahoma, Kansas and Minnesota (111)
Mycotrupes gaigei Olson and Hubbell *	Florida (123)*

Family Histeridae Gyllenhal, 1808 (Clown beetles, Hister beetles)	
Acritus acaroides Marseul *	Texas (205)*
Acritus exiguus (Erichson)	Southernmost Québec and Ontario south to Florida and Texas (31), New Brunswick (30), Ontario (30), Québec (30)
Acritus nigricornis (Hoffmann)	Southern Alberta (30) (31), British Columbia (30) (31), southern Manitoba (30) (31), southernmost Québec (30) (31), Saskatchewan (30)
***Atholus americanus* (Paykull) *** **= *Hister americanus* Paykull in Blume (22)** **= *Atholus americanus* Paykull in Blume (22)**	Florida (152), Illinois (156)*, Iowa (152), Missouri (228)* (208)*, South Dakota (126)*, Washington (152), Manitoba (152), Ontario (30) (152), Québec (30) (152), Kansas, and east to Georgia, and Florida (17) (109)
Atholus bimaculatus (Linnaeus) * **= *Peranus bimaculatus* Linnaeus in Blume (22)**	California (153) (154)*, Texas (205)*, Alberta (30) (31) (152), British Columbia (30) (31), Manitoba (30) (31) (152), New Brunswick (30), Ontario (30) (31) (152), Québec (30) (31) (152), Saskatchewan (152), District of Columbia to Iowa and Washington (152)
Atholus sedecimstriatus (Say)	New Brunswick (30), Ontario Peninsula (30) (31), Southern Québec (30) (31), south to Florida and Texas (31)
Carcinops pumilio (Erichson)	Alberta (30), British Columbia (30), Manitoba (30), New Brunswick (30), Newfoundland (30), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30) Saskatchewan (30), Newfoundland to southwestern British Columbia (31)
Euspilotus assimilis (Paykull) * **= *Saprinus assimilis* Paykull in Blume (22)**	Southern Florida (31), Missouri (228)* (229)*, Texas (26)* (205)*, Manitoba (30), New Brunswick (30), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30), Iowa east to Connecticut and Florida (17)
***Euspilotus placidus* (Erichson) ***	Texas (26)* (205)*
Euspilotus scrupularis (LeConte)	Arizona (31), California (31), Florida (31), Georgia (31), eastern Oregon (31), Texas (31), Utah (31), Washington (31), southeastern British Columbia (31)
***Euspilotus vescus* (Marseul) ***	Texas (26)* (205)*
Geomysaprinus monilatus (Casey)	Manitoba (30), New Brunswick (30), Ontario (30), Québec (30), New Brunswick to Ontario Peninsula (31), southern Manitoba, south to northern Florida (31)
Geomysaprinus posthumus (Marseul) *	Texas (205)*
Gnathoncus barbatus Bousquet & Laplante	Alaska (30), Alberta (30), British Columbia (30), New Brunswick (30), Nova Scotia (30), Ontario (30), Québec (30), Saskatchewan (30), Nova Scotia to Ontario, southwest Saskatchewan to central British Columbia (31)

***Hister abbreviatus* Fabricius *[ES]**	Florida (31) (109)*, Georgia (109)*, Illinois (156)*, Louisiana (218), Massachusetts (124)[E], Minnesota (39)*, Nebraska (168)* (191)*, New York (170)* (213)*, Ohio (196), South Dakota (126)* (127)*[S], Texas (205)*, Alberta (30) (31), British Columbia (30) (31) (141)*, Manitoba (30) (31), New Brunswick (30) (31), Ontario (30) (31), Québec (30) (31), Saskatchewan (30) (31)
***Hister coenosus* Erichson ***	Florida (17), New Mexico (57), Texas (26)* (205)* (206)*, and gulf states (17)
Hister furtivus LeConte	Alberta (30), British Columbia (30), Manitoba (30), New Brunswick (30), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30), Saskatchewan (30), Nova Scotia to British Columbia (31), south to Arizona (31), Georgia (31), New Mexico (31)
***Hister incertus* Marseul ***	Florida (17), Indiana (197) (17), Kansas (17), New York (197), Pennsylvania (197), Rhode Island (197), Texas (26)* (205)* (206)*, Wisconsin (197)
Hister nomus Erichson *	Hawaii (94)*
Hololepta vicina LeConte *	Texas (205)*
Margarinotus egregius (Casey)	Manitoba (30), New Brunswick (30), Nova Scotia (30), Ontario (30), Québec (30), Nova Scotia to southeastern Manitoba (31), south at least to Illinois and South Carolina (31)
Margarinotus faedatus (LeConte) * = *Hister foedatus* LeConte (39)	Minnesota (39)*, Ohio (196), New Brunswick (30), Nova Scotia (30), Ontario (30) Prince Edward Island (30), Québec (30), Nova Scotia to southern Ontario and south to Texas and Georgia (31)
Margarinotus harrisii (Kirby)	Alberta (30), British Columbia (30) Manitoba (30), New Brunswick (30), Ontario (30), Québec (30), Saskatchewan (30), Southeastern British Columbia to southern Manitoba (31), Ontario Peninsula and southern Québec (31)
Margarinotus interruptus (Beauvois)	Manitoba (30) New Brunswick (30), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30), Saskatchewan (30), Prince Edward Island and Nova Scotia to the Ontario Peninsula (31), southern Manitoba and Saskatchewan (31), south at least to South Dakota, Illinois and Pennsylvania (31)
Margarinotus lecontei Wenzel	Alberta (30), Manitoba (30), New Brunswick (30), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30), Saskatchewan (30), Nova Scotia to central Alberta and south to Texas and Georgia (31)
Margarinotus merdarius (Hoffman)	Alberta (30), British Columbia (30), Manitoba (30), New Brunswick (30), Nova Scotia (30), Ontario (30), Québec (30), Nova Scotia to eastern Manitoba (31), central Alberta to southwestern British Columbia (31)
Margarinotus obscurus (Kugelann)	Southwestern British Columbia (30) (31), Oregon (31), Illinois (31)
Margarinotus purpurascens (Herbst)	Southwestern British Columbia (30) (31)
Margarinotus rectus (Casey)	Idaho (31), Kansas (31), Oregon (31), Washington (31), British Columbia (30) (31)

Margarinotus umbrosus (Casey)	British Columbia to western Alberta (30) (31), south to California and east to Montana (31)
Onthophilus deflectus Helava	Southern Ontario south to Florida and Louisiana (31), west to Nebraska (31), Ontario (30)
Onthophilus kirni Ross *	Texas (205)*
***Onthophilus nodatus* LeConte ***	Texas (26)* (205)*, Oklahoma east to Florida, and North and South Carolina (97)
Onthophilus pluricostatus LeConte	Massachusetts and Michigan south to northern Florida and Louisiana (31) Québec (30)
Pachylister caffer (Erichson) *	Hawaii (94)*
***Phelister affinis* LeConte ***	Texas (26)*
Phelister haemorrhous Marseul *	Texas (205)*
***Phelister panamensis* LeConte ***	Texas (26)* (205)*
Phelister rouzeti (Fairmaire) *	Texas (205)*
***Phelister subrotundus* (Say) ***	Florida (17) (31), Indiana (17), Minnesota (39)*, Missouri (228)*, Nebraska (168)* (191)*, New York (17), South Dakota (125)*(126)*(127)*, Texas west to South Dakota (31), Ontario (30) (31), Québec (30) (31)
Phelister vernus (Say) *	Texas (205)*
Saprinus distinguendus Marseul	Michigan (31), Minnesota (31), North Dakota (31), South Dakota (31), Manitoba (30), Ontario (30) Québec (30) (31), Saskatchewan (30) (31), Northwest Territories (30) (31)
***Saprinus lugens* Erichson ***	Arizona, California, east to Iowa and Michigan (17), Texas (26)*, Alberta (30), British Columbia (30), Manitoba (30), Ontario (30), Québec (30), Saskatchewan (30), southern Québec to British Columbia (31), south to Mexico and southern Florida (31)
***Saprinus oregonesis* LeConte ***	Oregon, California, and east to Connecticut (17), Alberta (30) (31), British Columbia (30) (31) (141)*, Manitoba (30) (31), Saskatchewan (30) (31), south to California and New Mexico (31)
***Saprinus pennsylvanicus* (Paykull) *[E]**	Arizona, Colorado, and east to Connecticut (17), Nebraska (191)*, Ohio (196), Texas (26)* (205)* (206)* (190)*[E]
Saprinus profusus Casey	Ontario Peninsula and southern Manitoba (30) (31), south to Texas, west to Arizona (31)
Spilodiscus biplagiatus (LeConte) *	Texas (205)*
Spilodiscus ulkei (Horn)	Southwestern Saskatchewan and southern Alberta (31), south to southern Arizona (31), New Mexico (31), Texas (31)
Xerosaprinus acilinea (Marseul)	Alberta (30), British Columbia (30), Manitoba (30), Saskatchewan (30), Southwestern Manitoba to British Columbia (31), south to California and Texas (31)
***Xerosaprinus fimbriatus* (LeConte) ***	Texas (26)*
Xerosaprinus lubricus (LeConte) *	California (31) (17), British Columbia (30) (31) (141)*

= ***Saprinus lubricus* LeConte in Blume (22)**	
***Xerosaprinus orbiculatus* (Marseul) ***	Texas (26)* (205)* (206)*
Xerosaprinus plenus (LeConte) * = ***Saprinus plenus* LeConte in Blume (22)**	California, Arizona, and east to Kansas (109), New Mexico (31), Texas (26)*
***Xestipyge conjuctum* (Say) ***	Central Florida (31), Texas (26)* (205)* (206)*, Ontario (30), gulf states to Virginia (17)
Family Hydrophilidae Latreille, 1802 (Water scavenger beetles)	
Cercyon assecla Smetana	Alabama (199), Connecticut (199), District of Columbia (199), Illinois (199), Indiana (199), Iowa (199), Kansas (199), Maine (199), Maryland (199), Massachusetts (199), Michigan (199), Minnesota (199), Missouri (199), New Hampshire (199), New Jersey (199), New Mexico (199), New York (199), North Carolina (199), Ohio (199), Pennsylvania (199), Tennessee (199), Virginia (199), West Virginia (199), Wisconsin (199), Alberta (30) (199), New Brunswick (30) (199),Nova Scotia (30), Ontario (30) (199), Québec (30) (199), Saskatchewan (30)
***Cercyon haemorrhoidalis* (Fabricius) *[S]**	Alabama (199), Arizona (199), Arkansas (199), California (153)* (199), Connecticut (199), Delaware (199), District of Columbia (199), Georgia (199), Idaho (199), Illinois (156)* (199), Indiana (199), Iowa (199), Kansas (199), Kentucky (199), Louisiana (199), Maine (199), Maryland (199), Massachusetts (199), Michigan (199) (216)*[S], Minnesota (39)* (199), Missouri (199), New Hampshire (199), New Jersey (199) (227)[S], New York (199), North Carolina (199), Ohio (199), Oregon (199), Pennsylvania (199), Rhode Island (199), South Carolina (199), Tennessee (199), Texas (26)* (199), Utah (199), Vermont (199), Virginia (199), Washington (199), West Virginia (199), Wisconsin (199), British Columbia (30) (199), Labrador (30), New Brunswick (30) (199), Newfoundland (30) (199), Nova Scotia (30) (199), Ontario (30) (199), Prince Edward Island (30) (199), Québec (30) (149)* (199)
Cercyon impressus (Sturm)	Pennsylvania (199), Washington (199), British Columbia (30) (199)
***Cercyon lateralis* (Marsham) ***	California (199), Connecticut (199), District of Columbia (199), Illinois (199), Indiana (199), Iowa (199), Kansas (199), Kentucky (199), Maryland (199), Massachusetts (199), Michigan (199), Minnesota (39)* (199), Nebraska (168)*, New Hampshire (199), New Jersey (199), New Mexico (199), New York (199), Ohio (199), Oregon (199), Pennsylvania (199), Rhode Island (199), South Dakota (126)*(127)*(199), Tennessee (199), Virginia (199), Washington (199), West Virginia (199), Wisconsin (199), Alberta (30) (199) (72)*, British Columbia (30) (199), New Brunswick (30) (199), Newfoundland (30) (199), Northwest Territories (30) (199), Nova Scotia (30) (199), Ontario (30) (199), Québec (30) (199), Saskatchewan (30)

***Cercyon limbatus* Mannerheim ***	Alaska (30) (199), California (199) (171)*, Idaho (199), Nevada (199), New Mexico (199), Oregon (199), Texas (199), Washington (199), Wyoming (199), Alberta (30) (199), British Columbia (30) (199), Northwest Territories (30) (199), Yukon (30) (199)
Cercyon marinus Thomson	Alaska (30) (199), California (199), Colorado (199), Idaho (199), Iowa (199), Michigan (199), Minnesota (199), North Dakota (199), Oregon (199), South Dakota (199), Washington (199), Wisconsin (199),Wyoming (199), Alberta (30) (199), British Columbia (30) (199), Manitoba (30) (199), Northwest Territories (30) (199), Ontario (30) (199), Québec (30) (199), Saskatchewan (30) (199), Yukon (30) (199)
Cercyon minusculus Melsheimer [D]	District of Columbia (199), Illinois (199), Kentucky (199), Maine (199) , Maryland (199), Massachusetts (199), Michigan (199) New Hampshire (199), New Jersey (199), New York (199), North Carolina (199), Pennsylvania (199), South Dakota (199), Virginia (199), West Virginia (199), Wisconsin (199), British Columbia (30) (199), Manitoba (30) (199), New Brunswick (30) (199), Newfoundland (30) (199), Nova Scotia (30), Ontario (30) (199), Québec (30) (199) (33)[D], Saskatchewan (30)
Cercyon nigriceps (Marsham) * **= *Cercyon atricapillus* Marsham in Blume (22)**	Alabama (199), California (199), District of Columbia (199), Florida (199), Georgia (199), Idaho (199), Illinois (199), Indiana (199), Kansas (199), Louisiana (199), Maryland (199), Massachusetts (199), Michigan (199), Mississippi (199), Missouri (199), New Hampshire (199), New Jersey (199), New York (199), North Carolina (199), Oregon (199), Pennsylvania (199), Tennessee (199), Texas (20)* (199), Alberta (30) (199), Nova Scotia (30) (199), Québec (30) (199), Saskatchewan (30)
***Cercyon praetextatus* (Say) *[S]**	Alabama (199), Arkansas (199), California (199), Colorado (199), Connecticut (199), District of Columbia (199), Florida (199), Georgia (199), Illinois (199), Indiana (199), Iowa (199), Kansas (199), Kentucky (199), Louisiana (199), Maryland (199), Massachusetts (199), Michigan (199) (216)*, Minnesota (39)* (199), Mississippi (199), Missouri (199), Nebraska (168)* (199), New Hampshire (199), New Jersey (199) (227)[S], New York (199), North Carolina (199), North Dakota (199), Ohio (199), Oklahoma (199), Oregon (199), Pennsylvania (199), Rhode Island (199), South Carolina (199), South Dakota (126)*(127)*(199), Tennessee (199), Texas (199), Utah (199), Vermont (199), Virginia (199), West Virginia (199), Wisconsin (199), Wyoming (199), Manitoba (30) (199), Nova Scotia (30), Ontario (30) (199), Québec (30) (199)
***Cercyon pygmaeus* (Illiger) *[S]**	Arizona (199), California (199), Colorado (199), Connecticut (199), District of Columbia (199), Idaho (199), Illinois (156)* (199), Indiana (199), Iowa (199), Kansas (199), Kentucky (199), Maine (199), Maryland (199), Massachusetts (199), Michigan (199) (216)*[S], Minnesota (39)*, Missouri (199), Montana (199), Nebraska (168)* (199), New Hampshire (199), New Jersey (199) (227)[S], New Mexico

	(199), New York (199), North Carolina (199), Ohio (199), Oklahoma (199), Oregon (199), Pennsylvania (199), Rhode Island (199), South Dakota (127)*[S] (126)* (199), Tennessee (199), Texas (26)* (199), Utah (199), Vermont (199), Virginia (199), Washington (199), West Virginia (199), Wisconsin (199), Alberta (30) (199) (72)*, British Columbia (30) (199), Manitoba (30) (199), New Brunswick (30) (199), Newfoundland (30) (199), Nova Scotia (30) (199), Ontario (30) (199), Québec (30) (149)* (199), Saskatchewan (30) (199)
***Cercyon quisquillius* (Linnaeus) *[S]**	Arizona (199), Arkansas (199), California (199) (171)*, Colorado (199), Connecticut (199), Florida (199), Hawaii (94)*, Idaho (199), Illinois (156)* (199), Indiana (199), Iowa (199), Kansas (199), Kentucky (199), Maine (199), Maryland (199), Michigan (216)*[S] (199), Minnesota (39)* (199), Missouri (229)* (199), Nebraska (168)* (191)* (199), Nevada (199), New Hampshire (199), New Jersey (199), New Mexico (199), New York (199), North Carolina (199), Ohio (199), Oklahoma (199), Oregon (199), Pennsylvania (199), South Carolina (199), South Dakota (127)*[S] (126)* (199), Tennessee (199), Texas (26)* (199), Utah (199), Vermont (199), Virginia (199), Washington (199), Wisconsin (199), Wyoming (199), Alberta (30) (199) (72)*, British Columbia (30) (199), Manitoba (30) (199), New Brunswick (30) (199), Newfoundland (30) (199), Nova Scotia (30) (199), Ontario (30) (199), Québec (30) (149)* (199), Saskatchewan (30) (199)
***Cercyon unipunctatus* (Linnaeus) *[S]**	Connecticut (199), District of Columbia (199), Idaho (199), Illinois (199), Iowa (199), Maine (199), Maryland (199), Massachusetts (199), Michigan (199), Minnesota (39)*, New Hampshire (199), New Jersey (199), New York (199), Oregon (199), Pennsylvania (199), Rhode Island (199), South Dakota (127)*[S] (126)* (199), Wisconsin (199), Alberta (30) (199) (72)*, British Columbia (30) (199), Manitoba (30) (199), New Brunswick (30) (199), Nova Scotia (30) (199), Ontario (30) (199), Québec (30) (199), Saskatchewan (30) (199)
Cercyon ustulatus (Preyssler)	New Jersey (199), New York (199), Québec (30)
***Cercyon variegatus* Sharp ***	Alabama (199), Florida (199), Georgia (199), Louisiana (199), Mississippi (199), North Carolina (199), Texas (26)* (199)
Cercyon versicolor Smetana	Alabama (199), Arkansas (199), District of Columbia (199), Florida (199), Georgia (199), Illinois (199), Kansas (199), Louisiana (199), Maryland (199), Mississippi (199), Missouri (199), North Carolina (199), Pennsylvania (199), South Carolina (199), Tennessee (199), Texas (199), Virginia (199), West Virginia (199)
***Cryptopleurum minutum* (Fabricius) *[S]**	California (199), Colorado (199), Connecticut (199), Florida (199), Idaho (199), Illinois (199), Indiana (199), Iowa (199), Kansas (199), Maine (199), Maryland (199), Massachusetts (199), Michigan (199) (216)*[S], Minnesota (199) (39)*, Missouri (229)*, Montana (199), Nebraska (199), New Hampshire

	(199), New Jersey (199), New York (199), North Carolina (199), North Dakota (199), Ohio (199), Oregon (199)¸ Pennsylvania (199), Rhode Island (199), South Dakota (127)*[S] (126)* (199), Texas (26)*, Utah (199), Vermont (199), Virginia (199), Washington (199), West Virginia (199), Wisconsin (199), Alberta (199) (72)* (30), British Columbia (30) (199), Manitoba (30) (199), New Brunswick (30) (199), Newfoundland (30) (199), Nova Scotia (30) (199), Ontario (30) (199), Prince Edward Island (30), Québec (30) (199), Saskatchewan (30)
Cryptopleurum subtile **Sharp ***	California (199), Connecticut (199), District of Columbia (199), Idaho (199), Illinois (199), Indiana (199), Kentucky (199), Maine (199), Maryland (199), Massachusetts (199), Michigan (199), Minnesota (39)*, Mississippi (199), Missouri (199), Nebraska (168)*, New Hampshire (199), New Jersey (199), New York (199), North Carolina (199), North Dakota (199), Ohio (199), Oregon (199), Pennsylvania (199), South Carolina (199), South Dakota (199), Texas (26)*, Utah (199), Virginia (199), Wisconsin (199), Alberta (30), British Columbia (30) (199), Manitoba (30), New Brunswick (30), Newfoundland (30), Ontario (30) (199), Québec (30) (199), Saskatchewan (30) (199)
Helophorus orientalis Motschulsky *	Alberta (30), British Columbia (30), Manitoba (30), New Brunswick (30), Northwest Territories (30), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30) (149)*, Saskatchewan (30)
Megasternum posticatum (Mannerheim)	Alaska (30) (199), California (199), Oregon (199), Washington (199), British Columbia (30) (199)
Oosternum pubescens (LeConte) * **= *Cercyon pubescens* LeConte in Blume (22)**	Connecticut (199), District of Columbia (199), Florida (199), Georgia (199), Illinois (199), Indiana (199), Maryland (199), Massachusetts (199), Missouri (229)* (199), New Jersey (199), New York (199), North Carolina (199), Ohio (199), Pennsylvania (199), South Carolina (199), Tennessee (199), Virginia (199), West Virginia (199)
Phanenonotum exstriatum (Say)	Alabama (199), Arizona (199), Arkansas (199), District of Columbia (199), Florida (199), Georgia (199), Illinois (199), Indiana (199), Kansas (199), Louisiana (199), Maryland (199), Michigan (199), Mississippi (199), Missouri (199), New Jersey (199), New York (199), Ohio (199), Oklahoma (199), Pennsylvania (199), South Carolina (199), Tennessee (199), Texas (199), Virginia (199)
Sphaeridium bipustulatum **Fabricius *[S]**	California (153)* (199) (171)*, Colorado (199), Connecticut (199), Georgia (199), Idaho (199), Illinois (156)* (199), Indiana (199), Iowa (199), Kansas (199), Maine (199), Maryland (199), Massachusetts (199), Michigan (216)*[S] (199), Minnesota (39)*, Missouri (228)* (199), Nebraska (168)* (191)*, New Hampshire (199), New Jersey (227)[S] (199), New York (170)* (213)* (199), Ohio (199), Oregon (199), Pennsylvania (199), Rhode Island (199), South Carolina (199), South Dakota (127)*[S] (126)*, Tennessee (199), Utah (199), Virginia (199), Washington (199) Alberta (30) (199) (72)*, British Columbia (30) (141)* (199), Manitoba (30), New Brunswick (30) (199), Nova Scotia (30), Ontario (30) (199), Prince Edward Island (30), Québec (30) (149)*(199), Saskatchewan (30) (199)

***Sphaeridium lunatum* Fabricius ***[S]	Alabama (199), Arizona (199), California (153)* (199) (171)*, Colorado (199), Connecticut (199), Georgia (199), Idaho (199), Illinois (199), Indiana (199), Iowa (199), Kansas (199), Kentucky (199), Maine (199), Maryland (199), Massachusetts (199), Michigan (187)* (216)*[S](199), Minnesota (39)*, Missouri (229)* (199), Montana (199), Nebraska (168)* (191)* (199), New Hampshire (199), New Jersey (199), New Mexico (199), New York (170)* (213)* (199), North Carolina (199), Ohio (199), Oklahoma (199), Oregon (199), Pennsylvania (199), South Dakota (127)*[S] (126)* (199), Tennessee (199), Texas (26)* (199), Utah (199), Virginia (199), Washington (199), Wisconsin (199), Wyoming (199), Alberta (30) (199) (72)*, British Columbia (30) (141)* (199), Manitoba (30) (199), New Brunswick (30) (199), Newfoundland (30) (199), Nova Scotia (30) (199), Ontario (30) (199), Prince Edward Island (30), Québec (30) (149)* (199), Saskatchewan (30) (199)
***Sphaeridium scarabaeoides* (Linnaeus) ***[SA]	Alabama (28)* (29)*, Arizona (199), California (153)* (199) (171)*, Colorado (199), Connecticut (199), Delaware (199), District of Columbia (199), Georgia (199), Hawaii (94)*, Idaho (199), Illinois (156)* (199), Indiana (199) (188)* (189)*, Iowa (199), Kansas (199), Kentucky (199), Maine (199), Maryland (199), Massachusetts (199), Michigan (187)* (216)*[S] (199), Minnesota (39)* (199), Montana (199), Missouri (229)* (208)*, Nebraska (168)* (191)*, Nevada (199), New Hampshire (199), New Jersey (227)[S] (199), New Mexico (199), New York (170)* (213)* (199), North Carolina (199), North Dakota (199), Ohio (199), Oregon (199), Pennsylvania (199), Rhode Island (199), South Carolina (199), South Dakota (127)*[S] (126)*, Tennessee (199), Texas (19)*, Utah (199), Vermont (199), Virginia (199) (9)[A], Washington (199), West Virginia (199), Wisconsin (199), Wyoming (199), Alberta (30) (199) (72)*, British Columbia (30) (141)* (199), Manitoba (30) (199), New Brunswick (30) (199), Newfoundland (30) (199), Nova Scotia (30) (199), Ontario (30) (199), Québec (30) (199), Saskatchewan (30) (199)
Family Scarabaeidae Latreille, 1802 (Scarab beetles)	
Acrossus rubripennis (Horn) *[PEHMD] = *Aphodius rubripennis* Horn (85)	Maryland (197), Massachusetts (124)[E], Michigan (53)[M] (85), New Jersey (172)* (173)[H], New York (197), North Carolina (85), Ohio (85), Pennsylvania (197), Rhode Island (197), Wisconsin (131)[PHD] (85), New Brunswick (30) (220) (85), Nova Scotia (30), Ontario (30) (197) (85), Québec (30) (197) (85)
Agoliinus aleutus (Eschscholtz) **= *Aphodius aleutus* Eschscholtz in Blume (22)**	Alaska (30), California (17) (85) (138), Colorado (17) (138), New Mexico (57), Oregon (17) (85), Washington (17) (85), Alberta (30) (85), British Columbia (30) (85)

Agoliinus anthracus Gordon & Skelly * **= *Aphodius anthracinus* LeConte in Blume (22)**	Arizona (17) (138), Colorado (26)* (85), Idaho (85), Montana (85), New Mexico (57), Utah (17) (85) (138), Wyoming (85), Alberta (30) (85)
Agoliinus congregatus (Mannerheim) * **= *Aphodius congregatus* Mannerheim in Blume (22)**	Alaska (30) (85), California (17) (138), Montana (85), Washington (85), Alberta (30) (85), British Columbia (30) (141)*
Agoliinus cruentatus (LeConte) * **= *Aphodius cruentatus* LeConte in Blume (22)**	Arizona (85), Colorado (85), Florida (233), New Mexico (85), Texas (19)*, Utah (85)
Agoliinus explanatus (LeConte) = *Aphodius explanatus* LeConte (85); found in prairie dog dung (178)	Colorado (178) (85), New Mexico (85), Nebraska (178) (85), North Dakota (178) (85), Wyoming (178) (85), southcentral and southwestern Canada (178), probably in Montana (178)
Agoliinus leopardus (Horn) *[PHSDQ] = *Aphodius leopardus* Horn (85)	Alaska (30) (85), Michigan (187)*, Minnesota (85), North Carolina (85), North Dakota (98)*[SD], South Dakota (85), Wisconsin (131)[PHD], Wyoming (85), Alberta (30) (85) (75)*, British Columbia (30) (85), Manitoba (30) (85), New Brunswick (30) (220), Newfoundland (30), Northwest Territories (30), Nova Scotia (30) (158)[Q], Ontario (30), Québec (30), Saskatchewan (30), Yukon (30) (85)
Agoliinus manitobensis (Brown) * = *Aphodius manitobensis* Brown (85)	Maryland (85), Massachusetts (85), Michigan (187)*, New Jersey (172)*, New York (85), Pennsylvania (85), Alberta (30) (85), Manitoba (30) (85), New Brunswick (30) (220) (85), Nova Scotia (30), Ontario (30) (85), Québec (30) (85)
Aidophus parcus (Horn) * = *Aphodius knausii* Fall (85)	Florida (46), Georgia (46), Indiana (178) (46), Kansas (178) (46), Maryland (46), Mississippi (46), Nebraska (178) (191)* (46), New Jersey (46), New Mexico (178) (46), North Carolina (46), Oklahoma (178) (46), South Carolina (46), Texas (178) (46), Wisconsin (178) (46), Ontario (46), New Jersey south to Florida and west to Mississippi (178)
Alloblackburneus aegrotus (Horn) *[EH] **= *Aphodius campestris* Blatchley in Blume (22)**	Alabama (233) (85), Florida (123)* (233) (85), Georgia (233), Maryland (179)[EH] (174)[H], New Jersey (85), North Carolina (233) (16)* (14)*, South Carolina north to New Jersey (233)
Alloblackburneus lentus (Horn) *[PHSD] **= *Aphodius lentus* Horn in Blume (22)**	Florida (233), Illinois (17) (138), Indiana (85) (138), Iowa (234), Kansas (85), Massachusetts (138), Michigan (187)*, Minnesota (39)*, Nebraska (191)* (43), North Dakota (98)*[S] (85), Pennsylvania (138), Texas (85), Wisconsin (131)[PHD], Ontario (30) (85), Québec (30), Massachusetts to Georgia, west to Nebraska and Kansas (178)
Alloblackburneus rubeolus (Beauvois) *[PEH] **= *Aphodius rubeolus* Beauvois in Blume (22)**	Colorado (85), Florida (123)* (233) (85), Indiana (138), Maryland (179)[E] (174)[H], Massachusetts (124)[E] (138), Michigan (85), Missouri (17) (138), Nebraska (168)* (43) (85), New Jersey (172)*, North Carolina (135)* (16)* (14)*, Oklahoma (34), Texas (26)* (85) (64)[P], Wisconsin (131)[P], Ontario (30), Québec (233)
Alloblackburneus tenuistriatus (Horn) *[P] **= *Aphodius tenuistriatus* Horn in Blume (22)**	Kansas (85), Louisiana (85), New Mexico (85), Oklahoma (34), Texas (26)* (85) (64)[P], Nebraska and Kansas south to Louisiana, Texas and New Mexico (178)

Aphodius fimetarius (Linnaeus)[1] *PHSMKBDA (more likely *Aphodius pedellus* (De Geer) in Canada and the northern United States) **= *Aphodius fimetarius* Linnaeus in Blume (22)**	Arkansas (59)*, California (154)* (171)*, Florida (123)* (233), Massachusetts (82), Michigan (187)* (216)*S, Minnesota (39)*, Nebraska (178) (168)* (191)* (224)PHMKB (223)H, New Jersey (172)*, New York (170)* (213)* (231), North Carolina (15)* (135)* (16)* (14)*, North Dakota (98)*SDB, South Dakota (127)*S, Texas (19)* (64)P, Virginia (9)A, Wisconsin (131)PH, Alberta (30) (72)* (75)* (122)*, British Columbia (30) (141)*, Labrador (30), Manitoba (30), New Brunswick (30) (220), Newfoundland (30), Northwest Territories (30), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30) (149)*, Saskatchewan (30), Transcontinental except Arizona and Utah (233)
Aphonus tridentatus (Say) *	Iowa (234)*, Massachusetts (82), Ontario (30), Québec (30)
***Ataenius abditus* (Haldeman)**	Arizona (138) (36), California (17) (138) (36), Florida (233), Indiana (138) (36), Iowa (234), Massachusetts (138) (36), Nebraska (43), Oklahoma (34), New Brunswick (30) (220), Ontario (30), Québec (30)
***Ataenius apicalis* Hinton**	Alabama (233), Texas to Florida and north to Virginia (36), eastern half of the United States west to Kansas and Nebraska (178)
***Ataenius cognatus* (LeConte)**	Arizona (36), California (36), Kansas (36), Louisiana (36), New Mexico (36), Oklahoma (34), Texas (36)
***Ataenius cylindricus* Horn ***	Florida (123)*, north to Pennsylvania and New Jersey, west to Texas (36)
***Ataenius erratus* Fall ***	Alabama (36), Florida (123)* (233), Georgia (36), North Carolina (135)* (16)* (14)*, Ohio (221), South Carolina (36)
Ataenius gracilis (Melsheimer) *	Iowa (234)*, Minnesota (39)*, Nebraska (178), Ohio (221), Ontario (30), Québec (30), eastern half of the United States and extreme southeast of Canada (178)
***Ataenius imbricatus* (Melsheimer) *E**	Florida (123)*, Maryland (179)E, Minnesota (233) (39)* (36), Nebraska (43), North Carolina (135)* (16)* (14)*, Texas (26)*, Ohio (221), Ontario (30) (178), Québec (30), Michigan to Massachusetts and south to Florida (233) (36), eastern half of the United States (178)
Ataenius miamii Cartwright *	North Carolina (16)* (14)*
***Ataenius picinus* Harold ***	Florida (123)* (233), Texas (26)*, southern Arkansas and Louisiana east to Georgia (36)
***Ataenius platensis* (Blanchard) *CP**	Arkansas (59)*, Florida (123)* (233), Louisiana (218), North Carolina (135)* (16)* (14)*, Texas (26)* (38)C (19)* (64)P, California and Arizona east through Arkansas, Tennessee and North Carolina (36)

[1] Both species are difficult to morphologically distinguish and both occur across North America. Reports of *Aphodius fimetarius* in Canada and the northern tier states are likely misidentifications of *Aphodius pedellus*. For the distinction, consult Miraldo et al. (155).

