INSECTS ASSOCIATED WITH MONTANA'S HUCKLEBERRY (ERICACEAE: *VACCINIUM GLOBULARE)* PLANTS AND THE BUMBLE BEES (HYMENOPTERA: APIDAE) OF MONTANA

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Entomology

MONTANA STATE UNIVERSITY
Bozeman, Montana

April 2016

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DEDICATION

This work is dedicated to the amazing staff and students at Northpoint Expeditionary Learning Academy in Prescott, AZ. They challenged me to, not only teach, but also to exemplify the ten Expeditionary Learning Design Principles:

1. The Primacy of Self-Discovery
2. The Having of Wonderful Ideas
3. The Responsibilty for Learning
4. Empathy and Caring
5. Success and Failure
6. Collaboration and Competition
7. Diversity and Inclusion
8. The Natural World
9. Solitude and Reflection
10. Service and Compassion

ACKNOWLEDGEMENTS

I owe many people thanks for making this project happen. First to my advisor, Michael Ivie, who had the vision for the project, secured funding, and offered support and advice. Also, my committee members, Kevin O'Neill and Casey Delphia, offered suggestions and guidance throughout the process. All the people associated with the Ivie Lab offered me all sorts of help and encouragement: Tyler Kelly, Frank Etzler, Charles Hart, Hannah Bares, James Beck, Lisa Seelye, Adrian Massey, Paloma Amaral, and Donna Ivie. Thanks to all the other staff and students in the MSU entomology group who provided support, encouragement, and thought-provoking conversations throughout my two years at MSU.

My friends in Bozeman have cheered me on throughout this process. I especially want to thank Laurie Kerzicknik, Casey Delphia, Greg Ross, and all the awesome people at Shining Mountains Lutheran Church. Finally, my amazing family has always encouraged me to learn, explore, and challenge myself. Thank you all!

The project was funded through a grant from the Montana Department of Agriculture's Specialty Crop Block Grant Program. This is a contribution of the Montana Agriculture Experiment Station.

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ABSTRACT

A key factor in understanding the success of any crop plant is knowledge of the underlying interactions between that plant and its insect associates. However, no research project has ever explored the insect community associated with Montana's huckleberries, a culturally and economically important specialty crop in the state. Additionally, baseline knowledge on the composition and distribution of Montana's insect fauna is lacking in many ways. Without baseline knowledge of what insects are present, monitoring and/or conservation efforts are impossible. In 2014 and 2015, insects were sampled from huckleberry plants at 21 study sites in the mountains of Northwest and Southwest Montana to identify possible pollinators and potential threats. Bumble bees, andrenids, and vespids were found to be the most frequent flower visitors, while a variety of Lepidoptera, Diptera, Coleoptera, Hemiptera, and Hymenoptera were collected from the plants' leaves and stems. An attempt was made to distinguish between actual biological associates and casual plant visitors. Over 30 possible associates were identified. Several new host plant records were documented and an undescribed species of *Pristiphora* (Hymenoptera: Tenthredinidae) was discovered. Bumble bees collected from huckleberry study sites, bumble bees collected across the state during the summer of 2015, and historic museum specimens were used to compile the first inventory of *Bombus* species in Montana. Over 12,000 *Bombus* records were examined and 28 species have now been confirmed to be present in the state while four additional species are predicted to occur here. Data have been made available to the public through an online database in order to inform future research and conservation efforts.

INTRODUCTION

In all terrestrial ecosystems, arthropods and plants are continually interacting in complex and dynamic ways. Plants provide shelter, food, and oviposition sites for a variety of arthropods, while insects can provide pollination services and protection (Mello and Silva-Filho 2002). Insects and plants often have mutualistic relationships, but some insect herbivores can be extremely detrimental to plant productivity (Flint 2012). In both natural and agroecosystems, an understanding of the network of plant-insect interactions is key to developing effective management and conservation efforts.

Montana is known for its agriculture and is a leading producer of beef, wheat, peas, lentils, flax, honey, cherries, sugar beets, and seed potatoes (Montana Department of Agriculture (MDA) 2016). The state is also known for its large size, topographic diversity, and climatic variability, which support a large and diverse flora that is well-studied (Lesica *et al.* 1984, Lesica and Shelly 1991, Lesica 2012).

In contrast to the well-known flora of Montana, insects in the state have not been as well studied. Certain taxa (e.g. Cerambycidae) are known from published checklists (Hart *et al.* 2013) and agricultural pests (e.g. the wheat stem sawfly, *Cephus cinctus* Norton) have received considerable attention (Buteler *et al.* 2010, Beres *et al.* 2011, Peterson *et al.* 2011, Buteler *et al.* 2015). But Montana likely has tens of thousands of insect species, most of which have never been documented.

Concerns over declining pollinator populations are sparking entomological research projects across the U.S. and, based on the Pollinator Research Action Plan

issued by the White House (2015), more research projects are on the horizon. Wild, native bees are the least understood group of pollinators (Michener 2007) with biological and distribution information lacking for many groups. In Montana, there may be as many as 500-1,000 bee species (C. M. Delphia, personal communication 2016), but no comprehensive state inventory has ever been conducted.

Additional areas of concern in the study of insect populations include the spread of non-native pest species (Williams and Osborne 2009, Beggs *et al.* 2011, Lee *et al* 2011) and potential impacts of climate change (Giersch *et al.* 2015, Kerr *et al.* 2015). However, without baseline knowledge of which species occur in an area, population monitoring studies and conservation strategies are more-or-less useless.

Goals and Objectives

The overall goal of my thesis research was to fill in some of the existing gaps in baseline knowledge of insects in Montana. Additionally, because of my background in and passion for education, I wanted to make sure that my work could be used to educate the public, inspire young scientists, and support future research projects. Specific objectives for the two chapters of my thesis were:

Chapter 2

To provide an inventory of species associated with Montana's huckleberry plants. Huckleberry plants cannot be cultivated but are of economic, ecological, and cultural value in Montana. No work has ever been conducted on the insects associated with this important plant, though lack of pollinators or the presence of

invasive pests could negatively affect productivity and have both economic and ecological effects.

A study like this focusing on one plant species in a poorly sampled area has the potential to uncover new host plants records and new, undescribed insect species. Additionally, the insect inventory associated with the huckleberry plants will add to the overall knowledge of the insect community in Montana's western coniferous forests.

Chapter 3

As an outgrowth of studying pollinators of huckleberries, the paucity of information on the identity and distribution of Montana's bees became obvious. The bumble bee project naturally evolved out of the huckleberry project, after it was discovered that species commonly collected in different regions of Montana varied considerably and current literature (Colla *et al.* 2011, Koch *et al.* 2012, Williams *et al.* 2014) was not sufficient in describing the distributions of species within the state. Therefore, a goal emerged to create a state inventory of bumble bees found in Montana along with county-level distribution data. This project is an important step in documenting bee species in Montana and can be used to inform future research and conservation efforts.

INSECTS ASSOCIATED WITH MONTANA'S HUCKLEBERRY (ERICACEAE: *VACCINIUM GLOBULARE*) PLANTS

Introduction

Crops and livestock of primary economic importance in the State of Montana include wheat, barley, oats, corn, alfalfa, cattle, sheep, goats, pigs, and chickens (USDA 2014, MDA 2016). Specialty crops, such as honey and sweet cherries, add an additional component to Montana's economy (USDA 2014). One of the most important of these specialty crops in Montana, which also holds a strong cultural association, is the huckleberry, *Vaccinium globulare* Rydberg (Jahrig *et al.* 1997).

In 1996, 59,000 pounds of huckleberries were processed by Montana facilities. Most of these berries (85%) were from northwestern Montana, while the rest came from northern Idaho (Jahrig *et al.* 1997). Jams, jellies and preserves accounted for 55% of that year's huckleberry product sales of $1.16 million (Jahrig *et al.* 1997). However, this is mostly likely a gross underestimate of the huckleberry's economic value because it was based on only 14 of the state's major huckleberry manufacturers (Jahrig *et al.* 1997) and by 2010, at least 30 Montana companies were known to be making hundreds of local huckleberry products (Skornogoski 2010).

Aside from the commercial pickers and huckleberry manufacturers, there are many individual entrepreneurs picking huckleberries for personal use or to sell to local businesses (Vasquez and Buttolph 2010, ACD personal observation 2014),

especially in the Northwest portion of the state. One small cafe owner in Libby, MT estimated that she purchased hundreds of gallons of huckleberries in 2013, mostly from locals who spend their days out picking (ACD personal conversation 2014). Gallon bags of frozen huckleberries sold for $35-$45 each during the summer of 2014 (ACD personal observation 2014), but a bag can sell for as much as $70 at supermarkets in Bozeman (ACD personal observation 2016).

In addition to the berries' economic value, *V. globulare* is known to be of ecological importance in Montana. In the northwest region of the state, it is one of the most important food sources for bears in late summer and fall (Mace and Jonkel 1986). Dietary analyses suggest that huckleberries make up 10% or more of grizzly bear diets in Glacier National Park (Martinka and Kendall 1986). In the Cabinet-Yaak region, in the far northwest corner of Montana, huckleberries appear to provide an even greater amount of food for bears, most likely due to the shrub's wide distribution and ability to thrive in previously disturbed landscapes (Kasworm *et al*. 2013). Because low berry production is detrimental for bears attempting to store fat before hibernation, huckleberry productivity surveys have been a part of grizzly bear recovery efforts by the United States Fish and Wildlife Service (USFWS) since 1989, with between 11 and 21 huckleberry transects evaluated each year (Kasworm *et al*. 2013). High levels of black bear damage to cultivated crops, beehives, and livestock are correlated with low berry and mast crop productivity (Rogers 1976), further suggesting the value of wild berries to bear diets.

Huckleberry shrubs also play a role in forest succession and are a key understory species, contributing to a forest's overall diversity and long-term productivity (Kerns *et al*. 2004). *Vaccinium globulare* is specifically listed as an important shrub component of a climax forest community in Montana. Research has shown that undisturbed forests contain the least productive huckleberry patches while the most plants were found on slopes that were disturbed by fire 10-50 years earlier (Martin 1979). Greatest fruit production is associated with these previously burned sites before the reestablishment of a coniferous tree overstory (Lesica 2012). Once the overstory is reestablished, shrubs do not die out, but tend to grow taller and flower less, thereby decreasing berry production.

Finally, there is a strong cultural association to the huckleberries in Montana. Over the last two decades, Montana huckleberry products have gained recognition worldwide (Jahrig *et al.* 1997). But their cultural importance goes deeper than products for tourists. Before the arrival of white settlers in the 1800s, Northwest tribes relied on huckleberries as a major food source and entire villages would relocate to prime picking sites for as long as the berries were ripe (Richards and Alexander 2006). Ceremonial first fruits celebrations were a part of berry-picking traditions, along with feasts and periodic prescribed burns (Richards and Alexander 2006). Use of wild huckleberries by white settlers in Montana coincided with technological advances of the canning industry and by the mid-1920s commercial berry picking operations in Montana were well established, providing important jobs during the 1930s when the state's mining and timber industries collapsed

(Richards and Alexander 2006). The industry declined during and after World War II, and this downward trend persisted until the 1980s when it experienced a revival, primarily as a cultural symbol of state pride (Richards and Alexander 2006). The cultural importance of the huckleberry industry in Montana has continued into the 21st century.

The huckleberry plants known from across the western U.S. are members of the heath family Ericaceae (Order: Ericales), which contains approximately 35 genera of herbs, shrubs, and trees (USDA-NRCS 2015). Within the family Ericaceae, western huckleberries, along with cranberries, grouse whortleberries and blueberries, are in the genus *Vaccinium,* which contains 43 species in North America (USDA-NRCS 2015). These species are not closely related to the eastern huckleberry, which is in the genus *Gaylussacia*, or the garden huckleberry, which is in the genus *Solanum* (USDA-NRCS 2015).

Of the seven species of *Vaccinium* known to occur in Montana, *V. globulare* is the most common and widespread, with records in all of the western, mountainous counties. *Vaccinium membranaceum* Douglas ex Torr. superficially resembles *V. globulare*, and some sources consider the two species synonymous (Vander Kloet 1988, Consortium of Pacific Northwest Herbaria 2013). In the Pacific Northwest, *V. membranaceum* is more widespread, occurring from coastal British Columbia south to California and less commonly east into Alberta, Idaho, Montana, and Wyoming. It is sporadic in the Montana portion of its range (Vander Kloet 1988, Lesica 2012). *Vaccinium globulare* is more commonly found further inland and is most abundant

where British Columbia, Alberta, Idaho, and Montana converge (Lloyd 1996, Lesica 2012). For this project, we considered the two species to be separate and focused on *V. globulare*, the huckleberry plant most commonly encountered in Montana (Lesica 2012, M. Lavin personal communication 2015).

The "Globe Huckleberry" or "Blue Huckleberry," *V. globulare,* is known for large, sweet berries (Lesica 2012). It is a spreading shrub with grayish bark that grows up to one and a half meters tall (Lloyd 1996). Like all other *Vaccinium*, *V. globulare* is rhizomatous, with rhizomes being the primary method of reproduction. These plants depend on mycorrhizae to help pull nutrients out of the acidic, often nutrient-poor soils in which they grow (Vander Kloet 1988). Flowers are urn-shaped, mature before the leaves (Lesica 2012), and individual flowers can produce a relatively large amount of nectar, visible to the naked eye as drop of liquid filling the inside of the flower (ACD personal observation 2014). Each berry contains many seeds and the seeds are animal dispersed (Lesica 2012).

Due to their economic and ecological importance, several studies have been conducted on huckleberries of the Pacific Northwest, primarily focused on understanding succession or as part of grizzly bear recovery efforts. In these studies, berry production has been linked to fire (Lesica 2012), climate (Holden et al. 2012), snow cover (Stark and Baker 1992), rainfall, soil pH, elevation, slope, and aspect (Martin 1979). Despite this accumulation of knowledge, *V. globulare* cannot be successfully cultivated and all harvest depends on wild plants (Gough 1998,

Barney 1999). Additionally, one key aspect of *V. globulare* biology that has yet to be investigated is the impact of insects.

Insect/plant associations can include pollinators, herbivores, frugivores, and the predators and parasitoids associated with them. These associates may be polyphagous generalists or monophagous specialists. Published host plant data have documented numerous arthropod species associated with the genus *Vaccinium*, but no insect species have been specifically recorded to be associated with *V. globulare.* Only one species, the fruit-infesting tenthredinid *Pristiphora macnabi* (Ross) has a recorded association with *V. membranaceum* (Wong 1968). These host plant records are summarized in Appendix A and include insects in the orders Hymenoptera, Lepidoptera, Diptera, Hemiptera, and Coleoptera as well as two species of mites (Arachnida Subclass Acari).

Huckleberries, like many other fruit crops, are most likely insect-pollinated and, due to the structure of *Vaccinium* flowers (De Luca and Vallejo-Marin 2013), buzz pollination may be required. However, no specific pollinators associated with either *V. globulare* or *V. membranaceum* have been reported. Martin (1979) reports that fruit is set by insect pollination, but no species are reported. The loss of native bee populations in the Pacific Northwest following the eruption of Mt. St. Helens was implicated in a drastically unproductive year for *V. membranaceum* (Hunn and Norton 1984), but details of that native bee community were not reported. Stark and Baker (1992) suggest that pollination is achieved by bees and possibly by ants, but, again, no specific species were documented. *Vaccinium membranaceum* was

one of nine plants in a study on the factors limiting alpine seed production in British Columbia (Straka and Starzomski 2015). Potential pollinators recorded from this study included Lepidoptera, Diptera, and Hymenoptera (Tenthredinidae, Halictidae, Andrenidae), but these specimens were collected in pan traps, not in association with any particular plant.

Flowers of many species of plants require what is referred to as "buzz pollination." Buzz pollination is a description of the manner in which some bees collect pollen (i.e., by rapidly vibrating their bodies using their wing muscles to loosen pollen from anthers, effectively sonicating the flower). Bumble bees (*Bombus* spp.) are known to be buzz pollinators (De Luca and Vallejo-Marin 2013). In other regions of North America, small, native bees in the genera *Andrena* and *Halictus* have also been observed buzz pollinating *Vaccinium* flowers (Javorek *et al.* 2002). *Bombus* species, *Andrena* species, and *Apis mellifera* L. have been documented visiting the flowers of other species of *Vaccinium* across North America (Vander Kloet 1988) and *A. mellifera* has been used commercially in blueberry fields to supplement native bee populations (Kloet 1988). Montana's overall bee fauna has not been fully documented, and species inventories are just starting to be developed. Thus, we don't even know which bees inhabit most of the forests where *V. globulare* is found. In the midst of concern over declining bee populations (Chaplin-Kramer *et al.* 2014, Goulson *et al.* 2015) it is even more important to learn which pollinators are present in Montana's forests, in addition to which are

associated with *V. globulare,* because a lack of suitable pollinators could have both economic and ecological impacts on Montana's huckleberry industry.

Pollinators are not the only insects that affect plants. There are many insects, both native and introduced, that are considered pests of economically important crops. Martin (1979) reported observations of partial defoliation of *V. globulare* in Montana. This partial defoliation was attributed to either disease or insects and was connected to lower overall productivity, smaller berries, and fewer seeds per berry (Martin 1979). Stark and Baker (1992) also reported damage to *V. globulare* fruits and implicated leafcutting bees (Megachilidae), though this group of bees is known for damage to foliage of plants, not to fruits. The spotted-wing drosophila (SWD), *Drosophila suzukii* (Matsumura), is an invasive fruit fly from Southeast Asia that attacks healthy, ripening fruit (Lee *et al.* 2011). This fly has been known to cause serious damage to fruit crops including cherries, raspberries, strawberries, and plums (Lee *et al.* 2011). It was detected in Montana for the first time in 2011 (O'Neill *et al.* 2011). If SWD finds its way to Montana's huckleberries, there could be significant economic and ecological damage. Similarly, the German yellowjacket (*Vespula germanica* (Fabricius)) is an invasive wasp in North America known to be a scavenger of both sweets and meat (Bechinski *et al.* 2009). It has been in the northwestern U.S. since the 1970s and in Idaho since the 1980s (Bechinski *et al.* 2009). It has also been documented in Montana (Montana Entomology Collection, MTEC). If a non-native scavenger like *V. germanica* spreads into *V. globulare* habitat,

it could negatively affect production by robbing nectar from flowers or causing damage to fruits.

Due to the importance of insects as both pollinators and pests, the purpose of this project was to provide the first documentation of insects associated with *V. globulare* in Montana. Results from this work can be used to inform future research, conservation, and management efforts.

Materials and Methods

Study Sites

Sampling took place from June 5 to August 13, 2014 and from May 10 to August 4, 2015 at 21 sites in northwest and southeast Montana (Figure 1). During the summer of 2014, sampling was conducted at 12 sites in the Kootenai National Forest in northwest Montana (Lincoln and Sanders Counties; Figure 1). These sites were chosen to represent a diversity of elevations, slopes, aspects, and habitat types. Eight of the study sites are part of a long-term huckleberry-productivity study conducted by the USFWS (Kasworm *et al.* 2013). Other sites were found following the recommendations of Kootenai National Forest staff and locals in Lincoln and Sanders Counties.

During the summer of 2015, sampling was conducted at nine sites throughout the Custer-Gallatin National Forest in southwest Montana (Gallatin County). Sites were found using historic records of *V. globulare* in the Consortium of Pacific Northwest Herbaria database (Consortium of Pacific Northwest Herbaria

2013). Fewer sites were chosen during the 2015 field season to facilitate more frequent observations and sampling.

In general, the 2014 sites in the Kootenai National Forest were more remote. All were accessed via Forest Service roads and were at least 8 km from a main roadway. The sites in 2015 were accessed via hiking trails, but were generally less than 2 km from a main roadway. The four 2015 sites that were the most remote (two in the Boulder Valley of Sweet Grass County, one near Pioneer Falls in Madison County, and the Hidden Lakes Trail in Gallatin County) were only visited once or twice during the field season.

Due to different habitat types and variation in annual temperature, precipitation, and productivity, the *V. globulare* plants at the 2014 sites were very different from the plants at the 2015 sites. The *V. globulare* plants at the 2014 sites were much larger (approximately 0.5-1.2 m tall) than the plants at the 2015 sites (approximately 0.2- 0.6 m tall). The plants at the 2014 sites had 50 or more flowers or berries per plant, while many plants in 2015 did not even produce a single flower or berry.

In 2014, site visits were limited by weather, distance, and plant phenology (which is correlated to elevation, aspect, and canopy cover), and each site was sampled three, four, or five days during the season for approximately 3 h each. In order to visit the sites more frequently and sample more thoroughly, sampling in 2015 focused on four sites visited once every 7-10 days, while five additional sites were sampled only once or twice. *Vaccinium globulare* plants in the Custer Gallatin

National Forest are much more sparsely distributed than those in the Kootenai National Forest, so although the same amount of time was spent sampling, the time was split between smaller patches of plants spread out over a linear distance of approximately 1.5 km.

Sampling Procedure

Insects were collected from the *V. globulare* plants each field season beginning as soon as the flowers opened and continuing until the fruit was ripe. Insects sampled from different parts of the plant (i.e. flowers, leaves and stems, and fruit) were kept in separate vials.

Insects were individually collected between 0900 and 1600 h using a net, aspirator, or Bioquip® insect vacuum, depending on the type of insect. A beating sheet and sweep net were used to sample less visible insects from the plants' leaves and stems. Bees were placed in a killing jar with ethyl acetate, while other insects were placed in vials of 70% ethyl alcohol. Lepidoptera larvae found feeding on plants were collected, along with *V. globulare* foliage, to be reared in the lab.

All insects were taken to the MTEC at Montana State University (MSU) where they were cleaned, pinned, labeled, given a unique identifier (barcode), and uploaded to the MTEC X:BioD Database managed by The Ohio State University (http://mtent.org/Projects/huckleberry/huckleberry.html). Diptera specimens were chemically dried with hexamethyldisilizane (HMDS) following the online protocol of the California State Collection of Arthropods (Orozco and Gaimari 2015). Specimens were identified to the lowest taxon possible, using current literature and

the help of experts, and sorted into one of three categories: flower visitors, leaf and stem visitors, and fruit visitors.

Lepidoptera larvae were reared on *V. globulare* leaves collected at the study sites. The leaves and larvae were placed in plastic bags, kept in the lab at room temperature, and checked at least every other day for the emergence of adults. Adults that emerged were preserved in a freezer until they could be pinned, spread, labeled, and identified.

Pan Traps

Pan traps (355ml (12 oz) Solo® plastic bowls) were set up along the periphery of each study site during *V. globulare* anthesis in order to establish the overall community of bees for comparison. In 2014, yellow pan traps were set up 3 m apart in a linear transect along the edge of each study site. In 2015, four colors of pan traps (yellow, blue, pink, and white) were set up along the edge of each study site in a Latin Square design with 3 m between each bowl.

Red Solo® Cup Traps

Following the protocol established by the University of New Hampshire Cooperative Extension (2014), 532ml (18 oz) red Solo® cup traps were placed at seven study sites in 2014 and four study sites in 2015 to monitor for the presence of *D. suzukii*. These traps were established as the fruit was beginning to ripen with samples collected each week until the end of the field season.

Fruit Dissection

In 2015, damaged and undeveloped berries were collected from the plants and brought back to the MTEC lab for dissection. Berries were kept in closed petri dishes in a walk-in cooler at approximately 4°C until they could be dissected (See Appendix B for berry dissection notes).

Data Analysis

All specimen records were uploaded to the MTEC XBio:D database (http://mtent.org/Projects/huckleberry/huckleberry.html). Data were then extracted from the database into Excel® for analysis.

This study was observational in nature with the goal of surveying insects associated with the *V. globulare* plants. Sampling times and methodology were not standardized across all site visits over the two years, preventing quantitative analysis of diversity and abundance. Nevertheless, the data collected can begin to provide insights into the insects associated with the plant, and provides a foundation for further research.

Results

In total, 2,470 arthropod specimens were collected from the *V. globulare* plants over two years. The flower visitors, leaf and stem visitors, and fruit visitors are summarized in Tables 1-8. Species found in low numbers on plants were assumed to be incidental visitors in the absence of some behavior indicating a biological association. No *D. suzukii* were found in the red Solo® cup traps.

A total of 456 insects were collected from *V. globulare* flowers. These flower visitors (Table 1; Figure 2) included Diptera, Hymenoptera, and Thysanoptera. The hymenopterans consisted of seven genera of bees from four families, wasps from three families, and three genera of ants. The Diptera flower visitors consisted of members of seven families. Seven individual thrips were collected. Forty-seven percent of the total flower visitors were bumble bees of nine species (Figure 2).

A total of 1,954 arthropods were collected from the *V. globulare* leaves and stems. These arthropods represented twelve orders plus the subclass Acari (Figure 3). Thirty percent of the insects collected on leaves and stems were Diptera (Table 2). Twenty percent of the leaf and stem visitors were Hymenoptera (Table 3). Thirteen percent of the leaf/stem visitors were Hemiptera (Table 4). Four percent of the leaf and stem visitors were Lepidoptera (Table 5). Thirteen percent of the leaf and stem visitors were spiders (Table 6). Twenty percent of the leaf and stem visitors were other arthropods (Table 7).

Sixty insects were collected from *V. globulare* fruits and are summarized in Table 8 and Figure 4. Of these fruit visitors, the Tenthredinidae larvae and parasitoid wasps were found inside green or damaged berries. All others were collected from the surface of the fruits.

We collected 140 bees in 2014 and 92 bees in 2015 in the pan traps set up along the edge of the study sites during *V. globulare* anthesis (Table 9). In 2014, bees collected in pan traps represented eleven genera and the majority of the specimens collected (78%) were *Lasioglossum (Dialictus).* In 2015, bees collected in

pan traps represented twelve genera, with *Osmia* having the largest number of specimens (35%). These results suggest that the overall assemblage of bees in huckleberry habitat is larger and more diverse than the subset of bees visiting the huckleberry flowers.

Discussion

The 2,470 arthropod specimens collected from plants provide a baseline understanding of the insect community associated with *V. globulare* in Montana. The challenge in interpreting these data lies in determining which insects have an actual biological association with the plant and which are just incidental visitors, part of the larger forest understory ecosystem. Of the insects that have a true association with the plant, future questions to be addressed include 1) which insects are specialists on *V. globulare*?, 2) which insects are significant pollinators of *V. globulare*?, and 3) which insects might be causing significant injury to the plant? We used published biological information and the number of individuals collected to attempt to separate true plant associates with incidental visitors.