***Ataenius robustus* Horn ***	Arkansas (36), Illinois (36), Iowa (36), Missouri (228)*, Nebraska (178) (191)* (43), New Mexico (57), Wisconsin (36), Oklahoma (36), Kansas to South Dakota (36), central United States from South Dakota and Wisconsin south to Arkansas and Texas (178)
***Ataenius spretulus* (Haldeman) *[ESC]**	Arkansas (59)*, Florida (123)* (233), Idaho (36), Iowa (234)*, Maryland (179)[E], Massachusetts (124)[E], Minnesota (39)*, Missouri (228)*, Nebraska (178), New Jersey (172)*, North Dakota (98)*, Ohio (221), South Dakota (127)*[S] (126)*, Texas (38)[C], Utah (36), Ontario (30) (178), Québec (30), New Mexico east to Massachusetts and all states in the south (36)
***Ataenius strigatus* (Say) *[PH]**	Florida (233), Illinois (156)*, Iowa (234), Maryland (174)[H], Minnesota (39)*, Missouri (228)*, Nebraska (178) (168)* (43), New Jersey (172)*, New Mexico (57), Ohio (221), Oregon (36), Utah (36), Wisconsin (131)[PH], New Brunswick (30) (220), Ontario (30), Québec (30), Arizona east to Québec and Maine and all states to the south (36)
Ataenius texanus Harold * = *Ataenius punctifrons* Cartwright (39)	Minnesota (39)*, Nebraska (178), Ohio (221), central, northeastern and southwestern United States (178)
Ateuchus histeroides Weber *[PC]	Georgia (237)*, Louisiana (175)[P], Missouri (148), Nebraska (178), South Carolina (41), Texas (64)[P] (38)[C] (114), eastern half of the United States (178)
Ateuchus lecontei (Harold) *[H]	Florida (123)*, Maryland (174)[H]
Australaphodius frenchi (Blackburn)	California (85) (46)
Blackburneus stercorosus (Melsheimer) *[PEHS] **= *Aphodius stercorosus* Melsheimer in Blume (22)**	Arkansas (59)*, Florida (85), Illinois (156)*, Iowa (234), Kansas (85), Massachusetts (124)[E], Michigan (216)*[S], Minnesota (39)*, Missouri (148) (228)*, Nebraska (178) (43), New Jersey (173)[H], New York (213)*, Oklahoma (34), South Dakota (126)*, Texas (26)* (85) (64)[P], Wisconsin (131)[PH], Ontario (30), Québec (30) (85), Québec to Florida (233), eastern half of United States west to Nebraska, Kansas and Texas (178)
Calamosternus granarius (Linnaeus) *[PHSKC] **= *Aphodius granarius* Linnaeus in Blume (22)**	Arkansas (59)*, California (154)* (171)*, Colorado (132), Florida (123)*, Georgia (85), Illinois (156)*, Iowa (234)*, Massachusetts (82), Michigan (187)* (216)*[S], Minnesota (39)*, Missouri (228)*, Nebraska (178) (224)[PHK] (223)[H], New Jersey (172)*, New Mexico (57), New York (170)* (213)*, North Carolina (15)* (16)* (14)*, North Dakota (98)*, South Dakota (127)*[S] (126)*, Texas (26)* (38)[C], Wisconsin (131)[PH], Wyoming (165)*, Alberta (30) (72)* (75)* (122)*, British Columbia (30) (141)*, Manitoba (30), New Brunswick (30) (220), Nova Scotia (30), Ontario (30), Québec (30) (149)*, Saskatchewan (30)
Canthon blumei Halffter & Halffter *[H]	Texas (52)*[H]
***Canthon chalcites* (Haldeman) [PEH]**	Louisiana (233), Maryland (179)[E], Missouri (148), Nebraska (178) (43), Oklahoma (34), Wisconsin (131)[PH], Ontario (30), all of the eastern United States except Vermont, New Hampshire, and Maine (89)

	(233), eastern half of United States, but no records west of Lake Michigan and north of Chicago, Illinois (178)
***Canthon cyanellus* LeConte *[C]**	Texas (20)* (38)[C] (114)
Canthon depressipennis LeConte *[PEG] **= *Boreocanthon depressipennis* LeConte in Blume (22)**	Florida (123)*, Georgia (66)[PEG], North Carolina (135)*, South Carolina (41), Texas to North Dakota, Arkansas, and gulf coastal states to North Carolina (233)
Canthon ebenus (Say) *[EP] **= *Boreocanthon ebenus* Say in Blume (22)**	Colorado (132), Nebraska (178) (191)* (43), New Mexico (57), Oklahoma (34), Texas (26)* (64)[P] (114) (190)*[E], Texas northward to South Dakota (178)
***Canthon humectus* (Say) ***	Texas (26)*
***Canthon imitator* Brown *[CPHE]**	Arizona (89), Colorado (132), New Mexico (57), Oklahoma (34), Texas (19)* (64)[P] (38)[C] (114) (52)*[HE]
***Canthon indigaceus* LeConte**	Arizona (89), Texas (89)
Canthon lecontei Harold * **= *Boreocanthon lecontei* Harold in Blume (22)**	New Mexico (17), Oklahoma (34), Texas (19)*
Canthon melanus Robinson *[E] **= *Boreocanthon melanus* Robinson in Blume (22)**	Arizona (89), Texas (190)*[E]
Canthon mixtus Robinson *[H] **= *Boreocanthon mixtus* (Robinson) in Blume (22)**	Texas (17)* (52)*[H]
***Canthon pilularius* (Linnaeus) *[PHMKB]**	Colorado (132), Florida (123)*, Iowa (234), Maryland (174)[H], Nebraska (178) (191)* (224)[PHMKB] (223)[H], North Carolina (15)* (135)* (16)* (14)*, North Dakota (98)*[B], South Carolina (41), Texas (26)* (114), Alberta (30) (122)*, Saskatchewan (30), all of the United States east of Rockies except northern New England (233)
Canthon praticola LeConte *[BH] **= *Boreocanthon praticola* LeConte in Blume (22)**	Arizona (17), Colorado (132), Nebraska (178) (43), North Dakota (98)*[B], South Dakota (84), Texas (26)* (52)*[H], Utah (84), Alberta (178) (75)* (122)* (30), British Columbia (30) (178), Manitoba (30), Saskatchewan (30), southward from Alberta and British Columbia through the central states to Texas and Arizona (178)
Canthon probus (Germar) *[P] **= *Boreocanthon probus* Germar in Blume (22)**	Florida (123)* (233) (17), Georgia (233) (17), Kansas (233) (17), Kentucky (233) (17), Texas (20)* (64)[P], New Jersey south to Florida and west to Arizona and Utah (178)
Canthon puncticollis LeConte * **= *Boreocanthon puncticollis* LeConte in Blume (22)**	Arizona (17), California (17), New Mexico (17), Texas (20)*
Canthon simplex LeConte * **= *Boreocanthon simplex* LeConte in Blume (22)**	Arizona (17), Colorado (132), Idaho (17), Oregon (17), Utah (17), Alberta (30), British Columbia (142)* (30)

***Canthon vigilans* LeConte *[P]**	Florida (123)*, Illinois (89), Massachusetts (82) and south through Florida (233), Michigan (89), Nebraska (43), New York (233), North Carolina (16)* (14)*, South Carolina (41), Texas (26)* (64)[P] (114), Ontario (30), Massachusetts south to Florida and west to Nebraska, Kansas and Texas (178)
Canthon viridis (Beauvois) *[PHC] **= *Glaphyrocanthon viridis* Beauvois in Blume (22)**	Illinois (233), Iowa (234), Kansas (178), Louisiana (175)[P], Minnesota (233), Missouri (148), Nebraska (178), Oklahoma (178) (34), South Carolina (41), Texas (178) (20)* (64)[P] (38)[C] (114), Wisconsin (224)[PH], Ontario (30), Indiana to New York and New Jersey, and south to Georgia, and Florida (233), all over eastern United States (178)
Cephalocyclus luteolus (Horn) **= *Aphodius luteolus* Horn in Blume (22)**	Arizona (85), New Mexico (57) (85) (138), Texas (85), Utah (85)
Chilothorax distinctus (Müller) *[PEHSMKBD] **= *Aphodius distinctus* Müller in Blume (22)**	California (85), Colorado (132), Florida (85), Illinois (156)*, Indiana (42)*, Iowa (234)*, Maryland (174)[H], Massachusetts (124)[E], Michigan (187)* (216)*[S] (53)[M], Minnesota (39)*, Missouri (228)*, Nebraska (178) (43) (224)[PHMKB] (223)[H], New Jersey (172)*, North Carolina (15)* (16)* (14)*, North Dakota (98)*[SD], Oklahoma (85), South Dakota (126)* (127)*[S], Texas (26)*, Utah (85), Wisconsin (131)[PH], Alberta (30) (72)* (75)* (122)*, British Columbia (30) (141)* (85), Manitoba (30), New Brunswick (220), Nova Scotia (30), Ontario (30), Québec (30) (149)*, Saskatchewan (30), Atlantic States (17) (138)
Colobopterus erraticus (Linnaeus) *[PHSMKA] **= *Aphodius erraticus* Linnaeus in Blume (22)**	Arkansas (59)*, Georgia (85), Indiana (17), Iowa (234)*, Michigan (187)* (216)*[S], Minnesota (39)*, Missouri (148) (85), Montana (85), Nebraska (178) (168)* (85) (224)[PHMK] (223)[H], New York (170)* (213)*, North Carolina (15)* (135)* (16)* (14)*, North Dakota (98)*, South Dakota (178), Virginia (9)[A], Wisconsin (131)[PH], Alberta (30) (72)* (75)* (122)*, British Columbia (85), Manitoba (30), New Brunswick (30) (220), Newfoundland (30), Nova Scotia (30), Ontario (30), Québec (30) (149)*, Saskatchewan (30) , eastern states west to the Dakotas (178)
***Copris fricator* (Fabricius) *[PHMKB]** = <u>*Copris tullius*</u> Oliver (127)	Illinois (156)*, Iowa (234)*, Kansas (178), Michigan (187)*, Minnesota (39)*, Missouri (148), Nebraska (178) (43) (224)[PHMKB] (223)[H], New Jersey (172)*, New York (213)*, Oklahoma (178) (34), South Dakota (178) (126)* <u>(127)*</u>, Texas (178) (26)* (114) (110), Wisconsin (131)[PH], Ontario (30), Québec (30), eastern United States and Ontario except Maine, Georgia, Florida, and Mississippi (150), eastern United States west to South Dakota (178)
Copris fricator fricator Fabricius *	Massachusetts (82), Nebraska (191)*
Copris incertus Say *	Hawaii (94)*
***Copris inemarginatus* Blatchley**	Florida (233)
Copris minutus (Drury) *[PEHCA]	Florida (123)*, Georgia (66)[P] (237)*, Iowa (178), Kansas (178), Louisiana (175)[P], Maryland (179)[EH] (174)[EH], Massachusetts (82), Missouri (178), New Jersey (172)* (173)[HC], Nebraska (178), North

	Carolina (15)* (16)* (14)*, Oklahoma (178) (34), Texas (178) (26)*, Virginia (9)[A], Québec (30), Kansas and Iowa east through New Hampshire and south through Florida, and gulf states (150), eastern half of United States from New Hampshire south to Florida and west to northeastern Texas (178)
***Copris remotus* LeConte ***	Oklahoma (150), Texas (26)*
Cryptoscatomaseter acuminatus (Cartwright) [D] = *Aphodius acuminatus* Cartwright (85)	Arizona (178) (85), Kansas (178) (85), Nebraska (178) (85), Texas (178)[D] (85)
Cryptoscatomaseter iowensis (Wickham) *[P] = *Aphodius iowensis* Wickham (85)	Illinois (178) (85), Indiana (178) (85), Iowa (178) (85), Kansas (178), Nebraska (178) (85), North Dakota (85), Wisconsin (178) (131)[P], Alberta (30) (178) (85) (75)*, Manitoba (30) (178) (85), Saskatchewan (30)
Cryptoscatomaseter magnificens (Robinson) [P] = *Aphodius magnificens* Robinson (85)	Illinois (178) (85), Indiana (178) (85), Iowa (234), Kansas (178) (85), Minnesota (178) (85), Nebraska (178) (85), North Dakota (178) (85), Oklahoma (178) (85), Texas (178) (85), Wisconsin (178) (131)[P]
Cryptoscatomaseter punctissimus (Brown) [P] = *Aphodius punctissimus* Brown (85)	Colorado (85), Illinois (178) (85), Indiana (178) (85), Iowa (178) (85), Kansas (178) (85), Minnesota (85), Montana (178) (85), Nebraska (178) (85), Oklahoma (178) (85), Wisconsin (178) (131)[P], Alberta (30) (178) (85), Manitoba (30) (178) (85)
Dellacasiellus kirni (Cartwright) [P] = *Aphodius kirni* Cartwright (85)	Indiana (85), Iowa (234), Louisiana (85), New Mexico (178) (85), Texas (178) (85) (64)[P], Wisconsin (178) (131)[P], Manitoba (30) (178) (85), Indiana south to Louisiana (178)
Deltochilum gibbosum (Fabricius) [P]	Texas (64)[P]
Deltochilum gibbosum gibbosum (Fabricius) [P]	Louisiana (175)[P], Missouri (148), South Carolina (41)
Dialytes criddlei Brown [D]	Nebraska (178), North Dakota (98)[D] (85), Wyoming (85), Alberta (178), Manitoba (30) (85), Saskatchewan (178)
Dialytes striatulus (Say) *[PHE] = *Trox striatulus* Say (85)	Georgia (85), Illinois (197), Indiana (197), Maryland (197), Massachusetts (124)[E], Mississippi (85), Nebraska (85), New Jersey (172)*, New York (197), North Dakota (85), Pennsylvania (197), Rhode Island (197), Wisconsin (178) (131)[PH], Manitoba (30), New Brunswick (30) (220), Nova Scotia (30), Ontario (30) (197), Québec (30) (197), North Dakota, south to Georgia, Mississippi and Nebraska (178)
Dialytes truncatus (Melsheimer) *[PEH] = *Aphodius truncatus* Melsheimer (85)	Georgia (85), Indiana (197), Iowa (234)*, Maryland (197), Massachusetts (124)[E], Michigan (197), Missouri (148), New Jersey (173)[H], New York (197), Oklahoma (85), Pennsylvania (197), Rhode Island (197), Wisconsin (131)[PH], Ontario (30) (197), Québec (30) (197)
Dialytes ulkei Horn [PH]	Maryland (197), Pennsylvania (197), Rhode Island (197), South Carolina (85), Wisconsin (131)[PH], Ontario (30), Québec (30) (197)
Diapterna hamata (Say) * **= *Aphodius hamatus* Say in Blume (22)**	Arizona (85), California (85), Indiana (17), Maine (17), Minnesota (85), Nevada (85), North Dakota (98)*, Oregon (17), Washington (85), Alberta (30) (85), British Columbia (30) (85), Manitoba (30) (85), Ontario (30) (85), Québec (30) (85), Saskatchewan (30) (85)

Diapterna pinguella (Brown) * = *Aphodius pinguellus* Brown (85)	Colorado (178) (85), Idaho (178), Nebraska (178) (85), North Dakota (178) (85), Wyoming (178) (85), Alberta (178) (30) (75)*, British Columbia (30) (85), Manitoba (178) (30) (85), Saskatchewan (30)
Diapterna pinguis (Haldeman) * = *Aphodius pinguis* Brown (85)	Iowa (85), Minnesota (85), Montana (85), Nebraska (85), Alberta (30) (75)*, Manitoba (30) (85), New Brunswick (30) (220), Newfoundland (30), Northwest Territories (30), Ontario (30) (85), Québec (30) (85), Saskatchewan (30) (85), Québec south to New York and west to Alberta, Nebraska and Montana (178)
***Dichotomius carolinus* (Linnaeus) *[PEHSA]**	Arizona (178), Arkansas (59)*, Florida (123)*, Georgia (66)[PES], Louisiana (175)[P], Maryland (179)[H] (174)[H], Nebraska (178), North Carolina (135)* (15)* (16)* (14)*, Oklahoma (34), South Carolina (41), Virginia (9)[A], Pennsylvania south to Florida (138) (233), west to Texas (20)* (139), South Dakota east through Indiana (233), New York to Florida and west to southern Texas (178)
***Dichotomius colonicus* (Say) ***	Texas (26)* (138)
Digitonthophagus gazella (Fabricius) *[PCHE] **= *Onthophagus gazella* (Fabricius) in Blume (22)**	Alabama (70) (67) (78)[2], Arkansas (59)* (67) (117), Arizona (78)[2], California (6) (78)[2], Florida (123)* (78)[2], Georgia (237)* (67) (78)[2], Hawaii (94)*, Illinois (78)[2], Indiana (78)[2], Kansas (78)[2] (143), Kentucky (78)[2], Louisiana (175)[P] (67) (78)[2] (117), Maryland (78)[2], Mississippi (67) (78)[2] (143), Missouri (78)[2] (143), New Jersey (78)[2], New Mexico (78)[2], North Carolina (135)* (15)* (16)* (14)* (78)[2], Ohio (78)[2], Oklahoma (67) (117) (78)[2] (143), Oregon (78)[2], Pennsylvania (78)[2], South Carolina (41) (78)[2], Tennessee (78)[2] (143), Texas (64)[P] (38)[C] (114) (67) (117) (78)[2] (25) (52)*[HE], Virginia (78)[2], West Virginia (78)[2]
Diplotaxis harperi Blanchard *	Iowa (234)*, Nebraska (178), South Carolina (41), most of the eastern United States west to Nebraska, Kansas and Oklahoma (178)
Drepanocanthoides walshii (Horn) *[PHSMKB] **= *Aphodius walshii* Horn in Blume (22)** = *Aphodius walshi* Schmidt (85)	Colorado (85), Iowa (85), Kansas (85), Minnesota (39)* (85), Nebraska (191)* (85) (224)[PHMKB] (223)[H] (43), North Dakota (98)*[S] (85), Oklahoma (34), South Dakota (85), Texas (85), Wisconsin (131)[PH], Alberta (30) (85), Manitoba (30) (85), Saskatchewan (30), central United States from Indiana to the Rocky Mountains and from North Dakota south to Kansas (178)
***Euoniticellus intermedius* (Reiche) *[HE]**	California (6), Florida (123)* (5)* (232)*, Texas (21) (52)*[HE]
Euphoria inda (Linnaeus) *	Iowa (234)*, Nebraska (178), throughout the United States east of the Rocky Mountains and in southern Canada (178), Alberta (30), British Columbia (30), Manitoba (30), Ontario (30), Québec (30), Saskatchewan (30)
Eupleurus subterraneus (Linnaeus) * = *Aphodius subterraneus* Linnaeus (85)	Maine (85), New Brunswick (30) (220) (85), Nova Scotia (30) (85), Ontario (30), Québec (30) (149)*

[2] These are locations predicted to be favourable for the establishment of *Digitonthophagus gazella* (Fabricius) as reported in Floate et al. (78).

Geomyphilus insolitus (Brown) [P] = *Aphodius insolitus* Brown (85)	Arkansas (85), Illinois (85), Indiana (85), Kansas (85), Louisiana (85), Oklahoma (85), Texas (85), Wisconsin (131)[P]
Irrasinus stupidus (Horn) * **= *Aphodius stupidus* Horn in Blume (22)**	Alabama (233), Florida (123)* (231), Georgia north to New Jersey (233) (85), North Carolina (16)* (14)*, Oklahoma (85), Texas (26)* (85)
Labarrus lividus (Olivier) *[CP] **= *Aphodius lividus* Oliver in Blume (22)**	Arizona (138), California (17) (154)*, Florida (138), Hawaii (94)*, Illinois (85), Indiana (17) (138), Kansas (85), Nebraska (178) (168)*, New Mexico (57), North Carolina (16)*, Oklahoma (34), Texas (38)[C] (19)* (85) (64)[P]
Labarrus pseudolividus Balthasar *[EHS] = *Aphodius pseudolividus* Balthasar (85)	Arkansas (59)*, California (85), Connecticut (197), Florida (123)*, Indiana (197), Iowa (85), Kansas (85), Maryland (179)[EH] (174)[EH], Massachusetts (197), Michigan (216)*[S], Nevada (85), New York (197), North Carolina (15)* (135)* (14)*, Rhode Island (197), Maryland to Florida (178) (85), west to Iowa, Kansas, Nebraska and California (178)
Lechorodius lutulentus (Haldeman) *[EP] **= *Aphodius lutulentus* Haldeman in Blume (22)**	Arkansas (59)*, Florida (233), Massachusetts (124)[E], North Carolina (16)* (14)*, Oklahoma (34) (85), Texas (20)* (85) (64)[P], middle and southern states (138), New Jersey to Florida (85), west to Missouri (85)
Lechorodius terminalis (Say) * **= *Aphodius terminalis* Say in Blume (22)**	Alabama (85), Arkansas (59)*, Florida (85), Georgia (85), Illinois (156)*, Iowa (85), Kansas (85), Louisiana (85), Nebraska (85), New Jersey (172)*, Oklahoma (85), Texas (17) (138), Wisconsin (85), Canada (30), middle states (17)
***Melanocanthon bispinatus* (Robinson) *[H]**	Florida (123)* (233), Maryland (174)[H], Rhode Island (17), South Carolina (41), Texas (114), Ontario (30), New Jersey and Atlantic coast states west along Gulf of Mexico to Mississippi (233)
***Melanocanthon granulifer* (Schmidt) ***	Florida (123)* (233), Texas (17)
***Melanocanthon nigricornis* (Say) *[PHMK]**	Florida (17), Georgia (17), Massachusetts (17), Michigan (187)*, Missouri (148), Nebraska (178) (43) (224)[PHMK] (223)[H], Oklahoma (34), Texas (20)* (64)[P], Wisconsin (131)[PH], central United States from Michigan and Wisconsin to Nebraska and Kansas south to Texas (178)
***Melanocanthon punctaticollis* (Schaeffer)**	Florida (233)
Melinopterus femoralis (Say) * **= *Aphodius femoralis* Say in Blume (22)**	Arkansas (59)* (85), Illinois (156)*, Michigan (85), Missouri (228)*, Montana (85), Nebraska (178) (43), North Dakota (85), Oklahoma (34), South Carolina (85), Tennessee (85), Texas (85), Alberta (pers. observ.), Ontario (30), Québec (30) (85), Pennsylvania to South Carolina and west to Nebraska and Texas (178)
Melinopterus prodromus (Brahm) *[PHMK] **= *Aphodius prodromus* Brahm in Blume (22)**	Iowa (85) (234), Maine (17) (138), Michigan (216)*, Minnesota (39)* (85), Missouri (228)*, Montana (85), Nebraska (178) (85) (224)[HMK] (223)[H], New York (170)* (213)*, North Carolina (16)* (14)*, South Dakota (126)* (127)*, Virginia (85), Wisconsin (131)[PH], Alberta (30) (72)* (75)* (122)*, British

	Columbia (30), Manitoba (30), New Brunswick (30) (220), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30), Saskatchewan (30), Nova Scotia to Michigan (85)
Nialaphodius nigritus (Fabricius) *[P] **= *Aphodius cuniculus* Chevrolat in Blume (22)**	Florida (233), Louisiana (175)[P], Texas (19)*
Oniticellus cinctus (Fabricius) *	Hawaii (94)*
***Onitis alexis* Klug**	California (6)
***Onthophagus alluvius* Howden & Cartwright *[P]**	Texas (64)[P] (19)* (114) (112)
Onthophagus brevifrons Horn [H]	Texas (52)[H]
Onthophagus browni Howden & Cartwright [H]	Texas (52)[H]
***Onthophagus concinnus* Laporte *[H]**	Florida (123)* (233), Maryland (174)[H], South Carolina (41), Pennsylvania and New Jersey south through Tennessee, Louisiana, Alabama, and Georgia (112)
***Onthophagus depressus* Harold**	Florida (233), Georgia (35), South Carolina (41)
***Onthophagus hecate* (Panzer) *[PEHSMKBDC]**	Illinois (156)*, Indiana (189), Iowa (234)*, Maryland (179)[EH] (174)[H], Michigan (187)* (216)[S], Minnesota (39)*, Missouri (148) (228)*, Nebraska (178) (191)* (224)[PHMKB] (223)[H], New Jersey (172)* (173)[HC], New York (170)* (219), North Carolina (15)*, North Dakota (98)*[SDB], Ohio (196), South Dakota (126)* (127)*[S], Texas (20)* (64)[P] (38)[C] (114), Wisconsin (131)[PH], New Brunswick (220), Transcontinental expect Idaho, Nevada, and Pacific coast states (112)
Onthophagus hecate blatchleyi Brown *	Florida (123)*
Onthophagus hecate hecate (Panzer) *[PA]	Arkansas (59)*, Louisiana (218) (175)[P], Massachusetts (82), Nebraska (168)*, North Carolina (135)* (16)* (14)*, South Carolina (41), Virginia (9)[A], Alberta (30), British Columbia (30), Manitoba (30), New Brunswick (30), Nova Scotia (30), Ontario (30), Québec (30), Saskatchewan (30)
Onthophagus incensus Say *	Hawaii (94)*
Onthophagus knausi Brown [DH]	Illinois (178), Kansas (178), Nebraska (178), Texas (178)[D] (52)[H]
***Onthophagus knulli* Howden & Cartwright**	Arizona (112), New Mexico (112)
***Onthophagus landolti* Brown ***	Oklahoma (112), Texas (26) *
***Onthophagus medorensis* Brown *[P]**	Arkansas (112), Kansas (130), Oklahoma (34), Texas (26)* (64)[P] (114)
***Onthophagus nuchicornis* (Linnaeus) *[PHS]**	Arizona (78)[3], California (78)[3], Colorado (78)[3], Connecticut (78)[3], Idaho (78)[3], Illinois (78)[3], Indiana (78)[3] (143), Iowa (78)[3], Kansas (78)[3], Kentucky (78)[3], Maine (78)[3], Maryland (174)[H], Massachusetts (82) (78)[3], Michigan (187)* (216)*[S], Minnesota (39)* (78)[3] (143), Missouri (78)[3], Montana (78)[3], Nebraska (78)[3], New Hampshire (78)[3], New Jersey (78)[3], New Mexico (78)[3], New York (170)* (213)*

[3] These are locations predicted to be favourable for the establishment of *Onthophagus nuchicornis* (Linnaeus) as reported in Floate et al. (78).

	(78)[3], North Carolina (78)[3], North Dakota (78)[3] (210), Ohio (78)[3], Oregon (78)[3], Pennsylvania (78)[3], Rhode Island (78)[3], South Dakota (78)[3], Tennessee (78)[3], Utah (78)[3], Vermont (78)[3], Virginia (78)[3], Washington (78)[3], West Virginia (78)[3], Wisconsin (131)[PH] (78)[3], Wyoming (78)[3], Alberta (30) (72)* (75)* (122)* (78)[3] (103), British Columbia (30) (141)* (78)[3], Manitoba (30) (78)[3], New Brunswick (220) (30) (78)[3], Newfoundland (30), Nova Scotia (30) (78)[3], Ontario (30) (78)[3], Québec (30) (149)* (78)[3], Saskatchewan (30) (78)[3], Canadian provinces and northern tier of states (112)
***Onthophagus oklahomensis* Brown *[P]**	Florida (123)* (233), North Carolina (135)* (16)* (14)*, Oklahoma (34), Texas (26)* (64)[P] (114), District of Columbia and Virginia, south through Tennessee and Kansas, and gulf coastal states (112)
***Onthophagus orpheus* (Panzer) *[PEHMKBDC]**	Connecticut (197), Florida (233), Illinois (197) (112), Indiana (197), Louisiana (175)[P], Maine (197), Maryland (197), Massachusetts (124)[E] (197), Michigan (197), Missouri (148), Nebraska (224)[HMKB] (223)[H], New Hampshire (197), New Jersey (197) (172)* (173)[HC] (112) and states to the south (112) , New York (197), Ohio (197) (196) (112), Pennsylvania (197) (112), Rhode Island (197), Texas (26)* (64)[P], Wisconsin (197) (131)[PHD], Ontario (197), Oklahoma north through Minnesota (112)
Onthophagus orpheus canadensis (Fabricius) *	Iowa (234)*, Massachusetts (82), Ontario (30), Québec (30), Nebraska (178), Ontario and New England States southward to northern Georgia and west to Minnesota and Iowa (178)
Onthophagus orpheus pseudorpheus Howden & Cartwright *	Nebraska (178)*, Manitoba (30), Saskatchewan (30), south central Manitoba though the central United States south to Kansas, Missouri, Arkansas and east to Ohio (178)
***Onthophagus pennsylvanicus* Harold *[PEHSMKBCAT]**	Arkansas (59)*, Colorado (132), Florida (123)*, Maryland (179)[EH] (174)[H], Massachusetts (124)[E] (82), Michigan (187)* (216)[S], Minnesota (39)*, Missouri (148), Nebraska (168)* (191)* (224)[PHMKB] (223)[H], New Jersey (172)* (173)[HC], New York (170)*, North Carolina (135)* (15)* (16)* (14)*, North Dakota (98)*[S], Ohio (196), South Dakota (126)* (127)*[S], Texas (64)[P] (19)* (38)[C] (114), Virginia (9)[A], Wisconsin (131)[PHCT], Ontario (30), all states east except Maine (112), all states east and south of South Dakota except Maine, Vermont and New Mexico (178)
Onthophagus sagittarius (Fabricius) *	Hawaii (94)*
***Onthophagus schaefferi* Howden & Cartwright ***	Texas (26)* (112)
Onthophagus striatulus (Beauvois) *[PEH]	Maryland (174)[H], Massachusetts (124)[E], Missouri (148), Nebraska (178), New Jersey (172)*, Ohio (196), Texas (64)[P], Wisconsin (131)[PH], Québec (30), eastern half of the United States westward to Nebraska, Oklahoma and Texas (178)
Onthophagus subaenus (Beauvois) [D]	Nebraska (178)[D], Pennsylvania south to Florida and west to Missouri, Kansas, Oklahoma and Texas (178)

Onthophagus taurus **(Schreber) *EHSA**	Alabama (67) (78)[4] (61), Arizona (78)[4], Arkansas (59)* (78)[4], California (6) (78)[4] (143), Colorado (78)[4], Connecticut (78)[4], Delaware (78)[4], Florida (123)* (67) (78)[4] (61), Georgia (67) (78)[4] (61), Idaho (78)[4], Illinois (78)[4], Indiana (78)[4], Iowa (78)[4], Kansas (78)[4], Kentucky (78)[4], Louisiana (78)[4], Maine (78)[4], Maryland (179)[EH] (174)[H] (78)[4], Massachusetts (78)[4], Michigan (187)* (216)*[S] (78)[4], Minnesota (78)[4], Mississippi (67) (78)[4] (61), Missouri (148) (78)[4] (143), Montana (78)[4], Nebraska (78)[4], Nevada (78)[4], New Hampshire (78)[4], New Jersey (172)* (173)[H] (78)[4], New Mexico (78)[4], New York (170)* (78)[4], North Carolina (15)* (135)* (16)* (14)* (67) (78)[4] (61) (163), North Dakota (78)[4], Ohio (78)[4], Oklahoma (78)[4], Oregon (78)[4], Pennsylvania (78)[4], Rhode Island (78)[4], South Carolina (41) (67) (78)[4] (61), South Dakota (78)[4], Tennessee (78)[4], Texas (78)[4], Utah (78)[4], Vermont (78)[4], Virginia (9)[A] (78)[4], Washington (78)[4], West Virginia (78)[4], Wisconsin (78)[4], Wyoming (78)[4]
Onthophagus tuberculifrons **Harold *EHP**	Florida (123)*, Maryland (179)[EH] (174)[H], Massachusetts (82), Missouri (148), New Jersey (172)*, North Carolina (16)* (14)*, Oklahoma (34), South Carolina (41), Texas (26)* (64)[P], north through Wisconsin, Michigan, Connecticut, and south through Florida and gulf states (112) (233)
Onthophagus velutinus Horn H	Texas (52)[H]
Oscarinus crassulus (Horn) * = *Aphodius crassulus* Horn (85)	Florida (123)*, Virginia to north Florida (85), west to Louisiana (85)
Oscarinus pseudabusus (Cartwright) *B **= *Aphodius pseudabusus* Cartwright in Blume (22)**	Colorado (85) (132), Kansas (85), Nebraska (178), North Dakota (178) (98)*[B] (85), Oklahoma (178) (85), South Dakota (178)
Oscarinus rusicola (Melsheimer) ***PHM**SDB **= *Aphodius ruricola* Haldeman in Blume (22)** = *Aphodius rusicola* Melsheimer	Arkansas (59)*, Illinois (156)*, Indiana (197), Iowa (234), Louisiana (218) (175)[P], Maryland (197) (174)[H], Massachusetts (82), Michigan (216)*[S] (53)[M], Minnesota (39)*, Missouri (228)*, Montana (85), Nebraska (168)* (43), New Jersey (172)*, New Mexico (57), New York (197)* (170)*, North Carolina (16)*, North Dakota (98)*[SDB], Oklahoma (34), South Dakota (127)*[S], Pennsylvania (197), Rhode Island (197), Texas (26)* (64)[P], Wisconsin (131)[PH], Alberta (30) (72)* (75)*, Manitoba (30), New Brunswick (30) (220), Newfoundland (30) (17) (138), Nova Scotia (30), Ontario (30) (197), Québec (30), Saskatchewan (30), south to north Florida and Texas (85), eastern half of United States west to Nebraska and New Mexico (178)
Oscarinus silvanicus (Cartwright) EH = *Aphodius silvanicus* Cartwright (85)	Maryland (179)[EH] (85), Virginia (85)
Oscarinus windsori (Cartwright) *	Florida (123)*, South Carolina (85)

[4] These are locations predicted to be favourable for the establishment of *Onthophagus taurus* (Schreber) as reported in Floate et al. (78).