Flower Visitors

Bumble bees made up 47% (Figure 2) of *V. globulare* flower visitors. All bumble bees collected in 2015 and 80% of those collected in 2014 were queens. Because mated, overwintered bumble bee queens are known to emerge in early spring and forage for nectar from any available flowers before initiating a new colony (Williams *et al.* 2014), it is not surprising to find them to be the most

common visitor during *V. globulare* anthesis in May and June. Many of the bumble bees visiting the flowers appeared to be buzz pollinating the flowers.

Nine different *Bombus* species were collected from the flowers, though only four accounted for 91% of the total: *Bombus bifarius* Cresson*, Bombus melanopygus* Nylander*, Bombus mixtus* Cresson*,* and *Bombus sitkensis* Nylander (Figure 5). All four of these species are common, western North American species known to inhabit montane environments in the western half of Montana (Williams *et al.* 2014, Dolan 2016b). *Bombus bifarius*, *B. melanopygus*, and *B. mixtus* were collected across multiple sites in both years. *Bombus sitkensis* was only collected at sites in the Kootenai National Forest in 2014 coincident with the fact that its range in Montana is limited to the far northwest (Williams *et al.* 2014, Dolan 2016b). Of the remaining five *Bombus* species, *Bombus flavifrons* Cresson is another common western Montana bumble bee, known to be found in montane forests (Dolan 2016b) and was collected at multiple sites in both years. Two species (*Bombus insularis* (Smith) and *Bombus flavidus* Eversmann) are social parasites of the subgenus *Psithyrus* that are commonly collected in the western half of Montana (Dolan 2016b). Both of these species were collected at multiple sites in 2014. The remaining two species, *Bombus centralis* Cresson and *Bombus occidentalis* Greene are widespread in Montana, but more commonly collected in valleys, foothills, plains, or urban areas (Williams *et al.* 2014, Dolan 2016b). These last two species were only collected in 2015 at the Lava Lake site in the Custer-Gallatin National Forest.

Because bumble bees are known to be efficient pollinators, especially for plants like *V. globulare* with poricidal anthers (De Luca and Vallejo-Marin 2013), and because *Bombus* species were the most frequent *V. globulare* flower visitors, it is likely they are important pollinators of this plant. However, *Bombus* species are also widely known to be nectar robbers (Irwin *et al.* 2010), collecting a nectar reward without contributing pollination services. Exclusion experiments (Kearnes and Inouye 1993) are needed to elucidate the roles of different flower visitors in the pollination of *V. globulare.*

Bees in the genus *Andrena* accounted for 10% of the flower visitors observed at study sites in 2014-2015 (Table 1; Figure 2). Of those, 87% appeared to be of one species, *Andrena* cf. *thaspii* Graenicher (Figure 6). *Andrena* are difficult to identify to species, but all species whose biology is known are solitary ground-nesters (Michener 2007) and many are known to forage in low temperatures when other bees are not yet active (LaBerge 1980). Thus, the role of *Andrena* in the pollination of early season flowers like *V. globulare* may be substantial. *Andrena thaspii* is known to be widespread in boreal regions of Canada and the U.S. and has been recorded from Montana (LaBerge 1980). There is a great deal of intra-specific variability (LaBerge 1980) that makes positive identifications difficult.

Honey bees (*A. mellifera)*, which are not native to North America, were only collected from *V. globulare* flowers at one study site in 2014, the site closest to the town of Troy. They were absent from the flowers and the pan traps at all of the other sites, indicating that, in general, this domesticated pollinator is not common in

huckleberry habitat in Montana. Honey bees are known to be important pollinators, but do not have the ability to buzz pollinate (De Luca and Vallejo-Marin 2013), so it is likely that they are opportunistically collecting nectar from *V. globulare* when it is available, without contributing pollination services.

Pan traps were set along the periphery of study sites during *V. globulare* anthesis in order to establish the bee community for comparison. Table 9 compares the bees collected on *V. globulare* flowers with those collected in pan traps. Bumble bees represented 78% of the bees collected on flowers, but only 5% of those in pan traps. *Lasioglossum (Dialictus)* represented 49% of the bees collected in pan traps, but less than 1% of the flower visitors. The diversity of bees collected in pan traps was higher (14 genera) than that of bees collected on flowers (9 genera). This may suggest that 1) not every bee in *V. globulare* habitat is using the *V. globulare* flowers as forage and 2) not every bee that is foraging in an area can be collected with pan traps. However, differences in sampling methods could also have affected these results. Other studies have shown that one sampling method alone (e.g. pan traps or netting) is not adequate for assessing the true composition of a native bee assemblage (Roulston *et al.* 2007, Grundel *et al.* 2011, Wood *et al.* 2015), and conducting a complete bee inventory in any habitat is extremely difficult. For the current study, differences in bee diversity on flowers and the greater assemblage of bees collected in pan traps may be explained by date, temperature, weather, diversity of floral resources, phenology of floral resources, and phenology of the bee species. An exploration of these differences may be of interest for future studies.

Wasps in the family Vespidae, subfamily Vespinae, made up 23% of the insects observed visiting flowers (Figure 2) across multiple sites in both years. Like bumble bees, overwintered Vespinae queens emerge from hibernation in the spring and use the carbohydrates in nectar for energy (Akre *et al.* 1980). Fifty-six percent of the Vespinae collected from *V. globulare* flowers at multiple sites in both years were *Dolichovespula arenaria* (F.), the aerial yellowjacket (Figure 7). This species is known to be one of the most common and widespread yellowjackets in boreal forests of North America (Akre *et al.* 1980). Two other *Dolichovespula* species, *Dolichovespula maculata* (L.) and *Dolichovespula norvegicoides* (Sladen), accounted for 26% of the Vespinae flower visitors (Figure F). *Dolichovespula maculata* was only collected at sites in northwest Montana in 2014. *Dolichovespula norvegicoides* was collected at a single site in 2014, but at multiple sites in 2015. Though little is known of the biology of these two species, they are both common in boreal forests of North America (Akre *et al.* 1980). *Dolichovespula arctica* (Rohwer) and *Vespula austriaca* (Panzer), which together constitute 4% of the Vespinae flower visitors, are social parasites of other Vespinae. Three *D. arctica* individuals were collected at two sites in 2014 and one *V. austriaca* was collected in 2014. Four species, *Vespula acadica* (Sladen), *Vespula consobrina* (Saussure), *Vespula atropilosa* (Sladen), and *Vespula vulgaris* (L.), together account for the remaining 14% of vespid flower visitors. Of these, *V. consobrina* was collected only in 2014, while the others were collected at multiple sites in both years. No invasive *V. germanica* were collected at any of the study sites.

Unlike bees that actually forage for pollen as a source of protein for larvae, individual Vespinae visiting flowers are only seeking nectar for energy before constructing nests or seeking out prey as a protein source for larvae (Akre *et al.* 1980). So, while there may be some incidental pollen transfer, it is unlikely that these flower visitors are contributing pollination services. Additionally, on two occasions in 2014, *D. maculata* was observed biting through the outside of a flower (T. T. Kelly, M. A. Ivie, personal communication 2014), a behavior associated with primary nectar robbers (Irwin *et al.* 2010).

Stark and Baker (1992) reported seeing ants maneuvering in and out of *V. globulare* flowers and alluded to the possibility of ants as pollinators. Ten percent of the insects observed visiting flowers in 2014-2015 were ants from the genera *Formica*, *Camponotus*, and *Tetramorium* (Table 1; Figure 2). All of these genera are known to be scavengers or predators but also feed on nectar or honeydew and are commonly seen visiting flowers. While ants may be pollinators in certain specialized systems (Hickman 1974), the role of ants in pollination has been shown to be negligible, despite high frequency of flower visits (Chacoff and Aschero 2014). In fact, several studies have shown that ant flower visitors can actually disrupt pollination and fruit set (Ashman and King 2005, Dutton and Frederickson 2012).

Thrips (Thysanoptera) were collected from inside the flowers at two different sites in 2015. These insects are known to be abundant inside flowers,

feeding on both pollen and nectar (Willmer 2011). Thrips have traditionally been considered pollen destroyers because they suck the contents out of individual grains, but research in the last twenty-five years has shown that they can be pollinators of certain plants, including some Ericaceae (Willmer 2011).

Eight Empididae individuals and seven Syrphidae individuals were collected from *V. globulare* flowers in 2014-2015, along with one individual each of five other families of Diptera (Table 1). Both the Empididae and Syrphidae are known to have adults that feed on nectar (McAlpine *et al.* 1981), and some syrphids are known to be pollinators (Larson *et al.* 2001, Willmer 2011). The role of other flower-visiting Diptera, especially night-flying Nematocera, as pollinators has not yet been fully investigated, though it may be substantial (Larson *et al.* 2001), and in this study no night sampling was conducted.

Leaf/Stem Visitors

A large, diverse assemblage of arthropods was collected from the leaves and stems of *V. globulare* throughout the sampling period (Tables 2-7; Figure 3). Based on the number of individuals collected and known biological information, an attempt was made to determine which taxa were actual biological associations and which were just casual visitors.

Diptera. Diptera were the most numerous taxa found on the leaves and stems of *V. globulare* throughout the sampling period, with 577 individuals from 34 families collected (Table 2; Figure 3). Many of these are members of families that

inhabit moist forest understories and places where there is decaying organic matter, both of which accurately describe all *V. globulare* study sites. Based on what is known about the life history of the Diptera families collected (McAlpine *et al.* 1981 and 1987; Table 2), only four groups are likely to be biologically associated with the plant: Agromyzidae, Anthomyiidae, Scathophagidae and Tephritidae.

Larvae of all Agromyzidae are leaf miners, and the genus *Phytobia* has been recorded on other species of *Vaccinium* (Spencer 1990). The agromyzids collected were from the genera *Aulagromyza* and *Phytomyza*, neither of which are known to be associated with *Vaccinium.* Snowberry (*Symphoricarpos* spp.) is a known host for some *Aulagromyza* species (Meijer *et al.* 2012) and is common in the understory communities of Montana forests (Lesica 2012) where *V. globulare* is also found. This information, along with the fact that the leaves did not show evidence of leaf miner feeding, indicates the specimens collected likely came from a nearby non-*Vaccinium* host plant.

Anthomyiidae were collected from flowers of lingonberry plants (*Vaccinium vitis-idaea* L.) in Europe (Jones *et al.* 2014), and larvae of this family are known to feed and develop in roots, stems, flower heads or foliage (McAlpine *et al.* 1981). Twenty-one adult anthomyiids representing six species were collected from the leaves of *V. globulare* at six different study sites in 2015. Only one individual of this family was collected from the flowers and none were observed ovipositing. However, roots, rhizomes, and stems at these sites were not examined for larvae, so this Diptera family is one that may be of interest for further investigation.

Scathophagidae are often associated with dung, but larvae of this family have a variety of feeding habits—some are predators, some are found scavenging in rodent burrows, and some are phytophagous as leaf miners (McAlpine et al. 1981). Additionally, there is one record of a scathophagid species feeding on Ericaceae shrubs in Scotland (Horsfield and MacGowan 1997). Of the Scathophagidae collected from *V. globulare*, nine of the twelve specimens are in the genus *Scathophaga*, which is a group known to lay eggs in dung (McAlpine *et al.* 1987), so it is unlikely that this group is biologically associated with the plant.

The fourth Diptera family collected in this study and possibly phytophagous on huckleberries was Tephritidae. Tephritid larvae are known to feed on living plant matter and many form galls (McAlpine *et al.* 1981). However, only one specimen in this family was collected, so it is also unlikely to have an important biological association with *V. globulare.*

Hymenoptera**.** Hymenoptera were the second most common group collected from *V. globulare* leaves and stems (Figure 3). Of the 385 Hymenoptera specimens collected, 56% were wasps, 29% were ants, 13% were sawflies, and 2% were bees (Table 3; Figure 8). All the wasp families collected are known to be predators or parasitoids, the ant genera are known to be generalist predators or scavengers, and all bees are known to collect pollen and feed on nectar (Goulet and Huber 1993). So the only Hymenoptera with a potential association with the plants' leaves or stems are the sawflies.

One individual of *Pristiphora macnabi* (Ross) (Tenthredinidae) was collected in 2015. This species has been reared from berries of *V. membranaceum* in Coeur d'Alene, Idaho (Wong 1968). The specimen collected from *V. globulare* in the Gallatin National Forest is a new state record and a new host plant record for this species. Forty-two individuals of an undescribed *Pristiphora* species were collected from the leaves and stems of the *V. globulare* plants at five sites, also in Gallatin National Forest, just after anthesis. No individual was observed ovipositing, but larvae, presumed to be this species, from other Gallatin National Forest sites were found inside green, undeveloped berries late in the summer. Larvae of this group were also found inside green, undeveloped fruits collected at one site in Sanders County in 2015. Because the larvae were collected from sites other than where adults were collected, it is unclear at this time if the adults and larvae are the same species.

Of the nine other sawflies collected, four were Cimbicidae, known to feed on oak, willow, or honeysuckle; four were various other Tenthredinidae, known to feed on foliage or make galls; and one was in the family Argidae, known to feed on a variety of plants (Goulet and Huber 1993).

Hemiptera**.** Hemipterans are known for their piercing/sucking mouthparts, and many of the members of this order are known to be phytophagous and cause economic damage to crops (Schuh and Slater 1995). This group has the potential to be a threat to the health of the *V. globulare* plants in Montana. Two hundred fifty-five individuals from a variety of Hemipteran families were collected from the leaves

and stems of *V. globulare* plants (Table 4; Figure 9), but based on the numbers collected and known biological information (Schuh and Slater 1995; Table 4), only the Cicadellidae, Aphididae, and Miridae suggest any biological association with the plants.

No individual hemipteran taxon was consistently collected on *V. globulare* plants across multiple sites and years. However, two groups, the leafhoppers (Cicadellidae) and aphids (Aphididae) (Figure 9) constituted 77% of the 255 Hemiptera collected. Both of these families are known to contain species of economic concern.

The Cicadellidae collected were keyed to subfamily and sorted into seven morphospecies. All specimens belonged to the subfamilies Typhlocybinae and Aphrodinae. Typhlocybinae is a large, diverse, and widespread subfamily of leafhoppers with many species known to be of economic importance (Beirne 1956). In other parts of the world, Typholcybinae are associated with trees, shrubs, or other low plants and most species have a very narrow host plant range or are specialists on a single plant (Le Quesne and Payne 1981), though species recorded on *Vaccinium* have been collected on multiple host plants (Dmitriev 2016). Aphrodinae is a relatively small but widespread subfamily of leafhoppers with some species known to vector plant pathogens (Beirne 1956).

Much of the research on leafhoppers and their hosts has focused on agroecosystems and the damage caused by this group is often initially overlooked or attributed to some other cause due to the individual insects' small size and cryptic

nature (Fox 1928, Beirne 1956). The only known attempt to catalog the leafhoppers in Montana was in 1928 and was primarily a survey for the sugar beet leafhopper (Fox 1928). Nothing is known about the assemblage of species that inhabit the forested, montane habitats in the state. However, leafhoppers have been shown to be destructive in native grasslands (Wilbur 1954) and evidence has suggested that non-crop plants may be a source of economically important pest species (Lamp *et al.* 1994). Additionally, species of *Vaccinium* have been shown to have natural resistance to certain Cicadellidae (Meyer and Ballington 1990), suggesting species present on *V. globulare* may be specialized.

Of the 112 leafhopper specimens collected from *V. globulare*, 84 were of a single species, *Dikraneura carneola* (Stål). This species appears to be polyphagous and is a known vector of Western-X disease of stone fruits (*Prunus* spp.) (Kaloostian 1952). Western-X, caused by a phytoplasm, can cause serious damage to fruit crops like sweet cherry, chokecherry, plum, and peach. The phytoplasm is vectored by leafhoppers, and plants such as clover (*Medicago* and *Trifolium* spp.) and dandelion (*Taraxacum officinale* F. H. Wigg) are known weed hosts able to harbor the pathogen (Gubler and Teviotdale 2015). Since so little is known about the leafhopper fauna in Montana's forests, the *V. globulare* / insect association found here is one that warrants further study. Possible questions to be addressed include 1) are the *D. carneola* leafhoppers collected on *V. globulare* carrying the Western-X pathogen? 2) is *V. globulare* susceptible to Western-X disease? and 3) could *V. globulare* be a

reservoir host of the Western-X pathogen or a reservoir host of *D. carneola* populations?

The distribution of aphids on the *V. globulare* plants suggests that there is little cause for concern. They were rarely collected from the plants, and were in small numbers when they were (never more than two individuals on a plant). The individuals collected were a diverse assemblage, plus, in healthy ecosystems, aphid populuations are typically kept under control by natural enemies. This suggests there is not a specialized aphid species attacking huckleberry plants.

Twenty Miridae specimens were collected from *V. globulare* leaves and stems (Table 4). Seventeen of these were *Lygus hesperus* Knight, the western tarnished plant bug, which is a species known to cause significant damage to fruits and berries (Zalom *et al.* 2014). All *L. hesperus* were collected from leaves and fruit at just one site in 2015, while the berries were ripe. Additionally, some of the berries at this site were observed to have puncture wounds and appeared deflated or smashed. The presence of this species, especially in association with damaged fruit, suggests the potential for economic damage and may warrant further study.

Lepidoptera. The Lepidoptera are one of the most economically important insect orders because the larvae of most species are phytophagous (Triplehorn and Johnson 2005). Seventy-eight individual Lepidoptera were collected from the leaves and stems of *V. globulare* (Table 5). Sixty-nine of these were collected as larvae and reared at the MTEC lab. The other nine specimens were collected as adults from the plants. Individuals collected as adults were in the moth families Tortricidae and

Crambidae. Larvae reared to adults were in the moth families Gelechiidae, Tortricidae, Geometridae, and Lasiocampidae and three reared individuals were *Polygonia faunus* (Edwards) (Nymphalidae), a brush-footed butterfly known from Canada south through the Rocky Mountains (Scott 1986).

The three adult Crambidae moths collected are known to feed on grasses and sedges (R. Brown personal communication 2015). All the other Lepidoptera were collected and reared in the lab after being observed feeding on leaves. All of these taxa are known to be polyphagous and have been recorded using *Vaccinium* plants in North America as hosts (Robinson *et al.* 2010). However, *V. globulare* is a new host plant record for every Lepidoptera species collected in this study.

Forty-five percent of the reared Lepidoptera were *Neotelphusa praefixa* (Braun) (Figure 10), a Gelechilidae species known to use *Vaccinium* as a host. These microlepidopteran larvae were observed feeding on *V. globulare* from late May to June, removing interveinal tissue and causing skeletonization of the leaves. They then sealed themselves between two leaves to pupate, emerging as adults in two to three weeks. This species was previously only known from *Vaccinium pallidum* (Robinson *et al.* 2010).

Other reared Lepidoptera included *Acleris albicomana* (Clemens), *Rhopobota naevana* (Hübner), *Clepsis persicana* (Fitch), and *Olethreutes glaciana* (Möschler), all species in the leaf-rolling family Tortricidae (Table 5). Additionally, three individual *A. albicomana* were collected as adults from the plants. Six other Tortricidae were

collected as larvae, reared, and identified to genus: three *Olethreutes* and three *Choristoneura*. One Geometridae from the *Dysstroma truncata* (Hufnagel) species-group, eight Lasiocampidae (*Malacosoma disstria* (Hübner)), and the three Nymphalidae (*P. faunus)* were also reared from the *V. globulare* plants.

Other Groups Collected From Leaves/Stems**.** Two hundred fifty-eight spiders were collected from the leaves and stems of *V. globulare* (Table 6; Figure 3), but over half of these (141 out of 258) were immature. Spiders are known predators, and *V. globulare* shrubs provide habitat for both hunting spiders and orb-weavers that prey on the other arthropods found on and around the plant.

Two hundred fifty Collembola (Table 7; Figure 3) were collected from the *V. globulare* leaves and stems. Of those, 98% were Sminthuridae, the globular springtails. Because this group is so widespread and common on a diversity of vegetation (Triplehorn and Johnson 2005) and were observed on other understory plants at the *V. globulare* study sites, it is unlikely that they have a specialized association with this particular plant.

A variety of other miscellaneous arthropods were collected from the leaves and stems of *V. globulare* plants (Table 7). However, due to the low numbers collected and the known biological information summarized in Table 7, none of these appear to have a biological association with the plant.

Fruit Visitors

Sixty individual insects were collected from the *V. globulare* fruits in the two years (Table 8; Figure 4). Of these, all sawfly larvae, four eupelmid wasps, and one braconid wasp were dissected out of damaged or undeveloped berries, while the rest were collected from the surface of the fruit. The Tenthredinidae larvae were found feeding inside berries, which they had hollowed out and filled with frass. Three larvae were still alive and feeding, four were no longer alive but still in one piece, many were no longer alive and in multiple pieces. All of the live and whole individuals were dissected out of green, undeveloped berries that were still on the plant when the rest of the plants' berries were ripe. However, some purple, damaged fruits also had frass and the remains of larvae inside. The four Eupelmidae and the one Braconidae dissected out of the berries were only found in berries with Tenthredinidae larvae, suggesting a parasitoid/host relationship (See Appendix B for berry dissection notes).

Sawfly larvae (*Pristiphora* sp.) were collected at different sites than those where the adult *Pristophora* were collected earlier in the summer. Additionally, because two different *Pristiphora* species were collected as adults, it is not known if the adults collected from the plants and the larvae found inside the berries are of the same species.

The insects collected externally from the fruits included three ant genera, four families of Hemiptera, and two cantharid beetles (Table 8). The majority of

these species are generalists and are likely to be casual visitors based on low numbers collected and known biological information summarized in Table 8. *Lygus hesperus* is a species known to be economically damaging to strawberries, fruit trees, and other crops (Zalom *et al.* 2014), so this insect's association with the *V. globulare* fruits may be of interest (see above discussion of leaf and stem visiting Hemiptera).

No *D. suzukii* were collected in the monitoring traps placed at the study sites. This suggests little cause for concern regarding potential damage by this invasive fruit fly, at least at the current time and the locations sampled. The lack of *D. suzukii* around ripe huckleberries may suggest that populations have not spread into the remote, more intact habitats of Montana where huckleberries are found, they are not able to thrive in Montana's climate, or the phenology of the insects' development does not match huckleberry fruit development. Similarily, no *V. germanica* were collected at any of the *V. globulare* study sites, suggesting that this invasive species has not spread into the remote areas of western Montana where huckleberries grow.

Recommendations for Further Study

An observational study such as this is valuable for recording baseline data and suggesting further research. In the case of *V. globulare*, one direction for future research is an exploration of the roles various flower visitors play in pollination and fruit set. Not all floral visits result in pollination and effectiveness in pollination varies by insect and plant species. Pollinator exclusion experiments (Kearnes and

Inouye 1993) would be valuable in analyzing the costs and benefits to the plant of floral visits by different organisms and could help determine which insects are necessary for maximum pollination and fruit set and which might disrupt effective pollination.

The Cicadellidae are a large group of insects that have the potential to impact *V. globulare* productivity through foliage damage or by vectoring pathogens. The leafhopper fauna of Montana (especially in the forests of Montana) remains poorly known and, because many of these insects tend to specialize on a narrow range of host plants (Le Quesne and Payne 1981), a survey of Montana's unstudied/understudied habitats may reveal new species and new host associations. Specifically, the *V. globulare* / *D. carneola* association is one that should be addressed, since *D. carneola* is a known vector of Western-X disease (Kaloostian 1952).

The role of *L. hesperus* as an agricultural pest is well known (Zalom *et al.* 2014), but less is known of its impact on forest plants or wild, specialty crops like *V. globulare.* A more focused study of the hemipterans associated with *V. globulare* and their impact on productivity would be valuable. Additionally, because *L. hesperus* was only collected at one site in the current study, and that site was one with a great deal of human traffic, a look at the role of humans in the spread of pest species from agricultural fields to natural habitats may be valuable.

The Anthomyiidae collected from the *V. globulare* plants are of interest because some genera of this family are known to be associated with *Vaccinium* (Jones *et al.* 2014). A natural history study that more closely observes the behaviors of these flies (e.g. when and where they oviposit and if there are larvae in the roots or stems) could uncover the nature of their relationship with *V. globulare.*

Observations of *V. globulare* plants for additional individuals of the previously undescribed *Pristiphora* species would also be of interest. Nothing is yet known about the range, life span, mating, ovipositing, or overwintering habits of this sawfly. Attempts to observe and measure these activities, as well as to rear larvae from fruit and look for associations with other nearby plants would help elucidate the role of *V. globulare* as this species' primary host plant.

Acknowledgements

This project would not have been possible without the help and support of a large number of people. I would like to thank my graduate committee, Michael Ivie, Kevin O'Neill, and Casey Delphia for valuable feedback throughout the project. Tyler Kelly, Paloma Amaral, and Hannah Bares assisted with fieldwork. Tyler Kelly and Paloma Amaral also helped process specimens. Wayne Kasworm, Tabitha Graves, Mike Giesey, Kristina Boyd, and several anonymous Lincoln/Sanders County locals helped locate huckleberry sites. Matt Lavin answered all my plant taxonomy questions. Justin Runyon helped identify the Diptera. Casey Delphia, Harold Ikerd, and Terry Griswold helped identify the Hymenoptera. David Smith helped identify the Tenthredinidae and is

co-author on the description of the new *Pristiphora* species. Richard Brown identified most of the Lepidoptera and Sangmi Lee identified the Gelechiidae. Christopher Dietrich identified the Typhlocybinae and shared known Typhlocybinae host plant records. Lauren Kerzicnik identified the spiders. Frank Etzler, Charles Hart, Vinicius Ferreira, and Micheal Ivie helped identify the Coleoptera. The project was funded through a grant from the Montana Department of Agriculture's Specialty Crop Block Grant Program titled "Huckleberry Challenges: Pollinator Mysteries, Pests and New Invasive Threats." This is a contribution of the Montana Agricultural Experiment Station.

Table 1. Insects Collected on *Vaccinium globulare* Flowers. In 2014-2015, 246 insects from three orders were collected from *V. globulare* flowers.

Hymenoptera Family	Genus/Species	Number
Bees		
Apidae	*Anthophora ursine* Cresson	1
	Apis mellifera Linnaeus	8
	Bombus sitkensis Nylander	55
	Bombus mixtus Cresson	55
	Bombus melanopygus Nylander	54
	Bombus bifarius Cresson	31
	Bombus flavidus Eversmann	7
	Bombus flavifrons Cresson	7
	Bombus centralis Cresson	2
	Bombus insularis (Smith)	2
	Bombus occidentalis Greene	1
Andrenidae	*Andrena* cf. *thaspii* Graenicher	38
	Andrena sp.	2
	Andrena candida Smith (?)	1
	Andrena nigrocaerulea Cockerell	1
	Andrena nivalis Smith	1
	Andrena topazana Cockerell	1
Halictidae	*Lasioglossum* spp.	3
	Halictus rubicundus (Christ)	2
Megachilidae	*Osmia* spp.	4
Wasps		
Cynipidae		1
Ichnerumonidae		1
Vespidae	*Dolichovespula arenaria* (Fabricius)	58
	Dolichovespula maculata (Linnaeus)	15
	Dolichovespula norvegicoides (Sladen)	13
	Vespula acadica (Sladen)	7

Table 1 Continued.

Hymenoptera Family	**Genus/Species**	**Number**
Wasps continued		
Vespidae continued	*Vespula consobrina* Saussure	4
	Dolichovespula arctica (Rohwer)	3
	Vespula vulgaris (Linnaeus)	2
	Vespula austriaca (Panzer)	1
	Vespula atropilosa (Sladen)	1
Ants		
Formicidae	*Formica* spp.	36
	Camponotus spp.	9
	Tetramorium sp.	2
Diptera Family		**Number**
Empididae		8
Syrphidae		7
Ceratopogonidae		1
Mycetophilidae		1
Sciaridae		1
Tachinidae		1
Anthomyiidae		1
Thysanoptera Family		**Number**
Thripidae		7

Table 2. Diptera Collected on *Vaccinium globulare* Leaves/Stems. Families in bold indicate those with a potential biological association with the plant.

Family	**Number**	**Notes on Biology[1]**
Phoridae	100	Adults found in damp places on decomposing organic matter.
Mycetophilidae	83	Abundant in humid areas, especially woodlands; some visit flowers, some feed on honeydew.
Sciaridae	78	Larvae feed on decaying plant material, excrement, and fungi. Adults found near larval habitat.
Empididae	42	Adults most often found in moist vegetation, on tree trunks, or on water. Most feed on nectar and eat protein (some predaceous, some feed on pollen, some feed on dead insects in spider webs).
Muscidae	42	Adults are predacious, pollenophagous, bloodsucking or saphrophagous on dung/decaying organic matter. Larvae found in a variety of habitats.
Chironomidae	36	Associated with water. Most larvae are known to be microphagous. Adults have been known to not feed, feed on nectar, or feed on honeydew.
Cecidomyiidae	31	Larvae may be mycophagous or gall-makers. Some are phytophagous in flower heads or stems without making galls. Some may be predators or parasitoids.
Agromyzidae	**26**	**All larvae feed on living plant tissue, forming a mine/channel in plant tissue. Some are seed feeders or stem borers, or are known to attack roots, twigs, or trunks.**
Anthomyiidae	**21**	**Larvae are mostly phytophagous or saprophagous and live in stems, roots, flower heads, or foliage.**

Table 2 continued.

Family	Number	Notes on Biology[1]
Syrphidae	17	All "probably" visit flowers to gather nectar and pollen. Some species play a role as pollinators. Larvae have a variety of feeding habits.
Chloropidae	14	Adults are commonly collected in low vegetation. Larvae have a variety of feeding habits.
Scathophagidae	**12**	**Larvae have a variety of feeding habits.**
Heleomyzidae	10	Larvae are found in many types of decaying organic matter. Adults can be found in moist, shaded woods near larval habitats.
Ceratopogonidae	8	Adults found in moist areas around larval habitat. Larvae are found in damp habitats (bark, moss, soil, plant debris).
Tipulidae	7	Associated with moist, temperate environments. Adults typically found in low vegetation near streams or in forest.
Sphaeroceridae	7	Associated with all kinds of organic decay.
Bibionidae	6	Larvae are mainly scavengers in leaf litter/organic matter, though some may feed on plant roots. Adults have been observed visiting flowers.
Pipunculidae	5	Endoparasites of Homoptera, especially Cicadellidae and Delphacidae. Adults often seen hovering (like Syrphids) over vegetation seeking hosts.
Calliphoridae	5	Adults visit flowers or rest on low foliage near carrion where they lay their eggs.
Tachinidae	4	Larvae parasitic on other arthropods.
Dolichopodidae	3	Adults and larvae are predacious.
Sepsidae	2	Most often found on dung. Otherwise found on decaying matter, flowers, or with ants.

Table 2 continued.

Family	Number	Notes on Biology*
Platypezidae	2	Adults most often observed in damp woods at times of day (based on sun) when birds are not active. Feed on honeydew or fungi.
Drosophilidae	2	Larvae feed on microorganisms. Some are found in flowers or sap flows in tree wounds. Some could be leaf miners, ectoparasites of Cercopidae, or predators.
Dryomyzidae	2	Have been reared from decaying organic matter including carrion. May be predators.
Ephydridae	2	Found in aquatic and semiaquatic environments. Some larvae may be leaf miners. Adult biology is unknown.
Lauxaniidae	2	Larvae are known to be in leaf litter, rotting tree stumps, or animal dung. Adults are sedentary and shade loving, commonly collected on low foliage in damp woods near water.
Asilidae	2	Adults are predatory. Immatures are cryptic in soil or rotting wood and little is known of their biology.
Sciomyzidae	1	Larvae are predators, parasites, saprophages, or parasitoids.
Hippoboscidae	1	Adults are all ectoparasitic on vertebrates. Larvae form puparia in substrate near hosts.
Rhagionidae	1	Adult biology is poorly known. Larvae have been found in damp soils rich with organic matter.
Tabanidae	1	Most adults are blood-feeders. Others are known to visit flowers. Larvae inhabit wetland soils and are predators.
Tephritidae	**1**	**Larvae feed on living plant tissue, many species form galls.**
Trixoscelididae	1	Nothing is known of immatures. Adults are collected on flowers & vegetation.

[1]Biology notes from McAlpine *et al.* 1981 and 1987.

Table 3. Hymenoptera Collected on *Vaccinium globulare* Leaves/Stems. In 2014-2015, 385 Hymenoptera individuals were collected. Families in bold indicate those with a potential biological association with the plant.

Hymenoptera Family	**Number**	**Notes on Biology[1]**
Sawflies		
Tenthredinidae *Pristophora* new sp.	**42**	**New species.[2]**
Tenthredinidae *Pristophora macnabi* Ross	**1**	**Larvae known to feed inside fruits of *Vaccinium* (Wong 1968).**
Tenthredinidae, other	4	Most larvae are external feeders on foliage. Some make galls.
Cimbicidae	4	Larvae are known to feed on elm, willow, honeysuckle, or snowberry.
Argidae	1	Larvae usually feed on various trees or shrubs.
Ants		
Formicidae, *Formica* spp.	71	Predators. Also feed on honeydew or sap.
Formicidae *Tetramorium* spp.	27	Scavengers or predators.
Formicidae *Tapinoma* spp.	6	Found in any moist habitat. Feeds on sweets and scavenged proteins.
Formicidae *Camponotus* spp.	5	Have a highly generalistic diet.
Formicidae *Lasius* sp.	1	Scavengers.
Wasps		
Ichneumonidae	73	All known to be parasitoids or predators.
Braconidae	67	All are parasitoids.
Diapriidae	36	Most are parasitoids of immature Diptera. Common in moist, wooded areas.
Chalcidoidea	27	Most are parasitoids. Some gall feeders.
Platygastridae	3	Most are parasitoids on the larvae of Cecidomyiidae.
Figitidae	2	All are parasitoids.
Dryinidae	2	Parasitoids of Hemiptera Auchenorryncha. Adults can be predators of Cicadellidae.

Table 3 Continued.

Hymenoptera Family	Number	Notes on Biology[1]
Wasps continued		
Crabronidae	2	Predators.
Vespidae *Dolichovespula maculata* (Linnaeus)	1	Predators.
Vespidae: Eumeninae	1	Predators. Prey usually is Lepidoptera larvae.
Eucharitidae	1	Parasitoids of ant pupae.
Bethylidae	1	Parasitoids of Lepidoptera and Coleoptera larvae.
Bees		
Apidae *Bombus (Psithyrus) flavidus* Eversmann	2	Social parasites.
Apidae *Nomada* sp.	2	Social parasites.
Megachilidae *Osmia* sp.	1	Mason bee, known to visit *Vaccinium* flowers.
Andrenidae *Andrena* sp.	1	Mining bee.
Halictidae *Lasioglossum (Dialictus)* sp.	1	Sweat bee.

[1]Biology notes from Goulet and Huber 1993.
[2] For more information on these *Pristophora,* see text.

Table 4. Hemiptera Collected on *Vaccinium globulare* Leaves/Stems. Families in bold indicate those with a potential biological association with the plant.

Family	Number	Biology Notes[1]
Sternorrhyncha		
Aphididae spp.	**84**	**Very large, diverse group. Found on almost all types of plants.**
Psyllidae	7	Phytophagous. Host-plant relationships are usually very specific.
Pseudococcidae	3	Known to be phytophagous. Some are of economic importance.
Auchenorrhyncha		
Cicadellidae Typhlocybinae *Dikraneura carneola* (Stål)	**84**	**Is polyphagous and is a known vector of western-X disease of stone fruits (*Prunus* spp.) (Kaloostian 1952).**
Cicadellidae Aphrodinae spp.	**23**	**Common and widely distributed. Some known to vector diseases.**
Cicadellidae spp. (Immature)	5	Very large, diverse group that live on almost all types of plants. Species usually specialize on a narrow range of host plants.
Cercopidae	13	Known to feed on a variety of shrubs, trees, and herbaceous plants.
Heteroptera		
Miridae *Lygus hesperus* Knight	**17**	**Has been reported from more than one hundred species of plants in 24 families; known to cause damage to fruit crops (Scott 1977).**
Nabidae	8	Predators.
Pentatomidae 5 *Banasa* sp. 1 *Euschistus* sp.	6	Generalist plant feeders.
Miridae spp.	3	Most are phytophagous, some are predators.
Lygaeidae sp.	1	Most feed on seeds.
Piesmatidae sp.	1	Sap-feeders.

[1]Biology notes from Schuh and Slater 1995 unless otherwise cited.

Table 5. Lepidoptera Collected on *Vaccinium globulare* Leaves/Stems. All were collected as larvae and reared unless otherwise noted.

Family	Number	Known Host Plant Information[1]
Gelechiidae		
Neotelphusa praefixa (Braun)	34	Larvae known to feed on *Vaccinium palladium* Aiton.
Tortricidae		
Acleris albicomana (Clemens)	15 9 reared, 6 collected as adults	Larvae known to have a variety of host plants including *Vaccinium* spp. but not previously on *V. globulare*.
Rhopobota naevana (Hubner)	4	Larvae known to have a wide variety of host plants including *Vaccinium* spp. but not previously on *V. globulare*.
Clepsis persicana (Fitch)	3	Larvae known to have a wide variety of host plants including *Vaccinium* spp. but not previously on *V. globulare*.
Olethreutes glaciana Möschler	1	Larvae known to have a wide variety of host plants including *Vaccinium* spp. but not previously on *V. globulare*.
Olethreutes spp.	3	Larvae known to have a wide variety of host plants including *Vaccinium* spp. but not previously on *V. globulare*.
Choristoneura spp.	3	Larvae known to have a wide variety of host plants including *Vaccinium* spp. but not previously on *V. globulare*.
Lasiocampidae		
Malacosoma disstria (Hubner)	2 larvae 4 pupae 2 adults	Larvae known to have a wide variety of host plants including *Vaccinium* spp. but not previously on *V. globulare*.
Nymphalidae		
Polygonia faunus (Edwards)	3	Larvae known to have a wide variety of host plants. Scott (1986) includes "*Vaccinium* (sometimes in Michigan)" in his list of host plants.
Geometridae		
Dysstroma truncata (Hufnagel) species group	1	Larvae known to have a wide variety of host plants including *Vaccinium* spp. but not previously on *V. globulare*.
Crambidae		
Crambidae Crambini	3 All collected as adults	Most species in this tribe feed on grasses and sedges (Brown, personal communication 2015).

[1]Host plant records from Robinson *et al.* 2010 unless otherwise cited.

Table 6. Spider Families Collected on *Vaccinium globulare* Leaves/Stems.

Family	Adults	Immature	Biology Notes[1]
Araneidae	65	73	"Orb weavers." Often collected with beat sheet or sweep net. Common and diverse family.
Dictynidae	14	2	"Meshweavers." Arboreal, making webs on foliage, flowers, branches, or dried stalks of plants. Sometimes webs are small within one folded leaf.
Linyphiidae	13	5	"Sheet web spiders." Found in leaf litter, the ground surface, or in vegetation. Semi-permanent webs, hunt upsidedown. Generally feed on soft bodied insects (Collemboa, Diptera).
Miturgidae	10	18	"Prowling spiders." Wandering hunters. Most are ground dwellers, some arboreal. Construct white sac-like retreats in a folded or rolled leaves or under rocks.
Salticidae	4	11	"Jumping spiders." Predators.
Theridiidae	4	13	"Cobweb weavers." Sedentary predators, some ground dwellers. Usually build webs under some sort of cover (i.e. rocks, leaves, branches).
Gnaphosidae	1	0	"Ground spiders." Found in leaf litter, under rocks, and in decomposing wood. Are wandering generalized predators, use silk only for draglines, retreat, and egg sacs.
Philodromidae	1	0	"Running crab spiders." Active predators on leaves and stems of plants.
Tetragnathidae	1	0	"Longjawed orb weavers." Common, widespread in various vegetation.
Thomisidae	4	19	"Crab spiders". Most are ambush predators, some are wandering hunters.

[1]Biology notes from Ubick *et al.* 2005 and Bradley 2013.

Table 7. Miscellaneous Arthropods Collected on *Vaccinium globulare* Leaves/Stems.

Coleoptera		
Family	**Number**	**Biology Notes[1]**
Cantharidae spp.	20	Adults are often found on flowers (though these were not found associated with flowers). Larvae are predators.
Elateridae (Six different genera)	14	Adults are phytophagous and live on flowers, under bark, or in vegetation. Larvae live in soil or rotting wood.
Curculionidae 3 *Sibinia* spp. 2 *Magdalis* spp. 1 *Panscopus* sp.	6	*Sibinia* is associated with legumes; *Magdalis* larvae mine in bark of dead/dying trees, adults are associated with various trees; *Panscopus* is associated with forests.
Scraptiidae *Anaspis rufa* Say	6	Adults are often collected from flowers. Larvae are associated with dead logs or lichens.
Lycidae *Dictyoptera simpliceps* Mannerheim	2	Adults feed on nectar and honeydew. Larvae may be predators, probably feed on slime molds or bacterial/yeast slime.
Chrysomelidae *Syneta* sp. *Scelolyperus* sp.	2	Phytophagous, adults feed principally on flowers and foliage.
Coccinellidae *Anatis rathvoni* (LeConte) *Coccinella trifasciata* L.	2	Predators.
Buprestidae *Anthaxia inornata* (Randall)	1	Wood-borers. Adults can live on foliage of trees or shrubs.
Staphylinidae *Ontholestes cingulatus* (Gravenhorst)	1	Associated with carrion and fungi.
Other Miscellaneous Arthropods		
Order	**Number**	**Biology Notes[2]**
Collembola Sminthuridae	251	Common on a diversity of vegetation.

Table 7 continued.

Other Miscellaneous Arthropods - continued		
Order	**Number**	**Biology Notes[2]**
Subclass Acari	60	Have a diversity of habits and life histories—predators, parasites, scavengers, and plant feeders.
Thysanoptera	17	Known to cause plant damage with piercing, sucking, or rasping mouthparts. May vector disease.
Opiliones	7	Most are predacious.
Plecoptera	6	Adults generally do not feed. Nymphs associated with water.
Collembola	4	Most feed on decaying organic material or fungi.
Psocoptera	1	Associated with bark or foliage of trees and shrubs, under bark, or in leaf litter.
Chrysopidae	1	Adults may be predators. Some are known to visit flowers.

[1]Coleoptera biology notes from Arnett *et al.* 2002.
[2]Other biology notes from Triplehorn and Johnson 2005.

Table 8. Insects Collected on *Vaccinium globulare* Fruits. Families in bold indicate those with a potential biological association with the plant.

Family	Number	Biology Notes[1]
Hymenoptera		
Tenthredinidae Sawfly larvae	**25**	***Pristophora* spp. known to use *Vaccinium* as a host.**
Formicidae 6 *Formica* spp. 4 *Tetramorium* spp. 1 *Camponotus* sp.	11	Known to be predators and scavenge for sweet foods, like nectar and honeydew.
Eupelmidae	**4**	**Ectoparasites of larvae or prepupae that are usually concealed in plant tissue or cocoons.**
Braconidae	1	Known to be parasitoids.
Hemiptera		
Miridae ***Lygus hesperus* Knight**	**8**	**Known to be a pest of fruit and seed crops.**
Immature Heteroptera	4	Often are plant/sap feeders.
Aphididae	3	Plant/sap feeders. Some known to be pests on crops.
Nabidae	2	Predators.
Dictyopharidae	1	Chiefly grass feeders.
Coleoptera		
Cantharidae	2	Usually are found on flowers.

[1]Biology notes from Goulet and Huber 1993.

Table 9. A Comparison of Bees Collected on *Vaccinium globulare* Flowers vs. Bees Collected in Pan Traps.

Bee Genus	2014 Flowers	2014 Pan Traps	2015 Flowers	2015 Pan Traps
Andrena	23	4	21	9
Anthophora	1	0	0	1
Apis mellifera	8	0	0	0
Bombus	160	1	54	11
Dufourea	0	1	0	0
Halictus	2	1	0	19
Hoplitus	0	0	0	1
Hylaeus	0	2	0	0
Lasioglossum (Dialictus)	1	109	0	5
Lasioglossum (Evylaeus)	1	12	0	5
Lasioglossum (s.str.)	1	2	0	3
Nomada	0	1	0	4
Osmia	4	4	0	32
Panurginus	0	0	0	1
Sphecodes	0	3	0	1
TOTAL:	201	140	75	92

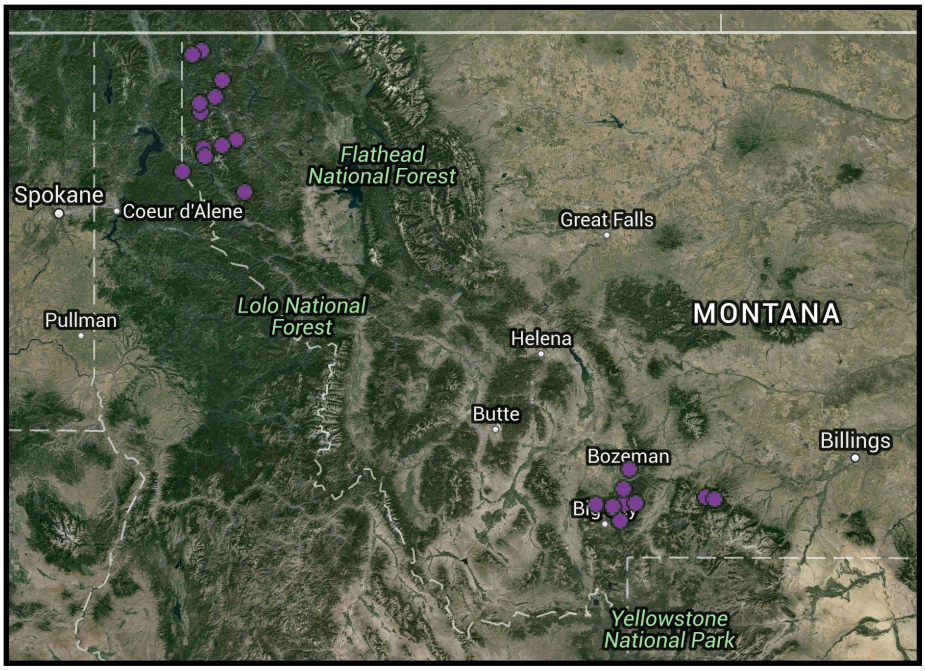


Figure 1. Map of Huckleberry Study Sites. Sampling was conducted at 21 sites in northwest and southwest Montana in 2014 and 2015.

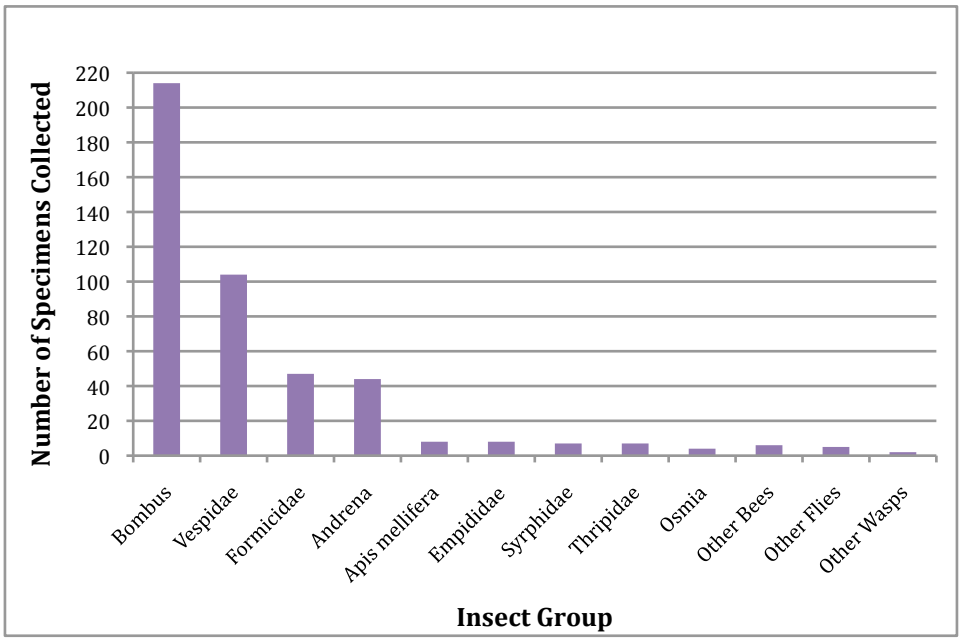


Figure 2. *Vaccinium globulare* Flower Visitors. In 2014-2015, 246 insects were collected from *V. globulare* flowers.

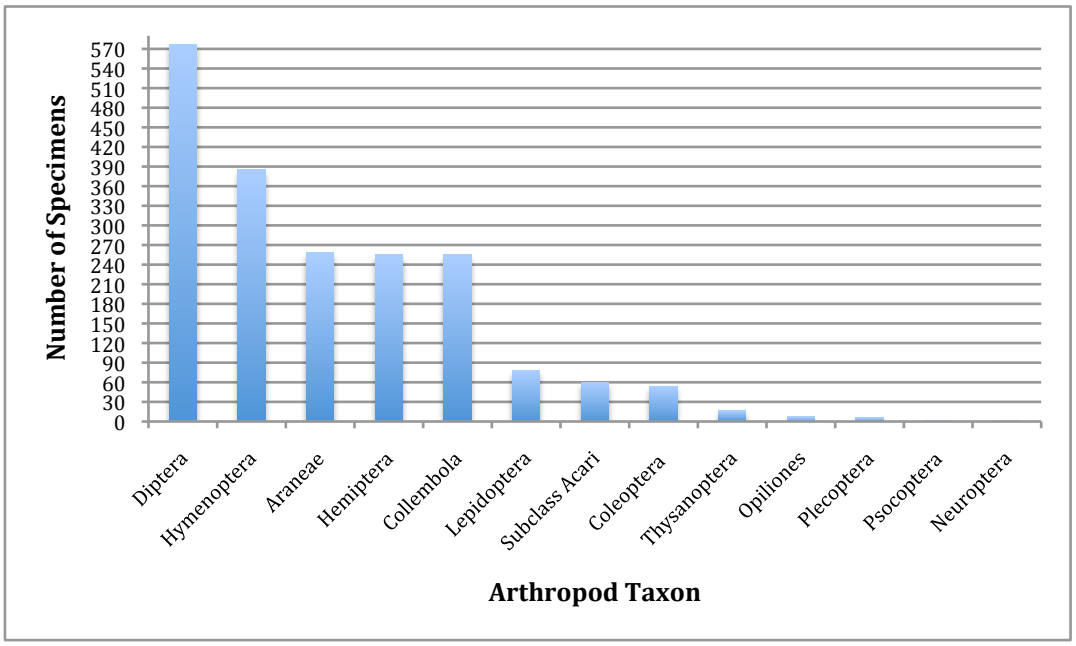


Figure 3. *Vaccinium globulare* Leaf and Stem Visitors. In 2014-2015, a total of 1,954 arthropods were collected from *V. globulare* leaves and stems.