= *Aphodius windsori* Cartwright (85)	
Otophorus haemorrhoidalis (Linnaeus) *[PHSB] **= *Aphodius haemorrhoidalis* Linnaeus in Blume (22)**	Arkansas (59)*, California (154)* (85), Colorado (26)* (132), Florida (233), Illinois (156)*, Indiana (197) (17), Iowa (234)*, Massachusetts (82), Michigan (216)*[S], Minnesota (39)*, Missouri (228)*, Nebraska (168)* (191)*, New Jersey (197) (178), New York (197) (170)* (213)*, North Carolina (15)* (135)* (14)*, North Dakota (98)*[B], Oregon (178), Rhode Island (197), South Dakota (127)*[S] (126)*, Texas (19)* (64)[P], Wisconsin (131)[*PH], Alberta (30) (72)* (75)* (122)*, British Columbia (30) (178) (141)*, Manitoba (30), New Brunswick (30) (220), Newfoundland (30), Nova Scotia (30), Ontario (30), Québec (30) (197) (149)*, Saskatchewan (30), south to northern Florida (85), eastern United States westward to the Dakotas, Nebraska and Kansas (178)
Parataenius simulator (Harold) * **= *Ataenius simulator* Harold in Blume (22)**	Florida (123)* (233), North Carolina (16)* (14)*, southeastern states from Maryland and Virginia to Tennessee and Mississippi (36)
Pardalosus pardalis (LeConte) **= *Aphodius pardalis* LeConte in Blume (22)**	California (17) (138), British Columbia (30) (17) (138), southern Idaho to southern British Columbia (85), south to central California (85)
***Phanaeus amithaon* Harold ***	Arizona (17)
***Phanaeus difformis* LeConte [P]**	Arkansas (118), Kansas (130), Louisiana (24), New Mexico (212), Oklahoma (34), Texas (64)[P] (114) (23)
***Phanaeus igneus* MacLeay *[PESG]**	Florida (123)*, Georgia (66)[PESG] (62) (60), South Carolina (41), Alabama to Florida, and north through North Carolina (233)
***Phanaeus mexicanus* Harold**	Arizona (17)
***Phanaeus quadridens* Say**	Arizona (88), New Mexico (57)
Phanaeus texensis Edmonds *[HE]	Texas (52) *[HE]
***Phanaeus torrens* LeConte ***	Georgia (60), Louisiana (17), Mississippi (17), Texas (26)*
***Phanaeus triangularis* (Say) ***	Kansas (138), Missouri (138), Nebraska (178), Texas (20)* (139), Texas to near the Atlantic Coast (178)
***Phanaeus vindex* MacLeay *[PEHSGKCA]**	Arizona (138), Arkansas (59)*, Florida (123)*, Georgia (66)[PESG], Iowa (234), Maryland (179)[EH] (174)[H], Massachusetts (82), Nebraska (178) (191)* (224)[PHK] (223)[H], New Jersey (172)* (173)[HC], New Mexico (57), North Carolina (135)* (15)* (16)* (14)*, South Carolina (41), Texas (64)[P] (24), Virginia (9)[A], Wisconsin (131)[PH], all of United States east of the Rockies except North Dakota, Minnesota, Wisconsin, Michigan, and northern New England (233) (24), eastern United States as far north as Massachusetts in the east and South Dakota in the west (178)
Planolinellus vittatus (Say) *[SBP] **= *Aphodius vittatus* Say in Blume (22)**	California (154)* (171)*, Colorado (26)*, Florida (5)*, Illinois (156)*, Nebraska (191)* (43), New Mexico (57), North Dakota (98)*[B], Oklahoma (34), South Dakota (127)*[S] (126)*, Texas (19)* (64)[P],

	Wyoming (165)*, Alberta (30) (72)* (75)* (122)*, British Columbia (30) (141)*, Labrador (30), Manitoba (30), New Brunswick (30) (220), Nova Scotia (30), Ontario (30), Québec (30), Saskatchewan (30), Maine to South Carolina west to Washington (178)
Planolinoides borealis (Gyllenhal) [M] = *Aphodius borealis* Gyllenhal (85)	Alaska (30) (181)[M], Alberta (30), British Columbia (30), Labrador (30), Manitoba (30), New Brunswick (30) (220), Newfoundland (30), Northwest Territories (30), Nova Scotia (30), Ontario (30), Québec (30), Saskatchewan (30), Yukon (30)
Planolinoides pectoralis (LeConte) * **= *Aphodius pectoralis* LeConte in Blume (22)**	California (17) (85) (138), Montana (85), Oregon (138), Washington (138), Wyoming (85), Alberta (30) (85), British Columbia (30) (141)* (85)
Planolinus tenellus (Say) *[S] = *Aphodius tenellus* Say (85)	Alaska (30) (85), California (85), New Mexico (85), south to North Carolina (85), North Dakota (98)*[S], Alberta (30), British Columbia (30), Manitoba (30), New Brunswick (220), Northwest Territories (30), Ontario (30), Québec (30), Saskatchewan (30), Yukon (30)
Platytomus longulus (Cartwright) *	Arkansas (59)*
Pseudagolius bicolor (Say) *[PEHSC] **= *Aphodius bicolor* Say in Blume (22)**	Arkansas (59)*, Florida (123)* (233), Illinois (156)*, Indiana (17), Iowa (234)*, Kansas to northern Florida and east Texas (85), Louisiana (175)[P], Massachusetts (124)[E], Michigan (216)*[S] (85), Minnesota (39)*, Missouri (228)*, Nebraska (178), New Jersey (172)* (173)[HC], North Carolina (16)* (14)*, Oklahoma (34), Texas (26)* (38)[C] (64)[P], Wisconsin (131)[H] (85), Ontario (30) (85), Québec (30), Canada (17) (138)
Pseudagolius coloradensis (Horn) *[PHMK] **= *Aphodius coloradensis* Horn in Blume (22)**	Arizona (85), Colorado (85), Iowa (85), Minnesota (85), Nebraska (178) (224)[PHMK] (223)[H] (43), New Mexico (57) (85), Oklahoma (85), North Dakota (98)*, South Dakota (126)* (127)*, Alberta (30) (85) (75)* (122)*, Manitoba (30) (85), Saskatchewan (30)
***Pseudocanthon perplexus* (LeConte) *[PC]**	Arkansas (59)*, Florida (123)*, Illinois (178) (17), Indiana (178) (17), Louisiana (175)[P], Nebraska (178), Texas (26)* (64)[P] (38)[C] (114), Arizona and New Mexico, east through Florida, and north to Virginia (233), Indiana to southeastern Arizona (178)
Scabrostomus peculiosus (Schmidt) [D] = *Aphodius peculiosus* Schmidt (85)	Kansas (178) (85), Nebraska (178) (85), Texas (178) (85)[D], Wisconsin (178) (85), Manitoba (30) (178) (85)
Tetraclipeoides denticulatus (Haldeman) **= *Aphodius denticulatus* Haldeman in Blume (22)**	California (85), Colorado (85), Montana (85), Nevada (85), New Mexico (57), Washington (85), Wyoming (17) (85) (138), Alberta (30) (85)
Tetraclipeoides testaceiventris (Fall) *[H] **= *Aphodius testaceiventris* Fall in Blume (22)**	Colorado (178) (85), Kansas (178) (17) (85), Nebraska (178) (85) (223)[H] (224)[H], Texas (178) (26)* (85)
Teuchestes fossor (Linnaeus) *[PEHSB] **= *Aphodius fossor* Linnaeus in Blume (22)**	Alaska (30), Colorado (132), Massachusetts (124)[E] (82), Michigan (187)* (216)*, Minnesota (39)*, Nebraska (178) (191)* (85), New York (170)* (213)*, North Dakota (98)*[B], South Dakota (127)* (126)*, south to Virginia (85), Wisconsin (131)*[PH], Wyoming (85) (165)*, Alberta (30) (72)* (75)*

	(122)*, British Columbia (30) (141)*, Labrador (30), Manitoba (30), New Brunswick (30) (220), Newfoundland (30), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30) (149)*, Saskatchewan (30), southern Canada and northern United States west to the Dakotas, Wyoming, Idaho, Kansas and Colorado (178)
Tomarus relictus (Say) *	Arizona (178), Iowa (234), Nebraska (178) (191)*, Manitoba (30), New Brunswick (30), Ontario (30), Prince Edward Island (30), Québec (30), Saskatchewan (30), eastern and central United States west to the Rocky Mountains (178)
Family Staphylinidae Latreille, 1802 (Rove beetles)	
Acrotona hebeticornis Notman *	Florida (115)*
***Aleochara bilineata* Gyllenhal ***	California (171), Alberta (30) (72)*, British Columbia (30), Manitoba (30), New Brunswick (30), Newfoundland (30), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30), Saskatchewan (30), Transcontinental in Canada, south to Oregon, Illinois, and Massachusetts (128)
***Aleochara bimactulata* Gravenhorst ***	California (154) (171)* (222), Massachusetts (124)[E], Minnesota (39)*, Missouri (208) (228)*, Nebraska (168)*, Ohio (196), South Carolina (37), South Dakota (126)* (127)*, Alberta (30) (72)*, British Columbia (30) (141)*, Labrador (30), Manitoba (30), New Brunswick (30), Newfoundland (30), Northwest Territories (30), Nova Scotia (30), Ontario (30), Québec (30) (149)*, Saskatchewan (30), Transcontinental (128)
Aleochara lacertina Sharp * **= *Aleochara imbricata* Casey in Blume (22)**	New York (213)*, Alberta (30), British Columbia (30), Manitoba (30), New Brunswick (30), Newfoundland (30), Nova Scotia (30), Ontario (30), Québec (30), Saskatchewan (30), widespread through southern Canada and United States (128) (157)
***Aleochara lanuginosa* Gravenhorst ***	California (171)*, Idaho (157), Minnesota (39)*, Oregon (157), Washington (157), Alberta (30), British Columbia (30) (157), New Brunswick (30), Newfoundland (30), Nova Scotia (30), Ontario (30), Québec (30) (149)*, northeastern United States (128), southern United States from Florida to California north to Utah, Kansas, and Pennsylvania (128)
***Aleochara notula* Erichson *[P]**	Florida (115)*, South Carolina (37), Texas (26)* (119)[P], Florida to California, north to Utah, Kansas, and Pennsylvania (128)
***Aleochara tristis* Gravenhorst ***	California (222), Minnesota (39)*, Missouri (230), Nebraska (157), New Brunswick (30), Newfoundland (30), Ontario (30), Québec (30) (149)* (128)
***Aleochara verna* Say *[PS]** **=*Aleochara bipustulata* (Linnaeus) *[S]**	Alaska (30), California (154), Florida (157), Minnesota (39)*, Missouri (229), Nebraska (168)*, New York (213)*, South Carolina (37), South Dakota (126)* (127)*[S], Texas (26)* (119)[P], Alberta (30), British Columbia (30), Labrador (30), Manitoba (30), New Brunswick (30), Newfoundland (30), Nova

	Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30), Saskatchewan (30), Yukon (30), widespread in Canada and United States (128), British Columbia to Québec (157)
Anotylus insignitus (Gravenhorst) *	Florida (115)*, Nebraska (168)*, South Carolina (37), Ontario (30), Québec (30)
Anotylus nanus (Erichson) *	Florida (115)*
Anotylus sobrinus (LeConte) *	Alberta (30) (72)*, British Columbia (30), Manitoba (30), Northwest Territories (30), Saskatchewan (30)
Anotylus suspectus (Casey) *[S] = *Oxytelus suspectus* Casey (127)	South Dakota (127)*[S], Manitoba (30), Ontario (30)
Anotylus tetracarinatus (Block) *	Minnesota (39)*, Nebraska (168)*, South Carolina (37), Alberta (30), British Columbia (30), New Brunswick (30), Nova Scotia (30), Ontario (30), Québec (30) (149)*
Autalia rivularis (Gravenhorst) *	Minnesota (39)*, Alberta (30), British Columbia (30), Labrador (30), New Brunswick (30), Newfoundland (30), Nova Scotia (30), Ontario (30), Québec (30)
Bisnius inquietus (Erichson) * **= *Philonthus inquietus* Erichson in Blume (22)**	Arizona (157), South Carolina (157), Texas (26)*, Ontario (30), Québec (30)
Bisnius sordidus (Gravenhorst) * **= *Philonthus sordidus* Gravenhorst in Blume (22)**	Alaska (30), California (171)*, Idaho (157), Indiana (157), New Mexico (157), Oregon (157), Washington (157), Alberta (30) (72)*, British Columbia (30), Manitoba (30), New Brunswick (30), Newfoundland (30) (157), Nova Scotia (30), Ontario (30), Québec (30), Saskatchewan (30)
Bryoporus rufescens LeConte *	Florida (115)*, South Carolina (37), Alberta (30), British Columbia (30), Manitoba (30), New Brunswick (30), Nova Scotia (30), Ontario (30), Québec (30), Saskatchewan (30)
Cilea silphoides (Linnaeus) *	Minnesota (39)*, Alberta (30), British Columbia (30), New Brunswick (30), Ontario (30), Québec (30)
Falagria dissecta Erichson *[S]	Minnesota (39)*, Nebraska (168)*, South Carolina (37), South Dakota (127)*[S], Alberta (30), British Columbia (30), Manitoba (30), New Brunswick (30), Nova Scotia (30), Ontario (30), Québec (30), Saskatchewan (30)
Gyrohypnus angustatus Stephens *	Nebraska (168)*, Alberta (72)*, British Columbia (30), New Brunswick (30), Newfoundland (30), Nova Scotia (30), Ontario (30), Québec (30)
Gyrohypnus fracticornis (Müller) * = *Gyrohypnus obsidianus* Melsheimer (127)	South Carolina (37), South Dakota (127)*, Alberta (30) (72)*, British Columbia (30), Manitoba (30), New Brunswick (30), Newfoundland (30), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30) (149)*, Saskatchewan (30)
Ischnosoma flavicolle (LeConte) * = *Mycetoporus flavicollis* (LeConte) (115)	Florida (115)*, New Brunswick (30), Ontario (30), Québec (30)

Lithocharis ochracea (Gravenhorst) *	Minnesota (39)*, Nebraska (168)*, South Carolina (37), British Columbia (30), New Brunswick (30), Nova Scotia (30), Ontario (30), Québec (30), Saskatchewan (30)
Lithocharis sororcula Kraatz *	Florida (115)*
Lobrathium gaudens (Casey) *	Nebraska (168)*
Lobrathium longiusculum Gravenhorst *	Nebraska (168)*, South Carolina (37), Ontario (30)
Neobisnius sobrinus (Erichson) *	Nebraska (168)*, South Carolina (37), New Brunswick (30), Newfoundland (30), Nova Scotia (30), Ontario (30), Québec (30)
Neohypnus attenuatus (Erichson) *	Florida (115)*
Neohypnus fragilis (Casey) *	Nebraska (168)*, British Columbia (30), Ontario (30)
Neohypnus obscurus (Erichson) *	Minnesota (39)*, South Carolina (37), Alberta (30), British Columbia (30), Manitoba (30), New Brunswick (30), Newfoundland (30), Nova Scotia (30), Ontario (30), Québec (30), Saskatchewan (30)
Neohypnus pusillus (Sachse) *	Florida (115)*, South Carolina (37)
Ontholestes cingulatus Gravenhorst *	Minnesota (39)*, Ohio (196), South Carolina (37), South Dakota (127)*, Alberta (30) (103), British Columbia (30), Manitoba (30), New Brunswick (30), Newfoundland (30), Northwest Territories (30), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30) (149)*, Saskatchewan (30)
Oxypoda sagulata Erichson *	South Dakota (127)*
Oxytelus incises Motschulsky *	Florida (115)*, New Brunswick (30), Ontario (30), Québec (30)
Phacophallus parumpunctatus (Gyllenhal) *	Nebraska (168)*, South Carolina (37), New Brunswick (30), Ontario (30), Québec (30)
Philonthus agilis (Gravenhorst) *	Minnesota (39)*
Philonthus carbonarius (Gravenhorst) * = *Philonthus varius* Gyllenhall (39)	Minnesota (39)*, Nebraska (168)*, British Columbia (30), Manitoba (30) New Brunswick (30), Newfoundland (30), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30), Saskatchewan (30), Yukon (30)
Philonthus caucasus Nordman * = *Philonthus dimidiatus* Sahlberg (39)	Minnesota (39)*, Alberta (30), British Columbia (30), Manitoba (30), Ontario (30), Québec (30), Saskatchewan (30)
***Philonthus cautus* Erichson ***	Florida (157), Georgia (157), Missouri (228)*, North Carolina (157)
***Philonthus cognatus* Stephens ***	California (157), North Carolina (157), Oregon (157), Washington (157), Alberta (30) (72)*, British Columbia (30) (141)*, New Brunswick (30), Newfoundland (30) (157), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30) (157)
Philonthus concinnus (Gravenhorst) *	Alaska (30), Minnesota (39)*, Alberta (30) (72)*, British Columbia (30), Manitoba (30), New Brunswick (30), Newfoundland (30), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30), Saskatchewan (30)

Philonthus cruentatus **(Gmelin) *[PS]**	California (154)* (171)*, Indiana (188)* (189)*, Michigan (157), Minnesota (39)*, Missouri (208)*, Nebraska (168)* (191)*, New York (213)*, South Carolina (37), South Dakota (127)*[S] (126)*, Tennessee (157), Texas (119)[P] (186), Alberta (30) (72)*, British Columbia (30) (141)*, Manitoba (30) (157), New Brunswick (30), Newfoundland (30) (157), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30) (149)*, Saskatchewan (30)
Philonthus debilis **(Gravenhorst) ***	California (157), Indiana (157), Minnesota (39)*, Nebraska (157), Alberta (30), British Columbia (30) (141)*, Manitoba (30), New Brunswick (30), Newfoundland (30) (157), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30) (157), Saskatchewan (30)
Philonthus discoideus (Gravenhorst) *	Hawaii (94)*, Minnesota (39)*, New Brunswick (30), Ontario (30), Québec (30)
Philonthus flavolimbatus **Erichson *[P]**	Arizona (157), California (157), Florida (115)* (157), New Mexico (57), South Carolina (37), Texas (119)[P] (186) (211)
Philonthus hepaticus **Erichson *[P]**	Arizona (157), California (157), Florida (115)* (157), Indiana (157), South Carolina (37), Texas (26)* (119)[P], British Columbia (30), New Brunswick (30), Canada (157)
Philonthus longicornis **Stephens ***	Alaska (30), Arizona (157), California (171)*, Florida (115)* (157), Hawaii (94)*, Indiana (157), Ohio (196), South Carolina (37), Manitoba (30), Newfoundland (157), Nova Scotia (30), Ontario (30), Québec (30)
Philonthus politus **(Linnaeus) ***	Alaska (30), California (171)*, Ohio (196), South Carolina (37), Alberta (30) (72)*, British Columbia (30), Labrador (30), Manitoba (30), New Brunswick (30), Newfoundland (30), Northwest Territories (30), Nova Scotia (30), Ontario (30), Québec (30), Saskatchewan (30), Canada and northern United States (157)
Philonthus rectangulus **Sharp *[PS]**	Alaska (30), California (154)* (171)*, Hawaii (94)*, Minnesota (39)*, Missouri (208)*, Nebraska (168)* (191)*, South Carolina (37), South Dakota (127)*[S], Texas (119)[P], Alberta (30), British Columbia (30) (141)*, Manitoba (30), New Brunswick (30), Newfoundland (30), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30) (149)*, Saskatchewan (30)
Philonthus rufulus Horn * **= *Philonthus alumnus* Erichson in Blume (22)**	Arizona (157), California (157), Florida (157), Missouri (228)*, Nebraska (168)*, New York (157), Texas (211) (108), British Columbia (30), Nova Scotia (30), Ontario (30), Québec (30)
Philonthus sanguinolentus (Gravenhorst) *	Alberta (72)*, British Columbia (30), Ontario (30)
Philonthus sericans (Gravenhorst) *[P] **= *Philonthus brunneus* Gravenhorst in Blume (22)**	Florida (157), Indiana (157), Minnesota (39)*, Nebraska (168)* (157), Texas (26)* (119)[P], New Brunswick (30) Ontario (30), Québec (30), Canada (157)
Philonthus umbrinus **(Gravenhorst) ***	California (154)*, Indiana (157), Missouri (228)*, New York (157), South Carolina (157), South Dakota (126)* (127)*, Ontario (30), Canada (157)

***Philonthus varians* (Paykull) ***	California (154)*, Illinois (156)*, Minnesota (39)*, Missouri (208) (228)*, Nebraska (168)*, New York (213)*, South Carolina (37), South Dakota (126)* (127)*, Alberta (30) (72)*, British Columbia (30), Manitoba (30), New Brunswick (30), Newfoundland (30), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (149)*, Saskatchewan (30), Canada and northern United States (157)
Philonthus ventralis (Gravenhorst) *	Florida (115)*, South Carolina (37), Ontario (30), Québec (30)
Platydracus maculosus (Gravenhorst) * **= *Staphylinus maculosus* Gravenhorst in Blume (22)**	Alabama (28), Missouri (228), Texas (26)*, Ontario (30), Québec (30)
***Platystethus americanus* Erichson *[PS]**	California (154)* (171)*, Connecticut (157), Florida (115)*, Illinois (156)*, Indiana (188)* (189)*, Minnesota (39)*, Missouri (209), Nebraska (168)* (191)*, New York (213)*, South Dakota (126)* (127)*[S], Texas (119)[P], Alberta (30) (72)*, British Columbia (30) (145), Manitoba (30), New Brunswick (30), Ontario (30), Québec (30) (149)* (157), Saskatchewan (30), Yukon (30)
Platystethus spiculus Erichson *	California (137), Florida (115)*
Rugilus angularis Erichson *	Florida (115)*, South Carolina (37)
Stenistoderus rubripennis (LeConte) *	Nebraska (168)*, South Carolina (37), Ontario (30)
Tachyporus nitidulus (Fabricius) *	Alaska (30), Nebraska (168)*, South Carolina (37), Alberta (30), British Columbia (30), Labrador (30), Manitoba (30), New Brunswick (30), Newfoundland (30), Northwest Territories (30), Nova Scotia (30), Ontario (30), Québec (30), Saskatchewan (30), Yukon (30)
Tinotus amplus Notman *	Florida (115)*
Tinotus brunnipes Notman *	Florida (115)*
Family Trogidae MacLeay, 1819 (Hide beetles)	
Omorgus scabrosus (Beauvois) [P]	Kansas (178), several eastern states west to Nebraska (178), Oklahoma (178), Texas (178), Wisconsin (131)[P], Ontario (30) (178)
Omorgus suberosus (Fabricius) [P]	Nebraska (178), South Carolina (41), Wisconsin (131)[P]
Trox foveicollis Harold [C]	Ontario (30), eastern United States and westward to Texas, Oklahoma and Nebraska (178)
Trox hamatus Robinson *[PHD]	Indiana (197), Kansas (178), Maine (197), Massachusetts (82), Missouri (148), Nebraska (178), New Jersey (172)* (173)[HD], New York (197), Oklahoma (178), Rhode Island (197), South Carolina (41), Texas (178), Wisconsin (131)[P], Ontario (30), Québec (30), eastern United States south to Georgia (178)
Trox robinsoni Vaurie [P]	Nebraska (178), Wisconsin (131)[P], Alberta (30) (178), Manitoba (30) (178), Québec (30), Saskatchewan (30)
Trox scaber (Linnaeus) *	Illinois (197), Indiana (197), Maryland (197), Massachusetts (82) (197), Michigan (197), New Jersey (197), New York (197), Pennsylvania (197), Rhode Island (197), Wisconsin (197), Alberta (30), British

	Columbia (30), Manitoba (30), New Brunswick (30), Nova Scotia (30), Ontario (30) (197), Québec (30) (197) (149)*, Saskatchewan (30), northern half of United States and Southern Canada (178)
Trox unistriatus Beauvois [PH]	South to Colorado (178), Florida (178), Louisiana (178), Nebraska (178), south to North Carolina (178), South Carolina (41), Texas (178), Wisconsin (131)[PH], Alberta (30), Manitoba (30), New Brunswick (30), Newfoundland (30), Nova Scotia (30), Ontario (30), Prince Edward Island (30), Québec (30), Saskatchewan (30)
Trox variolatus Melsheimer [PH]	Delaware (197), Illinois (197), Indiana (197), Kansas (178), Maryland (197), Massachusetts (197), Michigan (197), New Hampshire (197), New Jersey (197), New York (197), Ohio (197), Oklahoma (178), Pennsylvania (197), Rhode Island (197), South Carolina (41), Texas (178), Wisconsin (197) (131)[PH], New Brunswick (30), Nova Scotia (30), Ontario (30) (197), Prince Edward Island (30), Québec (30), eastern United States west to eastern Nebraska (178)

CHAPTER 3: DUNG BEETLE (COLEOPTERA: SCARABAEIDAE) DIVERSITY IN DIFFERENT HABITATS AND LOCATIONS IN SOUTHERN ALBERTA, CANADA

3.1 Abstract

Dung beetles (Coleoptera: Scarabaeidae) provide important ecosystems services on pasture ecosystems. Their nesting activities accelerate dung degradation, which reduces accumulation of dung pats as potential breeding sites for pest flies and parasites affecting livestock. By burying dung, they return nutrients to the soil and increase soil permeability to air and water. The extent of these services is influenced by the species and abundance of dung beetles present, which may be affected by habitat type and location. I examined the effect of habitat type (grassland and forest) and location (Purple Springs Grazing Reserve and Cypress Hills Interprovincial Park) on native rangeland pastures in southern Alberta, Canada. Using pitfall traps baited with cattle dung and operated from spring though autumn for two years, 112,367 individuals representing 18 dung beetles species were caught. Several species co-occurred in both habitats and locations, but each combination of habitat and location was dominated by a different species. *Chilothorax distinctus* (Müller) was the most abundant at Purple Springs (90%), *Diapterna hamata* (Say), was the most abundant in the open habitat (66%) and *Agoliinus leopardus* (Horn), was the most abundant in the forest habitat (81%). Overall, different locations and habitats affect the dung beetle species present in an area. However, future work should examine the presence of edge effects on these species in Cypress Hills Interprovincial Park.

3.2 Introduction

By virtue of their different nesting behaviours, dung beetles degrade cattle dung in pasture ecosystems (50, 93). Rollers (telecoprids) (Scarabaeidae: Scarabaeinae: Tribe Canthonini) construct a ball by breaking off a portion of the fresh dung pat and rolling it into a ball (90, 93). This activity is often done in pairs, with the male and female rolling the ball with their hind legs a distance away from the dung pat to be buried (90, 93). If a female lays an egg in the buried dung, it is termed a brood ball; if not, it is termed a food ball (90, 151). Both brood and food balls provide nourishment for developing dung beetle larvae. Tunnellers (paracoprids) (Geotrupidae; Scarabaeidae: Scarabaeinae) bury fresh dung in tunnels below the pat. Dwellers (endocoprids) (Scarabaeidae: Aphodiinae) (68) develop from egg to adult within the pat (93). Degradation occurs mainly due to the feeding activity of the developing larvae (74). A fourth group, the detritivores, do not use dung for breeding. Adults feed on fresh dung and may scatter it if a sufficient abundance of beetles are present. Eggs are laid in organic-rich soils where larvae feed on rotting organic matter (122, 193).

The most visually obvious activity of dung beetles is the degradation of dung pats, but they also offer several additional ecosystem services. Dung relocation by tunnellers and rollers helps the surrounding vegetation by increasing nutrient cycling and seed dispersal (162). As well, degradation also propagates the growth of new forage by freeing up the surface of the pasture. Burying dung provides increased nitrogen availability for plants instead of it being lost to the atmosphere due to volatilization (162). Tunnel formation increases soil aeration and water porosity to enhance plant growth (162). Dung beetles can also act as biocontrol agents to reduce pest fly populations such as face flies

(*Musca autumnalis* (DeGeer)) and horn flies (*Haematobia irritans* (Linnaeus)) that lay their eggs in fresh dung (63). Because dung beetles degrade dung pats, this reduces available breeding area for the flies, and damages their eggs (162).

Soil, vegetation and elevation are factors that affect dung beetle species present in an area and consequently the speed of cow dung degradation and the ecosystem services that they provide. In Texas, sites characterized by clay soils were less species rich than sites with sandy soils, presumably because clay soils are less conducive for tunnel formation (159). Densely vegetated sites can also hinder the rolling of brood balls or the location of dung pats (159). However, soil type was more important than vegetation to determine segregation of species (13, 159). Vegetative cover, specifically forests, have also been linked to harbouring different dung beetle species (64, 106, 177). In El Salvador, fewer species were present in untreed pastures compared to forested sites with each type of habitat supporting a different group of species (106). Different elevations also harbour different dung beetle species. Herzog et al. (101) reported that dung beetles are affected by elevational gradients in Bolivia, with a 57% species decrease of 23 species below 1000 m to 10 species above 1000 m.

The current study compared the dung beetle species diversity for: (i) two different habitats at the same location and (ii) the same habitat at two different locations in southern Alberta. For this purpose, dung-baited pitfall traps were established and maintained for two years from spring through autumn on native pastures at Cypress Hills Interprovincial Park and at the Purple Springs Grazing Reserve. This study will be the first to report the dung beetle species present in Cypress Hills Interprovincial Park. As well, the longevity of this study offers the chance to monitor species diversity over time. It is predicted that some species will have associations with each location and habitat.

3.3 Methods

3.3.1 Location Descriptions

Cypress Hills Interprovincial Park (CHIP) spans 40,000 ha of southeastern Alberta and southwestern Saskatchewan, Canada. The park is a ‘sky island’ with an elevation of roughly 1,400 m, which is approximatively 310 m above the surrounding prairie (102, 225). It is the highest point of elevation in Canada between the Rocky Mountains and Labrador (102). Daily precipitation (mm) and average temperature records (°C) were obtained from a weather station located in the park near the town of Elkwater (2). Weather records (1961 – 2013) identify the average precipitation as 322 mm (Apr. 1 – Sept. 30) and an average of 116 frost free days (≥ 0 °C) per year (2). Recent records (2011 – 2015) give a mean daily temperature of -10.4 °C and 17.3 °C for January and July, respectively (2).

Cypress Hills Interprovincial Park is a mosaic of forest and native grassland habitats. Forested sites have Grey Luvisol soils (86, 99) with stands of Lodgepole pine (*Pinus contorta* Douglas ex Loudon) (99, 161, 225) and trembling aspen (*Populus tremuloides* Michaux) (99, 161). Grassland sites have brown Chernozem soils (86, 99) and are dominated by shrubby cinquefoil (*Dasiphora fruticose* Linnaeus) and Plains rough fescue (*Festuca hallii* (Vasey) Piper); timber oatgrass (*Danthonia intermedia* Vasey) and June grass (*Koeleria macrantha* (Ledebour) Schultes) are also common (99, 225). It is thought that an active fire suppression program has caused the forest encroachment to expand (225). The reason for this program is that the local ranching community has used CHIP for the past 50 years to graze their cattle (192) from June to October (96).

Purple Spring Grazing Reserve (PSGR) is approximatively 2,700 hectares (4) in size and has an elevation of approximately 800 m (122). The landscape is characterized by gently rolling hills and sandy soil (4, 122). The dominant vegetation includes prickly rose (*Rosa acicularis* Lindley), silverberry (*Elaeagnus commutata* Bernhardi ex Rydberg), and buckbrush (*Ceanothus cuneatus* (Hooker) Nuttall) (122). Similar to CHIP, Purple Springs has cattle that graze yearly from May to October (4, 122). Daily average temperature records for Purple Springs were obtained from an Agriculture and Agri-Food weather station in Vauxhall, Alberta (1, 2). Weather records (1961 – 2013) identify the average precipitation as 240 mm (Apr. 1 – Sept. 30) and an average of 125 frost free days (≥ 0 °C) per year (2). Recent records (2011 – 2015) give a mean daily temperature of -9.3 °C and 18.5 °C for January and July, respectively (2).

3.3.2 Collection of Dung Beetles

To assess the effect of habitat (forest vs. pasture) on dung beetle assemblages, dung-baited pitfall traps were established and maintained at two sites over two years in Cypress Hills Provincial Park. At each site, a transect of 5 traps (ca. 10 m spacing) was placed in forested habitat and a second transect of 5 traps (ca. 10 m spacing) was placed about 100 m distant on adjacent open grassland. The reference names and locations of these sites are Cypress Hills Grassland Site 1 (CG1 = Lat. 49.657°; Long. -110.210°), Cypress Hills Forest Site 1 (CF1 = Lat. 49.656°; Long. -110.216°), CG2 (Lat. 49.630°; Long. -110.263°) and CF2 (Lat. 49.629°; Long. -110.264°) (Fig. 3.1).

To assess the effect of location (CHIP vs. PSGR), results obtained for sites CG1 and CG2 (n = 10 traps total) were compared with results obtained for two sites on open grassland at PSGR. One of these sites (PS1) was inside a small cattle exclosure (PS1 = Lat. 49.827°; Long. -111.895°). The second site (PS2) was located about a 1 km distance from the exclosure (PS2 = Lat. 49.849°; Long: -111.889°) (Fig. 3.2). Five dung-baited pitfall traps were established and maintained at each site over two years, with a separation of roughly 10 m between adjacent traps (n = 10 traps total).

The same type of dung-baited pitfall trap was used at both locations and in each year (Fig. 3.3). This trapping method is widely used and was employed in a similar fashion to other studies (59, 75, 113, 174). Each pitfall trap was composed of two nested (2 L volume) pails buried flush to the soil surface. This allows for both epigeal and flying insects to be caught. The top pail contained roughly 5-7 cm of a 1:1 water and propylene glycol (non-toxic antifreeze) killing solution. The bottom pail is used to maintain the shape of the trap when the top bucket is removed for collection. The bait (~250 mL) was suspended from a wire grid covering the mouth of the pail, which also excluded small mammals or reptiles and destruction if stepped on by roaming cattle. The baits were made from dung collected from cattle fed a diet of barley silage at the Lethbridge Research and Development Station (Agriculture and Agri-Food Canada) in Lethbridge, Alberta. Dung was collected fresh, homogenized, and then wrapped in 3-ply cheese cloth. Scores of baits were made and held at -15 °C until needed.

With rare exception, all traps were emptied and rebaited weekly from May to October in 2016 and 2017. Access to traps in some weeks was prevented by heavy rain or snow. The collected insects were stored in 70% ethanol at 7° C until counted and identified to species using dichotomous keys (83, 178). Scientific names for species of Aphodiinae identified in the current study follow the revision of Gordon and Skelley (85).

3.3.3 Seasonality Graphs

To help standardize the seasonality graphs, the number of beetles caught were combined into intervals of every two weeks and were divided by the number of trap days (i.e., the number of traps multiplied by the number of days they were left out). For example, in the last two weeks of September a combined total of 32,798 *C. distinctus* were collected at Purple Springs across both sites and years. During this time, there were 20 traps that were employed for 15 days (= 300 trap days). Therefore the number of *C. distinctus* for the last week of September is 109.3. This method was also used by Kadiri et al. (122).

3.3.4 Statistical Analysis

For analyses, trap catches were pooled for each combination of date and site; e.g., five samples/week (CG1, CF1, CG2, CF2, PS1, PS2). Preliminary tests prior to the Two-Way ANOVA revealed outliers that affected the homogeneity of the variances (Levene's Test, $P = 3.81 \times 10^{-5}$) and normality of the residuals (Shapiro-Wilk Test, $W = 0.65$, $P = 1.06 \times 10^{-10}$). Thus, the data were transformed using the natural log (ln) to correct for homogeneity (Levene's Test, $P = 0.71$) and normality (Shapiro-Wilk Test, $W = 0.98$, $P = 0.35$).

Captures of beetles between habitats (forest vs. grassland at CHIP) and locations (grassland sites at CHIP vs. PSGR) were compared using the non-parametric α diversity (within sample) tests Chao-1 index, Shannon index and Simpson's index. The Chao-1 index is a metric for species richness (40) and corresponds to the results from rarefaction analysis, which is also a metric for species richness. Rarefaction analysis, also known as species accumulation curves, plots the number of individuals versus the number of taxa. This can be used to pinpoint the ideal sampling effort to obtain the maximum species richness. As the curve plateaus, this indicates that an additional sampling effort will most likely result in the recovery of few or zero additional taxa. Both Shannon and Simpon's index are metrics for species diversity. Shannon index considers evenness and richness of the individuals (195). Values typically range from 1.5-3.5 (144) with smaller values indicating few taxa are present. Simpson's index (1-Dominance) captures the variance of species abundance and distribution (174) and ranges from 0 (one taxon dominates) to 1 (equal presence of all taxa).

The Jaccard index was used to compare the β diversity (between samples) for captures of beetles between habitats (forest vs. grassland at CHIP) and locations (grassland sites at CHIP vs. PSGR). The value is given as a percentage of similarity with higher values identifying a greater number of taxa shared between sites (144). Comparisons were made for captures in 2016 and again in 2017.

A Two-Way ANOVA (α = 0.05) was used to test for differences in the average number of dung beetles recovered using year (2016, 2017) and site (CG1, CF1, CG2, CF2, PS1, PS2) as fixed factors. Correspondence analyses were performed to assess the associations of individual species to different habitats and locations. These analyses produce plots that indicate the strength of these associations. In these plots, habitats or locations located spatially close together support a similar complex of species. In addition, species located spatially close to a habitat or location have a strong association to that factor.

Statistical tests and the correspondence analyses maps were performed using R (version 3.4.3) in RStudio. Species richness, diversity indices and rarefaction analysis were calculated using PAST (version 2.17c).

3.4 Results

3.4.1 Climatic Conditions

Daily precipitation and temperate from the sampling period was compared to historical data. Precipitation data for CHIP showed higher values for 2016 compared to 2017, especially for the end of July/beginning of August (Fig. 3.4A). These two months received four times the amount of precipitation in 2016 than 2017. A comparison of the precipitation data from 2011-2015 revealed that both 2016 and 2017 received less precipitation than normal, 16 mm (2016) vs. 7 mm (2017) vs. 322 mm. Data for October 2016 were missing from the database, so comparisons for this month could not be completed. Temperature data for CHIP was similar between 2016 and 2017 and was consistent with the previous four year (2011-2015) monthly averages (2) (Fig. 3.4B). In most cases there was only a difference of 1 °C . The precipitation data for CHIP is the total precipitation because snow and rainfall data were not separated in the database. Information for October 2016 is missing from the database (2).

Precipitation data for PSGR were missing for the sampling period from the Vauxhall station, which is roughly 30 km away from the grazing reserve and has been used in other studies that sampled at Purple Springs (122). Instead, data for snow (cm)

(Fig. 3.5A) and rain (mm) (Fig. 3.5B) were taken from the Agriculture and Agri-Food weather station located at the Lethbridge Research and Development Center (1). Although this weather station is 60 km away from Purple Springs, it would provide similar data. Precipitation data was similar for 2016 and 2017 except for the large snow fall at the beginning of November in 2017. A comparison of the precipitation data from 2011-2015 revealed that both 2016 and 2017 received less precipitation than normal, 10 mm (2016) vs. 7 mm (2017) vs. 240 mm. Temperature data for PSGR were similar to the previous four year monthly averages (2). In most cases there was only a difference of 1 °C except for the month of November (Fig. 3.5C). Data from 2016 shows that the temperature for November 2016 was 4.9 °C, which is much higher than 2017 (-2.3 °C) and the average from the previous four years (-1.9 °C).

3.4.2 Habitat and Location Comparison

A total of 112,567 dung beetles were recovered over the course of the study. A boxplot was constructed to show the spread of the data across sites and years (n = 5 traps/site) (Fig. 3.6).

At CHIP, 1,814 (12 species) and 3,130 (14 species) dung beetles were captured in 2016 and 2017, respectively (Table 3.1). In each year, species diversity and total abundance was higher in the grassland than in the forest (Table 3.1). Also, in each year *Diapterna hamata* (Say) was the most abundant species in grassland collections (66% of total collected at CG1 and CG2 across years) and *Agoliinus leopardus* (Horn) was the most abundant in forest collections (81% of total collected at CF1 and CF2 across years). At PSGR, 20,243 (12 species) and 87,180 (12 species) dung beetles were captured in 2016 and 2017, respectively (Table 3.2). Across both years and sites, *Chilothorax* *distinctus* (Müller) was the most abundant (90% of total collected at PS1 and PS2 across years) (Table 3.2).

A Two-Way ANOVA was used to test for differences in the average number of insects caught between years, habitats, sites and locations. The effect of site ($F_{5,48}$ = 174.173, P < 0.001), year ($F_{1,48}$ = 79.321, P < 0.001), and the interaction of both factors ($F_{5,48}$ = 8.716, P < 0.001) were found to be significant. A Tukey Kramer post hoc test for the habitat comparison at each site in CHIP revealed a significant difference at site one (P = 0.0036) and site two (P < 0.001) in 2016 and only at site one (P = 0.0458), not site two (P = 0.860) in 2017. A Tukey Kramer post hoc test for the location comparison of all combinations of sites and years between CHIP and PSGR showed a significant difference (P < 0.001 for all combinations) for both years. A Tukey Kramer post hoc test for the site comparison at PSGR showed a significant difference between years at site one (P < 0.001) and site two (P = 0.048).

Comparisons of the Jaccard index are reported in Table 3.3. In CHIP, the diversity of beetles recovered in grassland and forest habitats was more similar at site one (CG1 vs. CF1) than at site two (CG2 vs. CF2) in both 2016 and 2017. In comparisons of habitat and of location (CHIP vs. PSGR), the Jaccard index was higher in 2017 than in 2016. This result presumably reflects the higher number of individuals caught in 2017. Even though different species dominated each location and habitat, there was a large percentage of species overlap between habitats and locations.

The correspondence analysis plots indicate the strength of associations for each species associated with habitat and location in 2016 and 2017. The habitat plot (Fig. 3.7) should be viewed with reference to Table 3.1, and the location plot (Fig. 3.8) should be viewed with reference to Table 3.2. The habitat comparison indicates that most species are associated with the grassland habitat, which is consistent with the higher species diversity values. However, the relationship of some species should be interpreted with caution as they were recovered in low numbers (e.g., *D. hamata*, *P. coloradensis*, *T. fossor*, *O. haemorrhoidalis*, *C. granarius*, *P. vittatus* and *M. prodromus*) (Table 3.1). Dimension 1 (Dim1) and dimension 2 (Dim2) accounted for 68.8% and 27.3% of the variation, respectively. The combined total of 96.1% indicates almost all of the variation is represented on the plot (Fig. 3.7). The third dimension accounted for the remaining 3.9% and was excluded from the plot because of the small value, which did not contribute much variation. For the location comparison, the shorter the distance between the species and the location, the stronger the association (Fig. 3.8). Dimension 1 (Dim1) and dimension 2 (Dim2) accounted for 88.1% and 8.6% of the variation, respectively. The third dimension accounted for the remaining 3.3% of the variation and was excluded. Therefore, the combined total of the first two dimensions (96.7%) accounts for almost all of the variation.

Rarefaction analysis was completed for each of the six sites. Individuals recovered from CHIP grassland (CG1 & CG2) indicate that additional sampling would most likely result in the recovery of zero taxa because the curves have reached a plateau (Fig. 3.9). This result is supported from the Chao-1 index values as they are the same as the true number of taxa recovered (Table 3.1). However, the curves from CHIP forest (CF1 & CF2) indicate that additional sampling would recover more species, because the curves have plateaued (Fig. 3.9). This conclusion is also supported from the Chao-1 index values as they are higher than the actual number of taxa recovered. The curves from both sites and years at PSGR (PS1 & PS2) have plateaued indicating that future sampling would result in the recovery of no new taxa (Fig. 3.10). This is supported by the Chao-1 index values because they are the same as the true value of the number of taxa recovered (Table 3.2).

3.4.3 Seasonal Activity

Collection of dung beetles was sometimes hindered due to climatic conditions. Snowfall in early November of 2017 prohibited sample recovery at PSGR until late November (Fig. 3.5A). Similar issues occurred in CHIP, which caused traps not to be emptied for a few weeks at a time (Fig. 3.4A). Catches during these periods are representative of the extended time.

Each species exhibited one of two general patterns of adult seasonal activity. Unimodal species have one peak activity time, which is usually in the spring and early summer (75, 122). Bimodal species have two peak activity times, the first is usually in the spring/summer and the second in autumn (75, 122). The seasonality for each species is reported (Figs. 3.11-16). As well, detailed descriptions of each species are reported in the discussion.

3.5 Discussion

3.5.1 Species Descriptions

Rollers

Canthon pilularius (Linnaeus): This species is a roller (122, 178) and has a seasonal activity of April to September in Nebraska (178). This species is native to Alberta and is found within parts of the United States (Chapter 2). It exhibits a bimodal activity with the first peak in June and the second in September (122). Helgesen & Post (98) reported that late June and July are the peak activity times of *Canthon* species in North Dakota. Data collected from this experiment is consistent with these descriptions (Fig. 3.11A).

Canthon praticola LeConte: This species is as a roller (122, 178) and has a seasonal activity of May to November in Nebraska (178). Helgesen & Post (98) reported that late June and July are the peak activity times of *Canthon* species in North Dakota. *Canthon praticola* is native to Alberta and is found within the southwest of the United States (Chapter 2). It exhibits a bimodal activity with the first peak in May and the second in August (122). Data collected from this experiment indicates that the second peak of activity corresponds to the end of July rather than August (Fig. 3.11B).

Tunnellers

Onthophagus nuchicornis (Linnaeus): This species is of European origin and exhibits a bimodal activity with the first peak in May and the second in August (122). This species is a tunneller that is often associated with sandy soil (217). Its possible expansion through Canada and the United States has been predicted in Floate et al. (78). Based upon the seasonality data from Kadiri et al. (122) and the data collected from this experiment, it seems that the first peak in early summer is when the majority of individuals are present (Fig. 3.11C).

Colobopterus erraticus (Linnaeus): This species is of European origin (85, 178), prefers exposed habitats and overwinters as adults (133). Both adults and larvae are found at the dung pat with the larvae pupating in the soil under the pat (178). This species is a tunneller as it lays eggs at the end of tunnels formed under the dung pat (184). *Colobopterus erraticus* is found throughout the Midwest and east coast of the United States as well as throughout Canada (Chapter 2). Seasonal activity is reported as April to October for North America (85). In Alberta, this species is active from May to October (122) and lays its eggs at the end of May (184).It has two generations a year (133), which corresponds to a bimodal species activity (122). Data collected from this study supports the bimodal classification and the seasonal activity of May to October (Fig. 3.12A).

Dwellers

Agoliinus leopardus (Horn): This species is a Nearctic (158) dweller that feeds and develops within the dung pat (75). Most individuals are found associated with deer dung (75, 85, 158). This is a forest-dwelling dung feeder (85) that is found through Canada and the Midwest of the United States (Chapter 2). It has been caught in Kakwa Provincial Park, Alberta (3), which is similar to CHIP because it has areas dominated by Lodgepole pine and an elevation of roughly 1800 m (3). Most species in this genus live in high elevations or high latitudes (85). In terms of seasonality, Brousseau et al. (33) suggested that this species is active during July in Québec, but it was thought that this was not the peak of their active season. The seasonal activity is July to November for North America (85). Results from this study suggest that *A. leopardus* is active as early as the beginning of June and could exhibit a unimodal seasonality (Fig. 3.12B).

Aphodius pedellus (De Geer): Descriptions for this species are often grouped together with that of *Aphodius fimetarius* (Linnaeus) as they were thought to be synonyms until the findings of Wilson (226) and Miraldo et al. (155). They are morphologically similar, which makes it difficult to distinguish between the two species. In Alberta it is most likely *A. pedellus* not *A. fimetarius* (155), that is present, in contrast to previous literature from the province. Although little is known about life history differences, there appears to be distinct active seasons for each species. While both are active during the early summer, only *A. pedellus* has a second speak of activity in early autumn (155). This description indicates that it exhibits a bimodal activity, which corresponds to findings from this study (Fig. 3.12C).

Otophorus haemorrhoidalis (Linnaeus): This species is a European dweller found in Alberta (122), North Dakota (98) and throughout much of Canada and the United States (Chapter 2). It is common on pastures and adapted to open unshaded areas (85). Adults and larvae occur in the same dung pats (178); and overwintering occurring in the larval stage (133). *Otophorus haemorrhoidalis* exhibits a bimodal activity with the first peak in June and the second towards the end of September (122). This contrasts with the findings of Floate & Gill (75), who reported this species as being unimodal with the main activity being in the middle of June to the middle of August. The seasonal activity is listed as year round in southern latitudes and April to October in northern latitudes (85). This time frame corresponds to data collected in this study (Fig. 3.13A) and to those reported by Floate & Gill (75), Ratcliffe & Paulsen (178) and Kadiri et al. (122). In North Dakota, *O. haemorrhoidalis* is active from the middle of May to the middle July and the end of August to the beginning of November (98). In Sweden, adults occur from June to August (133).

Planolinellus vittatus (Say): This species is a native dweller of Alberta (122) and “prefers open pasture, but will tolerate dense shade” (85). *Planolinellus vittatus* has been reported throughout Canada and has a scattered distribution in the United States (Chapter 2). Seasonal activity is listed as year round (85). However, in North Dakota it is active from May to August (98), with peak times in late June and early July (98), and from April to September in Nebraska (178). *Planolinellus vittatus* has a unimodal activity with the peak at the end of May (122). Data collected from this study correlates with the seasonal activity reported in Kadiri et al. (122), but with peak activity at the beginning of June (Fig. 3.13B).

Planolinus tenellus (Say): This species prefers shaded areas (85). It is present later in the season, with a seasonal activity of April to October in North America (85). *Planolinus tenellus* is a native North American species (141), with records throughout Canada and limited data from the United States (Chapter 2). It appears to exhibit unimodal activity based on the data (Fig. 3.13C).

Pseudagolius coloradensis (Horn): This species is a dweller species native to Alberta (122) and is reported as a general surface dung feeder (85). Seasonal activity is listed as April to August in North America (85). In Alberta some individuals have been caught as late as September (122). *Pseudagolius coloradensis* has limited records from North America, which are limited to Canada and the Midwest of the United States (Chapter 2). This species exhibits a unimodal activity with the peak being in July (75, 122). The data collected supports this classification although the peak activity was in June (Fig. 3.14A).

Teuchestes fossor (Linnaeus): This species is a Palearctic euryphagous surface dung feeder that is common in exposed, unshaded pastures (85). In Sweden, *T. fossor* prefers exposed pastures and typically overwinters as larvae, rarely as adults (133). Seasonal activity is listed as April to September in North America (85). This is primarily a spring and fall species (178) and has extensive records throughout Canada and the United States (Chapter 2). This species exhibits a unimodal seasonality with peak activity at the beginning of June (122) and at the end of May (75). Data collected from this study indicates peak activity in beginning of June (Fig. 3.14B).

Detritivores

Diapterna hamata (Say): *Diapterna* species are typically associated with boreal regions and are mostly considered to be detritivores (85). In North Dakota, *D. hamata* is associated with boreal areas and has only been collected from cattle dung (98). The seasonal activity is May to July in North America (85). *Diapterna hamata* is reported throughout Canada and the United States excluding the east coast (Chapter 2). Results from this study extend the distribution from May to late August (Fig. 3.14C). This species most likely exhibits a unimodal seasonality with one peak of activity in spring and early summer (122).

Diapterna pinguella (Brown): This species is a detritivore that is restricted to moist locations (85). The seasonal activity of this species is March to October in North America (85). This species has few reports, which are limited to the Midwest of both Canada and the United States (Chapter 2). Helgesen & Post (98) reported this species as having a preference for humus near standing water. Only two individuals were recovered in the current study (CHIP grassland, June 2016). Therefore no conclusions can be drawn about their distribution in Alberta (Fig. 3.15A).

Calamosternus granarius (Linnaeus): This species is a detritivore (85). In Sweden, *C. granarius* is polyphagous and feeds on different types of material such as; dung carrion, compost and debris (133). The adults lay eggs in the dung pat, where the larvae develop then move to the soil to pupate (178). Seasonal activity is year round in North America (85). *Calamosternus granarius* has been reported throughout Canada and the United States (Chapter 2). In Sweden, adults occur from August to November, and then overwinter to appear again from April to May (133). Kadiri et al. (122) and Floate & Gill (75) reported this species as being unimodal with peak activity in the beginning of May and middle of June respectively. The data collected from this study exhibits a peak activity time of June, which corresponds to that of Floate & Gill (75) (Fig. 3.15B).

Chilothorax distinctus (Müller): This species is an European detritivore (85, 178). In Sweden, *C. distinctus* is highly polyphagous with only adults being recovered from dung pats and larvae found in decaying vegetable matter and "never in dung" (133). In Alberta, adults were seen feeding on fresh dung, and larvae usually feeding on manure under the ground (i.e., rotting organic matter) (193). This species overwinters as adults and will lay their eggs in manure or decaying plant material (193). Seasonal activity is reported as year round in North America (85) with peak abundances in the spring and fall (178). *Chilothorax distinctus* has been reported throughout Canada and the United States (Chapter 2). Adult *C. distinctus* have a bimodal pattern of seasonal activity (75, 122) with overwintered adults appearing in spring with a larger peak of new generation adults appearing in fall (98, 133, 193) prior to overwintering (133) (Fig. 3.15C). The differences in abundances between the two periods may incorrectly indicate that is it a unimodal species (122).

Melinopterus femoralis (Say): This species is a native general surface dung feeder (85). The seasonal activity is March to May and August to November in North America (85). To my knowledge, this is the first report of this species in Alberta (Chapter 2), with reports from the United States being limited to the Midwest and the South (Chapter 2). This species appears to have a unimodal species activity with the peak being in the middle of June or the beginning of July (Fig. 3.16A).

Melinopterus prodromus (Brahm): This is an introduced species from Europe to North America (85, 178). Adults are general dung feeders (85, 178) and are considered polyphagous, often found in compost and decaying vegetables (133). The larvae however, are reported as being obligate detritivores (85). Overwintering occurs as adults (133). Seasonal activity is March to May and September to November (85) and from January to November in Nebraska (178). In Sweden, adults are abundant in the late autumn and early spring (133). *Melinopterus prodromus* has been reported throughout Canada and the United States (Chapter 2). This species is reported as having a bimodal seasonal activity with peak active times in the beginning of May and the end of October (75, 122). Data collected from this study is consistent with these active times (Fig. 3.16B).

Planolinoides borealis (Gyllenhal): This species is widely distributed in Holarctic regions and is believed to be native to this area (85, 133). In Sweden, *P. borealis* is oligotropic and most likely prefers shaded areas as it found sporadically in open areas (133). In North America, it is primarily a forest inhabitant (85) with reports only from Canada and Alaska (Chapter 2). It overwinters as adults and larvae (133). The seasonal activity is April to November in North America (85), which is consistent with the collected data (Fig. 3.16C).

3.5.2 Future Directions and Conclusions

Results of the current study show an effect of habitat (grassland vs. forest) on the number and diversity of dung beetles. Throughout both years, a smaller proportion of dung beetles were caught in the forested pasture compared to the grassland, 17% and 30% for 2016 and 2017 respectively. A possibility for this large difference could be that the height and density of the forest prevented the dispersal of dung volatiles. Various species co-occurred in both habitat types at different abundances; however, each habitat was dominated by a different species (Tables 3.1 and 3.2). *Diapterna hamata* was the most abundant in the open habitat (66%) whereas *Agoliinus leopardus* was the most abundant in the forest habitat (81%). The former develops in organic-rich soils, whereas the latter develops in dung. What makes these results peculiar is that the two habitat types were in the same area, separated by roughly 100 metres. This is the first study to assess dung beetle diversity in Cypress Hills Interprovincial Park. Overall, these results indicate that some species have a preference of habitat or location while others do not.

In addition, the same habitat (e.g., grassland) at two different locations also harbours different species. For example, *Chilothorax distinctus* dominated the catch at Purple Springs Grazing Research (90% of total collection), but comprised only 1.9% of beetles recovered at CHIP. No rollers (e.g., *Canthon* sp.), were recovered from Cypress Hills, which is presumably due to the lack of sandy soil, which is an ideal texture for this genus (159).

The distance between the two habitats at CHIP is unlikely to be the cause of the difference in dung beetle species. A mark recapture study in Finland was able to determine dispersal distance of dung beetle species (185). Most beetles (73%) were recaptured within the pasture they were released and a small proportion (3%) being found in a different pasture, a minimum distance of 600 m (185). The only species whose density appeared to be unaffected by distance was *Aphodius prodromus* (Braham) (= *Melinopterus prodromus* (Braham)). Overall, this study indicates that dung beetle flight distance is species-dependant. This finding also explains why the same species were found in both habitats although in different abundances.

Other studies have found differences in dung beetle species in forested vs. open habitats. In Texas, Fincher et al. (64) compared the effects of tree cover on dung beetle species. Of the 238,000 beetles, 67.3% of them were recovered in open pasture versus the wooded habitat (64). However, there was a higher species diversity found in the wooded pasture (n = 20) than the open (n = 15). The same species, *Onthophagus oklahomensis* Brown was the most abundant in both the open and wooded pasture (64). Overall, species were either caught in one or both habitats and had different abundances if caught in both (64). Similar findings were observed in CHIP, with a higher number of individuals caught in the open pasture and different species abundances in both habitats.

An aspect of this study that could be the focus of future research would be the presence of edge effects. Sampling was conducted in both habitats, but not in the ecotone, also known as the transition zone between two areas (58). A study of forested and open habitat in the French Guiana revealed that the forested area was more species rich than the open area (58). However, at both locations there was a decrease in abundance towards the edge (58). In Brazil, it was found that the effect of habitat was greater than the ecotone area on dung beetle assemblages (51). Further sampling should be conducted in CHIP to see if there are edge effects on the dung beetle species present.

Modification in the manner with which baits were prepared might further improve the number of collected beetles. For example, when collections were made at PSGR in September 2017, small holes were noticed in the cheese cloth surrounding the dung bait (Fig. 3.17). These were deemed to be made by adult *C. distinctus*, which were observed crawling around on the bait. This species is an European detritivore (85, 178) that is well established in North America, with catches in the thousands being common in Alberta (122). We were unable to determine which traps these baits were from as it was noticed after they were collected and placed in a bag to be thrown out. This most likely had no effect on the weekly catch due to the large abundance of *C. distinctus* during this time. If cheese cloth is used to wrap baits, this issue can be avoided by using a style with smaller holes. Throughout the sampling period, a finer mesh was also used and this behaviour was not observed. Although *C. distinctus* was the only species noticed chewing through the cheese cloth, it is possible that a different species, maybe other detritivores, could chew through the cheese cloth. To my knowledge, this behaviour has not been previously reported. In addition, collections from PSGR in later November after the snowfall (Fig. 3.5A) recovered *C. distinctus* that were alive. It is uncertain if they remained alive during the snowfall or if they became motile once warm.

Overall, this study highlights that different dung beetle species are affected by habitat and location. It also indicates the importance of having multiple replicates, conducting sampling across years, and taking different habitats into consideration. In addition, this is the first study to give a detailed report of the dung beetle species located in Cypress Hills Interprovincial Park and expands the distribution of *Melinopterus femoralis* (Say) to include Alberta.

Figure 3.1. Map of the two sites at Cypress Hills Interprovincial Park, Alberta, Canada. Roughly 4.7 km between the two sites, and 0.12 km and 0.45 km between Cypress Hills grassland and forest at sites 1 and 2 respectively.

Figure 3.2. Map of the two sites at Purple Springs Grazing Reserve, Alberta, Canada. Roughly 2.6 km between the two sites.

Figure 3.3. Design of pitfall trap used in the current study. A metal grid over the mouth of a 2 L pail supports a bait of cow dung wrapped in cheese cloth, and excludes small animals. Non-toxic antifreeze in the pail is used as a preservative.

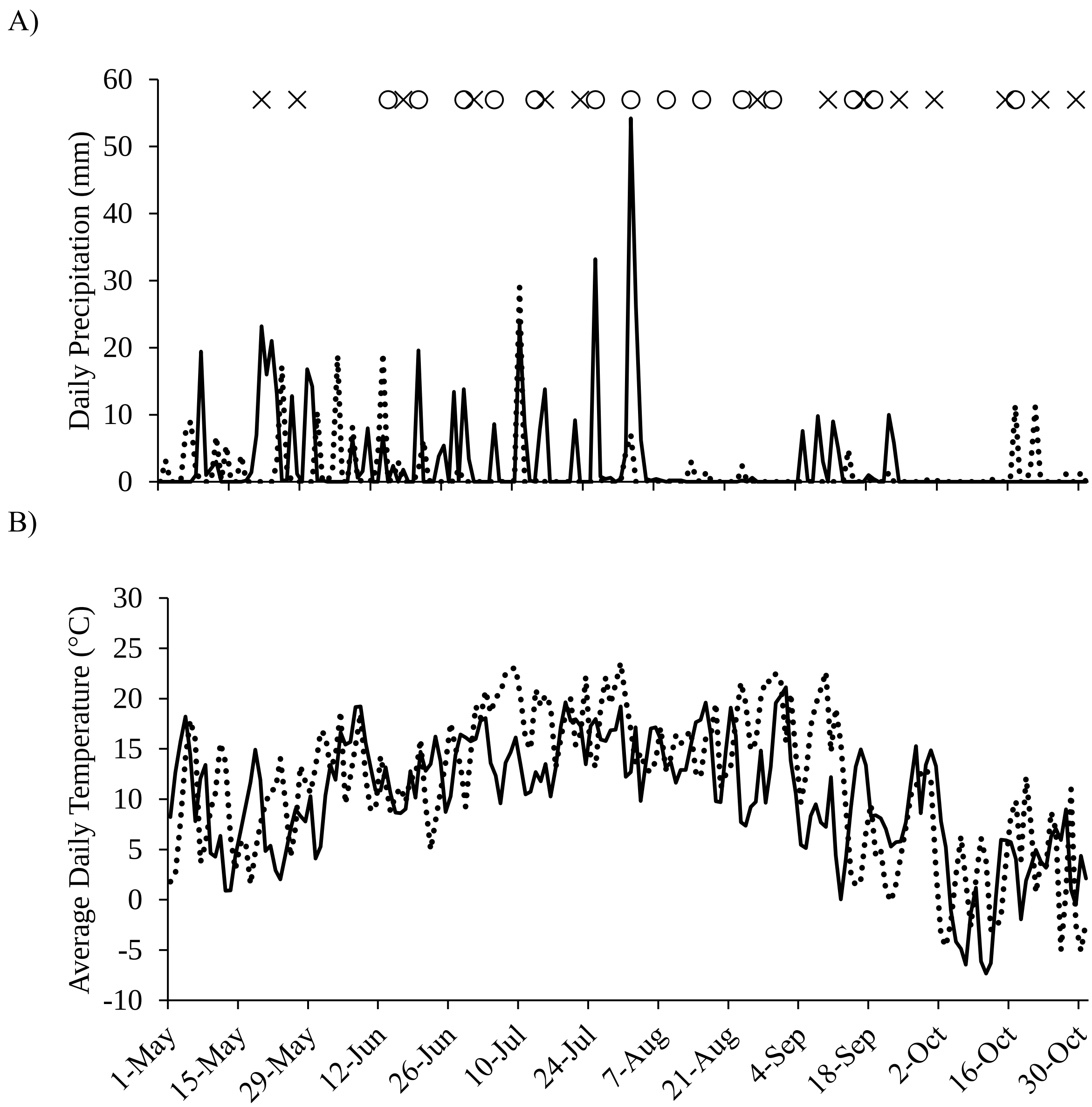

Figure 3.4. Daily precipitation (A) and average temperature (B) data for Cypress Hills Interprovincial Park from May 1st to October 30th. Solid lines, 2016; Dotted lines, 2017. The collection days for 2016 (X) and 2017 (O) are indicated.

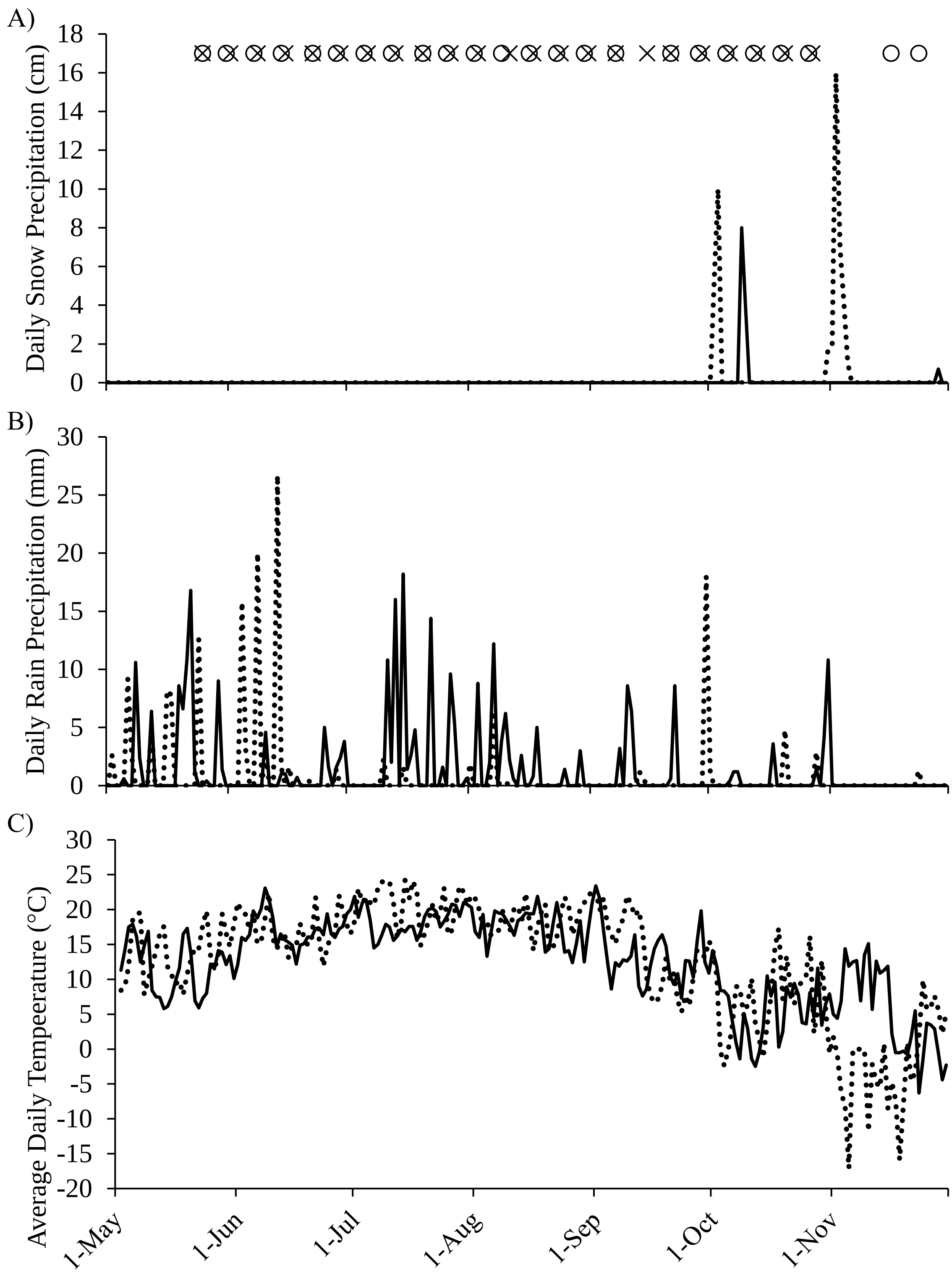

Figure 3.5. Daily snow (A), rain (B) precipitation and average temperature (C) data from Purple Springs Grazing Reserve from May 1st to November 30th. Solid lines, 2016; Dotted lines, 2017. The collection days for 2016 (X) and 2017 (O) are indicated.