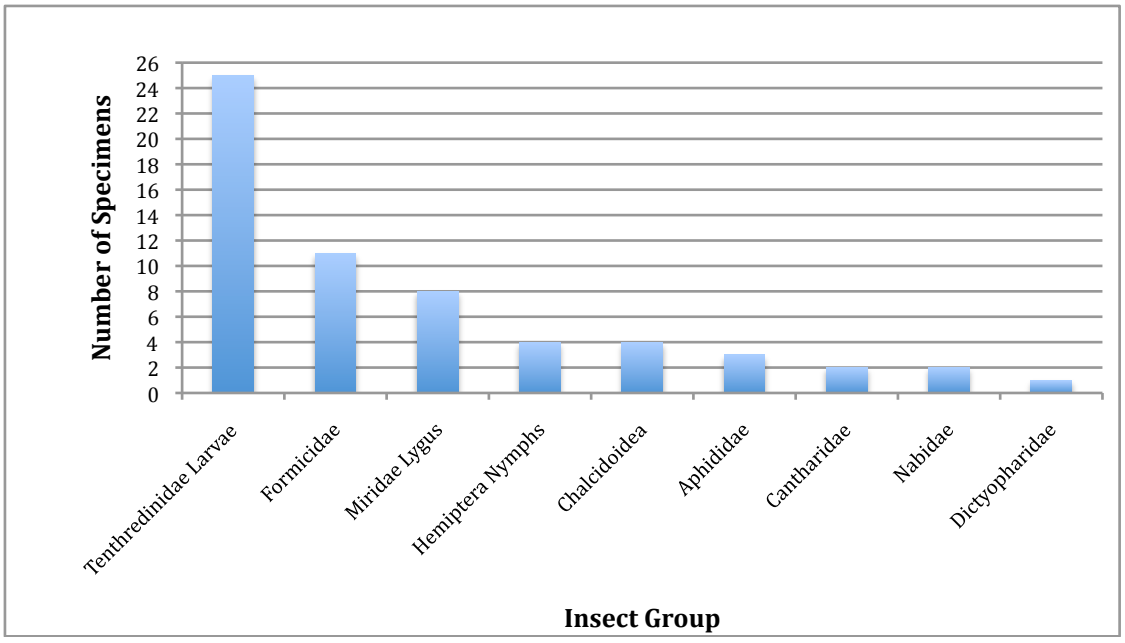


Figure 4. Insects Collected from *Vaccinium globulare* Fruits. In 2014-2015, 60 insects were collected from *V. globulare* fruits.

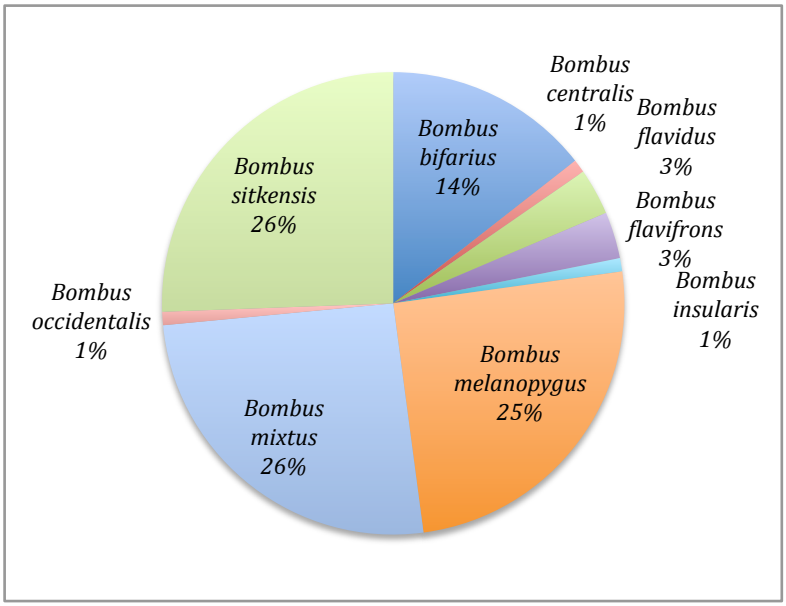


Figure 5. *Bombus* Species Visiting *Vaccinium globulare* Flowers. In 2014-2015, 214 total bumble bees were collected on *V. globulare* flowers. Four species made up 91% of the bumble bees collected.

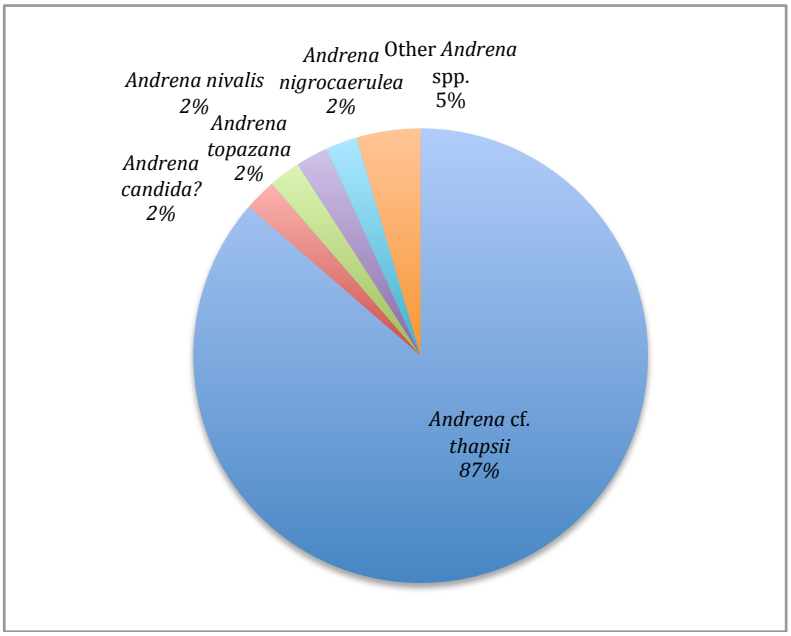


Figure 6. *Andrena* Species Visiting *Vaccinium globulare* Flowers. In 2014-2015, 44 total andrenids were collected from *V. globulare* flowers. 87% of these were just one species.

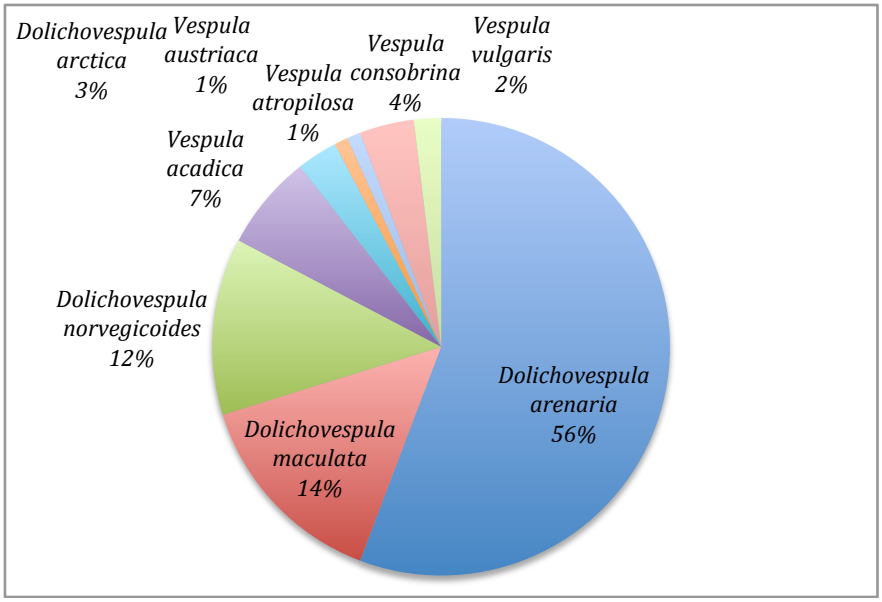


Figure 7. Vespinae Species Visiting *Vaccinium globulare* Flowers. In 2014-2015, 104 total vespids were collected visiting *V. globulare* flowers. Of these, 82% were just three species.

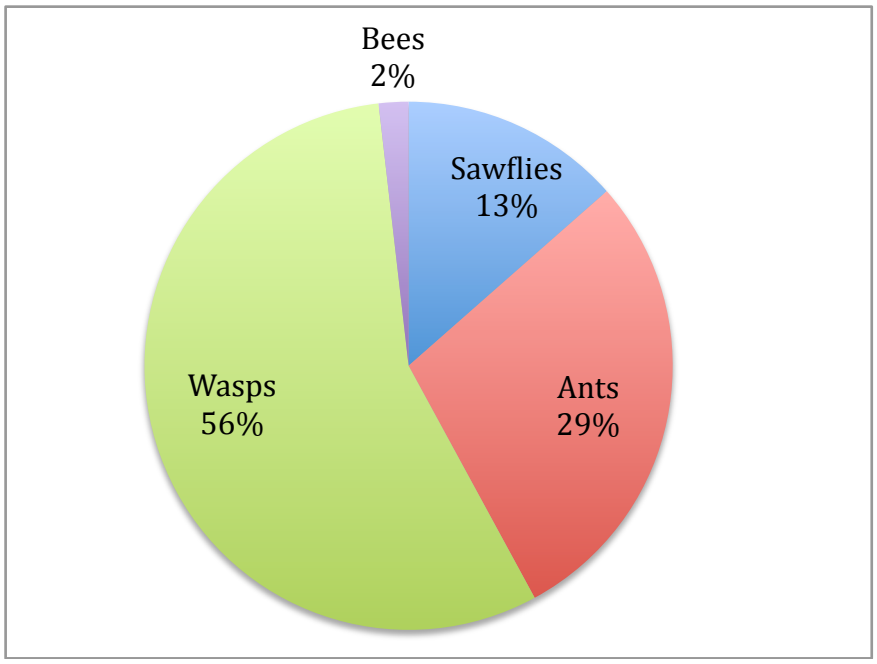


Figure 8. Hymenoptera on *Vaccinium globulare* Leaves and Stems. In 2014-2015, 385 total Hymenoptera specimens were collected.

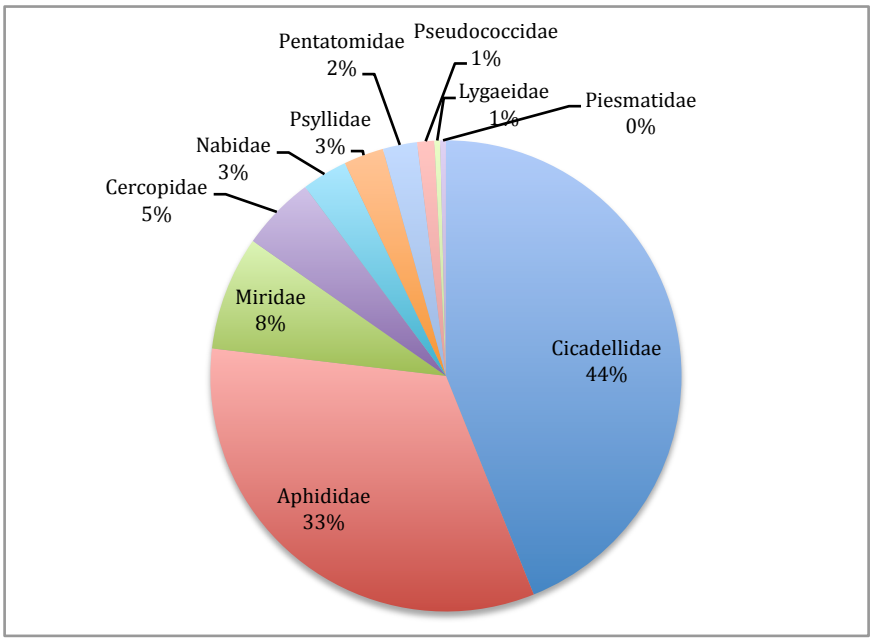


Figure 9. Hemiptera on *Vaccinium globulare* Leaves/Stems.
In 2014-2015, 255 total Hemiptera specimens were collected from *V. globulare* leaves and stems. Of these, 77% were leafhoppers and aphids.

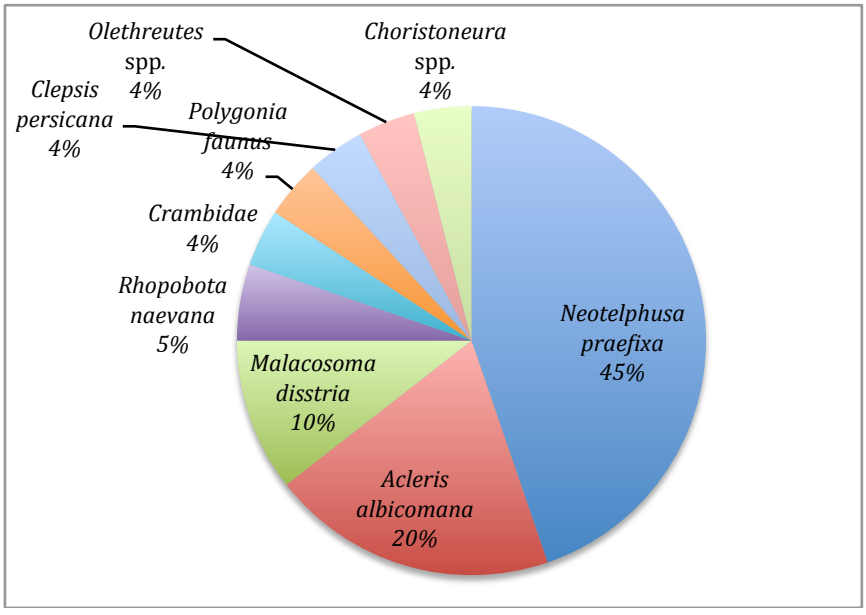


Figure 10. Lepidoptera on *Vaccinium globulare* Leaves/Stems.
In 2014-2015, 78 total Lepidoptera specimens were collected from *V. globulare* leaves and stems.

THE BUMBLE BEES OF MONTNA

Introduction

Shrinking ranges and declining populations of wild and managed bees (Hymenoptera: Apoidea) have recently been raising concerns worldwide (Chaplin-Kramer *et al.* 2014, Goulson *et al.* 2015). Hypotheses have been presented on causes of the observed declines, and predictions have been made about negative economic and environmental impacts (Holden 2006, Potts *et al.* 2010, Burkle *et al.* 2013). Factors proposed to play a role in population declines of pollinators include anthropogenic landscape changes, a lack of high quality food, the presence of pathogens and parasites, competition and pathogen transfer from non-native or commercial bees, pesticides, and climate change (Winfree *et al.* 2009, Goulson *et al.* 2015, Kerr *et al.* 2015).

Among pollinators, bumble bees (*Bombus* spp.) are one of the most recognizable species due to their large size and colorful bodies. Since they have the ability to sonicate or "buzz pollinate" certain types of flowers, they are also some of the most important pollinators for wild and cultivated plants that have poricidal anthers, like huckleberries (Ericaceae) and tomatoes (Solanaceae) (Harder and Barclay 1994, De Luca and Vallejo-Marin 2013). Like other bees, bumble bees worldwide have experienced declines and range contractions over the past two decades (Goulson *et al.* 2005, Williams and Osborne 2009, Cameron *et al.* 2011, Goulson *et al.* 2015). In the United States, Cameron *et al.* (2011) used historic

records and intensive sampling of present-day communities to show that four species, *Bombus affinis* Cresson, *Bombus occidentalis* Greene, *Bombus terricola* Kirby, and *Bombus pensylvanicus* (DeGeer), have had drastic reductions in their historic ranges over the last 20-30 years. Some estimates indicate that up to 25% of North American bumble bee species are facing some level of stress (Colla *et al.* 2012, Williams and Jepson 2014). In 2014, the International Union for Conservation of Nature (IUCN) Bumble Bee Specialist Group recommended five North American bumble bee species for "Critically Endangered" status, two for "Endangered" status, five for "Vulnerable" status, and one for "Near Threatened" status, while 28 species were considered to be of "Least Concern" (Williams and Jepson 2014). At least one *Bombus* species in North America, *Bombus franklini* Frison, known only from northern California and southern Oregon, may already be extinct (Williams *et al.* 2014).

Despite myriad studies focused on varying aspects of bumble bee biology amid concern over declining populations, large gaps in baseline knowledge still exist. Michener (2007) states that there may be as many as 250 bumble bee species worldwide, though some regions have been well studied while the fauna of other regions remains virtually unknown. In the U.S., checklists, range maps, and population-monitoring studies have been published on the bumble bees of some states (Severn 1926, Thorp *et al.* 1983, Colla *et al.* 2011, Warriner 2012, Koch *et al.* 2012), whereas other states have few published records.

In the U.S., Montana is one of the least-studied areas, partly because of having a sparse population and a vast area, much of which is difficult to access (Montana Wilderness Association 2015). Bumble bee range maps created using museum data and statistical models predict that 25-31 species might occur in Montana (Williams *et al.* 2014). Twenty-seven species have been reported in the literature (Franklin 1912, Milliron 1971 and 1973, Koch *et al.* 2012, Williams *et al.* 2014), but some of these reports are based on a single locality, and less than 500 specimens have been reported from the entire eastern half of the state (Williams *et al.* 2014).

Due to its large size, topographic diversity, and climatic variability, Montana supports vegetation zones ranging from relatively low-elevation, dry plains in the east to boreal and alpine zones in the west (Lesica 2012). Additionally, Montana is at the junction of known eastern and western North American bumble bee ranges (Koch *et al.* 2012). Alpine environments connected to the arctic via Canada provide a link for bumble bee species from the north, while xeric Great Basin elements approach from the south (Williams *et al.* 2014, Discover Life 2016). This diversity of landscapes and unique geographic placement make it likely that Montana contains a large and unique assemblage of bumble bee species.

Habitat and landscape changes have been cited as one of the primary factors threatening bumble bee populations (Goulson *et al.* 2015). Montana's history includes disturbances associated with mining, logging, agriculture, transportation, and recreation (Burlingame and Toole 1957, Wyckoff 2006), but no one has explored how these landscape changes could have affected bumble bee populations

in the state. However, before we can determine if and how bumble bee populations are changing, a baseline understanding of which species occur in Montana is necessary. The purpose of this project was to create a current inventory of *Bombus* species in the state and provide county-level distribution data. This information is meant to inform future research and conservation efforts.

Chronology of Bumble Bee Records in Montana (1883-2014)

The literature includes records of 27 species of bumble bees collected in Montana since 1883 (Table 10). Two other species (*Bombus borealis* Kirby and *Bombus bohemicus* Seidl) are recorded close to the Montana border (Williams *et al.* 2014), and three additional species (*Bombus cryptarum* (Fabricius), *Bombus morrisoni* Cresson, and *Bombus fraternus* (Smith) are predicted to be here based on geographic suitability modeling (Milliron 1973b, Williams *et al.* 2014).

The journals of Lewis and Clark (Moulton 2002) provide the first known mention of the existence of bumble bees in Montana, but provide no reliable taxonomic details. In the mid-19th century, Ezra Townsend Cresson (1864, 1878, 1879) published three papers describing new species and cataloguing the known North American Apidae. While these descriptions include species now known to occur in Montana and specimens were examined from localities throughout the western U. S. and Canada, no Montana specimens were cited.

A few decades later, in 1899, Robert Allen Cooley, the first entomologist of the Montana Agriculture Experiment Station in Bozeman founded the Montana Entomology Collection (Montana State University College of Agriculture 2015). In his role as State Entomologist, Cooley collected bumble bees from around the state and sent them to experts for identification. These specimens can still be found in the Montana Entomology Collection (MTEC), the National Museum of Natural History Collection (NMNH), and the Academy of Natural Sciences, Philadelphia Collection (ANSP). Among new species of Apoidea described by Austin Winfield Morrill in 1903 were four previously undescribed species of *Bombus* collected by Cooley in Montana (Morrill 1903).

In 1912, 22 species of *Bombus* and *Psithyrus* (which is now considered a subgenus of *Bombus*, Michener 2007) were recorded from Montana or predicted to be in Montana by Henry James Franklin (1912). After accounting for taxonomic changes in the last 103 years, these records represent 15 documented species and five predicted species (Table 10). Franklin (1915) later recorded the seventeenth Montana *Bombus* species from Hill County (Table 10).

Biological surveys of the states were conducted by the United States Department of Agriculture in the 1910s, including a 1919 expedition to the Missouri River Valley and the mountains of north-central Montana (Anonymous 1920). Bumble bees collected on that expedition are deposited in the NMNH collection and include four species (Table 10). While none of the species collected were new state

records, they all were new county records, and are the first specimens recorded from that part of the state.

Theodore Henry Frison clarified some of Franklin's taxonomic issues in 1923. He also recorded three additional species from Montana (Table 10).

In 1926, Harry Charles Severin published *The Bumble Bees of South Dakota*, documenting 26 *Bombus* species known to occur adjacent to Montana's eastern border. While none of these records were of specimens collected in Montana, data from neighboring areas are valuable when determining and predicting the ranges of bumble bee species.

Three decades later, Robert Kral (1955) recorded four *Bombus* species from northwest Montana, adding another species to the state list (Table 10). Later, three papers on the bumble bees of the eastern and far western U. S. were published, including keys, notes, and distributions maps (Stephen 1957, Mitchell 1962, and Thorp 1962). Unfortunately, Montana was outside the study areas of these works, though descriptions and geographic records for species known to be in Montana were documented in adjacent states.

In the early 1970s, Herbert Edward Milliron (1971, 1973a, 1973b) published a multi-volume monograph of the *Bombus* of the western hemisphere, in which he documented five species from Montana and created range maps predicting the presence of six others (Milliron 1971, 1973a, 1973b) (Table 10). However, two of his predicted species, *Bombus kirbyellus* Smith (currently synonomized with *Bombus*

kirbiellus Curtis, see species account*)* and *Bombus californicus* Smith, had already been documented from Montana (Franklin 1912, Franklin 1915).

Since Milliron's work in the early 1970s, published bumble bee research in Montana has included an exploration of pollination relationships on the Beartooth Plateau (Bauer 1983), territorial and mating behavior of male bumble bees (O'Neill *et al.* 1991), effects of forest management practices (Fultz 2005), diversity of bees on wildflower seed farms (Pearce *et al.* 2012), and alpine pollinator network mapping (Simanonok and Burkle 2014). None of these projects were focused specifically on surveying or mapping bumble bee populations, but each provides species records for different parts of the state (Table 10).

In 2011-2012, the United States Department of Agriculture and the Pollinator Partnership published *Bumble Bees of the Eastern United States* (Colla *et al.* 2011) and *Bumble Bees of the Western United States* (Koch *et al.* 2012). After examining museum specimens collected over the last 100 years, range maps and species descriptions were created to document eastern and western bumble bees. The maps include actual records as well as generalized range polygons predicting each species' larger distribution. No range maps in the eastern guide extend beyond the western borders of Minnesota and Iowa. However, the western guide documents 20 species from Montana and predicts the presence of four others (Table 10).

Finally, in 2014, Williams *et al.* published an identification guide to 46 known North American bumble bee species. Predictive range maps for each species were

created after compiling over 250,000 records and using software to model climatic suitability. These maps show records of 25 species in Montana or close to the border, while the predictive geographic suitability maps show that five more species could be present (Table 10).

Materials and Methods

Museum and Lab Collections

This study is based on 12,067 specimens of *Bombus* species from 25 North American collections and four databases. Tables 11 and 12 summarize the institutions, labs, and private collections that contributed data to this project. When a particular collection had a large number of *Bombus* specimens of the same species from the same locality, all determinations were checked and verified, but not every individual was added to the database.

All specimens were identified using keys from current literature: Williams *et al.* (2014), Koch *et al.* (2012), Colla *et al.* (2011), Thorp *et al.* (1983), and Stephen (1957). Taxonomy followed Williams *et al.* (2014) for all species except *Bombus fervidus* (Fabricius) and *B. californicus*, which we consider to be separate species, and *B. balteatus*, which we call *B. kirbiellus* (see species accounts for explanation). New state records, rare species, or difficult-to-identify specimens were verified by James Strange or Jonathan Koch at the Bee Biology and Systematics Laboratory (BLCU), Logan, UT or Robbin Thorp at the University of California, Davis.

Initially, 3,003 specimens from the Montana Entomology Collection (MTEC) at Montana State University (MSU) were examined. Determinations were verified, corrected, or made and each specimen was labeled with a unique identifier tag (barcode). Localities were georeferenced and verified or corrected and all records were uploaded to the MTEC XBio:D database (http://mtent.org/Projects/Bees%20of%20Montana/bumble_bees/bumble_bees.html) managed through The Ohio State University. Additionally, *Bombus* specimens deposited in other labs at MSU (Table 11) were examined, determined, and databased.

Lists of *Bombus* specimens collected in Montana were obtained from the Bee Biology and Systematics Laboratory (BLCU) database, the American Museum of Natural History (AMNH) database, the Yale University Peabody Museum (PMNH) database, and from Leif Richardson's (Williams *et al.* 2014) database. These lists of specimens were reviewed and other North American entomology collections were contacted for updated lists or loans. Requests for loans were made if there were 1) new state records, 2) new county records, 3) suspicious determinations, 4) range discrepancies, and/or 5) undetermined *Bombus* from Montana. On loaned specimens, we verified or updated historic determinations, identified undetermined specimens, georeferenced, and added the records to the database. Additional historic specimens deposited at the National Museum of Natural History (NMNH) in Washington, D.C. and the Academy of Natural Sciences in Philadelphia (ANSP) were examined and included.

Field Sampling

The review of museum specimens and the distribution of locations from which they were collected revealed that Montana has historically been undersampled (Figures 11 and 12), especially in the eastern half of the state. In April 2015, the database showed four counties (of the 56) with no *Bombus* records and seven others with less than three species documented. So, during the 2015 field season, collecting was focused on unsampled or undersampled regions of Montana (Figure 13). In cooperation with the Montana Department of Agriculture's Cooperative Agriculture Pest Survey (CAPS) program, 30 Japanese Beetle traps (Foley *et al.* 2011) and 29 yellow bucket traps (Brambila *et al.* 2014) were placed in 20 of Montana's 56 counties from March through August. In addition, between March and September, we collected bumble bees across the state, usually on flowers. Bumble bees collected by other labs at MSU and the United States Geological Survey (USGS) in Glacier National Park were also added to the database. Montana's County Extension Agents and Master Gardeners assisted with the project by sending *Bombus* specimens collected throughout the state.

As necessary, we cleaned the collected bumble bees by shaking them in a jar of hot soapy water, rinsing them with water and EtOH, and drying them with an electric hair dryer (Droege *et al.* 2012). Once cleaned, specimens were mounted, identified, and databased. Data were used to produce county-level range maps and graphs of each species' accumulation over time.

Data Analysis

Data were extracted from the XBio:D database into Excel® for analysis. Maps were generated using the locality information in the database. The EstimateS® (Colwell 2013) program was used to generate a Chao1 species richness prediction using each county as a sample. Species richness predictors estimate the total number of species present in a community. The Chao1 estimator is a commonly used estimator that is based on the number of rare groups found in a sample (e.g. singleton taxa and doubleton taxa) to adjust for the number of species present but not detected by sampling (Chao 1984, Gotelli and Colwell 2011). This estimator is a lower bound estimate, and often underestimates the true parameter (Chao 1984), but statisticians consider it a robust estimator of minimum species richness (Gotelli and Colwell 2011). A species accumulation curve was also generated using the EstimateS® (Colwell 2013) program. Each county was considered a sample, and samples were randomized 50 times to create the mean accumulation curve.

Results

During the study, 12,067 Montana *Bombus* records were added to the XBio:D database (http://mtent.org/Projects/Bees%20of%20Montana/bumble_bees/bumble_bees.html). Additionally, 645 specimens from Alberta, Canada were examined and 76 of those records were databased.

After sampling in all 56 counties (Figure 14), 28 *Bombus* species are now known to occur in Montana (Table 13; Figure 15; Figure 16). These species include

six that are typically considered to have eastern U.S. ranges (Koch *et al.* 2012): *Bombus auricomus* (Robertson), *Bombus bimaculatus* Cresson, *Bombus ternarius* Say, *B. borealis*, *B. pensylvanicus*, and *B. terricola*. The presence of *B. bimaculatus* in Montana is of special note, since its presence had not been documented or even predicted to be west of the eastern Dakotas and Nebraska (Williams *et al.* 2014). One of the 28 species is *B. impatiens*, another eastern species that is reared for commercial purposes. The specimens in our database were collected from a research project using commercial bees (see species accounts) in Choteau County. Because no specimen of *B. vosnesenskii* from Montana could be found to verify Frison's 1923 literature record, this species is not included in the 28.

Analysis with the EstimateS® program (Colwell 2013) yielded a Chao1 mean prediction of 28 species of *Bombus* for Montana (with standard deviation of 0.12 and 95% confidence interval of 28.0 to 28.2 species). The mean species accumulation curve generated with the EstimateS® program (Colwell 2013) reaches an asymptote at 28 species (Figure 17). The variation in sampling methodology by many individuals over the last 130 years prevents quantitative analyses of diversity and abundance comparisons by region. Nevertheless, the distribution maps (Figure 16) and numbers of specimens per species presented here (Figure 15) can provide insights into the relative abundance and ranges of *Bombus* species in Montana.

Patterns of Accumulation

The oldest specimens in the database were collected in 1883 (4 individuals, NMNH). Graphs of the accumulation of *Bombus* records from that time to the

present (Figures 18 and 19) highlight several periods when records of *Bombus* species in Montana increased dramatically. The first of these increases occurred during the first two decades of the 20th century, with 1904 and 1913 being the two biggest collecting years. This time period coincides with the work of Cooley, the first State Entomologist, and Franklin, who revised the New World *Bombus* in 1912-1913. In fact, most of the specimens in the database from this time period were initially determined by Franklin.

Another big year for *Bombus* collecting in Montana was 1946, when Severin, the North Dakota State Entomologist, was collecting in Montana. A third major increase in specimen records came from 1964 to 1966. Several parties, including Charles L. Remington, Beatrice Vogel and Christopher John Durden, and Thomas F. Walsh were collecting at localities all over Montana during that three-year period. From the late 1970s into the 1980s another large set of records was accumulated from two collectors in the Beartooth Mountains, Ernest Alden Wells and L. Walter Macior (see database, http://mtent.org/Projects/Bees%20of%20Montana /bumble_bees/bumble_bees.html, for specific record details).

In 1990 records began accumulating even more rapidly; 63% of the records in the database were collected between 1990 and 2015. This 25-year time frame coincides with several MSU entomology projects in the Michael A. Ivie and Kevin M. O'Neill labs, both of whom joined MSU in 1985. Also during this time, the Bee Biology and Systematics Lab in Logan, UT, did targeted collecting of *Bombus bifarius* Cresson and *B. occidentalis,* resulting in the accumulation of over 500 records in

2009. The Montana Department of Agriculture sent the bumble bees that were caught in CAPS program traps in 2009 and 2011 to the MTEC for mounting and identification, contributing over 500 more specimens. Laura A. Burkle joined the Ecology Department at MSU in 2011, and pollinator projects in her lab have contributed hundreds more specimens, especially in 2014. Finally, the greatest accumulation of records (over 3,000) came in 2015, and most of those specimens were collected for this project.

Discussion

Bumble bee sampling has now occurred in all 56 of Montana's counties. The number of *Bombus* specimens collected in the state has greatly increased since 2000 due, not only to the sampling effort associated with the current project, but also to the general increase in pollinator research projects over the last 15 years. With the exception of two species, *B. occidentalis* and *Bombus suckleyi* Greene (see species accounts for discussion of this), all species have experienced at least a 49% increase in the number of specimens known from Montana since 2000 (Table 14; Figure 20).

The intensive 2015 sampling did not uncover any new state records. There were, however, 113 new county records (Figure 21). Moreover, sampling increased sample sizes and added species records for previously undersampled localities (Figures 11, 12, and 15).

Additional sampling is still needed to fully understand the range and numbers of *Bombus* species in Montana. Over 50% of Montana's counties (29/56)

currently have less than 100 *Bombus* records (Figure 22) and two counties only have 12 records. The entire state presents a diversity of habitat types, vegetation, and elevations that, if sampled more completely, could provide additional insights into state and North American range and population trends for the 28 species known to occur here and may also reveal the presence of additional species.

Sampling Effort

Geographic variation in historic sampling effort is most certainly a factor in interpreting the data presented here. The cities with universities (MSU, Bozeman, in Gallatin County and University of Montana, Missoula, in Missoula County) and the most commonly visited areas of Montana (e.g. Glacier National Park in Flathead County) have the greatest number of specimens (Figure 11). The counties where entomologists have conducted research projects (e.g. Gallatin, Flathead, Carbon, and Meagher) have the most species (Figure 12). Additionally, the map of collection sites in Montana (Figure 14) matches up well with the state's major highways, indicating that much of the historical sampling of *Bombus* has been convenience sampling. Also, at least two of the projects that contributed data targeted limited subsets of *Bombus* species (O'Neill *et al.* 1991, Cameron *et al.* 2011), which may have skewed the relative abundance data presented here for those target species (*Bombus rufocinctus* Cresson, *Bombus griseocollis* (DeGeer), *Bombus nevadensis* Cresson, *B. occidentalis*, and *B. bifarius*). Furthermore, collecting in Lincoln and Sanders Counties in 2014 was part of a study focusing on insects associated with the huckleberry plant (*Vaccinium globulare* Rydberg, Dolan 2016a). Bumble bees were

only collected in specific habitats from one host plant, so these counties in northwest Montana may have more *Bombus* species than the data suggest.

Four Elusive Species

The Chao1 mean prediction of 28 *Bombus* species in Montana (Figure 17) indicates that we are statistically unlikely to find more species, among those historically present, than what we have already documented. However, based on known ranges and biological information, there are four *Bombus* species not yet recorded from Montana that may still be found. One of these is *B. cryptarum,* whose range is recorded as the tundra/taiga regions of the Mountain West from Alaska through southwestern Canada and across northwestern Canada to the Hudson Bay (Williams *et al.* 2014). The Canadian Rocky Mountains provide a continuous alpine environment south into northwestern Montana, allowing for the possibility of the occurrence of *B. cryptarum*. And, records from Canada show this species has been collected within 20 kilometers of Montana's northern border near Milk River, Alberta (JMLC).

Predictive geographic suitability maps extend the possible range of *B. morrisoni* from the deserts in the southwestern U.S. to the dry scrubland regions of southwestern Montana (Williams *et al.* 2014). There are records of this species in parts of Idaho near the Montana border, including one from Salmon, ID, just 17 kilometers southwest (Discover Life 2016). There are also records of *B. morrisoni* in southern Wyoming (Williams *et al.* 2014, Discover Life 2016), so it is possible that

the range of *B. morrisoni* extends into the state, especially in the desert-type areas of southwestern Montana (e.g. the Centennial Valley in Beaverhead County).

Bombus bohemicus is a species in the subgenus *Psithyrus* that has been recorded from New England across the Midwest and then north and west across western Canada to Alaska (Williams *et al.* 2014). It has not been documented from Montana, but there are records of it just to the north in Alberta and Saskatchewan, Canada (Williams *et al.* 2014). This species is very similar to *B. suckleyi*, which is thought to replace *B. bohemicus* in the west (R. W. Thorp, personal communication 2016). Montana, especially northeastern Montana, is a place where the ranges of these two species may overlap, though both of these species in the subgenus *Psithyrus* have been shown to be in decline (Williams *et al.* 2014)

None of the published predictive maps extend the possible range of *Bombus perplexus* Cresson into Montana (Williams *et al.* 2014). However, there are records of *B. perplexus* collected across the eastern United States to Minnesota and from Calgary, 225 kilometers north of the Montana border (Williams *et al.* 2014, BDUC 2015). This distribution pattern may suggest the presence of *B. perplexus* in the northeastern part of Montana.

Taxonomic Difficulties

When it comes to identifying bumble bees, a frequently-documented challenge is the extraordinary intra- and interspecific variation in the color patterns of the hair-like setae (hereafter referred to as hairs) occurring among members of a species (Milliron 1971, Williams 1998, Owen *et al.* 2010, Williams *et al.* 2015). This

difficulty is exacerbated by the tendency of multiple species to converge on similar color patterns when occupying similar geographic locations (Williams 1998). Recent DNA evidence confirms that species can be extremely difficult (or even impossible) to identify by morphological characters alone, as there appears to be phenotypic convergence of genetically distinct species (Koch 2015, Williams *et al.* 2015). In Montana, especially western Montana with its elevational diversity, the variation in color patterns is accompanied by noticeable differences in hair length and texture (Milliron 1971, ACD personal observations 2015), making identification even more challenging.

The distinction between *B. fervidus* and *B. californicus* is one example of these taxonomic difficulties. Some authors have considered these two species to be synonyms (Milliron 1973, Williams *et al.* 2014), but recent DNA evidence suggests that they are two distinct species (Koch 2015) and we have chosen to keep them separate (see species accounts for further discussion of this issue). Another pair of Montana species that is difficult to distinguish is *Bombus centralis* Cresson and *Bombus flavifrons* Cresson because of what appears to be phenotypic convergence and the blending of diagnostic characters (see species accounts for more information). Further complicating identification in Montana is the sympatric occurrence of morphologically similar species that have been considered allopatric species pairs in eastern vs. western North America (e.g. *B. auricomus / B. nevadensis, B. ternarius / Bombus huntii* Greene, and *B. terricola / B. occidentalis*). Future DNA work may provide important insights into the identities of and the relationships

between these morphologically similar species. See species accounts for specific information on how we distinguished between these species pairs for this project.

Notes on Sampling Methods

Many of the bumble bees collected in Montana over the last 130 years and examined for this project were captured using a net. However, many other methods were used in obtaining specimens, including pan traps, pitfall traps, flight intercept traps, bucket traps, and Japanese beetle traps. In many cases, the bumble bees collected by these traps would be considered "by-catch," since pitfall traps are commonly used to sample terrestrial arthropods while flight intercept traps, bucket traps, and Japanese beetle traps tend to target specific species, (e.g. certain Coleopteran taxa). Typically, non-target species collected in these types of traps are either stored, but not processed, or discarded. As Hung *et al.* noted (2015), even the small and biased samples of non-target bee species collected by these kinds of non-traditional methods could provide valuable insights when added to larger specimen and literature databases. In the current study, by-catch provided samples from a variety of localities throughout Montana that may not otherwise have been well represented (e.g. Ivie *et al.* 1998, Winton 2010).

Since bucket traps and Japanese beetle traps provided many *Bombus* specimens as by-catch in previous years, these traps were placed throughout remote areas of eastern Montana to specifically sample for bees from May through August, 2015. These traps were extremely effective at attracting and capturing bumble bees, resulting in the capture of many individuals of the same species in a

single trap. We advise that anyone utilizing these types of traps in the future should exercise caution since the large number of bees captured could drastically reduce populations of nearby colonies. Due to limitations in time and travel, our 2015 traps were set up in the spring and left up throughout the summer. Consequently, all castes of bees were collected, including a large number of queens. In the future, if these types of traps are used, we would caution against using them early in the spring or summer and late in the summer when queens are active, since the capture of queens has a greater impact on colony establishment than the collection of workers. In addition, large numbers of bees are attracted to the yellow color of the Japanese beetle traps and bucket traps and to the floral scents used as lures. We encourage the development and use of alternative trap colors and lures that are able to effectively collect target species while avoiding the unnecessary capture of non-target pollinators.

Key to Female Bumble Bees of Montana
(Adapted from Koch *et al.* 2012 with additional notes from Williams *et al.* 2014)

The following key is to female bumble bees only. To key out males, we recommend *Bumble Bees of North America* (Williams *et al.* 2014). The key includes all 28 species recorded from Montana along with four species that might be found here. Morphological characters used in the key are shown in Figure 23 and key terms are defined below. When color is used in the key, it is referring to the color of the body hairs unless otherwise stated.

One of the most challenging characters used to key out bumble bees is the length of the malar space (i.e. cheek) compared to its width. The length of the cheek is measured from the lower margin of the compound eye to the attachment of the mandible. The width of the cheek is measured below the compound eye and is the distance from the margin of the gena to the margin of the clypeus (see Figure 23d), which is best viewed in profile. In general there are three cheek lengths: 1) shorter than wide, 2) as long as wide and 3) longer than wide. There is considerable variability within these categories, and it takes practice to learn to identify these with confidence.

The species accounts that follow the key each contain a "Diagnosis" section where diagnostic characters are listed along with how to distinguish each species from morphologically similar species. After keying out a specimen, we recommend reading the species description and diagnosis to confirm your determination.

Definitions

Anterior scutum: The dorsal surface (i.e. top) of the thorax anterior to the wings (Figure 23a).

Basitarsus: The leg segment between the tibia and the tarsi (Figure 23b).

Cheek/malar space: The space between the compound eye and the attachment of the mandible (Figures 23c and 23d).

Clypeus: The region of the face below the antennal bases and above the mouthparts (Figure 23c).

Corbicular fringe: The long hairs that surround the corbicula/pollen baskets on the hind tibiae (Figure 23b).

Corbiculum: "Pollen basket"; The shiny, concave portion of the hind tibia (Figure 23b).

Coxa: The segment of the leg that attaches to the thorax (Figure 23b).

Gena: The side of the head below the eyes (Figure 23d).

Interalar band/space: Area between the wings (Figure 23a).

Metasoma: Referring to the third body segment (i.e. the abdomen; Figure 23a).

Occiput: The top of the head.

Tergite/terga/T1-T6: The segments on the dorsal surface (i.e. top) of the third body segment (i.e. abdomen). Tergal segments are counted starting from where the abdomen connects to the thorax (Figure 23a).

Scutellum: The dorsal surface (i.e. top) of the thorax posterior to the wings (Figure 23a).

Sternite/sterna/S1-S6: The segments on the ventral surface (i.e. bottom) of the third body segment (i.e. abdomen). Sternal segments are counted starting from where the abdomen connects to the thorax.

Key to Female Bumble Bees in Montana

1. Female: antenna with 12 segments; abdomen with six visible tergites.....2

1'. Male: antenna with 13 segments; abdomen with seven visible tergites

……..No key provided. (To key males to species, use Williams *et al.* 2014.)

2(1). Outer surface of hind tibiae concave and shiny; pollen baskets present; social species……..3

2'. Outer surface of hind tibiae convex and hairy; pollen baskets absent; social parasitics……..35

3(2). T2 and T3 with red or orange hairs, sometimes with yellow hairs intermixed at least medially……4

3’. T2 and/or T3 with yellow or black hairs……10

4(3). Scutum anterior to wing bases with yellow and black hairs intermixed, giving cloudy appearance……5

4’. Scutum anterior to wing bases with predominantly yellow or pale yellow hairs ……6

5(4). T2 with black hairs at least medially; integument of hind leg basitarsi brownish-orange and often lighter than the tibiae; corbicular fringes orange or brown……***Bombus bifarius*** **Cresson**

5’. T2 orange; corbicular fringes black, sometime with orange ……***Bombus melanopygus*** **Nylander**

6(4’). Cheek (i.e. malar space) distinctly shorter than wide; face with predominantly black hairs……***Bombus rufocinctus*** **Cresson**

6’. Cheek as long as wide; face with yellow hairs, at least centrally……7

7(6’). Scutellum with yellow hairs only……***Bombus huntii*** **Greene**

7’. Scutellum with yellow or pale yellow hairs divided by a line or triangle of black hairs……8

8(7'). T2 with black hairs at least medially; integument of hind leg basitarsi brownish-orange and often lighter than the tibi….***Bombus bifarius*** **Cresson**

8'. T2 orange……9

9(8'). T5 with yellow hairs on the lateral margins; hairs long and uneven; coxae with predominately black hairs.....***Bombus sylvicola*** **Kirby**

9'. T5 black; hairs short and even; coxae often with yellow hairs ……..***Bombus ternarius*** **Say**

10(3'). Cheek longer than wide (though sometimes only slightly longer than wide and appearing square).....11

10'. Cheek as long as or shorter than wide……25

11(10).Face with pale white or yellow hairs, sometimes with black hairs intermixed, giving cloudy appearance……12

11'. Face with predominantly black hairs.....16

12(11).T3 and T4 black……..***Bombus flavifrons*** **Cresson**

12'. T3 and T4 orange or yellow or brownish……13

13(12').T3 and T4 orange……14

13'. T3 and T4 yellow or brownish……15

14(13). Anterior scutum with black and yellow hairs intermixed, giving cloudy appearance ……..***Bombus flavifrons*** **Cresson**

14'. Anterior scutum with predominantly yellow hairs ……..***Bombus centralis*** **Cresson**

15(13'). T5 yellow or brownish……..***Bombus appositus*** **Cresson**

15'. T5 usually mostly black……..***Bombus borealis*** **Kirby**

16(11'). T5 and T6 with orange or pale orange hairs.....***Bombus kirbiellus*** **Curtis**

16'. T5 and T6 with black hairs.....17

17(16'). T3 with mostly black hairs……..18

17' T3 with yellow hairs at least medially……..21

18(17). T4 black.....19

18'. T4 yellow……..***Bombus californicus*** **Smith**

19(18). T2 with yellow hairs medially and black hairs laterally (yellow often in the shape of a "W")…… ***Bombus bimaculatus*** **Cresson**

19'. T2 yellow……..20

20(19'). Sides of the thorax with yellow hairs predominating ……..***Bombus vagans*** **Smith**

20'. Sides of the thorax usually with black hairs predominating ……..***Bombus perplexus*** **Cresson** (possibly in MT)

21(17'). Hairs between the wing bases completely or predominantly black……22

21'. Hairs between the wing bases predominantly yellow; if black hairs are present they form a small circle medially……***Bombus nevadensis*** **Cresson**

22(21). T4 black……23

22'. T4 yellow……24

23(22). T1 usually with yellow hairs; surface of clypeus with many pits and punctures ……***Bombus pensylvanicus*** **(DeGeer)**

23'. T1 with black hairs, at least medially, sometimes with yellow hairs intermixed; surface of clypeus smooth and shiny ……***Bombus auricomus*** **(Robertson)**

24(22'). T2 yellow……***Bombus fervidus*** **(Fabricius)**

24'. T2 with yellow hairs medially and black hairs laterally ……***Bombus californicus*** **Smith**

25(10'). Cheek shorter than wide……26

25'. Cheek as long as or slightly longer than wide……31

26(25). Hairs between the wing bases completely or predominantly black……27

26'. Hairs between the wing bases predominantly yellow; if black hairs are present they form a small circle medially……30

27(26). T1 yellow……..***Bombus rufocinctus*** **Cresson**

27'. T1 black……..28

28(27'). T2 yellow.....29

28'. T2 with black hairs or, if some yellow, along posterior margin only

……..…….***Bombus occidentalis*** **Greene**

29(28). T3 black……***Bombus cryptarum*** **(Fabricius)** (possibly in MT)

29'. T3 yellow……..…….***Bombus terricola*** **Kirby**

30(26'). T3 yellow, at least medially…..***Bombus morrisoni*** **Cresson** (possibly in MT)

30'. T3 black……***Bombus griseocollis*** **(DeGeer)**

31(25'). Scutellum with yellow or pale yellow hairs divided by a line or triangle of black hairs……..……***Bombus bifarius*** **Cresson**

31'. Scutellum not as above (with yellow hairs only, or yellow and black hairs intermixed throughout)……..……32

32(31'). T2-6 black……***Bombus impatiens*** **Cresson** (non-native, introduced in MT)

32'. T2-6 with some yellow and/or orange……..…33

33(32'). Anterior scutum with black and yellow hairs intermixed, giving cloudy appearance ……..……34

33'. Anterior scutum with yellow hairs only……..***Bombus frigidus*** **Smith**

34(33). Scutellum distinctly darker (with many black hairs intermixed with yellow) than anterior scutum……***Bombus sitkensis*** **Nylander**

34'. Scutellum and anterior scutum not as above (either with scutellum and anterior scutum similar in appearance, or with the anterior scutum appearing darker than scutellum)……***Bombus mixtus*** **Cresson**

35(2'). Occiput with predominantly black hairs; hairs of face predominantly black around bases of antennae; S6 with strongly produced lateral ridges……..37

35'. Occiput with predominantly yellow hairs……..36

36(35'). Hairs of face predominantly black around bases of antennae; lateral ridges not apparent on S6 (there may be small bumps); T6 often tightly curled under the abdomen……..***Bombus flavidus*** **Eversmann**

36'. Hairs of face predominantly yellow around bases of antennae; S6 with evenly rounded lateral ridges……..***Bombus insularis*** **(Smith)**

37(35). Hairs on the side of the thorax predominantly yellow; T4 yellow but with a triangle of black hair medially; S6 lateral ridges extending laterally beyond T6……***Bombus suckleyi*** **Greene**

37'. Hairs on the side of the thorax predominantly black, T4 yellowish-white to white, at least medially; S6 ridges barely extending laterally beyond T6 ……***Bombus bohemicus*** **Seidl** (possibly in MT)

Species Accounts

In this section, species are presented in alphabetical order. Common names are from Williams *et al.* (2014). For each species, information is provided on its distribution, historical collection records, and key characters used to identify females to species.

Bombus (Subterraneobombus) appositus Cresson, 1878
White-Shouldered Bumble Bee

Bombus appositus is a commonly collected bumble bee in Montana. In North America, it is considered a western bee, known to occur in the Rocky Mountain region from New Mexico to Alberta and British Columbia (Williams *et al.* 2014). In Montana, it has been most commonly collected in the western counties, though one specimen was recorded as far east as Valley County (MTEC).

Two specimens of *B. appositus* were collected in Bozeman in 1899, the earliest known records of this species in the state. Seventy-five specimens were collected in Gallatin, Missoula, Lewis and Clark, Hill, and Ravalli Counties between 1899 and 1911 (MTEC, NMNH, UMEC, and EMEC). Most of these individuals were determined by Franklin, and they are likely the Montana records he published in his *Bombidae of the New World* (1912). Though no specific locality was given in the 1912 publication, Franklin did note that his specimens were from the western portion of the state, also noting that this species seemed to be confined to the mountainous regions of the western U.S. Between Franklin's 1912 work and 1973 when Milliron published *A Monograph of the Western Hemisphere Bumblebees*, no

other literature records for *B. appositus* were published. However, this species was consistently collected over the last 115 years, ≥5 individuals collected each decade (Figure 18a). The database currently contains 302 specimens of *B. appositus* from 25 Montana counties (Figure 16a).

Diagnosis: *Bombus appositus* is a large bumble bee with pale yellow to gray-white hairs on the face. Metasomal T1-T5 are yellow to orange-brown. Its cheek is longer-than-wide and the hairs on the side of the thorax are predominantly black.

Bombus appositus is most easily confused with *B. fervidus* and *B. borealis* in Montana. However, *B. fervidus* has black hairs on the face and only T1-T4 are yellow. *Bombus borealis* has many black hairs on T5.

Bombus (Bombias) auricomus (Robertson, 1903)
Black and Gold Bumble Bee

Bombus auricomus is a common eastern North American bumble bee species. It is known to occur throughout eastern temperate forests west to the Great Plains (Williams *et al.* 2014). Prior to this study, the westernmost records of *B. auricomus* were along the western borders of North Dakota and South Dakota, though Milliron (1971) predicted its occurrence in Montana. We documented five specimens of *B. auricomus* in four Montana counties reaching as far west as Pondera County (Figure 16b).

The question of the presence of *B. auricomus* in Montana is a taxonomic issue more than anything else. At various times throughout their taxonomic histories, *B. nevadensis* and *B. auricomus* have been considered both separate species and

subspecies (Hurd 1979). Currently they are considered two separate species, with *B. nevadensis* occurring in western North America and *B. auricomus* in eastern North America (Williams *et al.* 2014). The distinction between eastern and western North America is often split at the 100th meridian, but that division is totally arbitrary. Since Montana's eastern border is near the 100th meridian, eastern Montana is one area where eastern and western species ranges may overlap, which means *B. auricomus* and *B. nevadensis* may be sympatric there. While *B. nevadensis* has been well documented throughout the state (252 specimens in 41 counties; Figure 16s), the presence of *B. auricomus* was uncertain prior to this study. In addition to including Montana in his map predicting the range of *B. auricomus*, Milliron (1971) discussed both the possibility of *B. nevadensis/B. auricomus* hybrids and the possibility of melanic forms of each species that would be essentially indistinguishable.

The main morphological difference used to tell these two species apart is the presence or absence of a distinct black interalar band. *Bombus auricomus* typically has a strong black interalar band, while *B. nevadensis* usually has yellow hairs predominating on the thorax with only a circle of black hairs medially. Another diagnostic character used to discern these two species is the size and spacing of punctations between the eyes and the ocelli (Williams *et al.* 2014), but the spacing differences are very subtle making this character somewhat unreliable.

Some individuals of these two species are especially difficult to distinguish since the circular patch of black on *B. nevadensis* is sometimes expanded into a nearly complete interalar band, making it more closely resemble *B. auricomus*. For this study, we relied on a complete black band being a diagnostic character of *B. auricomus.* Therefore, if the black hairs on the thorax extended to the wing bases, even if there were a few yellow hairs intermixed, we determined the specimen to be *B. auricomus.* If, however, the majority of the hairs touching the wing bases were yellow, we determined it to be *B. nevadensis.*

The identity of the five specimens of *B. auricomus* collected in Montana since 1971 (Figure 18b) were confirmed by Robbin Thorp at the University of California, Davis. These records expand the known range of *B. auricomus* west to the foothills of the Rocky Mountains in Pondera County (111. 506°W), and suggest an extensive area of *B. auricomus / B. nevadensis* sympatry across the eastern two-thirds of Montana.