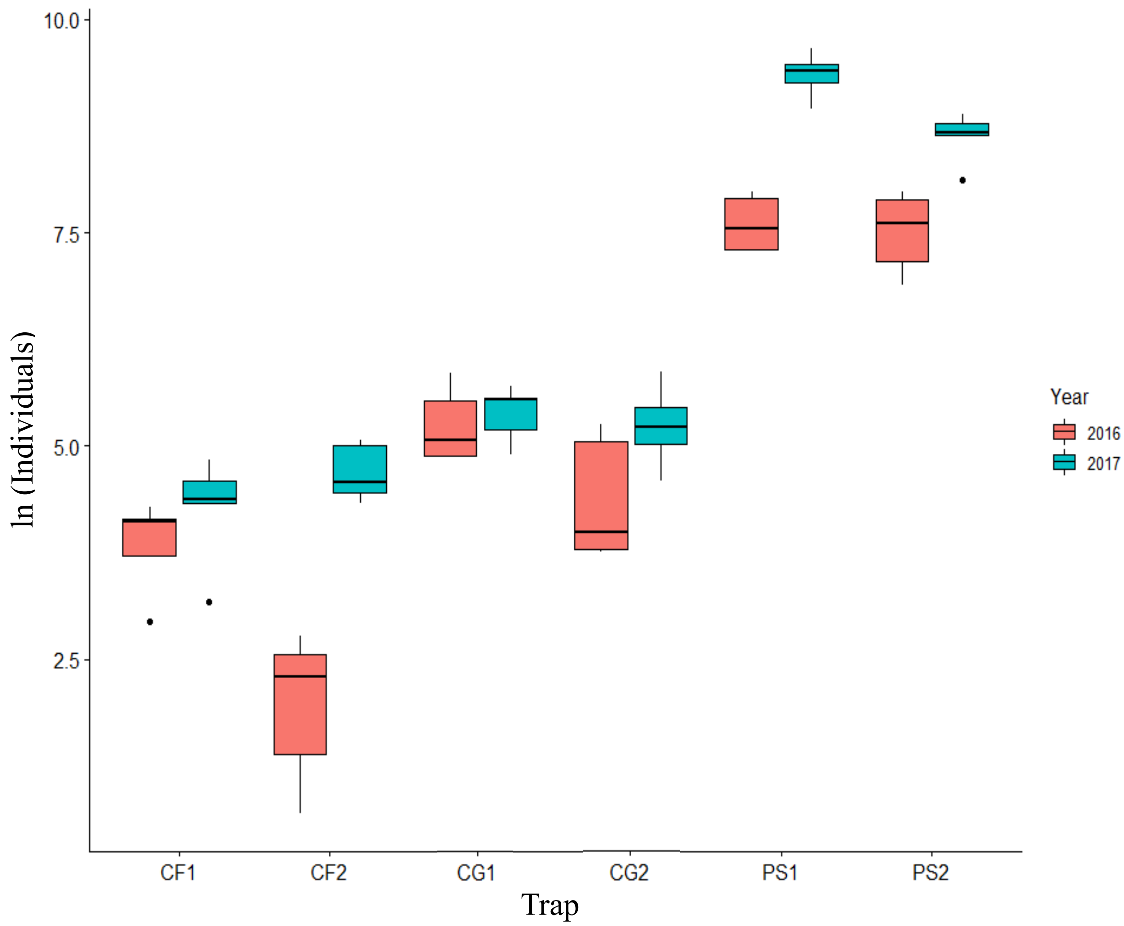

Figure 3.6. A boxplot of the natural log (ln) of the individuals caught at each site across both years; 2016 = pink, 2017 = green. (CF1 = Cypress Hills forest site 1; CF2 = Cypress Hills forest sites 2; CG1 = Cypress Hills pasture site 1; CG2 = Cypress Hills pasture site 2; PS1 = Purple Springs site 1; PS2 = Purple Springs site 2)

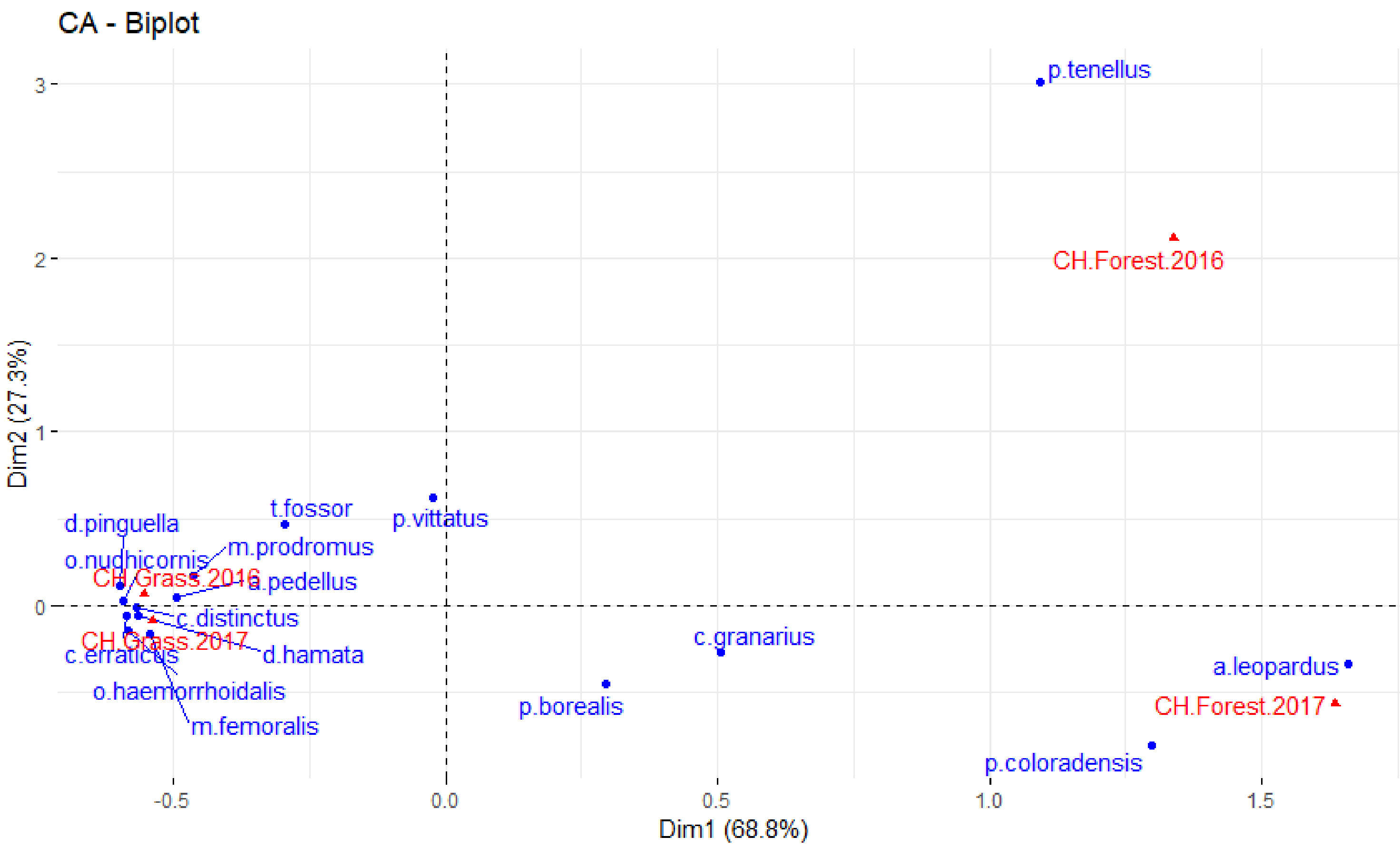

Figure 3.7. Correspondence Analysis of the dung beetle species caught in the forest and grassland in Cypress Hills Interprovincial Park. Species in blue; habitats in red.

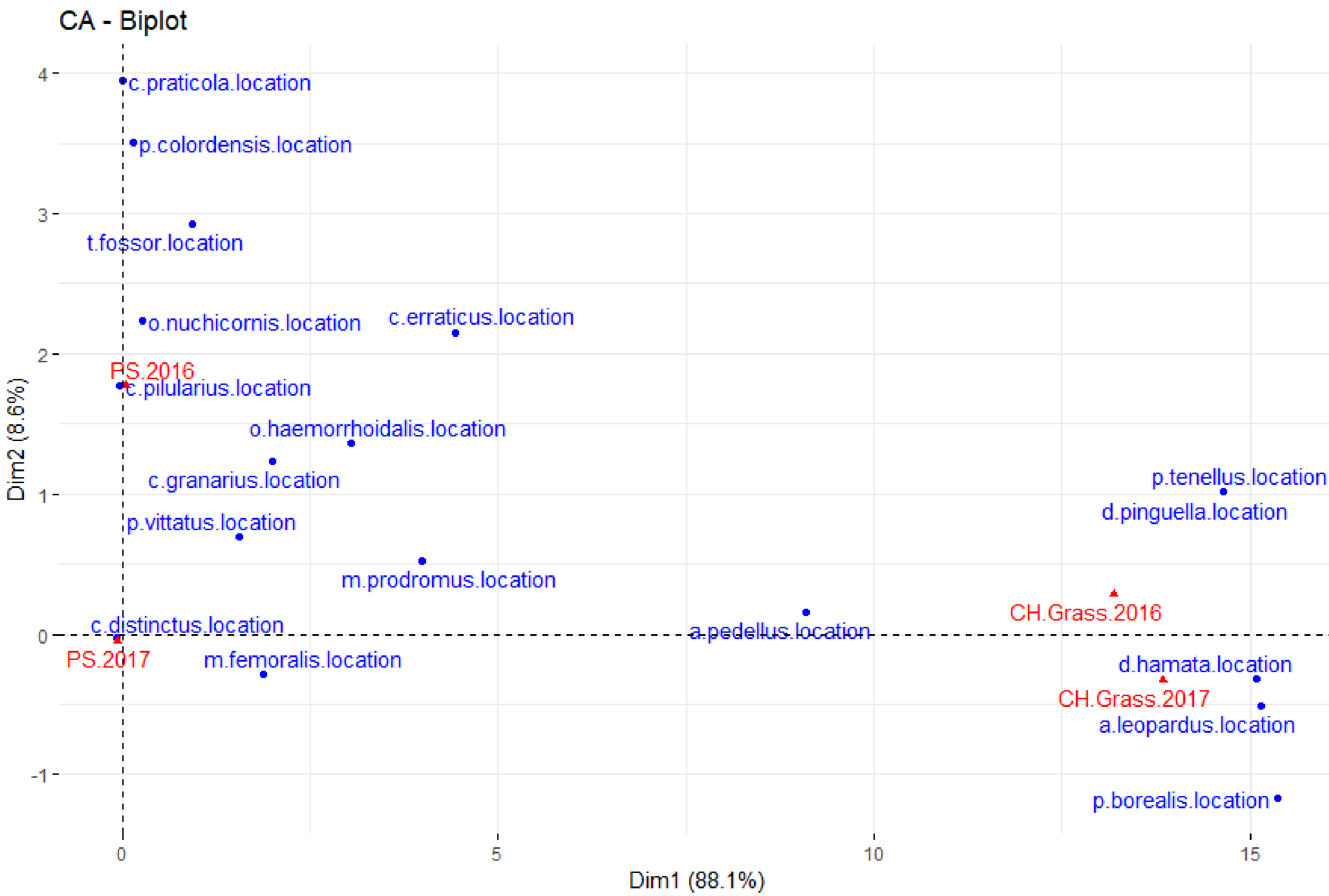

Figure 3.8. Correspondence Analysis of the dung beetle species caught in Purple Springs Grazing Reserve and Cypress Hills Interprovincial Park grassland (CG1 & CG2). Species in blue; locations in red.

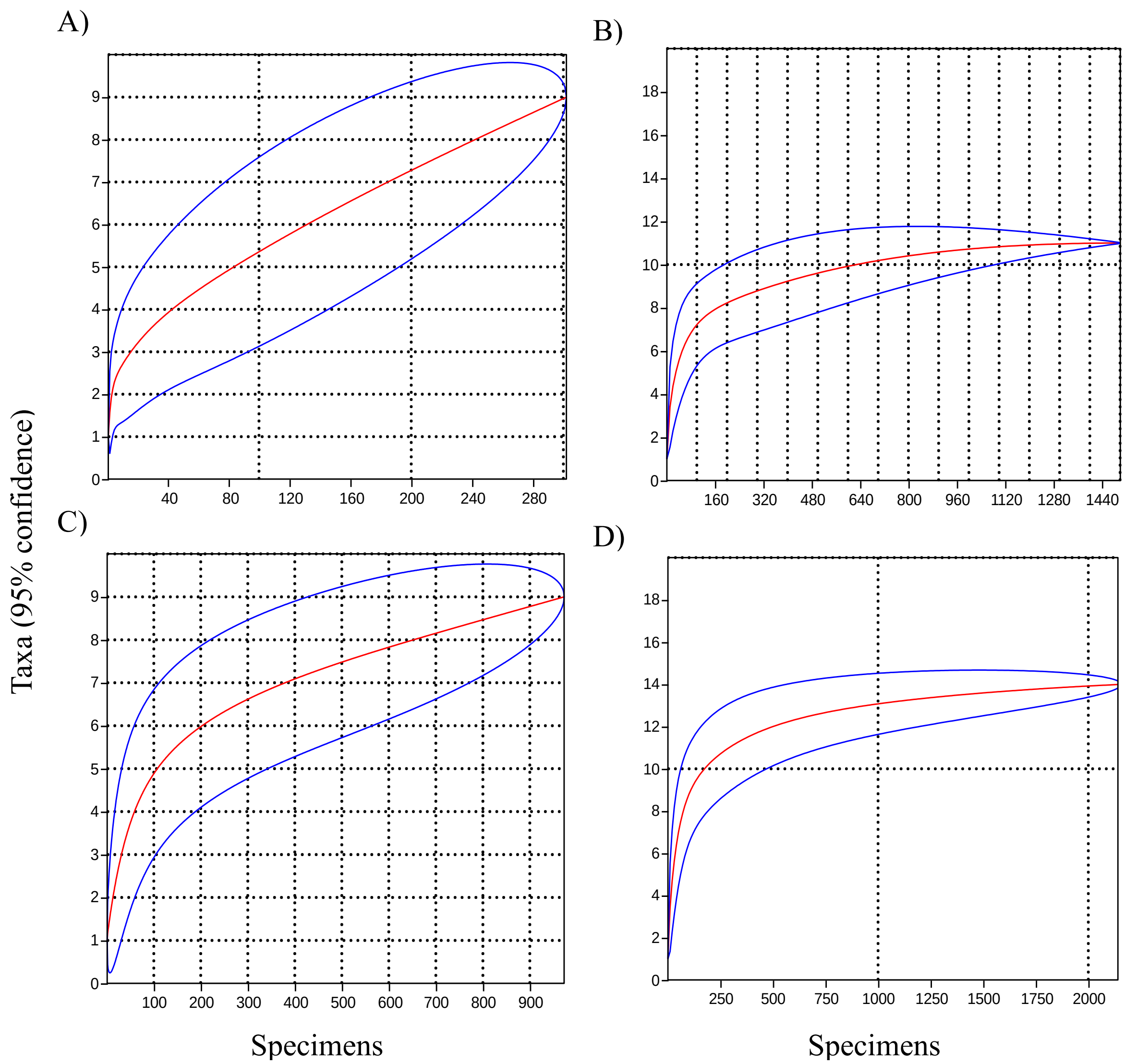

Figure 3.9. Rarefaction curves for Cypress Hills Interprovincial Park grassland and forest for 2016 and 2017 (inner red lines) with the corresponding 95% confidence interval (outer blue lines). A= CHF 2016; B= CHG 2016; C = CHF 2017; D = CHG 2017

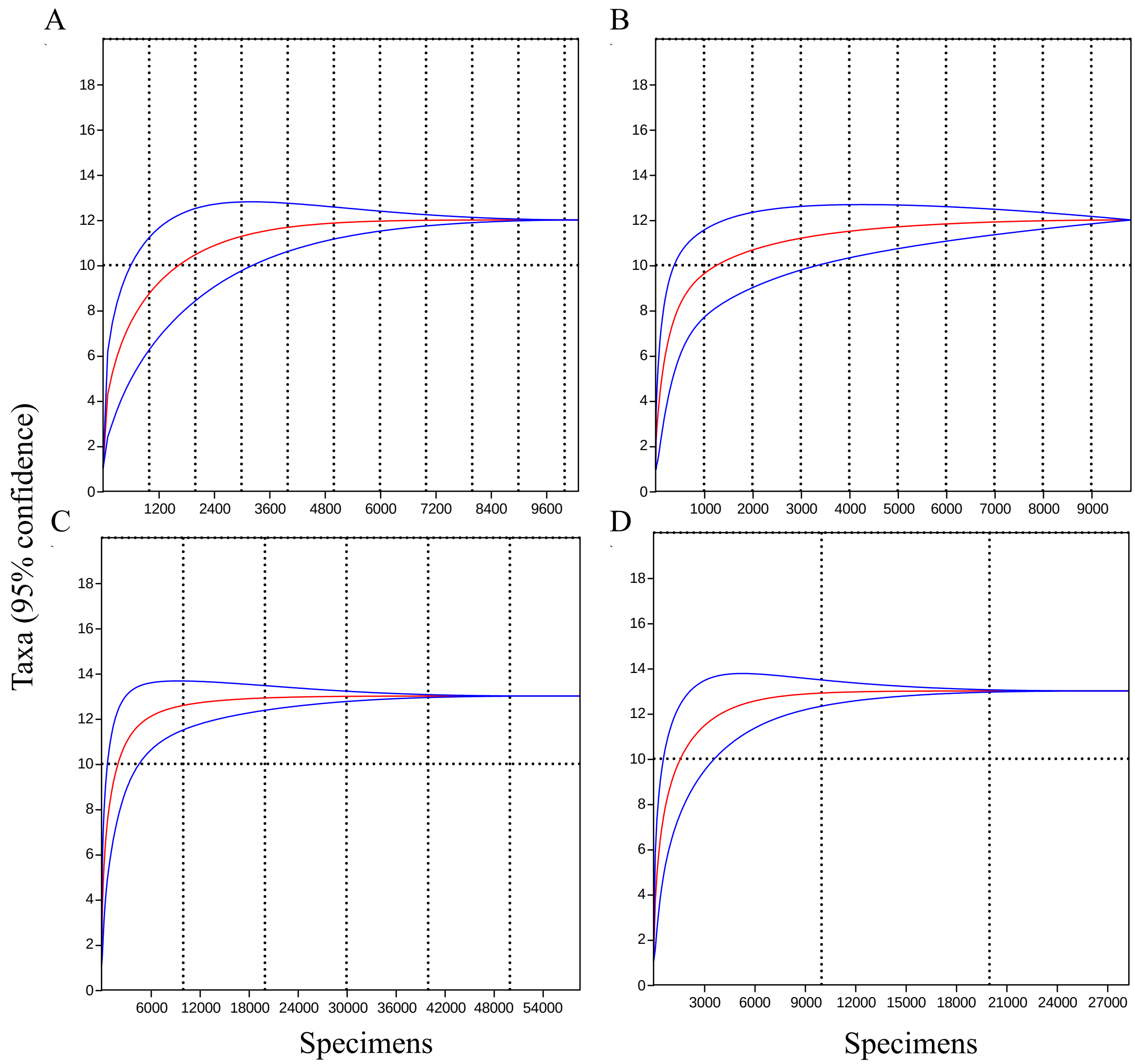

Figure 3.10. Rarefaction curves for Purple Springs Grazing Reserve for 2016 and 2017 (inner red lines) with the corresponding 95% confidence interval (outer blue lines). A = PS1 2016; B = PS2 2016; C = PS1 2017; D = PS2 2017

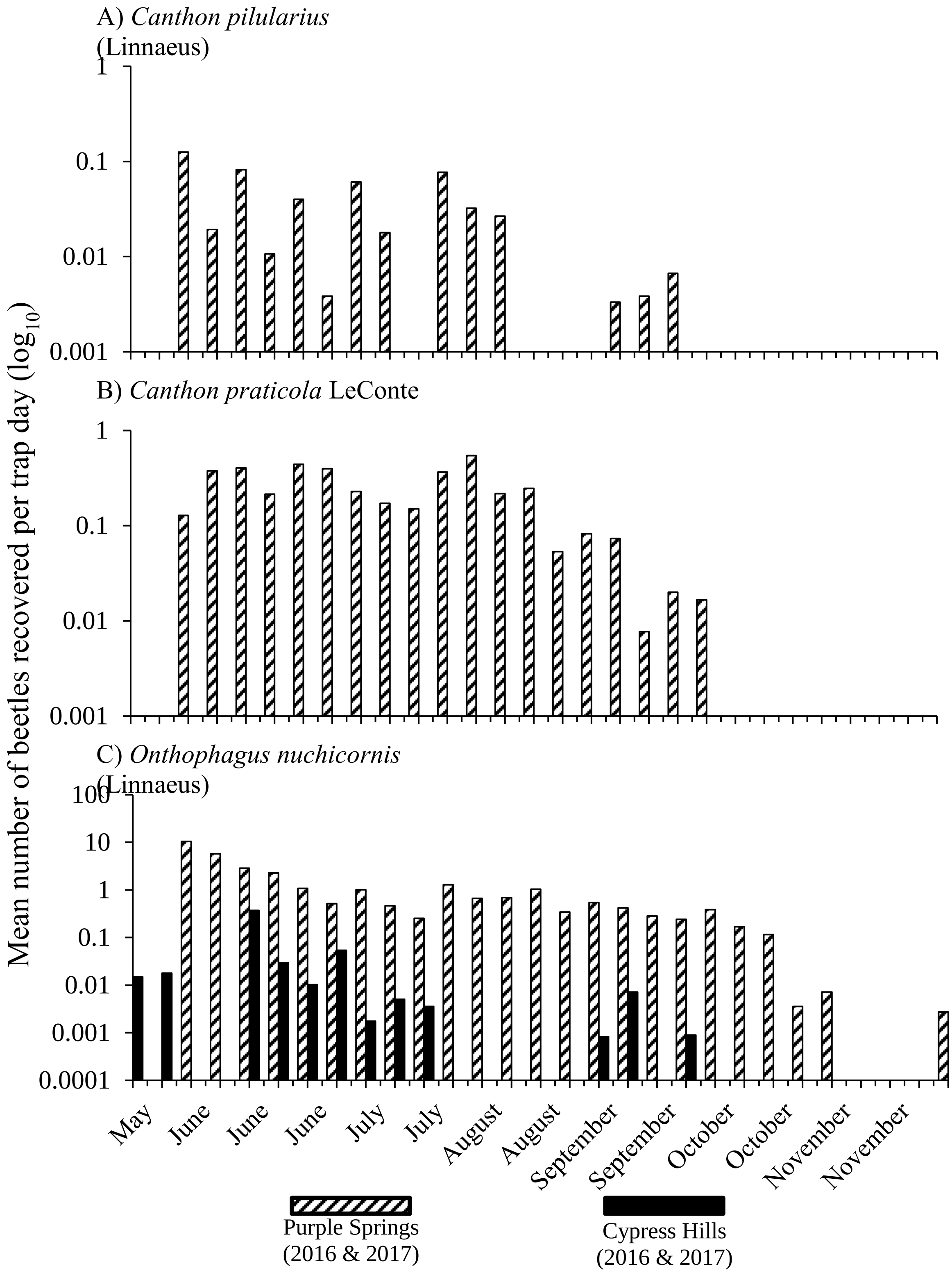

Figure 3.11. Seasonal activity of *Canthon pilularius*, *Canthon praticola*, and *Onthophagus nuchicornis* from 2016 and 2017. Locations: hatched bars (Purple Springs Grazing Reserve); black bars (Cypress Hills Interprovincial Park).

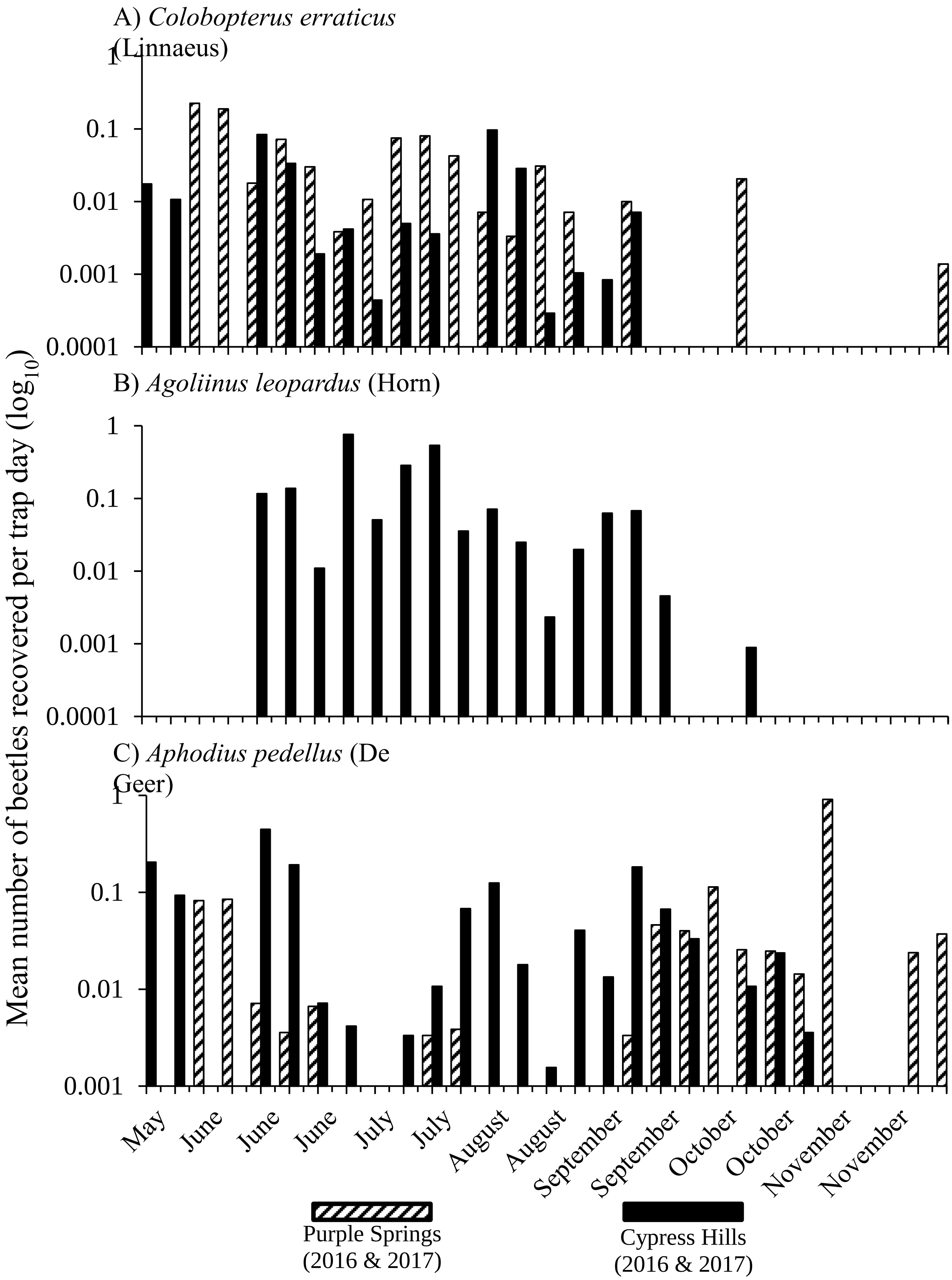

Figure 3.12. Seasonal activity of *Colobopterus erraticus*, *Agoliinus leopardus*, and *Aphodius pedellus* from 2016 and 2017. Locations: hatched bars (Purple Springs Grazing Reserve); black bars (Cypress Hills Interprovincial Park).

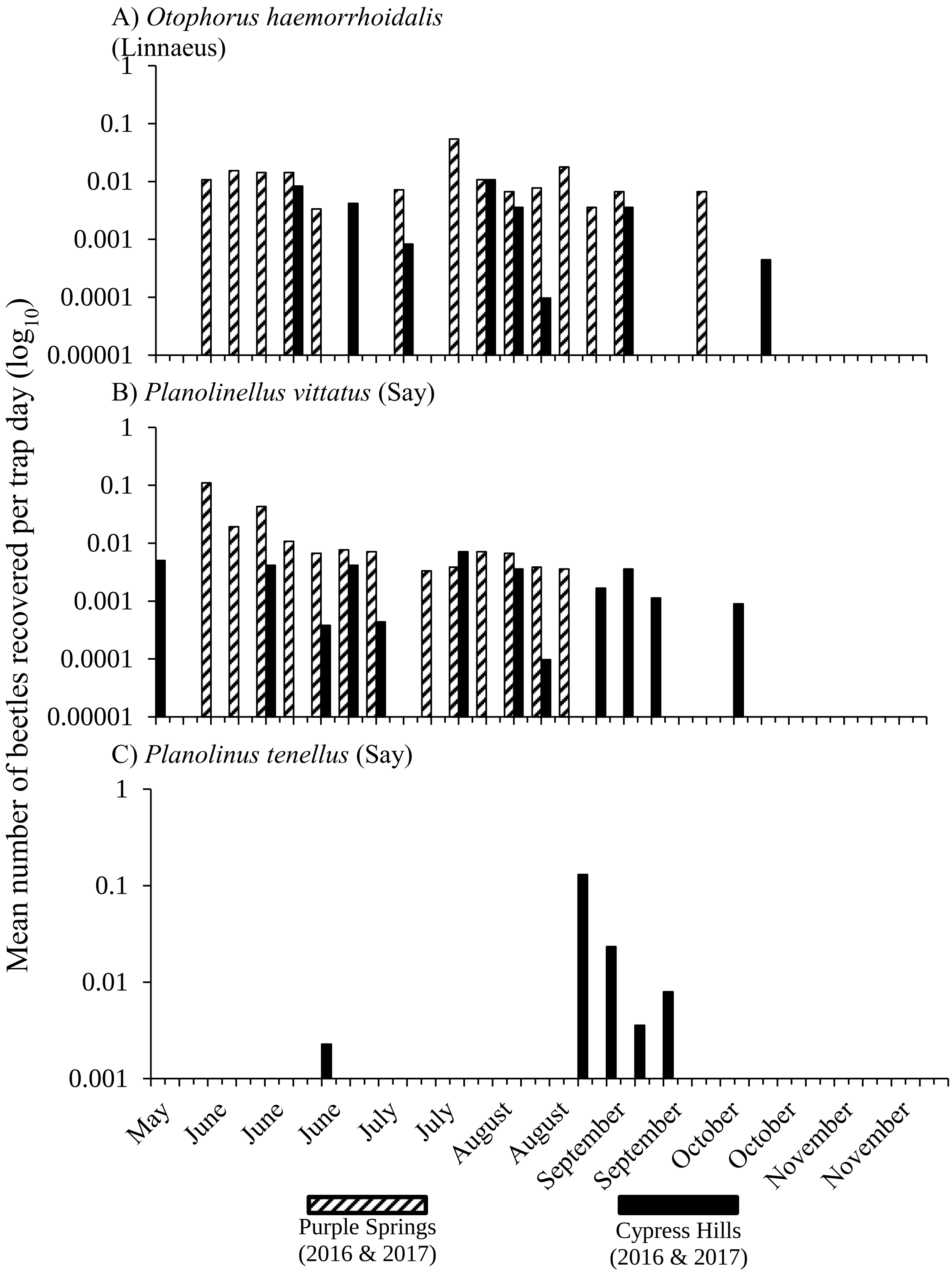

Figure 3.13. Seasonal activity of *Otophorus haemorrhoidalis*, *Planolinellus vittatus*, and *Planolinus tenellus* from 2016 and 2017. Locations: hatched bars (Purple Springs Grazing Reserve); black bars (Cypress Hills Interprovincial Park).

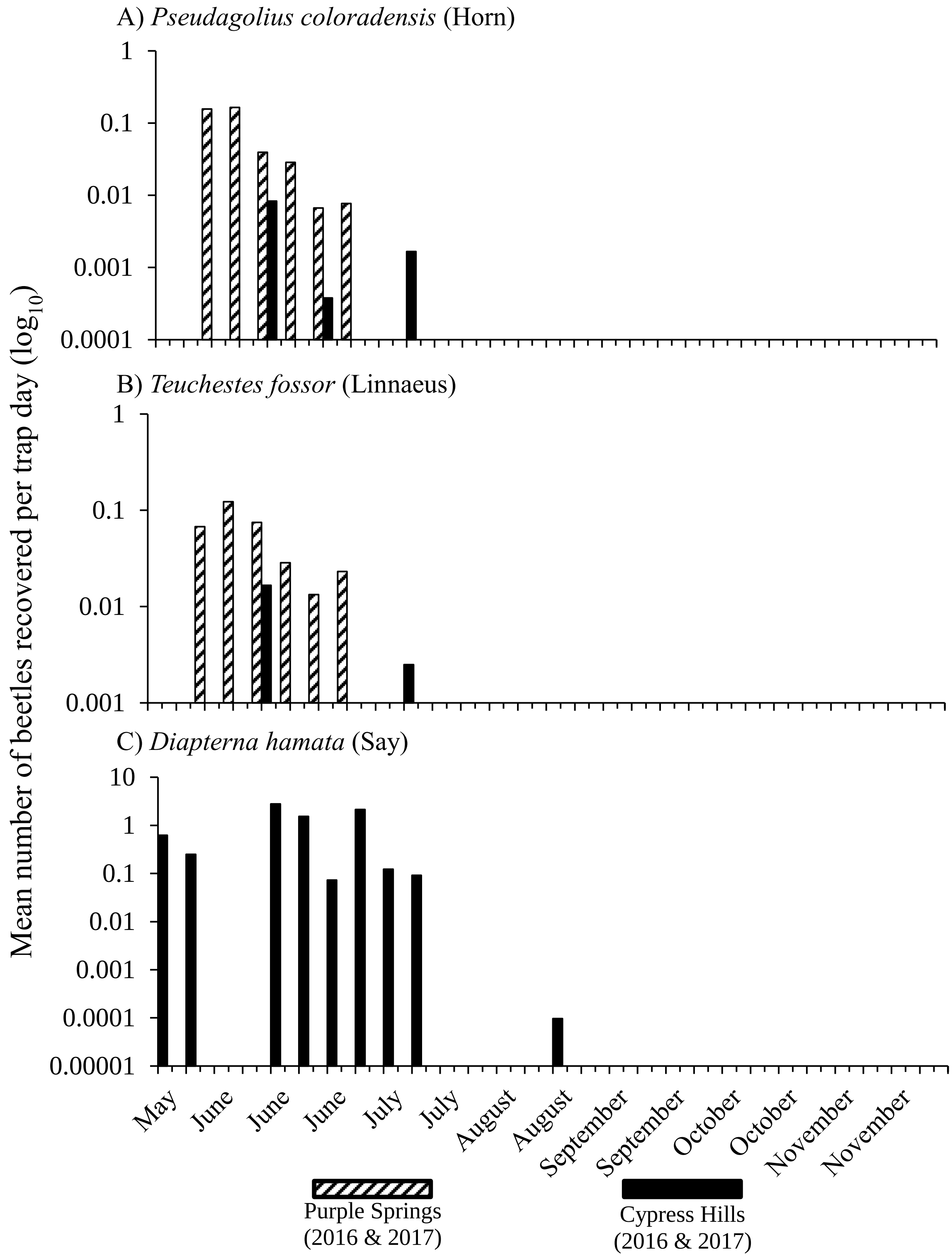

Figure 3.14. Seasonal activity of *Pseudagolius coloradensis, Teuchestes fossor,* and *Diapterna hamata* from 2016 and 2017. Locations: hatched bars (Purple Springs Grazing Reserve); black bars (Cypress Hills Interprovincial Park).

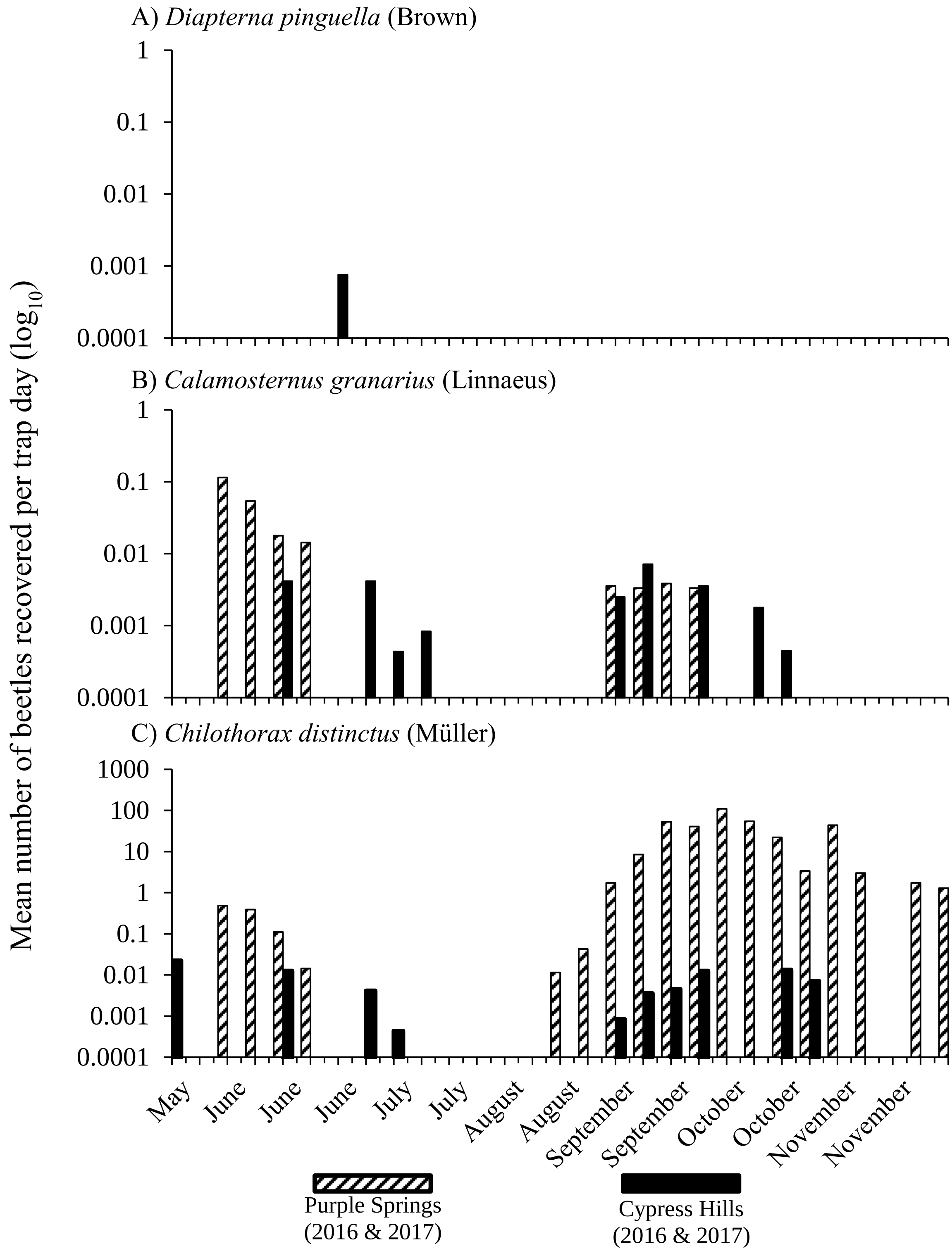

Figure 3.15. Seasonal activity of *Diapterna pinguella*, *Calamosternus granarius*, and *Chilothorax distinctus* from 2016 and 2017. Locations: hatched bars (Purple Springs Grazing Reserve); black bars (Cypress Hills Interprovincial Park).