Diagnosis: *Bombus auricomus* is a large bumble bee with a longer-than-wide cheek, black hairs on the face, and yellow hairs on Metasomal T2 and T3. Metasomal T1 may be yellow, black, or a mixture of both. The anterior scutum is yellow and there is a strong black interalar band. However, in some individuals, the scutellum may also be black so that the only yellow on the thoracic dorsum is anterior to the wings.

Bombus auricomus is most easily confused with *B. nevadensis*, which also has a longer-than-wide cheek, black hairs on the face, and yellow hairs on T2 and T3, but

B. nevadensis has many yellow hairs on the thoracic dorsum, so that most of its surface is yellow with only a small circular patch of black hairs medially.

Bombus (Pyrobombus) bifarius Cresson, 1878
Two Form Bumble Bee

Bombus bifarius is considered common throughout its range in western North America from Alaska to New Mexico (Williams *et al.* 2014). It is the most abundant bumble bee in the database from Montana, though it is known from the western two-thirds of the state only (Figure 16c).

The earliest record of *B. bifarius* in Montana is a specimen that was originally determined to be *Bombus edwardsii* Cresson, collected in 1883 near Yellowstone National Park. Early in the 20th century, there was some confusion with the names *B. bifarius* and *B. edwardsii.* What Franklin (1912) considered to be *B. edwardsii* was explained to be *B. bifarius* by Frison (1923). This species has been consistently collected throughout western Montana since the first specimen in 1883, and is still one of the most commonly seen bees in the western forests and mountains (Figure 18c). *Bombus bifarius* was one of eight targeted bumble bee species surveyed nationwide between 2007 and 2009 (Cameron *et al.* 2010). In that study, it was shown to have a stable population and range despite declines of sympatric *Bombus* species. The targeted collecting by Cameron *et al.* in 2009 added over 500 Montana records of this species in the database (BLCU).

DNA evidence has shown that two species with divergent color patterns, *B. bifarius* and *Bombus nearcticus* Handlirsch, share a close relationship and thus have

been synonymized (Williams *et al.* 2014). There is a red form (*B. bifarius s. str.*) and a dark form (*B. bifarius nearcticus*) which both occur in Montana. The database currently has 1,911 records of *B. bifarius* from 37 of the 56 counties (Figure 16c).

Diagnosis: *Bombus bifarius* can be identified by a line or triangle of black hair that divides the scutellum into two patches of light colored hair. The metabasitarsus is almost always brownish-orange, making it appear distinctly lighter than the metatibia. Black hairs are always present and usually predominate on metasomal T2, at least medially. The cheek is about as long as it is wide, though sometimes it appears shorter than wide, especially in small workers. The light-colored body hairs on the face and thorax often appear more white or gray than yellow. There may be orange on T2 and T3. The variation in *B. bifarius* color morphs makes it possible to confuse individuals of this species with several other species in Montana at first glance. As a result *B. bifarius* comes out in our key in three different places.

Bombus (Pyrobombus) bimaculatus Cresson, 1863
Two-Spotted Bumble Bee

Bombus bimaculatus is one of the most abundant and widespread bumble bee species in the eastern United States, reported as far west as the eastern Dakotas and Nebraska, and is commonly collected in both forests and urban green spaces (Williams *et al.* 2014). In the summer of 2011, two individuals were caught in Montana Department of Agriculture CAPS program traps, one in Yellowstone County

and one in Valley County (MTEC). In 2015, 16 more individuals were collected, three of which were collected by Master Gardener volunteers in Powder River and Valley Counties (Figure 16d; Figure 18d).

The database currently has 18 records of *B. bimaculatus* from seven Montana counties, all new state and county records for this species (Figure 16d). These records establish a substantial westward expansion of the known range of *B. bimaculatus,* and it is likely that future sampling efforts will reveal the presence of this species in other eastern Montana counties.

Diagnosis: Key characters used to identify *B. bimaculatus* include a cheek that is about as long as it is wide and black hairs on the face. There is a black circle of hairs located medially on the thoracic dorsum instead of an interalar band, though sometimes many yellow hairs are intermixed with the black. Metasomal T1 is yellow, T2 is black laterally with yellow hair medially, and T3-T6 are entirely black. Often the yellow hairs on T2 form a W-shape.

Bombus bimaculatus is most easily confused with *B. griseocollis* and *Bombus vagans.* However, *B. griseocollis* can be differentiated by its cheek which is shorter than it is wide. *Bombus vagans* also has a cheek that is just longer-than-broad, but T1 and T2 will be entirely yellow.

Bombus (Subterraneobombus) borealis Kirby, 1837
Northern Amber Bumble Bee

Bombus borealis is known to inhabit the temperate and boreal forests of the eastern United States, west through the northern Great Plains of North Dakota into

Canada (Williams *et al.* 2014). In Montana, it has been collected in five of the northernmost counties and further south in Gallatin and Lewis and Clark Counties (Figure 16e).

No record or prediction of *B. borealis* in Montana was recorded in the literature until 2014, when Williams *et al.* (2014) published a map showing records along the northern border. However, the ANSP collection has one specimen of *B. borealis* collected in Montana before 1922, though no specific date or locality was recorded on the label. The MTEC has one specimen of *B. borealis* collected in Hill County in 1926 and the SEMC has one collected in Bozeman in 1931. No other individuals of this species were collected in Montana until 75 years later, when two were taken in Sheridan County (Figure 18e). The database currently has 20 specimens of *B. borealis* from eight Montana counties (Figure 16e). The patchy distribution of this species in Montana, suggests that more sampling is necessary to fully assess its range.

Diagnosis: *Bombus borealis* has yellow hairs on metasomal T1-T4, many black hairs on T5, yellow hairs on the face, and a cheek that is longer than it is wide. The side of the thorax has predominantly black hairs.

This species is most easily confused with *B. appositus* and *B. fervidus* in Montana. However, the hairs of T1-T5 are predominantly yellow in *B. appositus* and *B. fervidus* has black hair on the face.

Bombus (Thoracobombus) californicus Smith, 1854
California Bumble Bee

Bombus californicus is known from coastal California, Oregon, and Washington and throughout the intermountain western U.S. from Colorado and Utah north to Idaho and Montana. Individuals have been recorded as far east as South Dakota (Koch *et al.* 2012). It is not a commonly collected bumble bee and is a species that may be in decline (Koch *et al.* 2012). In Montana, this species has been collected in mountainous regions of the west (Figure 16f) but is relatively uncommon.

Historically, there has been difficulty distinguishing between certain forms of *B. californicus* and *B. fervidus* (Stephen 1957), and the two have been considered synonymous by some (Milliron 1973a, Williams *et al.* 2014). However, data have shown that where the two species are seemingly sympatric, they generally occur in different habitats. *Bombus fervidus* occurs mostly in the prairies and *B. californicus* occurs in forested foothills (Thorp *et al.* 1983). New molecular data provide further evidence that the two are distinct species, though they can be phenotypically convergent (Koch 2015). Based on this, we treat them as separate species in Montana. The two are sympatric in the western counties, though our collection sites and observations support their ecological distinction. *Bombus fervidus* is widespread in the prairie-type habitats of eastern Montana and was collected all across the state to the western border. *Bombus californicus* was collected only in the mountainous regions of western Montana (compare Figure 16f and Figure 16h).

The first record of *B. californicus* in the literature was from Beaver Creek (Hill County), documented by Franklin in 1915, but collected in 1913 (SEMC). Between 1913 and 2015, this species was sporadically collected throughout western Montana, with most (68%) of the records from just three decades: the 1960s, 1990s, and 2010s (Figure 18f).

Bombus californicus is recommended for "Vulnerable" status on the IUCN Red List, with analyses showing patterns of decline (Hatfield *et al.* 2015a). Records in Montana support this conservation status as only seven individuals are in the database from 2014-2015. However, these low numbers may also be a result of low sampling effort in the parts of Montana where *B. californicus* can be found, since no standardized monitoring projects have been undertaken. The database currently has 91 records of *B. californicus* from 19 Montana counties (Figure 16f).

Diagnosis: *Bombus californicus* has several different color morphs, some more cryptic than others. Characters used to identify *B. californicus* include a longer-than-wide cheek and black hairs on the face. There is always yellow on metasomal T4 while T1-T3 are variable in color, though there is always at least some black. Some forms have T1-T3 completely black while others have T1-T3 almost completely yellow with only small patches of black laterally on T2. Identification is complicated by a spectrum of intermediate color patterns between these two extremes (Koch 2015).

This species is most easily confused with *B. fervidus* and some keys treat them as one species. *Bombus fervidus* in Montana has only yellow hairs on T1-T4.

Bombus (Pyrobombus) centralis Cresson, 1864
Central Bumble Bee

Bombus centralis is known to be a moderately common bee throughout its range, which includes the Rocky Mountain region and the desert highlands of Arizona and New Mexico (Williams *et al.* 2014). It is also widespread in Montana, known from 47 counties (Figure 16g).

Two *B. centralis* individuals were collected in Bozeman in 1901 (MTEC, NMNH), while the earliest literature reference was in 1912 (Franklin 1912). Since that time, it has been consistently documented across Montana (Figure 18g). While it is now known from nearly every part of the state, before 1980 records existed for just 22 of the 56 counties, with all collection localities near cities, roads, national parks, or Agricultural Experiment Stations.

The biggest issue with *B. centralis* is a taxonomic one, as certain individuals are very similar to *B. flavifrons* individuals. Both species have a longer-than-wide cheek and a hair pattern of metasomal T1: yellow, T2: yellow, T3: orange, and T4: orange. The key morphological character that separates these two species is the amount of black hair intermixed with the yellow on the anterior scutum. However, this character is not often clear-cut. In fact, the blending of diagnostic characters occasionally makes separation impossible (Stephen 1957, ACD personal observation 2015). Some individuals can easily be identified as one species or the other, but in many cases there appears to be more of a spectrum of *B. centralis-B. flavifrons* than two distinct species groups. In general, *B. flavifrons* is found in more forested, montane areas, while *B. centralis* is found more in the plains and valleys. Since these

habitats often overlap in Montana, the species also spill over into both habitats. This species pair is one for which future genetic comparisons may be of interest.

We used the amount of black on the anterior scutum and the general length of the body hairs as our main diagnostic characters. If only a few black hairs were intermixed on the anterior scutum and the body hairs were generally short and even, we identified the specimen as *B. centralis.* If more than just a few hairs were intermixed on the anterior scutum and the hairs were generally longer and more uneven, we identified the specimen as *B. flavifrons.* If an individual seemed to fall right in the middle of the *B. centralis / B. flavifrons* spectrum, we defaulted to an identification of *B. flavifrons*, based on advice from James Strange at the Bee Biology and Systematics Lab in Logan, UT. A few especially difficult specimens were identified only as *Bombus* sp. with a note indicating the specimen was either *B. flavifrons* or *B. centralis.*

In 2015, 215 *B. centralis* were added to the database, with 13 new county records from the eastern part of the state (Figure 24). In these specimens from eastern Montana, *B. centralis* was observed to have unexpected morphological variability. Here, the individuals were obviously distinct from *B. flavifrons*, which are not commonly collected in the plains of eastern Montana. However, T2 had a crescent shape of orange hair along the mid-line with yellow hair laterally. The most recent literature does not record a color morph in which T2 has orange hairs (Stephen 1957, Thorp *et al.* 1983, Koch *et al.* 2012, Williams *et al.* 2014), but this variation was documented by Franklin (1912). Some literature attributes patches of

unusually colored hair to mutations during the pupal stage of development (Williams *et al.* 2014), while other authors have contemplated the possibility of hybridization between species (Milliron 1971). It is unclear if one of these explanations could be valid in this case or if these individuals are presenting an uncommon but normal color morph.

The database currently contains 641 records of *B. centralis* in 47 counties (Figure 16g). The locations of the nine counties lacking *B. centralis* records suggest that more sampling in the future will reveal this species to be present throughout all of Montana's 56 counties.

Diagnosis: Diagnostic characters for *B. centralis* are a longer-than-wide cheek and a hair patter of metasomal T1: yellow, T2: yellow, T3: orange, and T4: orange. There are no black hairs intermixed with the yellow on the anterior scutum. Some individuals' cheeks are only slightly longer than wide, and some individuals have orange hairs medially on T2. This species is most similar to *B. flavifrons.* However, *B. flavifrons* has black hairs intermixed with the yellow on the thoracic dorsum and is often found in more forested mountain areas, while *B. centralis* is more common in the valleys.

Bombus (Thoracobombus) fervidus (Fabricius, 1798)
Yellow Bumble Bee

Bombus fervidus is known to be widespread coast-to-coast across the mid-latitudes of North America (Williams *et al.* 2014). It is also widespread in Montana, known from 47 counties (Figure 16h).

The earliest-known record of *B. fervidus* is a specimen collected in June 1899 by Cooley and determined by Franklin in 1908. Throughout the following 115 years, *B. fervidus* was one of the most consistently collected species across Montana (Figure 18h). Both Franklin (1912) and Milliron (1973a) listed Montana as part of its known range, and the most recent maps (Koch *et al.* 2012 and Williams *et al.* 2014) document known specimens from various parts of the state. Gaps still existed in undersampled regions until 2015, when collecting trips and trap placement targeted some of the remote eastern counties, resulting in nine new county records (Figure 25).

As discussed above (see *B. californicus*), some sources consider *B. fervidus* and *B. californicus* to be synonymous (Milliron 1973a, Williams *et al.* 2014). However, due to recent DNA evidence (Koch 2015) and habitat differences (Thorp *et al.* 1983), we have chosen to treat them as separate species.

The IUCN Red List recommends *B. fervidus* for "Vulnerable" status (Hatfield *et al.* 2015a), as it appears to be in slow decline in parts of its range (Williams *et al.* 2014), especially in the eastern U.S. (Koch *et al.* 2012). This Red List status includes *B. californicus* in its definition of *B. fervidus*, which may account for most of the reports of decline. However, published studies have shown that *B. fervidus s. str.* has also had a slow and steady decline since the 1930s (Hatfield *et al.* 2015a). In Montana, *B. fervidus* is still commonly collected; 242 specimens from 22 counties were added to the database in 2015.

The database now contains 688 records of *B. fervidus* from 47 Montana counties (Figure 16h). The location of the nine counties without records in the state suggests that future sampling will reveal the presence of *B. fervidus* across all 56 counties.

Diagnosis: *Bombus fervidus* is easy to identify by its longer-than-wide cheek, black hairs on the face, and yellow hairs on metasomal T1-T4. The sides of the thorax are also mostly yellow.

This species is most easily confused with *B. californicus, B. appositus,* and *B. borealis.* However, *B. appositus* has yellow hairs on the face, the sides of the thorax are predominantly black, and T5 is yellow. *Bombus borealis* has a yellow face and the sides of the thorax are predominantly black. *Bombus californicus* has some black on T1-T3, though sometimes that black is confined to small lateral patches on T2.

Bombus (Psithyrus) flavidus Eversmann, 1852
Fernald Cuckoo Bumble Bee

Bombus flavidus is a social parasite known from colonies of *B. rufocinctus, B. occidentalis, B. appositus,* and members of the subgenus *Pyrobombus*. Morphological and DNA evidence supports the synonymy of *Bombus fernaldae* (Franklin) from North America and *B. flavidus* from Europe and Asia, so the two are now considered members of the same species (Williams *et al.* 2014).

Bombus flavidus is uncommon but seems to be widespread across North America from New England to the Pacific Coast (Koch *et al.* 2012). Documentation of its presence is scattered, with records from the boreal and temperate forests of the Northeast, the Appalachian Mountains, the Mountain West, and the Pacific Coast (Williams *et al.* 2014). In Montana, records are restricted to the mountainous western half of the state (Figure 16i).

In 1912, Franklin predicted that *Psithyrus tricolor* Franklin is likely found in Montana, though he had not documented any individuals collected here. Nothing was said about the presence of *B. fernaldae* in Montana, though he cited evidence to support his hypothesis that *P. fernaldae* is the female of *P. tricolor* (Franklin 1912). Those two species were later synonymized (Frison 1922). The first actual record of *B. flavidus (= fernaldae)* in the literature did not appear until 2005 (Fultz 2005).

The earliest specimen of *B. flavidus* from Montana in the database is from 1929. After that, it was not collected again until the 1950s and the majority of the *B. flavidus* records in the database came from the last two years (Figure 18i). Currently the database contains 158 records of *B. flavidus* from 19 Montana counties (Map 16i).

Little is known about this species and its conservation status though one major threat to any species in the subgenus *Psithyrus* would be the loss of suitable hosts (NatureServe Explorer 2015). Bumble bees in the subgenus *Pyrobombus*, as well as other possible hosts (e.g. *B. rufocinctus*), appear to have stable populations in North America, including those in Montana, which indicates little current cause for

concern for *B. flavidus.* However, more work is needed to ascertain which species are actually the hosts in North America, and to truly assess its abundance and distribution.

Diagnosis: Like all species in the subgenus *Psithyrus*, *B. flavidus* lacks pollen baskets on the hind tibia. Characters used to identify this species include black hair on the face and yellow hairs on the top of the head. Often metasomal T6 is tightly curled under the abdomen, so that the tip of the abdomen actually points anteriorly. The lateral keels (small ridges) on metasomal S6 are so small they are barely noticable.

This species is mostly easily confused with *B. insularis* and *B. suckleyi*, the other two species in the subgenus *Psithyrus* known from Montana. *Bombus insularis* has yellow hairs at the bases of the antennae as well as on the top of the head and *B. suckleyi* has no yellow hair on the face or the top of the head. Both *B. insularis* and *B. suckleyi* have more strongly produced lateral keels on S6.

Bombus (Pyrobombus) flavifrons Cresson, 1863
Yellow Head Bumble Bee

Bombus flavifrons is considered common across its range, which includes the Rocky Mountain region from southern New Mexico and Arizona north to Alaska and east into northwestern Canada to the Hudson Bay (Williams *et al.* 2014). It is common in Montana as well, though it has only been collected in the western two-thirds of the state (Figure 16j).

The earliest *B. flavifrons* specimens in the database were collected in 1900 (MTEC). Since then, this species has consistently been collected (Figure 18j), and the database currently contains 488 *B. flavifrons* records from 30 counties (Figure 16j).

As discussed above (see *B. centralis*), identification of *B. flavifrons* in the parts of its range where it is sympatric with *B. centralis* can be difficult. There is variation in color patterns and often a blending of diagnostic characters that often makes these two species indistinguishable (Stephen 1957, ACD personal observation 2015). This is also a case where elevational diversity is associated with noticeable differences in hair length and texture (Milliron 1971, ACD personal observation 2015), further complicating identification. We used the amount of black intermixed with the yellow hairs on the anterior scutum and the general length of the body hairs as main diagnostic characters when distinguishing between these two species. If only a few black hairs were intermixed and the body hairs were generally short and even, we identified the specimen as *B. centralis.* If more than just a few hairs were intermixed and the hairs were generally longer and more uneven, we identified the specimen as *B. flavifrons.* If an individual seemed to fall right in the middle of the *B. centralis / B. flavifrons* spectrum, we defaulted to an identification of *B. flavifrons*, based on advice from James Strange at the Bee Biology and Systematics Lab in Logan, UT. A few especially difficult specimens were identified only as *Bombus* sp. with a note indicating the specimen was either *B. flavifrons* or *B. centralis.*

Diagnosis: *Bombus flavifrons* has a longer-than-wide cheek and a hair pattern of metasomal T1: yellow, T2: yellow, T3: orange, and T4: orange. There are black hairs intermixed with the yellow on the anterior scutum, and generally the body hairs are long and uneven.

This species is easily confused with *B. centralis. Bombus centralis* has few black hairs intermixed with the yellow on the anterior scutum and the body hairs tend to be shorter and more even. Additionally, *B. centralis* is more commonly collected in the valleys of western Montana and across the plains of eastern Montana, while *B. flavifrons* is more common in forested montane areas.

There is a dark form of *B. flavifrons* in which the orange hairs on T3 and T4 are replaced with black. This form can easily be confused with *B. vagans*, but has not been observed in Montana. *Bombus vagans* can be distinguished from this dark form by having few or no yellow hairs laterally on T3 and T4 and on S3-S5, while *B. flavifrons* would have many yellow hairs laterally on T3 and T4 and on S3-S5.

Bombus (Pyrobombus) frigidus Smith, 1854
Frigid Bumble Bee

Bombus frigidus is known to inhabit the tundra/taiga and boreal regions of North America, from eastern Canada west to Alaska and in the mountains of the western U.S. to Oregon and Colorado (Williams *et al.* 2014). In Montana, it has been collected in the mountains of the western counties, in the foothills of Golden Valley County, and in the Little Rocky Mountains of Blaine County (Figure 16k).

Franklin recorded *B. frigidus* from localities in Alaska and northern Canada (1912), noting that this species is rare in the southern portion of its range. He did, however, correctly predict it would be found in the high altitude areas of western Montana. In 1929, two individuals of *B. frigidus* were collected in the Little Rocky Mountains in Blaine County (MTEC) and five others were collected in the 1950s and 1960s in Gallatin, Glacier, and Carbon Counties (PMNH, NMNH, and MTEC). More specimens of this species were added between 1980 and 2015 as research projects took collectors to high altitude locations specifically to collect bumble bees (Figure 18k).

There currently are 59 records of *B. frigidus* from nine Montana counties (Figure 16k). It is possible that future sampling in other rarely visited mountain regions of Montana will reveal this species to be more widespread across the state.

Diagnosis: *Bombus frigidus* has a cheek that is approximately as long as it is wide. Its body hairs are long and uneven, the hairs on the face are black, and the hairs on the anterior scutum are yellow without black intermixed. Metasomal T2 is yellow without black hairs laterally and T5 (and often T4) is orange.

This species is most easily confused with *Bombus mixtus* and *B. kirbiellus. Bombus mixtus* has many black hairs intermixed with the yellow on the anterior scutum. Also, *B. mixtus* usually has black hairs laterally on T2 and often has orange hairs on T3. *Bombus kirbiellus* has a color pattern very similar to *B. frigidus*, but has an obviously longer-than-wide cheek.

Bombus (Cullumanobombus) griseocollis (DeGeer, 1773)
Brown-Belted Bumble Bee

Bombus griseocollis is one of the most widespread and abundant species in the eastern U.S. temperate forests and Great Plains and is known from lower elevations in the Rocky Mountains (Williams *et al.* 2014). It is common in Montana east of the continental divide (Figure 16l).

The first specimens of *B. griseocollis* in Montana were collected in 1904 in Yellowstone and Custer Counties (MTEC). One hundred sixty-two other records document the presence of this species throughout eastern Montana from 1905 until 2014, and 190 more individuals were added in 2015 (Figure 18l). In the literature, *B. griseocollis* was primarily considered an eastern North American species, and there was no mention of its presence in Montana until 1973 (Milliron 1973b).

Bombus griseocollis is one of four Montana species (along with *B. rufocinctus, B. nevadensis*, and *B. auricomus*) in which males have eyes that are greatly enlarged. The enlarged eyes are associated with territorial behaviors connected to mating in these species (O'Neill *et al.* 1991).

The database currently contains 357 records of *B. griseocollis* from 38 Montana counties (Figure 16l). It is likely that future sampling in the six counties east of the continental divide without *B. griseocollis* records and at lower elevations west of the divide will reveal *B. griseocollis* to be a more widespread species in Montana.

Diagnosis: *Bombus griseocollis* has a cheek that is shorter than it is wide. The thoracic dorsum is predominately yellow with only a small circle of black hairs between the wings. Metasomal T1 has yellow hairs, T2 can have yellow or brown hairs and may have black laterally, and T3-T6 are all entirely black. The integument beneath the hairs on T1 and T2 is dull and matte-looking.

This species is most easily confused with *B. rufocinctus.* However, *B. rufocinctus* has many black hairs between the wings, usually forming an interalar band, and the integument beneath the hairs of T1 and T2 is shiny. Also, *B. rufocinctus* usually has at least some yellow or orange hairs on T3, T4, T5 or T6.

Bombus (Pyrobombus) huntii Greene, 1860
Hunt Bumble Bee

Bombus huntii is a common western bumble bee known to inhabit the Rocky Mountains from the Sierra Nevada east to the Great Plains (Williams *et al.* 2014). It is the most widespread bumble bee known in Montana (Figure 16m).

Bombus huntii is also represented by one of the oldest specimens from the state. One individual (NMNH) was collected in 1883 near Yellowstone National Park (Park County), along with one individual of *B. bifarius* and an unidentifiable *Bombus* specimen. Another individual of *B. huntii* (NMNH) was collected in the same year along the Yellowstone River north of Custer (Yellowstone County). Since then, *B. huntii* has consistently been collected across Montana, though the majority of specimens (78%) were taken from 1990-2015, and 965 individuals were added to the database in 2015 alone (Figure 18m).

This species is very similar to *B. ternarius,* which is common in the eastern North American forests and boreal regions north and west into British Columbia. In fact, *B. huntii* is said to replace *B. ternarius* in the interior western U.S., while *B. ternarius* replaces *B. huntii* in the north (Williams *et al.* 2014). Across much of Montana, however, these two species appear to be sympatric (compare Figure 16m with Figure 16z).

The database currently contains 1,840 records of *B. huntii* from 53 Montana counties (Figure 16m). It is likely that future sampling efforts will reveal this species to be present in all 56 counties.

Diagnosis: *Bombus huntii* has a cheek that is about as long as it is wide and a hair pattern of metasomal T1: yellow, T2 and T3: orange, T4: yellow, T5 and T6: black. Hairs on the face, anterior scutum, and scutellum are all yellow without any black intermixed. All hairs on the coxae are black.