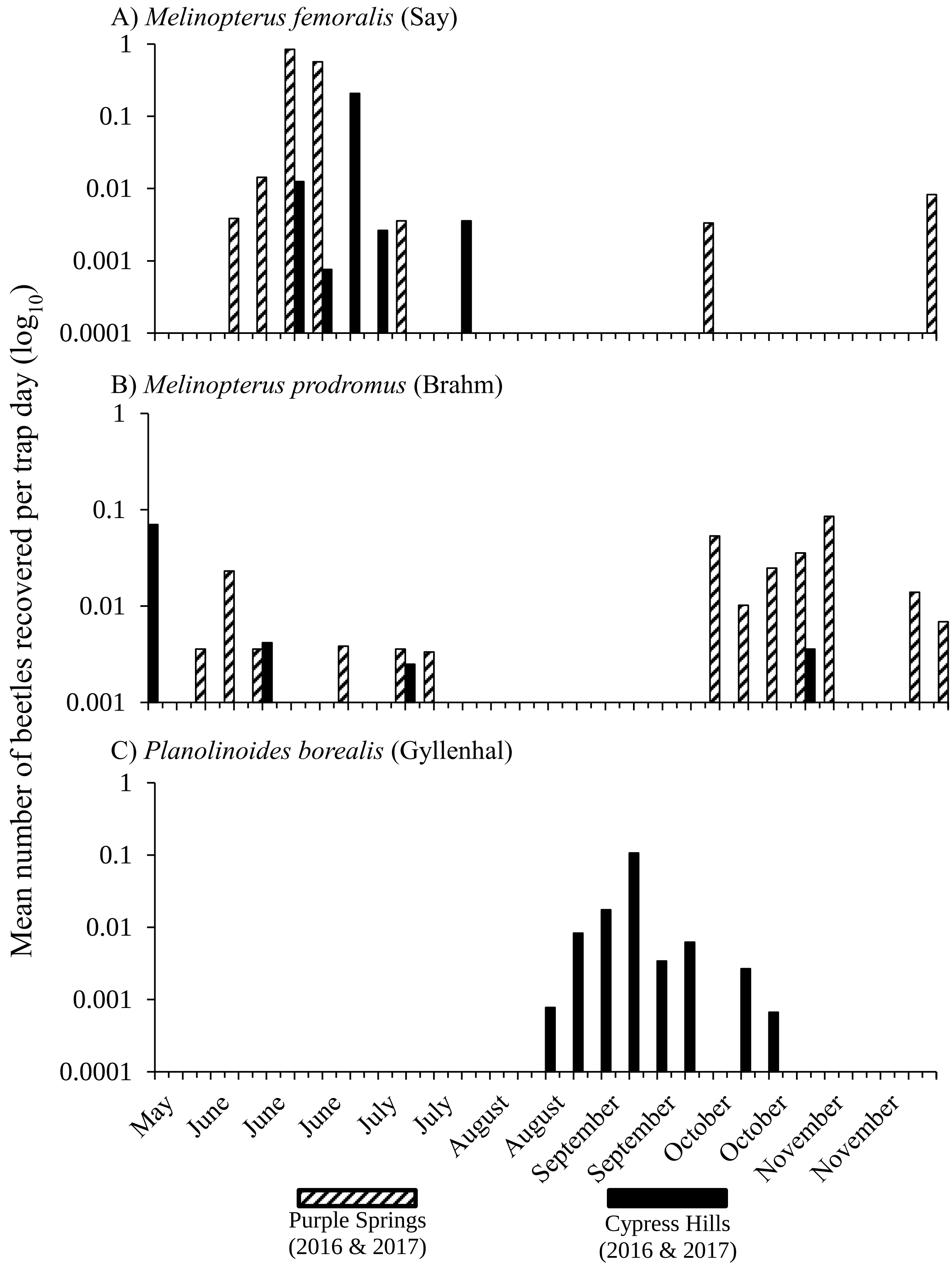

Figure 3.16. Seasonal activity of *Melinopterus femoralis*, *Melinopterus prodromus*, and *Planolinoides borealis* from 2016 and 2017. Locations: hatched bars (Purple Springs Grazing Reserve); black bars (Cypress Hills Interprovincial Park).

Figure 3.17. Cattle dung wrapped in 3-ply cheese cloth with small holes created by adult *Chilothorax distinctus* (Müller).

Table 3.1. The species caught at each sampling location in Cypress Hills Interprovincial Park during 2016 and 2017.

Species	Location						
	CH Grass 2016	CH Forest 2016	CH Grass 2017	CH Forest 2017	2 Year Total	% Grass	% Forest
Agoliinus leopardus (Horn)	3	140	27	889	1059	0.8	80.7
Planolinus tenellus (Say)	29	138	0	0	167	0.8	10.8
Planolinoides borealis (Gyllenhal)	0	0	52	31	83	1.4	2.4
Aphodius pedellus (De Geer)	317	16	337	14	684	17.8	2.4
Diapterna hamata (Say)	948	1	1472	25	2446	66.0	2.0
Calamosternus granarius (Linnaeus)	0	1	9	7	17	0.2	0.6
Planolinellus vittatus (Say)	4	3	7	1	15	0.3	0.3
Pseudagolius coloradensis (Horn)	0	0	1	4	5	0.0	0.3
Melinopterus prodromus (Brahm)	29	1	2	1	33	0.8	0.2
Chilothorax distinctus (Müller)	35	1	60	0	96	2.6	0.1
Melinopterus femoralis (Say)	0	0	61	1	62	1.7	0.1
Teuchestes fossor (Linnaeus)	2	1	4	0	7	0.2	0.1
Onthophagus nuchicornis (Linnaeus)	111	0	51	0	162	4.4	0.0
Colobopterus erraticus (Linnaeus)	32	0	62	0	94	2.6	0.0
Otophorus haemorrhoidalis (Linnaeus)	0	0	12	0	12	0.3	0.0
Diapterna pinguella (Brown)	2	0	0	0	2	0.1	0.0
Total Abundance	**1512**	**302**	**2157**	**973**	**4944**		
Species Richness	**11**	**9**	**14**	**9**			

Estimated Species Richness				
Chao-1	**11**	**19**	**14**	**12**
Species Diversity				
Shannon index (H)	**1.18**	**1.01**	**1.18**	**0.43**
Simpson's index (1-D)	**0.55**	**0.57**	**0.51**	**0.16**

Table 3.2. The species caught at each sampling location in Purple Springs Grazing Reserve during 2016 and 2017.

Species	Location					
	PS1 2016	PS2 2016	PS1 2017	PS2 2017	2 Year Total	% Abundance
Chilothorax distinctus (Müller)	8222	7794	55120	25089	96225	89.6
Onthophagus nuchicornis (Linnaeus)	1447	1707	2485	2787	8426	7.8
Canthon praticola LeConte	585	120	368	39	1112	1.0
Aphodius pedellus (De Geer)	20	27	173	203	423	0.4
Melinopterus femoralis (Say)	0	0	311	110	421	0.4
Colobopterus erraticus (Linnaeus)	70	48	61	47	226	0.2
Canthon pilularius (Linnaeus)	4	37	6	91	138	0.1
Pseudagolius coloradensis (Horn)	28	35	33	14	110	0.1
Teuchestes fossor (Linnaeus)	7	39	33	11	90	0.1
Melinopterus prodromus (Brahm)	5	2	61	14	82	0.1
Planolinellus vittatus (Say)	10	4	43	6	63	0.1
Calamosternus granarius (Linnaeus)	8	8	15	28	59	0.1
Otophorus haemorrhoidalis (Linnaeus)	7	9	20	12	48	0.0
Total Abundance	**10413**	**9830**	**58729**	**28451**	**107423**	
Species Richness	**12**	**12**	**13**	**13**		

Estimated Species Richness				
Chao-1	**12**	**12**	**13**	**13**
Species Diversity				
Shannon index (H)	**0.71**	**0.66**	**0.30**	**0.46**
Simpson's index (1-D)	**0.35**	**0.34**	**0.12**	**0.21**

Table 3.3. The Jaccard index values comparing the species similarity of dung beetles recovered in pitfall traps in different habitats and different locations in 2016 and 2017. Comparisons are based on the total number of individuals recovered at each of six sites (*n* = 5 pitfall traps/site).

Comparison	Similarity Value
Habitat (grassland vs. forest)	
2016 – Site 1 (CG1 vs. CF1)	54%
2016 – Site 2 (CG2 vs. CF2)	22%
2017 – Site 1 (CG1 vs. CF1)	61%
2017 – Site 2 (CG2 vs. CF2)	33%
Location (PSGR vs. CHIP - grassland)	
2016 – PS (PS1 & PS2) vs. CG (CG1 & CG2)	44%
2017 – PS (PS1 & PS2) vs. CG (CG1 & CG2)	69%

CHAPTER 4: THE ATTRACTIVENESS OF FRESH AND FROZEN CATTLE DUNG ON THE COPROPHAGOUS INSECT COMMUNITY

4.1 Abstract

Dung-baited pitfall traps are one of the most commonly used methods to collect coprophagous insects. Trap catch may be affected by the age of the bait and (or) whether the bait is fresh or frozen at the time it is placed to bait the trap. To date, there are no concrete recommendations in regard to rebaiting time or whether fresh or frozen dung is more attractive. To help address the lack of comparisons and recommendations, this study assessed (i) which bait type (fresh or frozen) is more attractive, and (ii) how long each bait type remains attractive. Paired pitfall traps were used (n = 10) with bait types alternating within each pair. Four experiments were done between June and August of 2017 and 2018, two per year. The combined data from all four experiments showed that frozen dung attracted on average 22% more insects than fresh dung. In terms of daily catch, frozen dung attracted significantly more insects than fresh dung for the first three days. However, after this period, the average insect catch was the same for both treatments. Overall, frozen dung attracts more insects than fresh dung over a three-day period.

4.2 Introduction

Dung-baited pitfall traps are commonly used to collect coprophagous insects (33, 113, 179, 215). The equipment required for this method is inexpensive and easy to obtain, the traps are quick to set up and empty, and yield large numbers of insects of diverse coprophagous taxa. In North Carolina, Bertone et al. (14) recovered 30 species of dung beetles and Price et al. (174) recovered 19 species of dung beetles in Maryland. However, the number and diversity of the taxa recovered in the traps partially reflects the age and type of the baits.

Studies have used rebaiting times of one (14, 66), two (134, 187), three (13), five (113) or seven days (39, 55, 59, 76), but those testing the optimal rebaiting time are rare. A lack of consistent rebaiting time is an issue that has also been raised by Hector et al. (95). They compared trap catch from pitfall traps rebaited and emptied every one, two or seven days (95). They found that not removing the caught insects had a negative effect and caused pig dung to be less attractive (95). Howden & Nealis (113) compared rebaiting every day to every fifth day. They found that most attractiveness was lost after the second day, with a reduction of both species and individuals seen over the five day period (113). Aruchunnan et al. (10) compared rebaiting times of one, two or five days. They found that the number of species and individuals also decreased over time (10). However, they mentioned that some species prefer fresh dung (i.e., *Copris agnus* and *Onthophagus aphodiodes*) while others prefer older desiccated dung (i.e., *Onthophagus peninsularis* and *Onthophagus sumaveiensis*) (10). Therefore, rebaiting time can depend on the species or time of interest.

Similar to rebaiting time, various studies either freeze dung baits (69, 71, 146), or make baits from fresh dung (174, 187). Freezing baits allows for hundreds to be made at once and used at a later date, while fresh baits would begin attracting insects instantaneously. Some studies incorporate both methods by freezing the dung then thawing it prior to making baits (14, 167). Unlike rebaiting time, very little investigation has been done to determine the effect of freezing on the attractiveness of the dung.

Pimsler (170) compared the attractiveness of fresh and frozen cattle dung over a period of one day and found frozen baits to be more attractive.

To help address the lack of comparisons and recommendations, this study assessed: (i) which bait type (fresh or frozen) is more attractive and (ii) the length of time each bait type is attractive for. It was predicted that both bait types would become less attractive with time as they being to desiccate. However, frozen baits may be attractive for longer as they first need to thaw before they can dry out. Identifying the optimal combination of bait type and rebaiting time will maximize captures of coprophilous species.

4.3 Methods

4.3.1 Study Sites

This experiment was replicated four times, twice in 2017 and twice in 2018. Experiments one, two, and three, were conducted at the Lethbridge Research and Development Station (Agriculture and Agri-Food Canada) in Lethbridge, Alberta, Canada (Lat. 49.695°; Long. -112.7675°) (Fig. 4.1). The site was adjacent to tame pasture with cattle and traps were set outside the pasture one metre from the fence line. Experiment four was completed at Purple Springs Grazing Reserve, Alberta, Canada (Lat. 49.827°; Long. -111.895°) (Fig. 4.1). This area is roughly 2,700 hectares (4) and is characterized as gently rolling hills with dry mixed grassed and sandy soil (4, 122). There are also cattle that roam yearly from May to October (4, 122).

The location change in 2018 was because of a lack of dung beetles with the previous sampling efforts. There were higher abundances of non-dung insects such as ants, springtails and grasshoppers with the other three trials. Purple Springs Grazing Reserve (PSGR) has been sampled for dung beetles in the past, with great success and large abundances of various species (122). The traps were set up inside of an exclosure at PSGR to prevent cattle disruption. As well, the exclosure allows for the fence line element to remain constant between both sites and years.

In 2017, collections were made from June 14th to June 29th (Experiment One) and again from August 26th to September 10th (Experiment Two). In 2018, collections were made from June 5th to June 21st (Experiment Three) and again from July 31st to August 15th (Experiment Four). Two different time periods were chosen to try to capture the entirety of the dung insect community because different species are active at different times of the year in Alberta (75, 122).

4.3.2 Dung Insect Collection

In the current study, dung-baited pitfall traps were constructed from two nested buckets (2 L capacity). They were buried flush with the soil surface to catch both epigeal and flying insects. Dung beetles are attracted to dung from the emitted volatiles and can walk or fly to and from the food source. Ensuring that the pitfall trap is flush with the soil prevents the exclusions of epigeal arthropods. The top bucket of the pitfall trap contained roughly 5-7 cm of a 1:1 water and propylene glycol (non-toxic antifreeze) killing solution. In 2018 after the last experiment, the traps did not contain non-toxic antifreeze as they were used to collect live dung beetles, which were dissected (see Appendix 1). The bait was suspended from wire mesh covering the pail, which is secured into the ground (Fig. 4.2). This ensured that no larger animals such as ground squirrels and mice were accidentally caught and prevented larger animals from drinking the liquid. Once collected, insects remained in 70% ethanol at 7 °C until identified.

Baits were made from roughly 250 mL of cattle dung wrapped in 3-ply cheese cloth and secured with a twist tie. To prevent confusion, all frozen baits were secured with a green twist tie and fresh baits with a white twist tie (Fig. 4.2). Across both years, the dung was collected from cattle at the Lethbridge Research and Development Station that were fed a diet of barley silage. To maintain consistency, dung was collected from the same pen of animals for the duration of the experiment. Frozen baits were made a few days ahead of time and stored in a freezer at -15 °C until used.

Traps were set up in pairs, with one fresh bait and one frozen bait separated by roughly one metre (Fig. 4.2) and each subsequent pair was separated by roughly seven metres. A white stake was placed in between the pair to allow for easy discovery. The experiment was conducted in a staggered fashion. Each day baits for a single pair were put out and collections were made for the pairs that were previously baited (Fig. 4.3). Seven days of collections were made for the ten pairs ($n = 70$). Collections and set up were done each day between 8:00 a.m. and 10:00 a.m.. In 2017, all frozen baits were placed closer to the fence line. However, in 2018, the bait treatments alternated between frozen and fresh along the fence line to help eliminate any bias.

The paired nature of the traps minimizes confounding effects associated with the trap position. Floate (71) was able to show that pitfall traps set up in a line often recover different amounts of insects. This remained true when two different treatment types were used and alternated (71). Although the two different treatment types alternated within each pair to help reduce bias, this may not have made a difference. Floate (71) showed that *Onthophagus nuchicornis* (Linnaeus) was continually recovered in higher abundances from one treatment type no matter the position.

In addition to different trap positions, two different sites were used to capture the effects on the coprophagous insect community. This method tests the rigour of the findings between the two locations and is a common practice of other studies (75, 122). Trapping throughout different years and seasons also improves the rigour of a study and is able to better encompass the entirety of the coprophagous insect community. Several dung beetle species have different active seasons which have been thoroughly documented in Alberta (75, 122) and North Carolina (14). Although many active seasons overlap, trapping too early or late may result in the exclusion of several species. Finally, staggering the baiting of the traps over time takes into account catch variation due to daily weather, which could otherwise confound the interpretation of the results. Only the first and last day of the experiment has a single pair of traps in the field, while every other day will have baits of different ages.

4.3.3 Insect Processing

Incidental insects were removed from the total prior to analysis because they are not members of the dung insect community and do not require fresh dung for breeding or nutritional resources. However, they are found on or near the dung pat because they have walked onto it by chance (74, 156). The incidental insects that were removed included; spiders (Araneae), harvestmen (Opiliones), ants (Formicidae), springtails (Collembola), mites (Acari), leaf hoppers (Cicadellidae), moths (Lepidoptera), thrips (Thysanoptera), aphids (Aphidoidea), grasshoppers (Orthoptera), ticks (Ixodoidea), and crane flies (Tipulidae). These species were excluded from the totals in experiments one and two and composed 73% and 56% of the relative abundance for experiments three and four respectively. Removing these insects allowed for direct comparisons between experiments. In both years, all insects were identified to at least Order, with dung beetles being identified to species (Table 1). In 2018, however, a greater number of morphological taxa were identified. This difference reflected a greater familiarity with the insect taxa by staff sorting samples in 2018 than in 2017.

The insects were then divided by Order (Coleoptera, Diptera and Hymenoptera) and behaviour (i.e., coprophagous (Chironomidae, Sarcophagidae, Calliphoridae, Scathophagidae, Sepsidae, Scarabaeidae and Hydrophilidae), predators (Staphylinidae and Histeridae), fungus feeders (Ptiliidae), parasitoids (Tachinidae, Ichneumonidae and Proctotrupidae) and incidentals (Elateridae and Dermaptera)). This was done to assess the effect of bait type and age on the different members of the dung insect community.

Although Hydrophilidae are considered to be coprophagous and predators (74, 133), species belonging to the *Sphaeridium* genus develop in dung (133). The species recovered from the traps was *Sphaeridium lunatum* Fabricius, which was included with the coprophagous insects instead of the predators because it is known to eat dung (105). It should be noted that there were some insects included in the Order analysis that did not belong into the behavioural categories such as wasps, bees, and syrphid flies as they are pollinators that were most likely attracted to the yellow bucket, not the dung bait.

4.3.4 Climatic Conditions

Weather data was collected for all four experiments from Agriculture and Agri-Food Canada weather station data (1). Weather data for Purple Springs Grazing reserve (experiment four) was collected from the weather station in Vauxhall, Alberta, which is consistent with other published literature (122).

4.3.5 Statistical Analysis

Comparisons of the two treatments were completed through non-parametric α diversity (within sample) tests such as Chao-1 index, Shannon index and Simpson's index. The Chao-1 index is a metric for species richness (40) and corresponds to the results from rarefaction analysis, which is also a metric for species richness. Rarefaction analysis, also known as species accumulation curves, plots the number of individuals versus the number of taxa. This can be used to pinpoint the ideal sampling effort to obtain the maximum species richness. As the curve plateaus, this indicates that an additional sampling effort will most likely result in the recovery of few or zero additional taxa. Both Shannon and Simpson's index are metrics for species diversity. Shannon index considers evenness and richness of the individuals (195). Values typically range from 1.5-3.5 (144) with smaller values indicating few taxa are present. Simpson's index (1-Dominance) captures the variance of species abundance and distribution (174) and ranges from 0 (one taxon dominates) to 1 (equal presence of all taxa).

Raw counts were used for the statistical analysis and were pooled by day and treatment for One-Way ANOVA analysis, which was used to test for differences in the average number of insects caught from frozen or fresh baits (α = 0.05). A Paired-T test was used to test the difference between bait treatments for each day (α = 0.05). This test was used because of the paired nature of the trap set up.

Statistical tests were preformed using R (version 3.4.3) in RStudio. Species richness, diversity indices and rarefaction analysis were calculated using PAST (version 2.17c).

4.4 Results

4.4.1 Weather Data

The average temperature across the 17-day sampling period was 16.9 °C, 20.7 °C, 16.1 °C and 20.4 °C for experiments one, two, three, and four, respectively. Average values for each day can be seen in Figure 4.4. A One-Way ANOVA ($F_{3,64} = 13.22$, $P = 8.16 \times 10^{-7}$) with a Tukey Kramer post-hoc test revealed no significant difference in average temperatures between experiments one and three (P = 0.815) and between experiments two and four (P = 0.989).

4.4.2 Experiment One

A total of 1,610 insects were caught in pitfall traps baited with either frozen (913 insects) or fresh (697 insects) baits, which represented 27 and 23 different morphospecies, respectively (Table 1). The estimated species richness according to the Chao-1 index was 24 and 30, respectively. This indicates that additional sampling would be expected to recover more taxa. However, the rarefaction analysis for the combined sampling effort reveals that adequate sampling was conducted because the curve has plateaued (Fig. 4.5). Shannon index values were 2.35 and 2.43 for frozen and fresh baits, respectively. Because the values are close together this indicates that the evenness and richness of the two communities are similar and permits an easier comparison. Simpson index values of 0.85 and 0.86 for frozen and fresh baits, respectively, are both closer to 1 than 0, which indicates that there is an equal presence of most taxa, instead of a few dominant species.

On average, more insects were caught using frozen baits (13.0 ± 1.7 SE) than with fresh baits (10.0 ± 1.7 SE) across all seven days (*n* = 70), but this difference was not significant (One-Way ANOVA, $F_{1,138} = 1.635$, $P = 0.203$). Day one was the only day that was marginally insignificant in the average amount of insects collected from frozen baits compared to fresh baits (Paired T-test, t = 2.1955, df = 9, P = 0.056). There was no significant difference for days two (t = 0.487, df = 9, P = 0.638), three (t = 1.10, df = 9, P = 0.300), four (t = -0.675, df = 9, P = 0.517), five (t = 0.620, df = 9, P = 0.550), six (t = 1.55, df = 9, P = 0.155), and seven (t = 1.66, df = 9, P = 0.131) (Fig. 4.6a).

Insects were then grouped by Order (Coleoptera = 45.3%, Diptera = 44.5%, Hymenoptera = 9.6%) and by behaviour (coprophagous = 30.9%, predators = 18.1%, parasitoids = 5.2%, incidentals = 0.7%). One-Way ANOVAs were performed for each Order and behaviour. There was no significant differences seen between the Orders; Coleoptera ($F_{1,1818} = 2.57$, $P = 0.109$), Diptera ($F_{1,838} = 1.27$, $P = 0.26$), and Hymenoptera ($F_{1,838} = 0.662$, $P = 0.416$). There was also no significant differences seen between the coprophagous ($F_{1,1538} = 0.459$, $P = 0.498$), parasitoids ($F_{1,278} = 1.501$, $P = 0.222$), and incidentals ($F_{1,278} = 0.227$, $P = 0.634$). The only behavioural group that had a significant different between the fresh and frozen dung baits were the predators ($F_{1,418} = 6.95$, $P = 0.008$).

4.4.3 Experiment Two

A total of 3,432 insects were caught in pitfall traps baited with either frozen (2,132 insects) or fresh (1,300 insects) baits, which represented 18 and 26 different morphospecies, respectively (Table 1). The estimated species richness according to the Chao-1 index was 18 and 26, respectively. This indicates that additional sampling would not recover more taxa. This conclusion is support by the rarefaction analysis, because the combined sampling effort reveals that adequate sampling was conducted because the curve has begun to plateau (Fig. 4.5). Shannon index values were 1.88 and 1.84 for frozen and fresh baits, respectively. Because the values are close together this indicates that the evenness and richness of the two communities are similar and permits an easier comparison. Simpson index values 0.77 and 0.74 for frozen and fresh baits, respectively, are both closer to 1 than 0 which indicates that there is an equal presence of most taxa, instead of a few dominant species.

On average, more insects were caught using frozen baits (30.5 ± 3.7 SE) than with fresh baits (18.6 ± 2.1 SE) across all seven days (n = 70), which was a significant difference (One-Way ANOVA, $F_{1,138}$ = 7.815, P = 0.006). Paired T-tests for days one (t = 3.22, df = 9, P = 0.011), two (t = 5.41, df = 9, P = 0.0004), three (t = 3.85, df = 9, P = 0.004), and four (t = 2.47, df = 9, P = 0.035) showed a significant difference in the average amount of insects collected from frozen baits compared to fresh baits. There was no significant difference for days five (t = 0.050, df = 9, P = 0.961), six (t = 1.24, df = 9, P = 0.2447), and seven (t = -0.756, df = 9, P = 0.469) (Fig. 4.6b).

Insects were then grouped by Order (Coleoptera = 72.7%, Diptera = 21.5%, Hymenoptera = 5.3%) and by behaviour (coprophagous = 15.7%, predators = 57.1%, parasitoids = 4.0%, incidentals = 0.6%). One-way ANOVAs were performed for each Order and behaviour. There was a significant for Coleoptera ($F_{1,1818}$ = 10.89, P = 0.0009), but not for Diptera ($F_{1,838}$ = 3.023, P = 0.0825) or Hymenoptera ($F_{1,978}$ = 0.067, P = 0.796). For the behavioural groups, there was a significant difference for coprophagous ($F_{1,1538}$ = 4.941, P = 0.0264) and predators ($F_{1,418}$ = 8.55, P = 0.004) but there was no significant difference for parasitoids ($F_{1,278}$ = 0.126, P = 0.723) and incidentals ($F_{1,278}$ = 1.48, P = 0.225).

4.4.4 Experiment Three

A total of 1,228 insects were caught in pitfall traps baited with either frozen (721 insects) or fresh (507 insects) baits, which represented 29 and 31 different morphospecies, respectively (Table 1). The estimated species richness according to the Chao-1 index was 30 and 36 respectively. This indicates that additional sampling using frozen baits could recover more taxa than use of fresh baits. However, the rarefaction analysis for the combined sampling effort reveals that adequate sampling was conducted because the curve has begun to plateau (Fig. 4.5). Shannon index values were 2.25 and 2.34 for frozen and fresh baits, respectively. Because the values are close together this indicates that the evenness and richness of the two communities are similar and permits an easier comparison. Simpson index values were 0.81 and 0.83 for frozen and fresh baits, respectively, are both closer to 1 than 0, which indicates that there is an equal presence of most taxa, instead of a few dominant species.

On average, more insects were caught using frozen baits (10.3 ±1.6 SE) than with fresh baits (7.2 ± 1.1 SE) across all seven days (*n* = 70), but this difference was not significant (One-Way ANOVA, $F_{1,138}$ = 2.44, P = 0.12). Day two was the only day that was marginally insignificant in the average amount of insects collected from frozen baits compared to fresh baits (Paired T-test, t = 2.23, df = 9, P = 0.052). Paired T-test for days one (t = 0.707, df = 9, P = 0.497), three (t = 1.36, df = 9, P = 0.205), four (t = -0.420, df = 9, P = 0.685), five (t = 0.525, df = 9, P = 0.612), six (t = 1.835, df = 9, P = 0.100), and seven (t = 1.34, df = 9, P = 0.213) revealed no significant difference (Fig. 4.6c).

The insects were then grouped by Order (Coleoptera = 47.5%, Diptera = 38.7%, Hymenoptera = 13.8%) and behaviour (coprophagous = 10.7%, predators = 36.6%, fungus feeders = 3.3%, parasitoids 7.6%, incidentals = 0.5%). One-way ANOVAs were performed for all Orders and behaviours. There was no significant difference for any Order; Coleoptera ($F_{1,1958}$ = 1.51, P = 0.219), Diptera ($F_{1,1398}$ = 2.27, P = 0.132) or Hymenoptera ($F_{1,1118}$ = 0.642, P = 0.423). There was also no significant difference for any of the behavioural groups; coprophagous ($F_{1,1538}$ = 2.11, P = 0.147), predators ($F_{1.418}$ = 0.653, P = 0.42), parasitoids ($F_{1,418}$ = 0, P = 1), and incidentals ($F_{1,278}$ = 0.505, P = 0.478).

4.4.5 Experiment Four

A total of 1,846 insects were caught in pitfall traps baited with either frozen (797 insects) or fresh (1,049 insects) baits, which represented 23 and 25 different morphospecies, respectively (Table 1). The estimated species richness according to the Chao-1 index was 28 and 27 respectively. This indicates that additional sampling could recover more taxa. However, the rarefaction analysis for the combined sampling effort reveals that adequate sampling was conducted because the curve has plateaued (Fig. 4.5). Shannon index values were 1.76 and 1.72 for frozen and fresh baits, respectively. Because the values are close together this indicates that the evenness and richness of the two communities are similar and permits an easier comparison. Simpson index values 0.71 and 0.71 for frozen and fresh baits, respectively, are both closer to 1 than 0, which indicates that there is an equal presence of most taxa, instead of a few dominant species.

On average, more insects were caught using fresh baits (15.0 ± 2.1 SE) than frozen (11.4 ± 3.4 SE) across all seven days (*n* = 70), but this difference was not significant (One-Way ANOVA, $F_{1,148}$ = 1.356, P = 0.246). There was no significant difference between the average amount of insect caught in frozen traps compared to fresh for days one (t = -0.842, df = 9, P = 0.422), two (t = 0.963, df = 9, P = 0.361), three (t = -0.650, df = 9, P = 0.532), four (t = -2.11, df = 9, P = 0.64), five (t = -1.30, df = 9, P = 0.225), six (t = -2.16, df = 9, P = 0.060), and seven (t = -1.94, df = 9, P = 0.084) (Fig. 4.6d).

Insects were then grouped by Order (Coleoptera = 44.0%, Diptera = 50.2%, Hymenoptera 5.8%) and by behaviour (coprophagous = 4.06%, predators = 9.2%, fungus feeders = 28.7%, parasitoids = 2.1%, incidentals = 0.05%). One-Way ANOVAs were performed on each Order and behaviour. The only Order than showed a significant difference was Hymenoptera ($F_{1,978}$ = 7.03, P = 0.008). The other two Orders, Coleoptera ($F_{1,1958}$ = 0.003, P = 0.954), and Diptera ($F_{1,978}$ = 3.41, P = 0.065) were not significant. There was also no significant differences seen between the predators ($F_{1,558}$ = 0.005, P = 0.945), parasitoids ($F_{1,418}$ = 1.99, P = 0.159), and incidentals ($F_{1,138}$ = 1.00, P = 0.319). The only behavioural group that had a significant different between the fresh and frozen dung baits were the coprophagous ($F_{1,698}$ = 3.921, P = 0.048).

4.4.6 All Experiments Combined

Combined across the four experiments, more insects were recovered with the use of frozen (16.3 ± 1.47 SE) versus fresh (12.7 ± 0.9 SE) baits (One-Way ANOVA, $F_{1,558}$ = 4.307, P = 0.0384). Days one (t = 2.73, df = 9, P = 0.009), two (t = 2.42, df = 9, P = 0.021), and three (t = 2.89, df = 9, P = 0.006) showed a significant difference in the average amount of insects collected from frozen baits compared to fresh baits (Fig. 4.7). There was no significant difference for days four (t = -0.510, df = 9, P = 0.613), five (t = -0.700, df = 9, P = 0.488), six (t = -0.032, df = 9, P = 0.974), and seven (t = -0.040, df = 9, P = 0.968).

The combined data for the coprophagous insects (flies and beetles), indicated a large drop-off in abundance after day two (Fig. 4.8). Day one had more beetles and flies from the frozen baits compared to the fresh baits. Day two had a larger abundance of beetles, specifically from the fresh baits (Fig. 4.8). After the second day, the average relative abundances for beetles and flies were very similar no matter the bait treatment.

4.5 Discussion

This study was able to determine that frozen baits are more attractive than their fresh counterpart. However, a significant difference was only seen from the combined data for days one, two, and three, after which the average number of insects caught was almost identical. These findings correspond to those from Howden & Nealis (113) who also saw a decrease in attractiveness after the second day of sampling. In South Dakota, Pecenka & Lundgren (167) found a decrease in both arthropod community complexity and abundance after the dung pat was more than a week old. Pimsler (170) found frozen baits to be more attractive than fresh, however their results are only based upon a trapping period of 24-hours. Overall, the peak colonization period of coprophagous insects, namely beetles and flies, occurs within one week of dung deposition (73).

The pattern of succession of coprophagous insects to dung pats usually follows a predictable pattern. Flies are early colonizers (73), with some species being present within minutes of deposition (74, 156). Oviposition usually occurs within one to two days after deposition (98) with some species taking upwards of 28 days to complete their full development (156). Fly colonization begins to decline within a few hours of deposition as a crust forms on the dung pat (74). Beetles are the next to arrive at dung pats and usually begin oviposition three days after deposition (98). Further colonization of coprophagous insects two to three weeks after deposition is scarce (74). Based on the data collected from this experiment, most coprophagous insects of interest were collected within the first two days (Fig. 4.8). This corresponds to peak activity periods of several species.

Colonization of parasitic wasps and predacious beetles such as Histeridae, Hydrophilidae and Staphylinidae, corresponds to the arrival of flies and beetles (74). The majority of wasps parasitize flies (74) while Histeridae (31, 162) and Hydrophilidae (156) predate on fly larvae and Staphylinidae predate on adult (133, 236) and larval (133) dung beetles as well as flies (162). Mites are also associated with dung pats as they usually have a phoretic relationship with flies and beetles (74). Their abundance in the pat increases from ten days to several weeks after deposition (74).