There are three species that can easily be confused with *B. huntii* in Montana: *B. ternarius*, *B. sylvicola*, and *B. melanopygus. Bombus ternarius* can be found in many of the same habitats as *B. huntii.* It is distinguished from *B. huntii* by a line or triangle of black hair dividing the yellow hairs on the scutellum. Additionally, in *B. ternarius*, there is often yellow hairs on the fore-coxae and there is usually a circle of yellow hairs on the face near the antennal bases with black hairs intermixed around the edges. *Bombus sylvicola* is also very similar to *B. huntii,* though it is known to inhabit higher elevation sites than where *B. huntii* is typically found. *Bombus sylvicola* typically has long, uneven hair, a black line or triangle dividing the yellow

hairs of the scutellum, and yellow hairs laterally on T5. Additionally, there is usually a yellow patch of hairs near the antennal bases. *Bombus melanopygus* is typically found in more forested, montane habitats than those of *B. huntii*. It has many black hairs intermixed with the yellow hairs on the anterior scutum.

Bombus (Pyrobombus) impatiens Cresson, 1863
Common Eastern Bumble Bee

Bombus impatiens is a common eastern North American species whose native range extends only as far west as Nebraska and Minnesota (Williams *et al.* 2014). It has been commercially reared for greenhouse pollination services and research since the 1980s (Koppert Biological 2015). Concerns have been raised about the transport of this species to the western U.S., and the possible consequences for native bees if feral *B. impatiens* colonies became established outside of their native range (Xerces Society *et al.* 2013). The U.S. Department of Agriculture's Animal and Plant Health Inspection Service (USDA-APHIS) does not regulate interstate movement of bees in the continental U.S. (USDA-APHIS 2015), so moving colonies of *B.* impatiens out of their native range into the western states is legal. Hives contain queen excluders in order to prevent the escape of new queens and the establishment of feral colonies (Koppert Biological 2015). Still, the use of these colonies is of some concern, with potential consequences including the development of feral colonies by escaped queens, pathogen spillover (McMahon *et al.* 2015), and competition with native pollinators (Potts *et al.* 2010, Morales *et al.* 2013).

There was one record of this species in Montana from a 2005 study (Fultz 2015), but this record could not be validated. Specimens from Fultz's study were examined and determinations were verified or corrected but no *B. impatiens* individuals were found (KMOC).

The database, however, currently contains seven specimens of *B. impatiens* from Montana (Figure 16n; Figure 18n). One verified specimen of *B. impatiens* was collected in Ravalli County in June of 1980 from a locality on the western side of the continental divide, well beyond the known range of *B. impatiens* and before the widespread use of *B. impatiens* as a commercial pollinator (SEMC).

The other six specimens of *B. impatiens* are from a MSU research project using commercially reared *B. impatiens* in a comparison between organic and conventional wheat fields in Chouteau County. These six records were added to the database as documentation of this exposure and in case feral colonies of this species are detected in that region in the future. At the end of the summer 2014 field season, several individuals of *B. huntii* were found inside these commercial *B. impatiens* colonies (MTEC 019701, MTEC 019702) documenting that native and commercially reared bees are interacting in the wild, providing a potential pathway for pathogen and parasite transfer from imported colonies to native bees.

Diagnosis: *Bombus impatiens* has a cheek that ranges from approximately as long as it is wide to just shorter-than-wide. Only metasomal T1 is yellow, T2-T6 are

all black. This species is most easily confused with *B. griseocollis* in Montana, but *B. griseocollis* has a shorter-than-wide cheek and T2 is yellow or brown, at least medially.

Bombus (Psithyrus) insularis (Smith, 1861)
Indiscriminate Cuckoo Bumble Bee

Bombus insularis is a social parasite known to breed in colonies of *B. appositus*, *B. fervidus*, *B. flavifrons*, *B. nevadensis*, and *B. ternarius.* It has also been recorded inside colonies of *B. rufocinctus*, *B. occidentalis*, and *B. terricola* (Williams *et al.* 2014). It is known from the Rocky Mountains north to Alaska and scattered across the tundra/taiga and boreal regions of Canada to the maritime regions of eastern Canada and the U.S. (Williams *et al.* 2014). It is moderately common in Montana, collected mostly in the western half of the state (Figure 16o).

The earliest record of *B. insularis* in Montana is a specimen collected in Bridger Canyon (Gallatin County) in 1899 and determined by Franklin in 1908 (MTEC). In 1903, Morrill described specimens of *Psithyrus insularis* collected by Cooley in Montana, and Franklin (1912) referenced specimens of both *P. insularis* and *Psithyrus consultus* Franklin from Montana. *Psithyrus consultus* has been synonymized with *B. insularis* (Frison 1922). Since the early 1900s, individuals of *B. insularis* have been sporadically collected across the state (Figure 18o).

This is a relatively common species in North America (Koch *et al.* 2012), though there may be declines in portions of its range due to declines in host species (Hatfield *et al.* 2014, Williams *et al.* 2014). It is currently listed by the IUCN as a

"Species of Least Concern," with a caveat that populations should frequently be monitored since its success depends on strong host populations (Hatfield *et al.* 2014). The database currently contains 389 records of *B. insularis* from 30 Montana counties (Figure 16o).

Diagnosis: Like all species in the subgenus *Psithyrus*, *B. insularis* lacks pollen baskets on the hind tibiae. Characters used for identification include yellow hairs on the face near the antennal bases and yellow hairs on the top of the head. The lateral keels (small ridges) on metasomal S6 are relatively large and rounded in cross-section.

This species is mostly easily confused with *B. flavidus* and *B. suckleyi*, the other two species within the subgenus *Psithyrus* known from Montana. *Bombus flavidus* has black hairs at the base of the antennae, T6 is usually tightly curled below the abdomen, and the lateral keels on S6 are so small they are barely noticeable. *Bombus suckleyi* has no yellow hairs on the face or the top of the head and has lateral keels on S6 that are much more strongly produced.

Bombus (Alpinobombus) kirbiellus Curtis, 1835
High Country Bumble Bee

Bombus kirbiellus is an uncommon bumble bee in North America where it inhabits the highest elevations of the Rocky Mountains from Colorado and New Mexico north to Alaska and northern Canada (Williams *et al.* 2014). In Montana, it has been collected at many high elevation sites, including Logan Pass (2,028m) and Jackson Glacier (2,181m) in Glacier National Park, the Flint Creek Mountains

(2,590m) in Granite County, Big Snowy Peak (2,530m) in Fergus County, and the Beartooth-Absaroka Mountains (~3,000m) in Carbon County (Figure 16p).

Over the past 100 years there have been many names and synonomies for *B. kirbiellus,* highlighting taxonomic difficulties in the arctic bumble bee subgenus, *Alpinobombus.* The work to sort out the taxonomy of this group is ongoing (Williams *et al.* 2015). In 1903, Morrill described four new species of bumble bees from Montana. Among these was *Bombus atrifasciatus* Morrill, now a synonym of *B. kirbiellus* (Franklin 1912), which was collected in Gallatin County by Cooley in July 1900 at an elevation of 2,865m and represents the first record of *B. kirbiellus* in Montana (Morrill 1903). In 1912, another species, *B. kirbyellus,* also now synonymous with *B. kirbiellus* (Hurd 1979), was redescribed by Franklin (1912). Some of the most current literature (Koch *et al.* 2012, Williams *et al.* 2014) called *B. kirbiellus* by the name *B. balteatus.* While Milliron (1973a) considered *B. balteatus* and *B. kirbyellus* to be distinct species, Hurd (1979) considered the two synonomous, and listed 20 other names for this species. Recent work incorporating DNA analysis shows that *B. balteatus* is confined to the Old World, and *B. kirbiellus* is the species in the new world (Williams *et al.* 2015).

Besides the type of *B. atrifasciatus* collected in 1900, Franklin's description in 1912, and two specimens collected in Glacier Park in 1937, there are no records of this species in Montana before 1961, and only nine specimens are recorded from the 1960s and 1970s (Figure 18p). More recently, various research projects took place in the Beartooth Mountains of Carbon County. These projects resulted in a dramatic

accumulation of *B. kirbiellus* records: Macior in the 1980s, Simanonok and Burkle in 2011, and the MTEC group in 2015. The database currently has 122 records of *B. kirbiellus* from six Montana counties (Figure 16p).

Diagnosis: *Bombus kirbiellus* can be identified by its longer-than-wide cheek, black hairs on the face, yellow hairs on metasomal T1 and T2, and orange or pale orange hairs on T4-T6. It is only known from high elevations. This species is most easily confused with *B. frigidus*, which has a very similar color pattern, but *B. frigidus* has a cheek that is about as long as it is wide.

Bombus (Pyrobombus) melanopygus Nylander, 1848
Black Tail Bumble Bee

Bombus melanopygus is known to be common throughout its range, which includes most of California, the southwestern U.S. deserts, and the Rocky Mountains. There are also records of this species scattered throughout the tundra/taiga regions of Alaska and northern Canada (Williams *et al.* 2014). Two color forms exist: the dark form (formerly *B. edwardsii;* Owen *et al.* 2010) is found primarily in California and Oregon, while the red form (*B. melanopygus s. str.)* is found in the northern and eastern portions of its range (Koch *et al.* 2012). In Montana, only the red form has been collected, and it is relatively common in the mountainous regions throughout the western portion of the state (Figure 16q).

Bombus edwardsii was recorded by Franklin (1912) to be in Montana, but what he considered *B. edwardsii* was actually *B. bifarius neararcticus* (Frison 1923). He only predicted the presence of *B. melanopygus*. The earliest specimens of *B.*

melanopygus in the database are seven specimens collected along Beaver Creek (Hill County) in 1913 (SEMC). Since that time, it has continued to be collected in the mountainous regions of Montana (Figure 18q). Just over one third of the specimens of *B. melanopygus* (131 of 357) were collected in 2014 (MTEC, LBLC, GLNP, UCRC). Many of these were collected as part of a project exploring the insects associated with Montana's huckleberry plants (Dolan 2016a). The database currently has 379 records of *B. melanopygus* from 19 Montana counties (Figure 16q).

Diagnosis: *Bombus melanopygus* has a cheek that is about as long as it is wide. The yellow hairs on the face and anterior scutum have many black hairs intermixed, giving the face and anterior scutum a dark or cloudy appearance. The yellow hairs of the scutellum are often divided by black hairs medially. Metasomal T1 is yellow, T2 and T3 are orange, and T6 is always black. The corbicular fringes are also black. There is a color morph of *B. melanopygus* that has black, instead of orange, on T2 and T3, but this color morph has not been documented from Montana.

This species is most easily confused with *B. huntii, B. ternarius*, *B. sylvicola,* and *B. bifarius.* In *B. huntii*, *B. ternarius*, and *B. sylvicola*, there will be few, if any, black hairs intermixed with the yellow on the anterior scutum. *Bombus bifarius* has at least some black on T2, and the corbicular fringes are usually orange. Additionally, the metabasitarsus of *B. bifarius* is almost always brownish-orange, making it appear distinctly lighter than the metatibia.

Bombus (Pyrobombus) mixtus Cresson, 1878
Fuzzy-Horned Bumble Bee

Bombus mixtus is known to be common throughout most of its range, which extends from the Pacific Coast through the Rocky Mountains north into western Canada and Alaska. There are scattered records as far east as the upper Midwest, northern Ontario, and New Brunswick (Williams *et al.* 2014). It is also common in Montana, with records throughout the forested, montane regions in the west (Figure 16r).

Six specimens of *B. mixtus* were collected in Gallatin County in 1900 and were determined by Franklin, who also documented the presence of *B. mixtus* in Montana (1912). Since that time, *B. mixtus* has been consistently collected throughout the western part of the state (Figure 18r), though its presence was not well documented in the literature until after 1980 (Bauer 1983, Fultz 2005, Koch *et al.* 2012, Williams *et al.* 2014). The database currently has 855 records of *B. mixtus* from 30 Montana counties (Figure 16r).

Diagnosis: *Bombus mixtus* has a cheek that is approximately as long as it is wide and there are black hairs mixed throughout the yellow on the anterior scutum, making it appear dark or cloudy. Usually metasomal T2 has yellow hair medially and black hair laterally. Metasomal T5 (and often T4 and sometimes T3) is orange, though sometimes the orange is very pale.

This species is most easily confused with *B. frigidus* and *Bombus sitkensis* in Montana. *Bombus frigidus* does not have black hairs mixed with the yellow on the

anterior scutum and T2 does not have black hair laterally. Similar to *B. mixtus*, *B. sitkensis* has black hairs mixed with yellow on anterior scutum. However, the scutellum of *B. sitkensis* has many more black hairs than the anterior scutum, so the thorax appears to have a front to back gradient of light to dark.

Bombus (Bombias) nevadensis Cresson, 1874
Nevada Bumble Bee

Bombus nevadensis is considered common throughout its range, which is in the western U.S. from the Pacific Coast east to the Great Plains (Koch *et al.* 2012). In Montana, this species is widespread. The database currently has 252 records in 41 counties all across the state (Figure 16s).

The earliest records of *B. nevadensis* are two specimens that were collected in Bozeman in 1899 (MTEC), and it has been consistently collected since that time (Figure 18s). This species is also well documented in the Montana literature (Table 10). *Bombus nevadensis* is the second of four species, along with *B. griseocollis*, *B. rufocinctus*, and *B. auricomus*, known from Montana in which the males have large, bulbous eyes associated with territorial behaviors (O'Neill *et al.* 1991).

As discussed above (see *B. auricomus*), the biggest issue surrounding *B. nevadensis* is its relationship with *B. auricomus* and the idea of *B. auricomus* "replacing" *B. nevadensis* in the East. Eastern Montana is the location where eastern and western ranges overlap and where these two species are sympatric. This leads to problems identifying forms that appear to be intermediate between the two

species. It may be of interest for a future study to look at where these two ranges overlap and how the species' characters converge.

We used the presence or absence of a black interalar band to distinguish between *B. auricomus* and *B. nevadensis* in Montana. If the black hairs on the thorax between the wings reached the wing bases, even if there were a few yellow hairs intermixed, we determined the specimen to be *B. auricomus*. If the hairs touching the wing bases were predominantly yellow, we determined the specimen to be *B. nevadensis*.

Diagnosis: *Bombus nevadensis* is a large bumble bee with short, even hair. The face is predominantly black and there is not a strong black interalar band--either the black band has many yellow hairs intermixed or the band is reduced to a black circle medially. Metasomal T2 and T3 (and usually T1) are yellow while the sides of the thorax are predominantly black.

This species is most easily confused with *B. auricomus* and *B. fervidus. Bombus auricomus* has a strong band of black hairs between the wings, with few to no yellow hairs intermixed. *Bombus fervidus* has yellow hair, not black, on T4 and also has a strong black interalar band.

Bombus (Bombus) occidentalis Greene, 1858
Western Bumble Bee

The range of *B. occidentalis* extends through the Mountain West from the Pacific Coast to the Great Plains, north to Alaska (Williams *et al.* 2014). This species was formerly one of the most common bees in the West and was even reared for

commercial use (Cameron *et al.* 2011). However, since the 1990s, its range has contracted, populations in California and British Columbia have experienced sharp declines (Williams *et al.* 2014), and it is now recommended by the IUCN for "Vulnerable" status (Hatfield *et al.* 2015b).

Bombus occidentalis was first collected in Bridger Canyon (Gallatin County) in 1889 (MTEC). Since that time, it has been one of the most commonly collected species in Montana, and is still frequently collected (103 specimens collected in 18 counties during summer 2015, Figure 18t).

However, from 2000-2015, the percent increase of *B. occidentalis* was just 36% (Table 14; Figure 20), compared to ≥49% for all other *Bombus* species collected, with the exception of one other species (see *B. suckleyi*). This relatively low percent increase is consistent with reports of this species' decline (Cameron *et al.* 2011, Hatfield *et al.* 2015b). Changes in the prey composition of natural enemies over the past 50 years may also be reflective of population declines in this species. Armitage (1965) found *B. occidentalis* to be the most common prey (35% of 203 *Bombus*) of the wasp *Philanthus bicinctus* Mickel at a site on the southern edge of Yellowstone National Park (50 km from Montana). Forty years later, however, Dukas (2005) found that *B. rufocinctus* was the primary prey of the wasp at the same site, though he does not indicate whether *B. occidentalis* was among the prey.

Bombus occidentalis has been thought to replace *B. terricola* in the west (see *B. terricola*), but we now have records of these two species being sympatric in the two northeastern-most counties of Montana (compare Figure 16t and Figure 16aa).

The database currently contains 1,046 records of *B. occidentalis* from 41 Montana counties (Figure 16t). The southeastern portion of the state is notably lacking records of this species.

Diagnosis: *Bombus occidentalis* is one of the most easily identified species in the state. It has a cheek that is shorter than wide and white or yellow hairs on metasomal T5 (and usually T4). Metasomal T1 and T6 are always black, T2 is usually black at least anteriorly, and T3 may be black or yellow.

This species is most easily confused with *B. terricola* in Montana, but *B. terricola* can be distinguished by always having yellow hairs on both T2 and T3. Though not yet recorded from the state, *B. cryptarum* is another species that could be confused with *B. occidentalis. Bombus cryptarum* always has black hairs on T1, yellow hairs on T2, and black hairs on T3.

Bombus (Thoracobombus) pensylvanicus (DeGeer, 1773)
American Bumble Bee

Bombus pensylvanicus was once one of the most widespread bumble bees in North America, ranging from the eastern U.S. through the Great Plains, with the subspecies *B. pensylvanicus sonorous* known from the deserts of the Southwest to Oregon (Williams *et al.* 2014). However, the IUCN now recommends this bee for "Vulnerable" status as recent studies have documented declines in both range and abundance, especially in the northernmost parts of its range (Hatfield *et al.* 2015c). *Bombus pensylvanicus* has rarely been collected in Montana, with only five specimens known from four counties (MTEC, PMNH; Figure 16u).

Writing about *B. pensylvanicus,* Franklin (1912) questioned its presence in Montana, noting that the species was common east of the Rocky Mountains, but surprisingly absent from the northernmost regions of the U.S. Milliron's (1973a) predictive range map for *B. pensylvanicus* just barely extends into the southeast corner of Montana and he had no Montana records. The map in Williams *et al.* (2014) suggests geographic suitability across the eastern two-thirds of Montana and shows three records: one in the southern part of the state, one on the Montana/North Dakota border, and one just north in Canada. The database contains one specimen of *B. pensylvanicus* collected prior to the present study, from Big Horn County in 1964 (PMNH). This likely is the record represented by the dot on the Williams *et al.* (2014) map.

In 2015, we collected four more specimens of *B. pensylvanicus* (Figure 18u) from three counties (Carter, Powder River, and Pondera). These records fit the geographic suitability model presented in Williams *et al.* (2014) and suggest the presence of this species across more of Montana. Sampling across the eastern two-thirds of the state could reveal a more widespread presence of this species, and may be of special interest given its conservation status.

Diagnosis: *Bombus pensylvanicus* has a cheek that is longer than it is wide. The hairs on the face and on the top of the head are black. The surface of the clypeus has many pits and punctures. Metasomal T2 and T3 (and often T1) have

yellow hairs while T4-T6 are black. The black hair between the wings forms a strong interalar band, though often the scutellum is also all black so that the only yellow on the thoracic dorsum is anterior to the wings.

This species is similar to, and easily confused with, *B. fervidus*, *B. nevadensis*, *B. auricomus*, *B. appositus*, and *B. borealis.* However, *B. fervidus* has T1-T4 yellow. *Bombus auricomus* and *B. nevadensis* both have a very smooth clypeus. *Bombus appositus* and *B. borealis* both have yellow hair predominating on the face and on T1-T4.

Bombus (Cullumanobombus) rufocinctus Cresson, 1863
Red-Belted Bumble Bee

Bombus rufocinctus is a widespread, common bee throughout the Rocky Mountains east through the northern U.S. and Canada to the Atlantic Coast (Williams *et al.* 2014). In Montana, it is one of the most widespread species, having been collected in all but four counties (Figure 16v).

Bombus rufocinctus is well known to be in Montana from the literature (Table 10). Four specimens of *B. rufocinctus* collected in the Bozeman area in 1899 are the earliest records of this species in the state (MTEC). Since that time, records of *B. rufocinctus* have steadily increased (Figure 18v) and the database currently has 1,391 *B. rufocinctus* records from 52 Montana counties (Figure 16v).

Bombus rufocinctus is the third species in Montana (along with *B. griseocollis*, *B. nevadensis*, and *B. auricomus)* in which the males have large, bulbous eyes associated with mate seeking and territory defense (O'Neill *et al.* 1991). While

searching for mates, these males are known to perch on plants or structures and chase any moving object (Williams *et al.* 2014).

Among the bumble bee species in Montana, *B. rufocinctus* has the most variable color patterns. This variability causes individuals to look similar to many other species and can lead to misidentifications if specimens are not carefully examined. There seems to be no geographic pattern associated with the various color morphs, and an individual colony may produce workers with many different color patterns (Williams *et al.* 2014).

Diagnosis: This species has incredible variation in coloration and superficially can be easily confused with many other species, so using the key for identification is the best strategy when dealing with *B. rufocinctus.* Characters used for identification include a distinctly shorter-than-wide cheek and black hair on the face. The integument under the hairs of metasomal T1 and T2 is shiny, and there is usually a distinct interalar band. Metasomal T2 almost always has a crescent of yellow medially, while T3 and T4 have hairs that are orange, black, yellow, or some combination of these colors.

Bombus (Pyrobombus) sitkensis Nylander, 1848
Sitka Bumble Bee

The range of *B. sitkensis* extends from Alaska south along the coast to California as well as through the Canadian Rocky Mountains into Idaho, Montana, and Wyoming (Williams *et al.* 2014). It is commonly collected throughout this range. As would be expected based on its known distribution, *B. sitkensis* has only

been collected in the northwestern corner of Montana (Figure 16w). Since its range in Montana is so limited, it is one of the less commonly collected species in the state.

Franklin predicted that *B. sitkensis* would be found in western Montana, though he only had records from Alaska, British Columbia, Washington, Oregon, Idaho, and California (1912). The first specimen of this species was not collected in Montana until August of 1934 in Glacier National Park (Flathead County; UCRC). Between 1934 and 2009 only 22 more individuals were collected (Figure 18w). The Bee Biology and Systematics Laboratory has 36 records of this species from the Hungry Horse Dam (Flathead County) in 2009 (BLCU), and huckleberry pollinator projects in northwest Montana in 2014 and 2015 added over 100 more records (MTEC, GLNP; Dolan 2016a). The database currently has 180 records of *B. sitkensis* from eight Montana counties (Figure 16w).

Diagnosis: *Bombus sitkensis* has a cheek that is about as long as it is wide (though sometimes it may appear slightly longer than wide) and long, uneven body hairs. There are many black hairs mixed with the yellow on the thoracic dorsum, with more black intermixed with yellow on the scutellum than on the anterior scutum, making the scutellum appear darker than the anterior scutum. Metasomal T1 and T2 are predominantly yellow, T3 is black, T4 has black hair anteriorly and brown/orange hair posteriorly, T5 is brown/orange, and T6 is black.

This species is most easily confused with *B. mixtus*, which has a similar color pattern and also can have long, uneven hairs. While *B. mixtus* does have black hairs intermixed with yellow on the scutellum like *B. sitkensis*, usually the anterior

scutum appears darker than the scutellum, though sometimes the amount of black hairs intermixed with yellow is similar between the anterior scutum and the scutellum of *B. mixtus*.

Bombus (Psithyrus) suckleyi Greene, 1860
Suckley Cuckoo Bumble Bee

Bombus suckleyi is an uncommon social parasite known to breed in colonies of *B. occidentalis,* though it has also been observed in nests of *B. terricola*, *B. rufocinctus*, *B. fervidus*, *B. nevadensis*, and *B. appositus* (Williams *et al.* 2014). Its range extends from the Pacific Coast east to Nebraska and from New Mexico north to Alaska (Koch *et al.* 2012). It also has been recorded across the Canadian Prairie Provinces to the Atlantic Coast in northeastern Canada (Williams *et al.* 2014). *Bombus suckleyi* is one of only three species on the IUCN Red List recommended for "Critically Endangered" status (Hatfield *et al.* 2015d). In Montana, *B. suckleyi* seems to have a patchy distribution, with records throughout the western half of the state and one record in Daniels County in the far northeast (Figure 16x).

The earliest record of *B. suckleyi* is from Bozeman in 1899 (NMNH). This individual is listed as a cotype of *Psithyrus latitarsus* Morrill (1903). *Psithyrus latitarsus* was later synonomized with *B. suckleyi* (Frison 1926). Records steadily accumulated from 1899 until the 1990s (Figure 18x). The database currently has 146 records of *B. suckleyi* from 19 Montana counties (Figure 16x).

Only five individuals of *B. suckleyi* have been added to the database since 2000 (MTEC, BLCU, KMOC) when sampling efforts in Montana substantially

increased, which is consistent with observations of this species' decline (Hatfield *et al.* 2015d). These five records represent only a 4% increase in the number of *B. suckleyi* specimens collected since 2000, which stands in stark contrast to the substantial increase in the numbers of most other Montana *Bombus* species since 2000 (Table 14; Figure 20). It has been hypothesized that the decline of *B. suckleyi* is associated with the observed decline of *B. occidentalis*, its primary host (Hatfield *et al.* 2015d). In Montana, which is at the center of the historic range of *B. occidentalis* (Cameron *et al.* 2011), there has not been a great deal of concern about population declines (but see *B. occidentalis* species account), so the low numbers of *B. suckleyi* collected in the past 15 years seem a bit surprising. No standardized population assessment has yet been conducted in Montana, so it is not appropriate at this time to form conclusions about the populations of any of Montana's species. However, it is clear that more work is needed to assess the true range, status, and habits of *B. suckleyi* and its primary host, *B. occidentalis*, in Montana.

Diagnosis: Like all species in the subgenus *Psithyrus*, *B. suckleyi* lacks pollen baskets on the hind tibiae. Characters used to identify this species include black hairs on both the face and the top of the head and very strongly produced lateral keels (ridges) on metasomal S6.

This species is mostly easily confused with *B. flavidus* and *B. insularis,* the other two species within the subgenus *Psithyrus* known from Montana. However, the abdomen of *B. flavidus* is usually tightly curled under, it has black hairs at the bases of the antennae, yellow hairs on the top of the head, and the lateral keels on S6

are barely noticeable. *Bombus insularis* has yellow hairs on both the face and top of the head and its lateral keels are not as strongly produced as those of *B. suckleyi.*

B. (Pyrobombus) sylvicola Kirby, 1837
Forest Bumble Bee

Bombus sylvicola is a boreal-alpine species that is common throughout high elevation habitats of the western U.S., north to Alaska and across the northernmost parts of Canada (Williams *et al.* 2014). In Montana, it has been collected throughout the mountainous counties in the west, though 55% (104 of the 187) of the records are from the Beartooth Plateau of Carbon County where the Beartooth Highway makes access to true alpine habitat easy (Figure 16y).