The colonization of some species is dependant on the season as some are early colonizers (e.g., *Scathophaga stercoraria* (Linnaeus) (18) and *Melinopterus prodromus* (Say) (75)) and some are more abundant later in the season (e.g., *Chilothorax distinctus* (Müller) (75)). However, the three species mentioned exhibit a bimodal seasonal activity, which means they would be more abundant in early spring and late fall compared to the summer months (18, 75). In addition to season; rainfall, wind, sunshine and humidity have all been shown to affect species of *Sepsis* and *Leptocera* (156). Moisture of a dung pat and the speed that it dries also affects fly succession (156).

Dung beetles are attracted to the volatile compounds that are emitted from dung (235) with each type of mammal dung containing unique volatiles (49). Cattle dung specifically contains at least 35 different volatile compounds with α–pinene and *p*-cresol being the most dominant (49). Research regarding the abundance of these compounds over time, and how they are affected by freezing could not be found. It is thought that presence of the volatile compounds would begin to decline over time as the pat dries out and forms a 'skin' or thin crust. This would correspond to a decrease in coprophagous insects beyond a one-week period.

During experiment four, there were large numbers of *Eumerus* sp. (Diptera: Syrphidae) from both the frozen (n = 315) and fresh (n = 493) baited traps. Most Syrphidae are considered pollinators. However, *Eumerus strigatus* (Fallen) is known to be attracted to rotting oatmeal presumably for oviposition (47). An examination of *Eumerus* mouthparts revealed the presence of accessory teeth and pharyngeal ridges, which permit these species to feed on the fluids of decaying matter, which would most likely include fungi and bacteria (180). This finding suggests that *Eumerus* are most likely saprophagous (180). However, a similar number of individuals were recovered each day, independent of bait treatment. High numbers of *Eumerus* sp. may have been recovered in this study because they were attracted to the yellow colour of the bucket, to the dung to feed and oviposit, or both.

Although some insects use colour as a visual cue (48, 166), there is no record of dung beetles exhibiting this behaviour. However, colour preference has been reported in the tribe Hopliini (Coleoptera: Scarabaeidae) (169). This preference is presumably due to their role as pollinators. If dung beetles do exhibit a colour preference, any effects should have been eliminated because each trap was constructed from the same colour pails (i.e., yellow).

Our results support the use of frozen dung over fresh when used as baits for pitfall trapping. During the first three days after the baits were set out, frozen baits attracted significantly more insects than fresh baits. Additional benefits include ease of transport to study sites where fresh cattle dung may not be readily available and making hundreds of baits at once that can be used later. Making large batches of baits can also save time by having them made in advance. In addition, baits made on the same day from the same animal would be very similar as factors such as diet and weather would be negligible.

Figure 4.1. Map showing the sampling points, in yellow dots, at Lethbridge Research and Development Station and Purple Springs Grazing Reserve as well as their relative distance from each other (~ 64.0 Km).

Figure 4.2. Pitfall trap set up at Lethbridge Research and Development Station to test the attractiveness of frozen baits (green twist tie on left) and fresh baits (white twist tie on right) on the dung insect community.

Pair	Treatment	Day																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	Fresh		1	2	3	4	5	6	7									
1	Frozen		1	2	3	4	5	6	7									
2	Fresh			1	2	3	4	5	6	7								
2	Frozen			1	2	3	4	5	6	7								
3	Fresh				1	2	3	4	5	6	7							
3	Frozen				1	2	3	4	5	6	7							
4	Fresh					1	2	3	4	5	6	7						
4	Frozen					1	2	3	4	5	6	7						
5	Fresh						1	2	3	4	5	6	7					
5	Frozen						1	2	3	4	5	6	7					
6	Fresh							1	2	3	4	5	6	7				
6	Frozen							1	2	3	4	5	6	7				
7	Fresh								1	2	3	4	5	6	7			
7	Frozen								1	2	3	4	5	6	7			
8	Fresh									1	2	3	4	5	6	7		
8	Frozen									1	2	3	4	5	6	7		
9	Fresh										1	2	3	4	5	6	7	
9	Frozen										1	2	3	4	5	6	7	
10	Fresh											1	2	3	4	5	6	7
10	Frozen											1	2	3	4	5	6	7

Traps Baited

Collection Day

Figure 4.3. A schematic illustrating the experimental setup. Green boxes identify when the traps were baited and yellow boxes identify the seven subsequent days that traps were emptied.

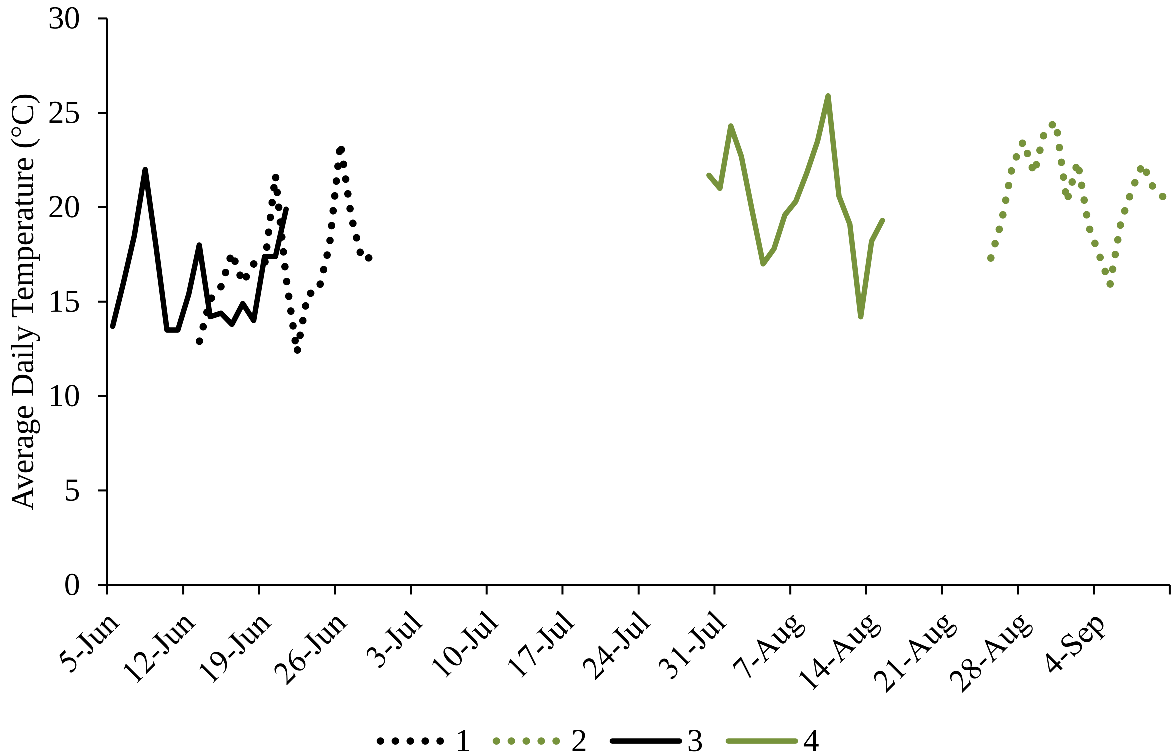

Figure 4.4. The daily mean temperatures for each of the four experiments (2017 = dotted lines; solid lines = 2018). Experiment 1 = black dots; Experiment 2 = green dots; Experiment 3; black line; Experiment 4; green line.

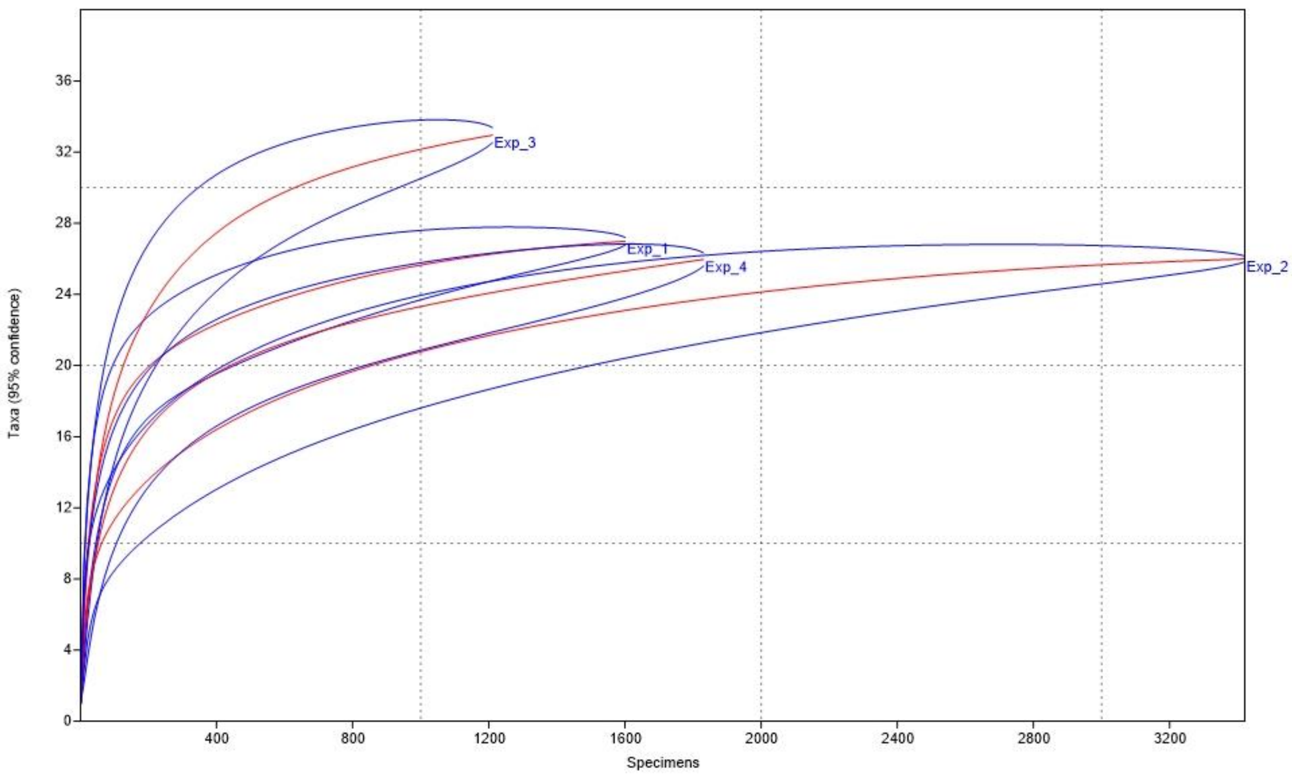

Figure 4.5. Rarefaction curves for each experiment (red lines) with the corresponding 95% confidence interval (blue lines).

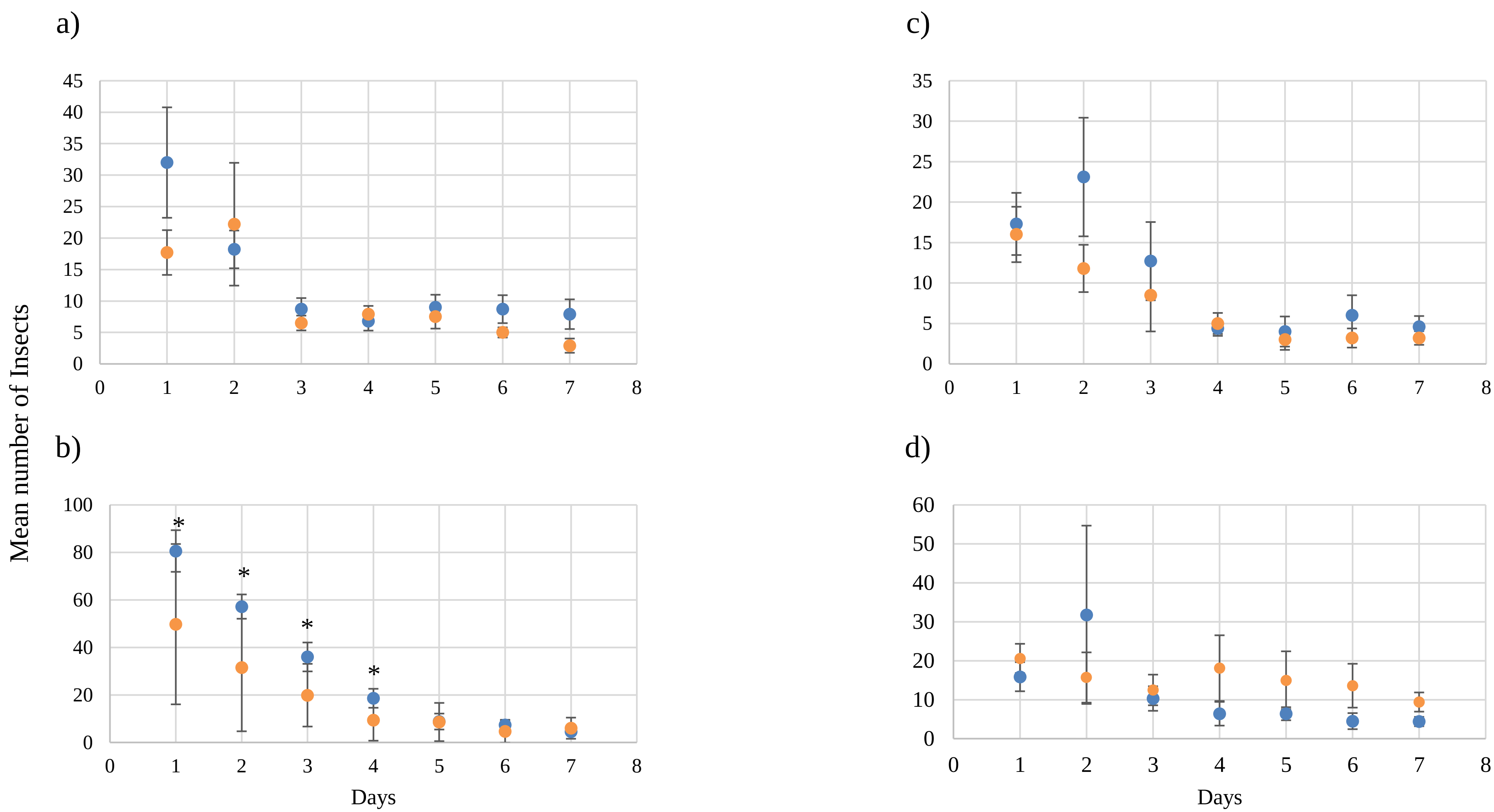

Figure 4.6. Values are means (± SE) of the insects caught in 10 traps for each combination of bait type (fresh = orange dots; frozen = blue dots) and bait age (day) for a) Experiment 1, b) Experiment 2, c) Experiment 3 and d) Experiment 4. Asterisks indicate the days that are significantly different.

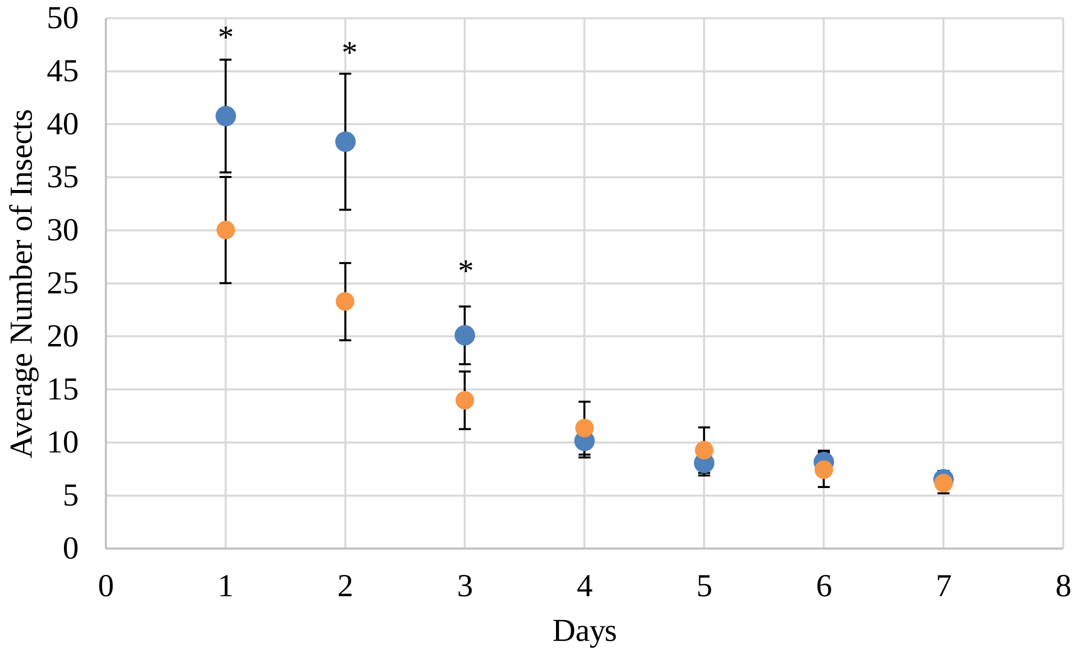

Figure 4.7. Values are means (±SE) of the insects caught across all four experiments (*n* = 40) of fresh (orange dots) and frozen baits (blue dots) Asterisks indicate the days that are significantly different.

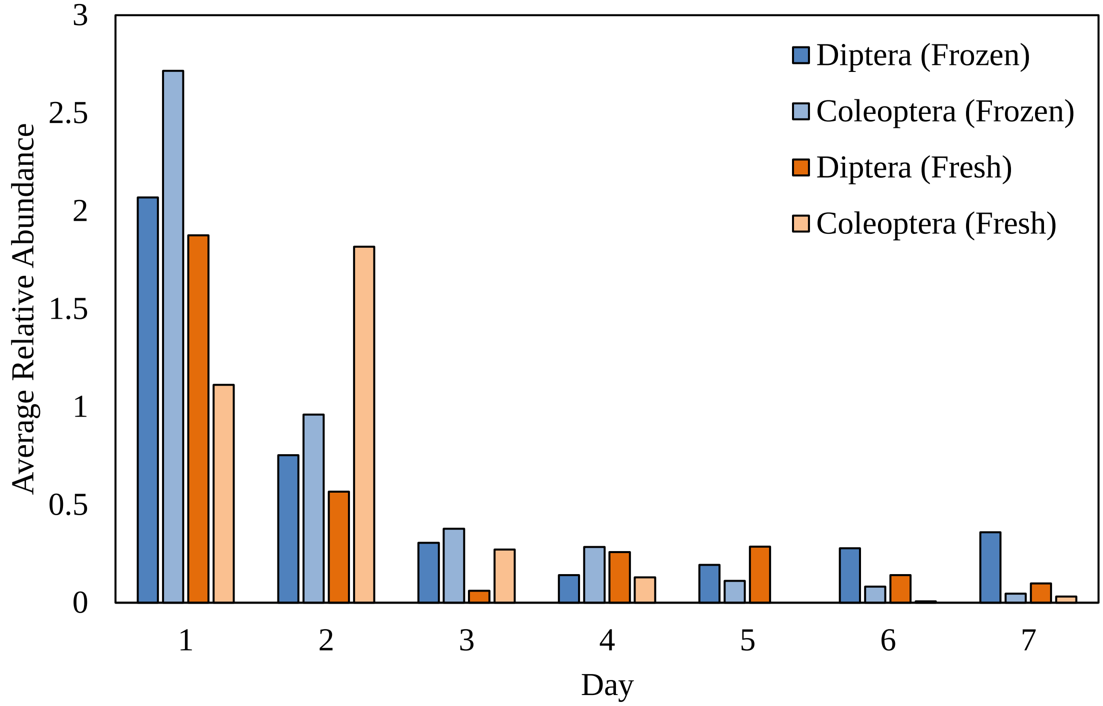

Figure 4.8. A bar graph depicting the average relative abundance of coprophagous Dipterans and Coleopterans from all four experiments for fresh (orange bars) and frozen baits (blue bars) (*n* = 40).

Table 4.1. Species caught from each experiment with diversity and richness values located at the bottom.

Species		Experiment One		Experiment Two		Experiment Three		Experiment Four	
		Frozen	Fresh	Frozen	Fresh	Frozen	Fresh	Frozen	Fresh
Chilopoda		1	—	—	—	—	—	—	—
Dermaptera	(I)	4	6	12	6	1	—	—	—
Coleoptera									
Curculionoidea		13	8	9	5	16	8	9	3
Elateridae	(I)	1	1	2	2	3	2	1	—
Histeridae	(Pr)	—	—	—	—	—	—	2	—
Hydrophilidae									
Sphaeridium lunatum	(C)	32	7	2	—	3	2	—	—
Nitidulidae		5	2	1	1	1	—	2	1
Ptiliidae	(F)	—	—	—	—	32	8	281	249
Scarabaeidae									
Aphodius pedellus	(C)	2	—	4	—	2	—	—	—
Chilothorax distinctus	(C)	—	—	187	117	1	3	—	—
Colobopterus erraticus	(C)	106	90	2	—	9	5	1	—
Calamosternus granarius	(C)	20	12	1	—	3	4	—	—
Canthon praticola	(C)	—	—	—	—	—	—	5	12
Diapterna pinguis	(C)	—	—	—	—	—	1	—	—
Melinopterus prodromus	(C)	3	—	—	—	—	—	—	—
Otophorus haemorrhoidalis	(C)	—	—	4	—	—	—	—	—
Onthophagus nuchicornis	(C)	2	1	—	—	—	—	7	24
Planolinellus vittatus	(C)	1	1	—	—	—	—	—	—
Silphidae									
Nicrophorus sp.		—	—	—	—	—	—	—	1
Staphylinidae									

Small (< 2.9 mm)	(Pr)	68	51	58	23	23	14	56	59
Med (3.0 - 5.9 mm)	(Pr)	84	38	974	554	236	172	25	20
Large (> 6.0 mm)	(Pr)	30	20	229	124	5	–	1	7
Tenebrionidae		–	–	–	–	–	–	12	19
Unknown		78	53	118	77	19	11	11	5
Diptera									
Calliphoridae									
Lucilia sp.	(C)	–	–	–	–	4	8	8	5
Chironomidae	(C)	13	3	1	2	18	8	–	–
Nematocera		–	–	–	–	37	38	6	9
Sarcophagidae	(C)	75	76	88	70	34	18	2	6
Scathophagidae	(C)	7	17	6	2	4	2	–	–
Sepsidae	(C)	22	8	26	26	1	1	2	3
Syrphidae									
Eristalis sp.		–	–	–	–	–	1	–	–
Eumerus sp.		–	–	–	–	13	7	315	493
Tachinidae	(Pa)	–	–	–	–	2	2	–	1
Unknown		275	220	315	203	161	116	22	54
Hymenoptera									
Adrenidae		–	–	–	–	9	3	3	2
Apoidea		–	–	2	–	–	–	–	–
Chalcidoidea		–	–	2	6	–	–	–	–
Chysididae		–	–	–	–	4	5	1	–
Cynipoidea		21	23	18	4	18	13	9	49
Ichneumonoidea	(Pa)	11	12	1	–	1	2	–	1
Proctotrupoidea	(Pa)	24	36	65	72	44	43	12	25
Sphecidae		–	–	–	–	1	1	3	1
Symphyta		1	–	–	–	4	2	1	–

Vespoidea	1	2	2	–	12	7	–	–
Unknown wingless	13	10	3	6	–	–	–	–
Total Abundance	**913**	**697**	**2132**	**1300**	**721**	**507**	**797**	**1049**
Species Richness	**27**	**23**	**26**	**18**	**31**	**29**	**25**	**23**
Estimated Species Richness								
Chao-1	30.33	24	26.86	18	36	29.86	27	28
Species Diversity								
Shannon (H)	2.43	2.35	1.84	1.88	2.34	2.25	1.72	1.76
Simpson (1-D)	0.86	0.85	0.74	0.77	0.83	0.81	0.71	0.71

C = Coprophagous; Pr = Predator; Pa = Parasitoid; I = Incidental, F = Fungivore

CHAPTER 5: USING WEIGHT TO ESTIMATE THE NUMBER OF *Chilothorax distinctus* (MÜLLER) CAPTURED IN DUNG BAITED PITFALL TRAPS

5.1 Abstract

Counting the number of individuals per insect species recovered from pitfall traps can be time-consuming, especially when one sample can contain thousands of individuals. This paper aims to provide cheaper and faster alternative methods than hand-counting. Three methods (wet weight, oven-dried weight, and air-dried weight) were used to estimate the number of *Chilothorax distinctus* (Müller) recovered from pitfall trap samples. A total of 31 different sample sizes ranging from 100 – 5,000 beetles were used to generate linear regression equations. The wet weight was taken for all samples, nine samples were dried in an oven, and 22 were dried at room temperature. No change in oven-dried weight was observed after three days independent of sample size, whereas it took a maximum of 15 days to achieve stabilization at air temperature. The regression equations were then validated with nine unknown samples. It was determined that estimates of beetle numbers were most accurate when based on the weights of individuals that were oven-dried for three days. In comparison with the time (associated salary dollars) needed to count beetles individually, using a bulk weight to estimate numbers in the current study equated to a per samples savings ranging from $8 (150 beetles/sample) to $130 (5,000 beetles/sample).

5.2 Introduction

Chilothorax distinctus (Müller) (Coleoptera: Scarabaeidae) is a common species of coprophagous insect across southern Canada. Overwintering adults emerge in spring to oviposit in organic rich soils or rotting accumulations of organic material (122, 193). Larvae complete development in late June, pupate in July and emerge as adults in autumn.

At that time, they can be attracted to fresh cattle dung in enormous numbers to feed and presumably mate. This species exhibits a bimodal seasonality, with the second active period (September – November) having the greater abundance of individuals (122, 156, 193).

Dung-baited pitfall traps are a common method used to collect data on the presence and relative abundance of coprophagous insect in a local area. Traps typically are emptied and rebaited once or twice per week. During such surveys, it is common to catch thousands *C. distinctus* in one trap over a one-week period (pers. observ.). In 1934, Seamans stated that "… the beetles [*C. distinctus*] appear in countless thousands. The air to a height of ten or fifteen feet seems filled with flying beetles. Clouds of them hover over manure piles or over horse droppings …" (193). Since then, their presence has persisted, with a three-year survey of dung beetles in Alberta collecting greater than 36,000 individuals (122). In Indiana, USA, more than 4,000 individuals were recovered from 13 dung pats in 24-hours (42).

The recovery of large numbers of insects in pitfall catches can be problematic. Once samples are returned to the lab from the field, insects are typically sorted by species, with the number of individuals being hand-counted. Occasionally, all but a few individuals may be of one species. These latter individuals often can be quickly removed, resulting in a large but unknown number of one conspecific. A literature search revealed few papers that have suggested faster alternative approaches to hand-counting, with even fewer focusing on how to estimate the number of individuals in sample. Atkins (11) used volume, weight, and hand-counting to estimate the number of honey bees, *Apis mellifera* Linnaeus (Hymenoptera: Apidae) in a sample. While all three methods were equally accurate, the volumetric method was found to be the quickest, and most efficient. Stark & Vargas (203) is one of the few papers to suggest using insect weights to estimate the abundance in a sample. They reported that using insect weight was the fastest and most accurate method to estimate the number of oriental fruit flies (*Dacus dorsalis* Hendel) and melon flies (*Dacus cucurbitae* Coquillett) in a sample (203).

The goal of this study was to assess the use of weight as a quicker method to process samples of *C. distinctus* recovered from pitfall traps. Using samples with different numbers of individuals, I developed linear regressions for comparing beetle numbers to their wet, air-dried, and oven-dried weights. I then validated use of these regressions to estimate beetle numbers by first using the equation to estimate the number of beetles in a sample, then hand-counting the number of individuals to achieve the exact number. Wet weight is the easiest to obtain but may offer the least accurate estimate as ethanol evaporation can cause rapid weight decrease. Oven-dried weight might be the most accurate, but this method assumes that everyone has access to an oven, which may not be possible when working in the field. For these reasons, all three methods were used and compared to determine which offers the best estimate.

5.3 Methods

5.3.1 Obtaining Samples of Chilothorax distinctus (Müller)

To recover *C. distinctus* for use in the present study, dung baited pitfall traps were placed at Purple Springs Grazing Reserve in Alberta, Canada (Lat. 49.827°; Long. -111.895°) (Fig. 5.1.). The grazing reserve is roughly 2,700 hectares of native rangeland grassland with sandy soil and cattle that graze yearly from May to October (4). Pitfall traps were constructed from two nested pails (2 L capacity) buried to the rim, with the dung bait suspended from wire mesh as outlined in other studies (80, 113, 122). Baits comprised 250 mL of fresh bovine dung wrapped in 3-ply cheese cloth and were frozen (-15° C) for at least 24-hours prior to use. The dung was collected from cattle fed a diet of barley silage and was homogenized before use to ensure an even consistency. Traps were emptied and rebaited weekly from May to October 2017. Insects recovered from traps were stored in 70% ethanol at 7° C until processed. Catch sizes of *C. distinctus* ranged from 0 to 5,000 per trap per week, depending upon the time in the summer (see Chapter 3).

5.3.2 Weight Treatments

Three types of weights were obtained for different samples of *C. distinctus*, each containing approximatively 100 up to roughly 5,000 individuals. Beetle numbers were determined using a Leica MZ8 dissecting microscope and a hand-counter. Beetle weight to the nearest 0.0001g was obtained using an electronic balance (A&D ER-182A). Wet weights were first obtained for a set of 40 samples for which *C. distinctus* numbers had not been manipulated. Wet weight is defined here as the weight of beetles removed from ethanol and placed on paper towel for one to three minutes and then weighed. Wet weights were also obtained for a set of 22 samples that were then held at room temperature (~21° C) and weighed daily (from six to 23 days) until no further decrease in weight was observed (air-dried weight). Wet weights also were obtained for a set of nine samples that were then held in an oven (~57° C) and weighed daily (from three to five days), until no further decrease in weight was observed (oven-dried weight). For these latter two sets of samples, beetle numbers were manipulated to span the range of beetles that might normally be recovered from a trap and for which bulk weights might be faster than individual counts by hand.

For the different sets of samples, beetle numbers and their corresponding weights were used to develop linear regression models to predict the number of beetles in a sample based on sample wet weight, air-dried weight or oven-dried weight. After the weights were collected, linear modeling was used to determine the equation of the line for both air-dried and oven-dried samples. The y-intercept was set to be zero for biological relevance; i.e., zero beetles should weigh zero grams. To test the accuracy of these models, they were used to estimate the number of beetles in a subset of samples for which the number of beetles was subsequently counted by hand.

To illustrate the potential savings in time and money achieved by using bulk weights to estimate the number of *C. distinctus*, the times taken to sort the samples were also recorded.

5.3.3 Statistical Analysis

To test the accuracy of the estimates using the generated linear equations, a One-Way ANOVA was done to test the differences between the true number of beetles and the predicted values for both the air and oven treatments. This was done using R (version 3.4.3) in RStudio.

5.4 Results

A total of 87,180 dung beetles were collected over the six-month period, with *C. distinctus* being the most abundant (92.0%).

Comparisons of weights obtained over sequential days showed different patterns of weight loss varying with sample size and method of drying. When dried in the oven, samples lost an average of 79% of their wet weight after 24-hours with no further weight loss observed thereafter (Fig. 5.2). In contrast, air-dried samples lost only 43% of their wet weight after 24-hours and continued to lose weight for up to an additional two weeks depending upon the number of beetles in the sample (Fig. 5.3). For both treatments, drying time depended on the number of beetles present in the sample. Use of either wet, air-dried (~21° C for at least six days) or oven-dried (~57° C for at least three days) weight was highly predictive of the number of beetles in a given sample (Fig. 5.4a: n = 40 samples, y = 99.25x , R^2 = 0.9812; Fig. 5.4b: n = 22, y = 361.54x, R^2 = 0.9565; Fig. 5.4c: n = 9, y = 480.03x, R^2 = 0.9708).

For the air-dried treatments, there was no statistical differences between the true value and the predicted values (One-Way ANOVA, $F_{2,9}$ = 0.089, P = 0.918). There was also no statistical difference found for the oven-dried samples (One-Way ANOVA, $F_{2,12}$ = 0.005, P = 0.995).

5.5 Discussion

Two drying techniques, air and oven, were used as alternative methods when determining sample sizes. It was decided to carry out both methods as budget or sampling location can hinder availability to an oven. Although both methods are equally easy to execute, oven-drying appears to be the better method. The air-dried weight of samples containing 150 beetles stabilized after two days, whereas samples of roughly 3,100 and 5,100 beetles continued to lose small amounts of weight even after eight and fourteen days, respectively (Fig. 5.3). However, oven-drying was independent of sample size with no further weight loss after 24-hours for samples containing up to 3,100 beetles.

Based on the coefficient of determination (R^2) values, the wet weight was the highest (0.9812) with oven-dried being second (0.9708) and air-dried being the third (0.9565). The R^2 values for all equations are close to one indicating the trend lines are well fit to the data. Although wet weight offers the best R^2 value, it may not be the best method because the weight quickly decreases presumably due to ethanol evaporation.

When testing the accuracy of the regression equations, it was noticed that either wet or dry weight offered the better estimate depending on the sample size (Tables 5.1 and 5.2). Due to the presence of outliers (Fig. 5.4a), these samples were recounted to ensure that the regression equations were as accurate as possible. Out of the 31 recounted samples, ten samples had a different number of *C. distinctus*, which ranged from 4 to 280 individuals. Half of the ten samples had more beetles than what was originally counted. These discrepancies highlight that hand-counting, especially with such large numbers, is still prone to some error.

A possible explanation as to why the weight of some samples appear to be outliers could be due to a loss of biomass. Radtke et al. (176) showed that storing insects in ethanol for a year did not change their volume, but it is likely that it changed their biomass. In addition, different storage solutions may increase the wet and dry weights of insects even after only one month in storage (129). Some of the insects used in this study may have been in ethanol longer than others due to the large number of collections each week. It would have been ideal to process the samples and weigh them as they were collected.

For illustrative purposes, the time and hence cost associated with processing was estimated for twelve samples (Fig. 5.5). Minimum wage in Alberta for 2018 was $15.00 an hour. To sort out and count about 1,000 *C. distinctus* in a sample of mixed insect species takes about one hour or $15.00. To put this into perspective, 12 samples of approximatively 1,000 beetles would cost $180 to sort and count. However, more than 5,000 beetles may be collected in one trap during the course of a few days, with hundreds of thousands of *C. distinctus* recovered over the course of a two- or three-year study (122). By quickly scanning a sample to remove unwanted debris and insects instead of examining each individual, both time and money will be greatly reduced. The time taken to sort samples can be quite variable depending on how much debris and additional insects are present as well as the experience of the individual.

Although using linear regression provides a quicker alternative to hand-counting, there are a few variables that can skew the estimated number. First, *C. distinctus* ranges in length from 4.0-5.7 mm and in width from 1.8-2.8 mm (85) (Fig. 5.6). This variability indicates that some samples may contain larger individuals while some may contain smaller individuals. Secondly, sexual dimorphism has been reported in this species, with males having a larger pronotum than females (85). The larger pronotum could make males heavier than females thus causing male-biased samples to weigh more than others. Christensen & Dobson (42) reported a female: male sex ratio for *C. distinctus* of 3:2 (n =122) and 1:3 (n = 281) in spring and autumn, respectively. Thus, sex ratio changes throughout the season could affect the size and weight of the beetles recovered.

Additional weight can also come from debris and insects stuck to the beetles such as mites or small Staphylinidae. Finally, the condition of the individuals may also influence the weight. If the body is missing parts such as heads, legs, and elytra, this could provide an imprecise weight.

A similar study conducted by Stark & Vargas (203), mentioned that fly weight may vary depending on time of year, location and availability of resources. Although there is no evidence of these latter two factors affecting *C. distinctus*, it is a possibility that should be considered. The beetles used for this study were all collected at the same location within the same year, which would minimize any effects that environment may have on the weight. Although the presented data set encompasses a wide range of sample sizes, there is the possibility of obtaining a number outside this range. Extrapolation may result in an imprecise number of *C. distinctus*. A suggested alternative method, would be to break up the sample into smaller groups that fall within the range to allow for a more accurate estimation.

Even though this method only used one species, it could be argued that these equations could be applied to other Aphodiinae of similar size e.g., *Planolinoides borealis* (Gyllenhal) (length: 4.0-5.9 mm, width: 2.3-2.9 mm), *Otophorus haemorrhoidalis* (Linnaeus) (length: 4.1-5.4 mm, width: 2.1-2.6 mm) or *Oscarinus lodingi* (Cartwright) (length: 4.0-5.2 mm, width: 2.0-2.7 mm) (85). Separate regression equations for other commonly recovered species such as; *Onthophagus nuchicornis* (Linnaeus) (over 60,400 (75)), *O. taurus* (Schreber) (over 57,000 (14)) and *Labarrus pseudolividus* (Balthasar) (over 230,000 (59)) would greatly benefit the counting process. Ultimately, this study adds to the scarce literature dealing with estimating individuals based upon weight. It also highlights that the three methods used can be applied to any species in addition to Scarabaeidae, which will ultimately offer a faster alternative method to hand-counting.

Overall, using an oven to dry samples is faster than air-drying especially if there are larger sample sizes involved. However, the use of any of the three treatments (wet, air, or oven) offer similar R^2 values and are all faster than hand-counting. Assuming one is available, there may be a slight advantage using oven-dried weight to estimate the number of individuals, rather than hand-counting or air-drying.

Figure 5.1. A pitfall trap baited with cattle dung used to collect dung beetles at Purple Springs Grazing Reserve.

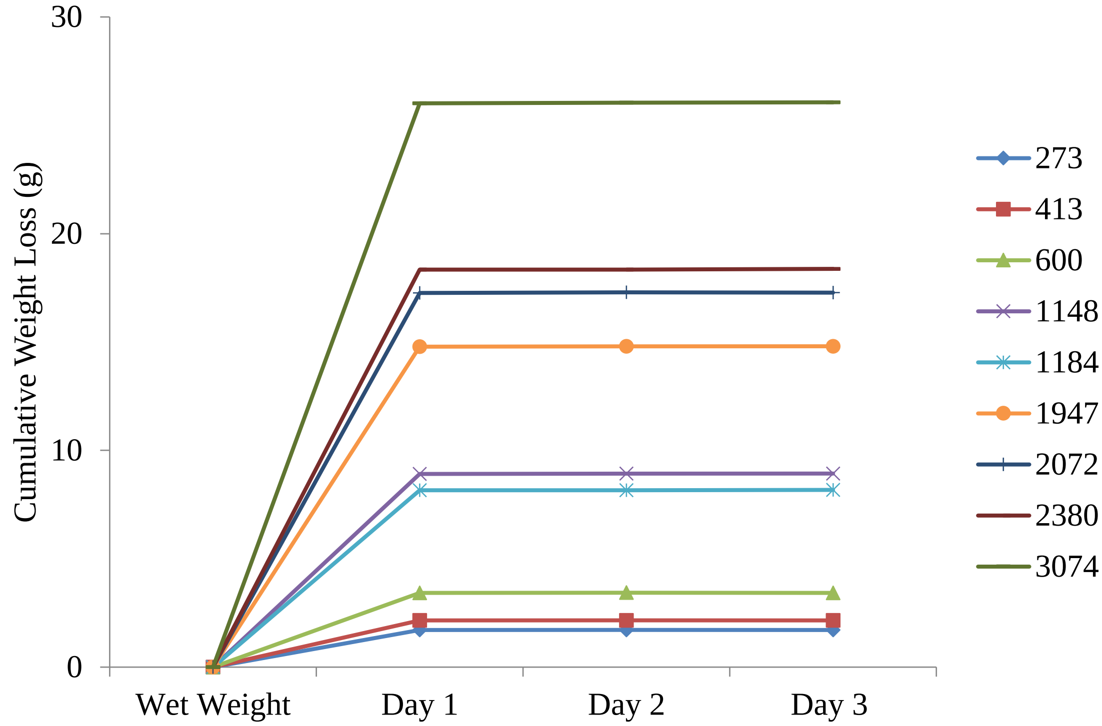

Figure 5.2. The cumulative weight loss after being dried in an oven (~57° C) for three days. The exact sample sizes used can be found in the legend.

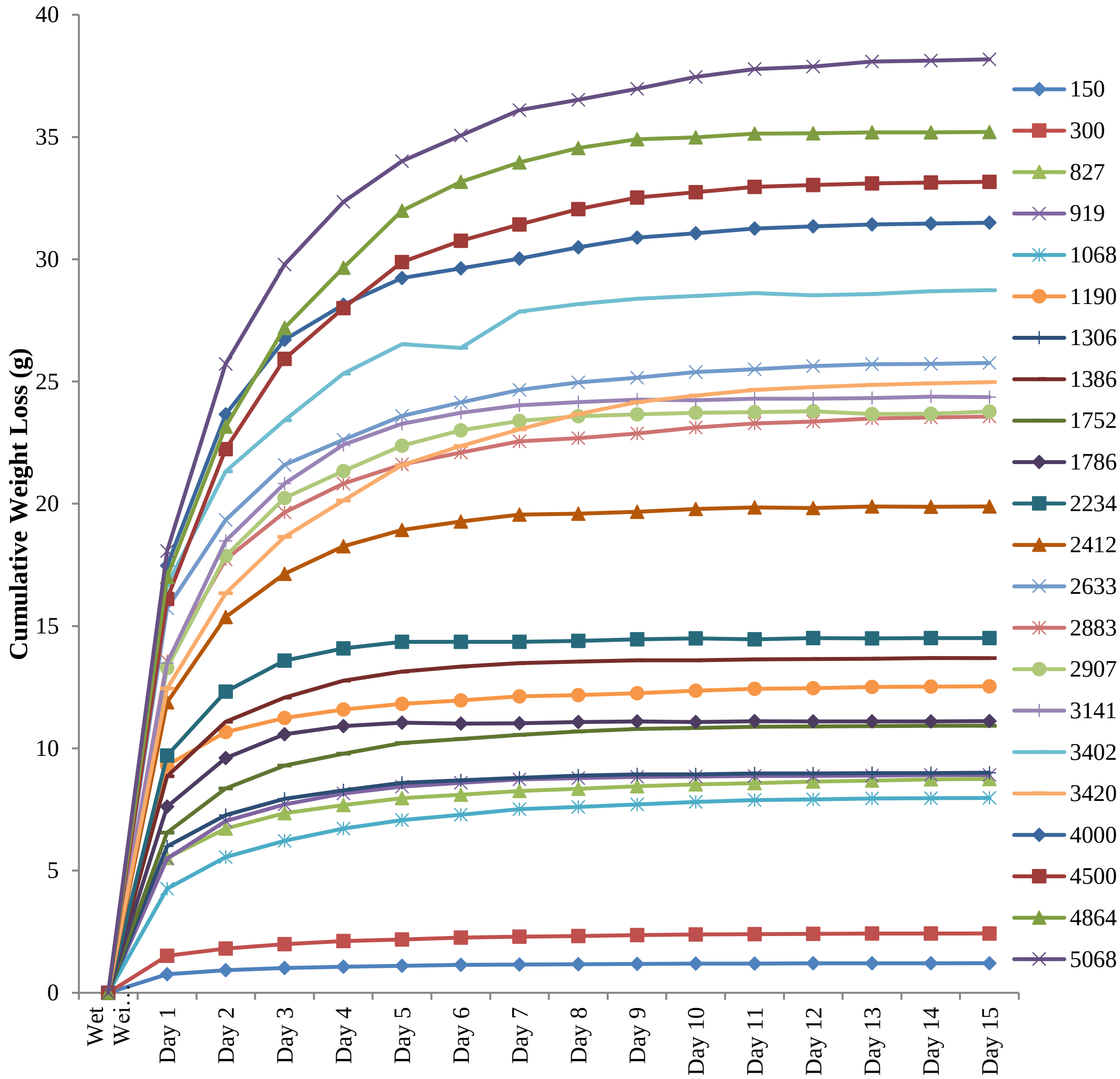

Figure 5.3. The cumulative weight loss after samples were dried at air temperature (~21° C) for fifteen days. The exact sample sizes used can be found in the legend.

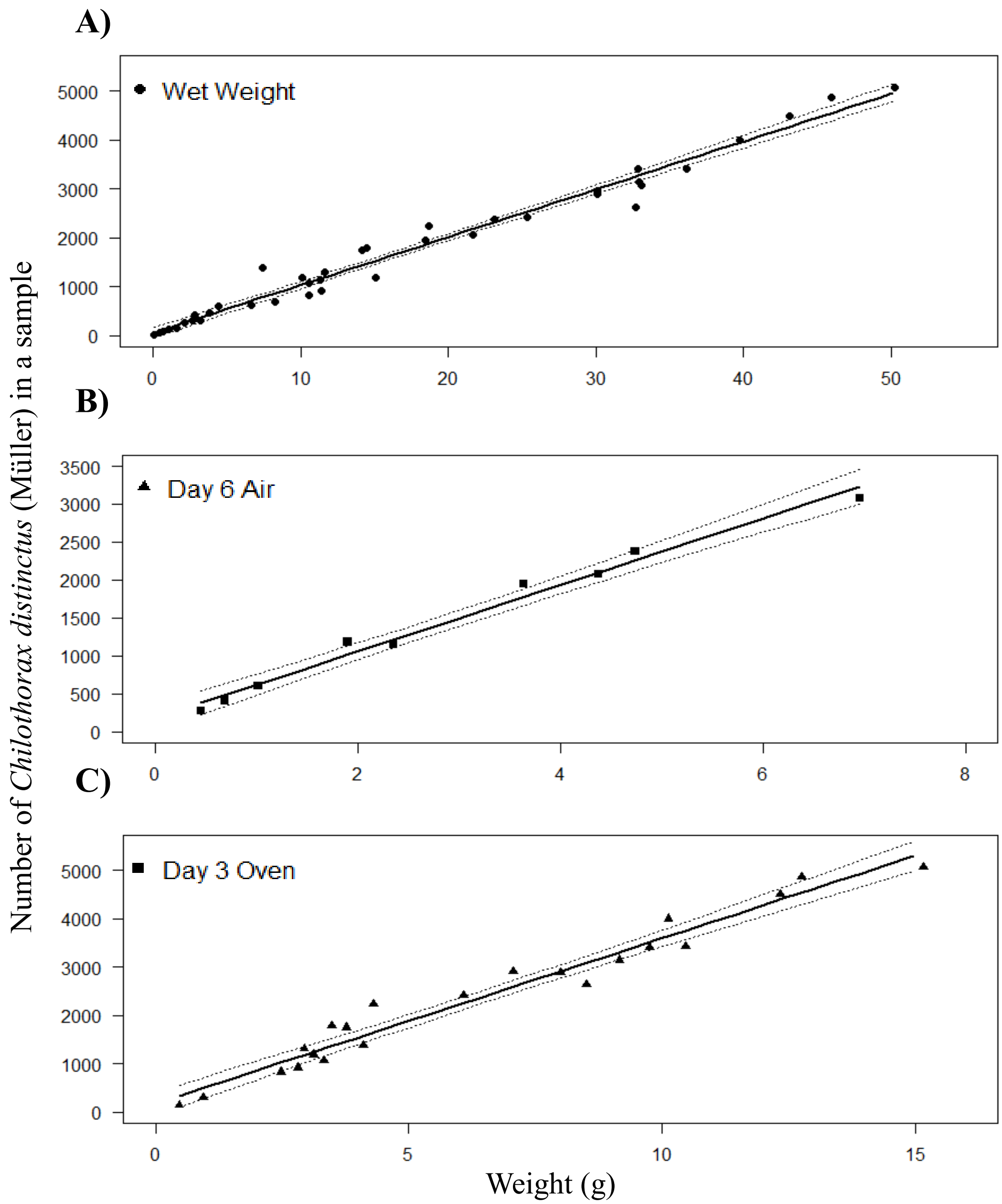

Figure 5.4. Scatter plots showing the weight and the corresponding number of *Chilothorax distinctus* (Müller) in a sample. The thick black line represents the linear regression while the dotted black lines are the 95% confidence intervals; **a)** wet weight, $y = 99.25x$, $R^2 = 0.9812$, **b)** dried at air temperature (~21° C) for 6 days, $y = 361.54x$, $R^2 = 0.9565$ **c)** dried at oven temperature (~57° C) for 3 days, $y = 480.03x$, $R^2 = 0.9708$

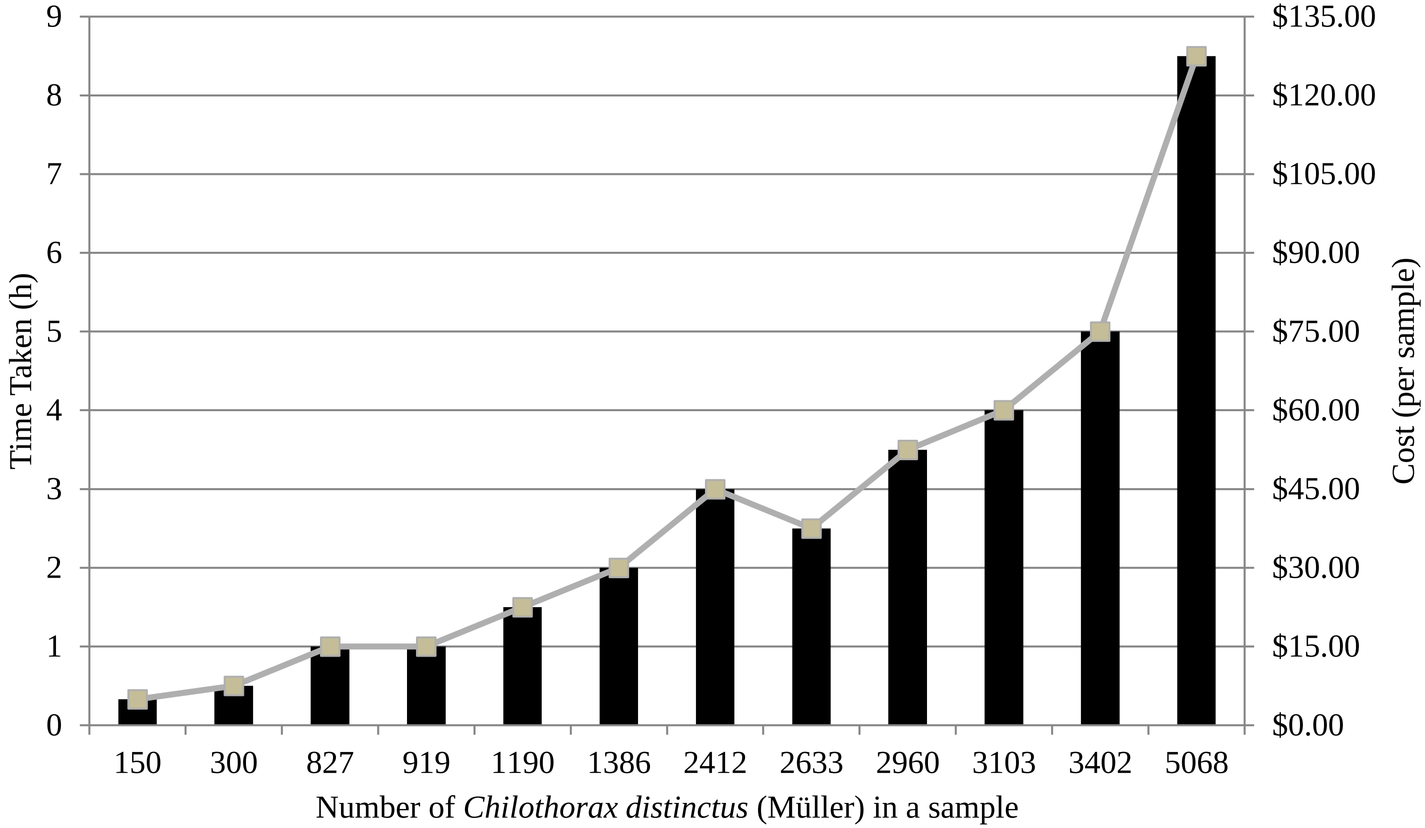

Figure 5.5. The time taken to count twelve samples of various sizes of *Chilothorax distinctus* (Müller) as well as the associated cost.

Figure 5.6. A dorsal view of *Chilothorax distinctus* (Müller). Photo taken by Henri Goulet.

Table 5.1. A comparison of the true number of *Chilothorax distinctus* (Müller) and the predicted number when air-dried. Values for wet weight are derived from the linear regression equations in Figure 3a. Values for dry weight are derived from the linear equation in Figure 5.3b.

True	Wet Weight (g)	Predicted	% Difference	Dry Weight (g)	Predicted	% Difference
200	2.0631	205	2.4	0.4675	169	16.8
589	6.2515	620	5.2	1.3328	482	20.0
1138	12.451	1236	8.2	2.9755	1076	5.6
1500	14.3685	1426	5.1	3.2806	1182	23.4

Table 5.2. A comparison between true number of *Chilothorax distinctus* (Müller) and the predicted number when dried in an oven. Values for wet weight are derived from the linear regression equation in Figure 3a. Values for dry weight are derived from the linear equation in Figure 5.3c.

True	Wet Weight (g)	Predicted	% Difference	Dry Weight (g)	Predicted	% Difference
216	1.748	173	21.8	0.3075	148	37.6
500	4.9277	489	2.2	1.0587	508	1.6
1600	15.2973	1518	5.2	3.3453	1606	0.4
2292	21.6235	2146	6.6	4.714	2263	1.3
2781	27.8345	2763	0.7	6.0185	2889	3.8

CHAPTER 6: GENERAL DISCUSSION AND CONCLUSION

7.1 Summary

Hundreds of different species of insects feed and breed in fresh cattle dung. Common taxa include species of beetles (Coleoptera), flies (Diptera), and wasps (Hymenoptera). Among these, dung beetles (Coleoptera: Scarabaeidae, Geotrupidae) typically dominate in terms of biomass and abundance. By virtue of their feeding and breeding activities, they accelerate the degradation of the dung pat to facilitate the cycling of nutrients in pasture ecosystems. Dung beetles have been the subject of thousands of studies with a search of Web of Science displaying over 2,900 results. The current thesis adds to this body of knowledge in a series of four chapters (Chapters 2-5) and one appendix.

Chapter 2 reviews information on the distribution of dung beetles (Geotrupidae and Scarabaeidae) and other coprophagous beetles (Histeridae, Hydrophilidae, Staphylinidae, and Troginae) in America north of Mexico. The most recent and complete data set regarding this information, was compiled by Blume in 1985 (22). Because this checklist is more than 30 years old, information in Blume is combined with data from a further 63 references published since 1985. The updated version includes current taxonomic classifications and different types of livestock dung. This list highlights that dung beetle diversity varies within countries and with different dung types. As well, it provides a resource to quickly determine the species of dung beetles in any given province or state.

Chapter 3 investigates dung beetle diversity in southern Alberta. This was achieved through two studies; study 1 compared the species recovered from two different habitats (forest and pasture) within the same vicinity, and study two compared the same habitat (pasture) at two locations (Cypress Hills Interprovincial Park and Purple Springs). Although there was a large overlap of similar species recovered at each location and habitat, there were different dominant species. *Chilothorax distinctus* (Müller) was the most abundant at Purple Springs (90%), *Diapterna hamata* (Say) in Cypress Hills pasture (66%) and *Agoliinus leopardus* (Horn) in Cypress Hills forest (81%). These results support that species abundance is dependant on habitat or characteristics such as soil (159) and vegetation (64, 106, 159, 177), even if these differences are in close vicinity.

Chapter 4 aimed to determine which bait type (fresh or frozen) is more attractive and the length of time each bait type is attractive for. This comparison was evaluated by using paired pitfall traps, each containing one bait type. The ideal combination of bait type and trapping length to obtain the most insects was determined to be using frozen baits over a period of three days, afterr which, there was no significant difference in the bait type used. This information adds to the scarce literature comparing rebating time and bait treatment and will be useful for designing future experiments as it offers a method to increase trapping efficiency.

In Chapter 5, three methods (wet weight, oven-dried weight and air-dried weight) were used to estimate the number of *C. distinctus* recovered from pitfall traps. Regression equations were created for each method and were tested using unknown samples. Although wet weight was the easiest to obtain, oven-drying offered the slightly more accurate estimate. It is important to consider various factors such as sexual dimorphism or small insects such as mites, stuck to the individuals that may affect the weight of the sample.

7.2 Practical Considerations and Future Directions

Developing an update of the distribution of the beetles associated with livestock dung is a good starting point; however, it would be more valuable to include all the members of the dung insect community; e.g., flies (Diptera), mites (Acarina) and parasitic wasps (Hymenoptera). Inclusion of this information would provide a more complete list of the insects you would expect to find associated with dung. In addition, periods of seasonal activity could be included for each species. Including distribution maps of each species would help to pinpoint the specific areas where these species were recovered and monitor range extensions over time.

In addition, information regarding niche or habitat preference would be useful to determine the species that would most likely be recovered. In the current thesis, sampling two habitats in the same vicinity indicated that some species may prefer or be better suited to live in either forested or open pasture. Future research sampling at the interface or ecotone of two habitats may offer additional information regarding species diversity. Studies determining the strength of habitat associations can provide insights to the persistence of a given dung beetle species if the habitat changes over time (forest encroachment) or space. The use of a transect from one habitat to another could determine at what distance specific species are the most abundant. This is important to consider when developing methods to reclaim the endangered native fescue grasslands.

Although pitfall traps are the preferred method used to recover coprophagous insects because of the inexpensive material and quick and easy set up, difficulty with the design may occur if there is limited access to fresh dung. Freezing dung baits has been shown to attract more coprophagous insects than fresh baits. However, this was only tested in Alberta, Canada where is the climate is hot and arid during summer months. Testing the attractiveness of the two bait treatments in more humid climate may indicate different results as the dung may take longer to desiccate. It would be beneficial to compare fresh and frozen dung throughout the entire active season of the dung insect community to determine if there is a difference earlier or later in the season. In addition, testing the effect of freezing on the volatiles associated with dung could reveal why frozen baits are more attractive. To date, no studies have reported on this relationship, or on the change of volatiles over time. This information would help to determine the ideal attractive period of dung.

The recovery of large numbers of individuals and taxa from pitfall traps are common and can often slow down the counting process. The development of regression equations to estimate the number of *C. distinctus* in a sample offers users an efficient method in both time and money. Although the equations were designed for *C. distinctus*, they could be used for other Aphodiinae of similar size such as *Planolinoides borealis* (Gyllenhal), *Otophorus haemorrhoidalis* (Linnaeus) or *Oscarinus lodingi* (Cartwright). This study highlights that it is possible to develop these equations for any insect. However, for the most accurate results, it is suggested that the insects used should not be stored in preservative for long periods as this could alter their weight (129, 176).

7.3 Conclusions

To understand the diversity of the coprophagous insect community as a whole requires the knowledge of various factors. This thesis identified that diversity can be monitored by using bait treatment, bait age, location and habitat. Depending on the nature of the research question, one or more of these may play a larger role. However, the effect of all factors should be equally considered when conducting sampling.

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APPENDIX 1: DUNG BEETLES AS POTENTIAL VECTORS OF LIVESTOCK PARASITES

Dung beetles (Coleoptera: Scarabaeidae) can be a vector of nematodes, trematodes or cestodes that are parasites of livestock. I examined this phenomenon for Canada by dissecting adults of two dung beetle species that are common in southern Alberta. Live adult *Onthophagus nuchicornis* (Linnaeus), a tunneller of European origin, and *Canthon praticola* LeConte a native roller, (Coleoptera: Scarabaeidae) (n = 20 individuals per species) were dissected using a LEICA MZ 8 dissecting scope and forceps. Live adult darkling beetles *Eleodes hispilabris* (Say) (Coleoptera: Tenebrionidae) (n = 12 individuals) were also dissected following the same protocol. These individuals acted as a control to compare to the dung beetles to see if the recovered nematodes were specific to dung beetles.

Results identified 75% and 80% of *C. praticola* and *O. nuchicornis*, respectively, to harbour nematodes (Table A.1). Images of the nematodes were taken using a LEICA DFC290 HD camera on a Leitz Dialux 22 compound microscope. The nematodes were roughly 1 mm in length with no distinctive physical markings (Figs A.1 and A.2). To identify the nematode species recovered, DNA extraction was followed as per the Qiagen DNeasy® Blood and Tissue Kit protocol. General methods were followed as described in Goater et al. (81) and was completed by Paul Coghlin (Agriculture and Agri-Food Canada, Lethbridge, Alberta, Canada). Amplification of the cytochrome oxidase subunit 1 (CO1) gene was carried out using the Folmer primers LCO1490 and HCO2198 (79) and sequencing was done in both directions at the University of Calgary Core DNA Services Lab (Calgary, Alberta, Canada). Sequences were aligned in BioEdit (version 7.2.5) and analyzed using Molecular Evolutionary Genetics Analysis (MEGA7). Successful amplification and sequencing was only obtained for nematodes extracted from *O. nuchicornis*. The resulting sequence was deposited into GenBank (Accession Number: MK518440). Comparison of this sequence to sequences in GenBank did not clarify the identity of the nematode species.

The absence of nematodes associated with the darkling beetles could suggest that the nematode found in *O. nuchicornis* could be specific to Scarabaeidae species. A generalist nematode may be more likely to develop a relationship with any beetle. It would be expected that a generalist nematode would infect all three species because they were in close contact for two weeks. However, the cold storage temperature may have prevented the nematodes from moving, thus transferring to a different species.

Future research could use different genes such as 28S (44) and 18S (140), which have been used to sequence nematode DNA. Using a different gene for the DNA sequencing may be more helpful in identifying the species of nematode.

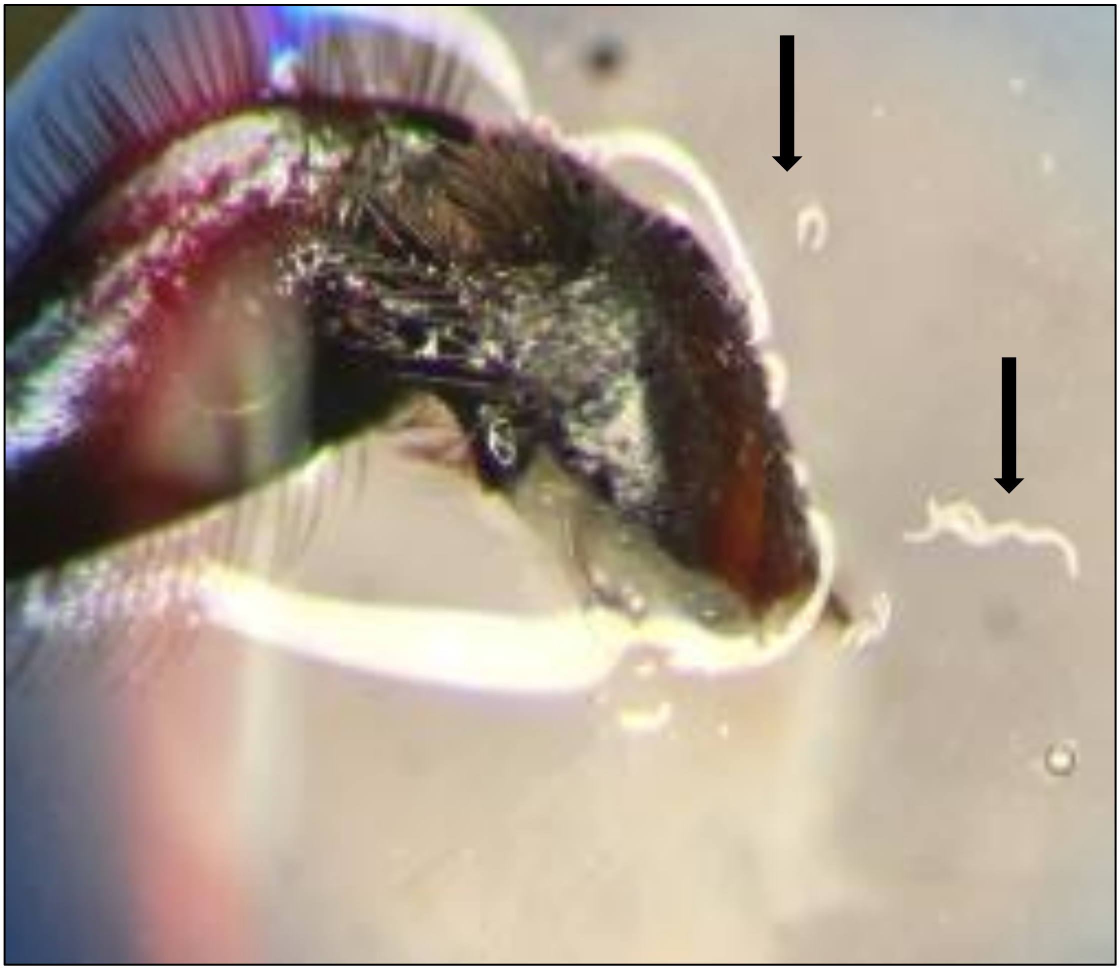

Figure A.1. Photo of a fore leg of a *Canthon praticola* LeConte taken under a LEICA MZ 8 dissecting scope (4.0x). Black arrows indicate small clumps of nematodes to the right of the femur.

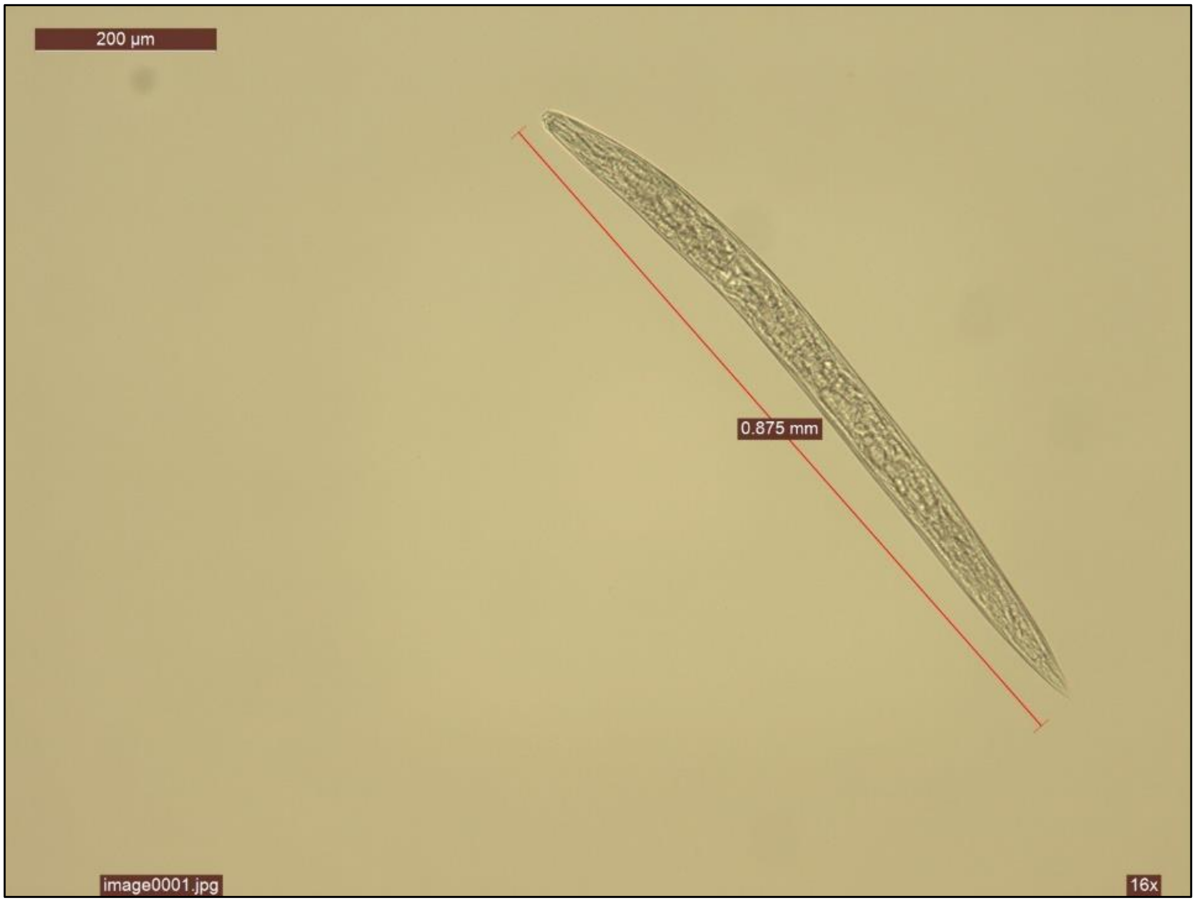

Figure A.2. Photo of the nematode recovered from Canthon praticola LeConte using a LEICA DFC290 HD camera on a Leitz Dialux 22 compound microscope.

Table A.1. A rough estimate of the number of nematodes found in each individual from each species.

Individual	*Canthon praticola*	*Onthophagus nuchicornis*	*Eleodes hispilabris*
1	0	50	0
2	40	40	0
3	0	10	0
4	10	50	0
5	>100	30	0
6	15	5	0
7	20	30	0
8	3	0	0
9	5	10	0
10	40	20	0
11	10	15	0
12	0	35	0
13	0	0	
14	0	15	
15	5	10	
16	50	0	
17	40	0	
18	1	10	
19	30	5	
20	40	1	