There are no records of *B. sylvicola* in the database until 1913. After that, only 42 individuals were collected until 1980 (Figure 18y), and there was no literature record of this species in Montana until 1983 (Bauer 1983). *Bombus sylvicola* was collected more often beginning in the early 1980s, when Macior was in Carbon County collecting high elevation bees. From 1990 until 2015, various MSU research projects and collecting trips led entomologists to higher elevations (in Beaverhead, Carbon, Gallatin, Glacier, Madison, Meagher, and Park Counties), which more than doubled our *B. sylvicola* records. The database currently has 187 records of *B. sylvicola* from 18 Montana counties (Figure 16y).

Diagnosis: *Bombus sylvicola* has body hairs that are relatively long and uneven. It also has a square cheek and hair pattern of metasomal T1: yellow, T2 and

T3: orange, T4: yellow, T5: black with yellow tufts laterally, and T6: black. The black hairs on the face are interrupted by a circle of yellow hair at the base of the antennae. The yellow hair on the scutellum is divided by a line or triangle of black hairs medially.

This species is most easily confused with *B. huntii*, *B. ternarius*, and *B. melanopygus*, though collecting at higher elevations reduces the likelihood of an individual being *B. huntii* or *B. ternarius.* *Bombus huntii* does not have black interrupting the yellow hairs of the scutellum, the face has only yellow hairs, and T5 is completely black. *Bombus ternarius* will often have yellow hair on the coxae and T5 will be completely black. *Bombus melanopygus* has many black hairs intermixed with the yellow on the anterior scutum making it appear cloudy.

There is a form of *B. sylvicola* in which the orange hair on T2 and T3 is replaced with black. This form has not been recorded in Montana, and is known primarily from the Sierra Nevada Mountains of California.

Bombus (Pyrobombus) ternarius Say, 1837
Tri-Colored Bumble Bee

Bombus ternarius is known to inhabit the eastern and northern portions of the U.S. and the eastern and southern portions of Canada (William *et al.* 2014). Koch *et al.* (2012) described the distribution of this species as common in the East, but rare in the West, with records from eastern Montana and the Black Hills east to New England. In Montana, *B. ternarius* has been found through much of the north and east (Figure 16z). *Bombus ternarius* is said to replace *B. huntii* in the north

(Williams *et al.* 2014), but throughout much of Montana these two species appear to be sympatric (compare Figure 16m and Figure 16z).

Frison (1923) records one specimen of *B. ternarius* from Montana. However, no other information on that specimen is given in his paper. No other record of *B. ternairus* appears in the literature until Kral (1955) recorded one on Eddy Peak in Sanders County, though no voucher from this study has been found for verification. Hurd (1979) lists Montana as part of the range of *B. ternarius*, but the geographic suitability map published by Koch *et al.* (2012) predicts that it might barely make it into the eastern part of the state. The range map published by Williams *et al.* (2014) shows records of *B. ternarius* right on Montana's northern and eastern borders, and the pattern of records plus geographic suitability strongly suggest that it would be found here, especially in the eastern and northern counties.

Only three specimens collected before 2000 are in the database: one undated specimen labeled only "Montana" (ANSP; this is likely Frison's 1923 specimen); one collected in Mineral County in August, 1931 (SEMC); and one from Gallatin County in June, 1973 (OSUC). Three individuals were collected in far northeastern Montana (Sheridan County) in 2006 and 2008. Then, in 2011, Montana Department of Agriculture personnel put green bucket traps across eastern Montana to monitor for invasive moth species (I. A. Foley, personal communication 2016). Those traps collected 108 *B. ternarius* individuals from nine counties in eastern Montana. Japanese beetle traps and yellow bucket traps were placed across eastern Montana again in 2015, and 185 *B. ternarius* were taken from nine counties (Figure 18z). The

database currently has 301 records of *B. ternarius* from 18 Montana counties (Figure 16z), and it has become one of the most commonly collected species in the northeastern portion of the state.

Diagnosis: *Bombus ternarius* has a cheek that is about as long as it is wide and hair pattern of metasomal T1: yellow, T2 and T3: orange, T4: yellow, and T5 and T6: black. The face is black with yellow hairs near the antennal bases, and the yellow hairs on the scutellum are divided by a line or triangle of black hairs. Often there are yellow hairs on the front coxae.

This species is most easily confused with *B. huntii*, *B. sylvicola*, and *B. melanopygus. Bombus huntii* is found in many of the same habitats, but the yellow hairs of the scutellum are not divided by black and the hairs on the face are predominantly yellow. *Bombus sylvicola* is typically found at higher elevations and has longer, more uneven body hairs, plus there are yellow tufts of hair laterally on T5. *Bombus melanopygus* has many black hairs mixed with the yellow on the anterior scutum making it appear cloudy.

Bombus (Bombus) terricola Kirby, 1837
Yellow-Banded Bumble Bee

The range of *B. terricola* extends from New England and eastern Canada north and west through the Great Plains and Black Hills to British Columbia and the Yukon Territory (Williams *et al.* 2014). Though previously common in the eastern

U.S., this species has been in decline in major parts of its range and is considered rare in the western U.S. (Koch *et al.* 2012, Williams *et al.* 2014). It has been recommended by the IUCN Red List for "Vulnerable" status (Hatfield *et al.* 2015e). *Bombus terricola* is one of the four most rarely collected Montana bumble bees.

Literature records placed *B. terricola* in Montana (Frison 1923, Kral 1955, Williams *et al.* 2014). However, upon examination of many of the specimens associated with those records, nearly all of the *B. terricola* records from Montana are *B. occidentalis* according to current taxonomic understanding (Koch *et al.* 2012, Williams *et al.* 2014). We did collect nine specimens of *B. terricola* from far northeastern Montana (MTEC): one from 2011 and eight in 2015 (Figure 16aa; Figure 18aa). There is one more verified *B. terricola* specimen determined by Franklin in 1922 (ANSP; this is likely Frison's 1923 specimen), but it lacks a date or specific locality. This individual is the earliest known record of *B. terricola* in Montana.

Bombus terricola is known to be in the Black Hills area of South Dakota (Koch *et al.* 2012) and has been predicted to be as far west as eastern Montana (Milliron 1971, Koch *et al.* 2012, Williams *et al.* 2014). It has been collected in Alberta east of Edmonton, and in northwestern Alberta near Valleyview and Grande Prairie (A. Sturm, personal communication 2015). Thus, it is possible that the range of *B. terricola* extends further into Montana than has been predicted.

Bombus terricola is said to more-or-less replace *B. occidentalis* in the eastern U.S. (Williams *et al.* 2014). A comparison of Figure 16t and Figure 16aa shows that

B. occidentalis has not yet been collected in the southeastern region of Montana, where *B. terricola* would be expected to be found, though the two species do seem to be sympatric in the northeastern part of the state.

Diagnosis: *Bombus terricola* has a cheek that is shorter than wide and a hair pattern of metasomal T1: black, T2 and T3: yellow, T4: black, T5 and T6: black or yellow. This species is most easily confused with *B. occidentalis* and *B. cryptarum.* However, in *B. occidentalis*, T2 has at least some black and in *B. cryptarum* (which has not been recorded from Montana, but may be here), T3 is black.

Bombus (Pyrobombus) vagans Smith, 1854
Half-Black Bumble Bee

Bombus vagans is a common bumble bee known from eastern Washington to New England, primarily along the Canadian border (Koch *et al.* 2012), and south through the Appalachian Mountains (Williams *et al.* 2014). The database shows patchy records of *B. vagans* in Montana (Figure 16ab). It's been collected throughout the mountainous northwestern counties, in the south-central counties, and in two counties in far eastern Montana. This patchy distribution suggests the need for more sampling throughout the state.

The first known specimen of *B. vagans* was collected by Cooley in Ravalli County in 1901. Since that time it has continued to be collected fairly regularly (Figure 18ab). The database currently contains 152 records of *B. vagans* from 18 Montana counties (Figure 16ab).

Diagnosis: *Bombus vagans* has a cheek that is longer than it is wide (though sometimes it may appear to be as long as it is wide) and a hair pattern of metasomal T1 and T2: yellow and T3-T6: black. Sometimes the yellow hairs on T2 are only along the anterior margin, with the posterior hairs black. The hairs on the face are black, but there are usually shorter yellow hairs inconspicuously mixed in, especially near the base of the antennae. The sides of the thorax are yellow.

This species is most easily confused with *B. bimaculatus*, *B. griseocollis*, and *B. perplexus.* In *B. bimaculatus*, T2 is black with yellow hairs only medially, often in a W- shape. The sides of the thorax are extensively black in *B. perplexus* (which is not yet known from Montana) and *B. griseocollis* has a cheek that is shorter than wide. There is a dark form of *B. flavifrons* that looks very similar to *B. vagans*, though this form has not yet been recorded from Montana. The dark form of *B. flavifrons* can be distinguished from *B. vagans* by having yellow hairs laterally on T3 and T4 and having S3-S5 extensively yellow.

Acknowledgements

This project would not have been possible without the help and support of a large number of people. Frank Etzler, Paloma Amaral, Charles Hart, Michael Ivie, Donna Ivie, Ian Foley, and Lauren Kerzicnik traveled many miles all over Montana during the summer of 2015 to collect bumble bees and/or put up insect traps. Paloma Amaral, Joe Wood, Dayane Andrade do Reis, Alyssa Piccolomini, Lisa Seelye, Elizabeth Reese, Justin Runyon, Adrian Massey, Frank Etzler, Charles Hart, Michael Ivie, Donna Ivie, Casey Delphia and Tyler Kelly helped process specimens. Lauren Kerzicnik forwarded a request for bumble bee collecting volunteers to the Extension Agents and Master Gardeners across the state, and served as the recipient of those specimens in the MSU Schutter Diagnostic Lab. Volunteers that sent in specimens included Patti Armbrister, Cynthia Mernin, Misty Miles, Sean Foley, Kevin Foley, and Katie Foley, Kari Lewis, Janet Hamill, and Patti Fulton. Tabitha Graves and Joe Giersh contributed specimens collected at their USGS project sites in Glacier National Park. James Beck created all maps included in this work. He also designed and manages the MTEC website. Tyler Kelly, Elizabeth Reese, and Lisa Seelye tested the key and offered valuable feedback. Norman Johnson, Joe Cora, and Sara Hemley offered a great deal of assistance throughout the process of databasing all the records. James Strange, Jonathan Koch, and Robbin Thorp verified troublesome identifications and answered morphological or diagnostic questions. Robert Peterson, Christopher Brown, and Tyler Kelly contributed photographs to the website. Catherine Delphia created figure 10.

I would like to thank the following individuals, collection managers, curators, and database managers for their contributions to the over 12,000 *Bombus* records from Montana. Brian Thompson, Hayes Goosey, and Ruth O'Neill contributed specimens from various 2015 research projects at MSU. Ian Foley, from the Montana Department of Agriculture, contributed specimens collected in CAPS project traps. Bethanne Bruninga-Socolar, from Rutgers University, New Brunswick, NJ, contributed records from her Ph.D. project in Montana. Leif Richardson, Harold Ikerd, Lawrence Gall, and John Ascher contributed lists of Montana *Bombus* from their databases. Jessamyn Manson, Monica Kohler, and Ashton Sturm, University of Alberta, Edmonton, shared records and observations about bumble bees in Alberta. The following loaned specimens or hosted a visit to examine specimens: Jason Weintraub, Greg Cowper, and Jon Gelhaus, Academy of Natural Sciences, Philadelphia, PA; Luciana Musetti, C. A. Triplehorn Insect Collection, The Ohio State University, Columbus, OH; Casey M. Delphia, Bozeman, MT; Catherine E. Siebert, Bozeman, MT; Christopher Grinter, Illinois Natural History Survey, Champaign, IL; the Kevin M. O'Neill Lab (which includes C. Delphia, J. Fultz, and A. Pearce) at Montana State University, Bozeman; the Laura Burkle Lab (which includes E. Reese, M. Simanonok, L. Heil, and S. Adhikari) at Montana State University; Jen Marangelo, Missoula Butterfly House and Insectarium; Michael Ivie, Montana Entomology Collection at MSU, Bozeman; John Swann, Museum of Zoology, University of Calgary, Alberta; Brian Harris, Sean Brady, and Floyd Shockley, National Museum of Natural History, Washington, D. C.; Leonard Munstermann and Lawrence Gall, Peabody

Museum of Natural History, Yale University, New Haven, CT; Jennifer Thomas and Zachary Falin, Snow Entomological Museum, University of Kansas, Lawrence; Virginia Scott, University of Colorado Musuem of Natural History, Boulder, CO.

This is a contribution of the Montana Agricultural Experiment Station.

Table 10. Literature Records of *Bombus* in Montana.

Citation	*Bombus* Species Documented
Morrill 1903	**Recorded:** *B. cooleyi*[1], *B. atrifasciatus*[2], *Psithyrus*[3] *latitarsus*[4], *P. insularis*
Franklin 1912	**Recorded:** *B. appositus, B. centralis, B. edwardsii*[5], *B. fervidus, B. flavifrons, B. huntii, B. kirbyellus*[6], *B. mixtus, B. occidentalis, B. nevadensis, B. rufocinctus, B. separatus*[7], *B. vagans, P. consultus*[8], *P. insularis, P. latitarsus*[4] **Predicted:** *B. californicus, B. frigidus, B. melanopygus, B. pensylvanicus, B. sitkensis, P. tricolor*[9]
Franklin 1915	**Recorded:** *B. californicus*
Anonymous 1920	**Recorded:** *B. bifarius, B. centralis, B. occidentalis, B. rufocinctus* (Species not listed in publication, but specimens are deposited at the Academy of Natural Sciences, PA)
Frison 1923	**Recorded:** *B. terricola, B. vosnesenskii*[10], *B. ternarius*
Kral 1955	**Recorded:** *B. edwardsii*[5], *B. occidentalis, B. ternarius, B. terricola*[11]
Milliron 1971	**Recorded:** *B. occidentalis*, *B. nevadensis* **Predicted:** *B. auricomus, B. terricola*
Milliron 1973a	**Recorded:** *B. appositus B. fervidus fervidus* **Predicted:** *B. fervidus californicus, B. kirbyellus*[6], *B. pensylvanicus*
Milliron 1973b	**Recorded:** *B. griseocollis* **Predicted:** *B. morrisoni*
Hurd 1979	**Recorded:** *B. nevadensis auricomus, B. sitkensis, B. ternarius, B. terricola terricola, B. vagans vagans*
Bauer 1983	**Recorded:** *B. appositus, B. bifarius nearcticus, B. flavifrons, B. frigidus, B. kirbyellus*[6], *B. melanopygus, B. mixtus, B. nevadensis nevadensis, B. occidentalis, B. sylvicola, P. insularis*
O'Neill *et al.* 1991	**Recorded:** *B. griseocollis, B. nevadensis nevadensis, B. rufocinctus*

Table 10 Continued.

Citation	*Bombus* Species Documented
Fultz 2005	**Recorded:** *B. appositus, B. californicus, B. edwardsii*[5]*, B. fernaldae*[9]*, B. fervidus, B. flavifrons, B. impatiens*[12]*, B. insularis, B. occidentalis, B. melanopygus, B. mixtus, B. rufocinctus, B. suckleyi,*
Pearce *et al.* 2012	**Recorded:** *B. centralis, B. fervidus, B. griseocollis, B. huntii, B. rufocinctus, B.* sp.
Koch *et al.* 2012	**Recorded:** *B. appositus, B. bifarius, B. californicus, B. centralis, B. fernaldae*[9]*, B. fervidus, B. flavifrons, B. frigidus, B. griseocollis, B. huntii, B. insularis, B. melanopygus, B. mixtus, B. nevadensis, B. occidentalis, B. rufocinctus, B. sitkensis, B. suckleyi, B. sylvicola, B. vagans* **Predicted:** *B. balteatus*[13]*, B. morrisoni, B. ternarius, B. terricola*
Simanonok and Burkle 2014	**Recorded:** *B. appositus, B. balteatus*[13]*, B. bifarius bifarius, B. bifarius neararcticus, B. centralis, B. fernaldae*[9]*, B. flavifrons, B. frigidus, B. insularis, B. melanopygus, B. mixtus, B. nevadensis, B. sylvicola*
Williams *et al.* 2014	**Recorded:** *B. appositus*, *B. balteatus*[13]*, B. bifarius, B. centralis, B. fervidus, B. flavidus, B. flavifrons, B. frigidus, B. griseocollis*, *B. huntii, B. insularis*, *B. melanopygus, B. mixtus, B. nevadensis*, *B. occidentalis*, *B. pensylvanicus, B. rufocinctus*, *B. sitkensis, B. suckleyi*, *B. sylvicola, B. terricola*[11]*, B. vagans* **Recorded Near Montana Border:** *B. borealis, B. ternarius, B. bohemicus* **Predicted**[14]**:** *B. bohemicus, B. cryptarum, B. fraternus, B. morrisoni, B. vosnesenskii*

[1]*B. cooleyi = B. bifarius* (Hurd 1979)
[2]*B. atrifasciatus=B. kirbiellus* (Hurd 1979, Williams *et al.* 2015)
[3]The genus *Psithyrus* is now considered to be a subgenus of *Bombus* (Michener 2000)
[4]*P. latitarsus = B. suckleyi* (Hurd 1979)
[5]*B. edwardsii = B. bifarius* (Frison 1923)
[6]*B. kirbyelleus = B. kirbiellus* (Hurd 1979, Williams *et al.* 2015)
[7]*B. separatus =B. griseocollis* (Hurd 1979)
[8]*P. consultus = B. insularis* (Williams *et al.* 2014)
[9]*B. tricolor = B. fernaldae = B. flavidus* (Hurd 1979, Williams *et al.* 2014)
[10]No other information was given for this record, and no voucher has been found for verification.
[11]Likely *B. occidentalis*, see discussion
[12]This record is not verified, see discussion
[13]*B. balteatus* is confined to the old world; *B. kirbiellus* is the species found in North America (Williams *et al.* 2015)
[13]Predicted via geographic suitability maps

Table 11. Labs, Institutions, and Individuals that Contributed *Bombus* **Specimens**.

Lab, Institution, or Individual	Number of Specimens Examined/Databased*
Academy of Natural Sciences, Philadelphia, PA (ANSP)	457/457
C.A. Triplehorn Insect Collection, The Ohio State University, Columbus, OH (OSUC)	170/170
Casey M. Delphia Personal Collection, Bozeman, MT (CMDC)	306/306
Catherine E. Seibert Private Collection, Bozeman, MT (CESC)	265/265
Glacier National Park Collection, West Glacier, MT (GLNP)	130/130
Illinois Natural History Survey, Urbana, IL (INHS)	62/62
Kevin M. O'Neill Lab Collection, Montana State University, Bozeman, MT (KMOC)	2,113/585
Laura Burkle Lab Collection, Montana State University, Bozeman, MT (LBLC)	1,967/400
Missoula Butterfly House and Insectarium, Missoula, MT (MBHI)	7/7
Montana Entomology Collection, Montana State University, Bozeman, MT (MTEC)	8,164/6,616
Museum of Zoology, University of Calgary, Calgary, AB, Canada (BDUC)	645/28
National Museum of Natural History, Washington, DC (NMNH)	182
Peabody Museum of Natural History, Yale University, New Haven, CT (PMNH)	139/462
Snow Entomological Museum, University of Kansas, Lawrence, KS (SEMC)	469
University of Colorado Museum of Natural History, Boulder, CO (UCMC)	159

*When a particular collection had a large number of *Bombus* specimens of the same species from the same locality, all determinations were checked and verified, but not every individual was added to the database.

Table 12. Institutions and Individuals that Contributed Databased *Bombus* **Records.**

Institution or Individual	N Records Uploaded
American Museum of Natural History, New York, NY (AMNH)	319
Bee Biology and Systematics Laboratory (USDA-ARS), Utah State University, Logan, UT (BLCU)	1,137
Essig Museum of Entomology, University of California, Berkeley, CA (EMEC)	17*
Jessamyn Manson Lab, University of Alberta, Edmonton, AB, Canada (JMLC)	36
Leif Richardson, from Williams *et al.* 2014 *Bumble Bees of North America*	1,820
M.T. James Museum, Washington State University, Pullman, WA (WSU)	41*
Patuxent Wildlife Research Center, Laurel, MD (PWRC)	68
Peabody Museum of Natural History, Yale University, New Haven, CT (PMNH)	323
R.M. Bohart Museum of Entomology, University of California, Davis, CA (UCDC)	29*
Rutgers State University, Brunswick, NJ (RUIC)	47**
University of California, Riverside, CA (UCRC)	56*
University of Massachusetts - Entomology, Amherst, MA (UMEC)	8**
W.F. Barr Entomological Collection, University of Idaho, Moscow, ID (WFBM)	55*

*Records were included in the files from BLCU and Leif Richardson
**Records were included in the file from AMNH

Table 13. The 28 *Bombus* Species Found in Montana. The species are organized by year of earliest detection in the state, based on the specimens in the database.

Species	Earliest Specimen (Year)	First Lit Record	Total Number of Specimens	Total Number of Counties
Bombus (Pyrobombus) bifarius Cresson, 1878	1883	Morrill 1903	1,911	37
Bombus (Pyrobombus) huntii Greene, 1860	1883[1]	Franklin 1912	1,840	53
Bombus (Subterraneobombus) appositus Cresson, 1878	1899	Franklin 1912	302	25
Bombus (Thoracobombus) fervidus (Fabricius, 1798)	1899[1]	Franklin 1912	688	47
Bombus (Psithyrus) insularis (Smith, 1861)	1899	Morrill 1903	389	30
Bombus (Bombias) nevadensis Cresson, 1874	1899[1]	Franklin 1912	252	41
Bombus (Bombus) occidentalis Greene, 1858	1899[1]	Franklin 1912	1,046	41
Bombus (Cullumanobombus) rufocinctus Cresson, 1863	1899	Franklin 1912	1,391	52
Bombus (Psithyrus) suckleyi Greene, 1860	1899	Morrill 1903	146	19
Bombus (*Alpinobombus) kirbiellus* Curtis, 1835	1900	Morrill 1903	122	6
Bombus (Pyrobombus) flavifrons Cresson, 1863	1900	Franklin 1912	488	30
Bombus (Pyrobombus) mixtus Cresson, 1878	1900	Franklin 1912	855	30
Bombus (Pyrobombus) centralis Cresson, 1864	1901[1]	Franklin 1912	641	47
Bombus (Pyrobombus) vagans Smith, 1854	1901	Franklin 1912	152	18
Bombus(*Cullumanobombus) griseocollis* (DeGeer, 1773)	1904	Franklin 1912	357	38
Bombus (Thoracobombus) californicus Smith, 1854	1913	Franklin 1915	91	19
Bombus (Pyrobombus) melanopygus Nylander, 1848	1913	Franklin 1912	379	19

Table 13 Continued.

Species	Earliest Specimen (Year)	First Lit Record	Total Number of Specimens	Total Number of Counties
Bombus (Pyrobombus) sylvicola Kirby, 1837	1913	Bauer 1983	187	18
Bombus (Subterraneobombus) borealis Kirby, 1837	1926[1]	**New State Record[2]**	20	8
Bombus(Psithyrus) flavidus Eversmann, 1852	1929[2]	Fultz 2005	158	19
Bombus (*Pyrobombus) frigidus* Smith, 1854	1929	Bauer 1983	59	9
Bombus (Pyrobombus) ternarius Say, 1837	1931[1]	Kral 1955	301	18
Bombus (Pyrobombus) sitkensis Nylander, 1848	1934[2]	Hurd 1979	180	8
Bombus (Thoracobombus) pensylvanicus (DeGeer, 1773)	1964	Willams *et al.* 2014	5	4
Bombus (Bombias) auricomus (Robertson, 1903)	1971	Hurd 1979	5	4
Bombus (Pyrobombus) impatiens Cresson, 1863	1980	Fultz 2005[3]	7	2
Bombus (Pyrobombus) bimaculatus Cresson, 1863	2011	**New State Record**	18	7
Bombus (Bombus) terricola Kirby, 1837	2011[1]	Kral 1955[4]	10	2

[1]Some specimens at ANSP have no recorded collection date. They were determined by Franklin in 1922, and may be part of E.T. Cresson's collection, which means they may have been collected as early as the mid-18th century (Weintraub 2015, personal communication).
[2]This species was predicted, but not confirmed, by earlier literature to be in Montana.
[3]This record of *B. impatiens* could not be verified. See text.
[4]The specimen recorded by Kral 1955 is likely *B. occidentalis*. See text.

Table 14. Comparison of *Bombus* Specimens Collected Before and After 2000. The year 2000 was the point where sampling efforts in the state of Montana substantially increased.

Species	Collected pre-2000	Collected between 2000-2015	Total Number Collected*	% increase from 2000-2015
B. appositus	202	99	301	49
B. auricomus	1	4	5	400
B. bifarius	903	1,003	1,906	111
B. bimaculatus	0	18	18	NA
B. borealis	2	17	19	850
B. californicus	50	39	89	78
B. centralis	223	416	639	187
B. fervidus	285	369	654	129
B. flavidus	26	132	158	508
B. flavifrons	166	316	482	190
B. frigidus	23	35	58	152
B. griseocollis	99	253	352	256
B. huntii	402	1391	1793	346
B. impatiens	1	6	7	600
B. insularis	249	135	384	54
B. kirbiellus	57	65	122	114
B. melanopygus	140	237	377	169
B. mixtus	354	497	851	140
B. nevadensis	126	121	247	96
B. occidentalis	766	277	1,043	36
B. pensylvanicus	1	4	5	400
B. rufocinctus	661	716	1,377	108
B. sitkensis	22	158	180	718
B. suckleyi	139	5	144	4
B. sylvicola	108	79	187	73
B. ternarius	3	298	301	9,933
B. terricola	1	9	10	900
B. vagans	54	98	152	181

*Specimens without a specific date on the label were excluded from these calculations.

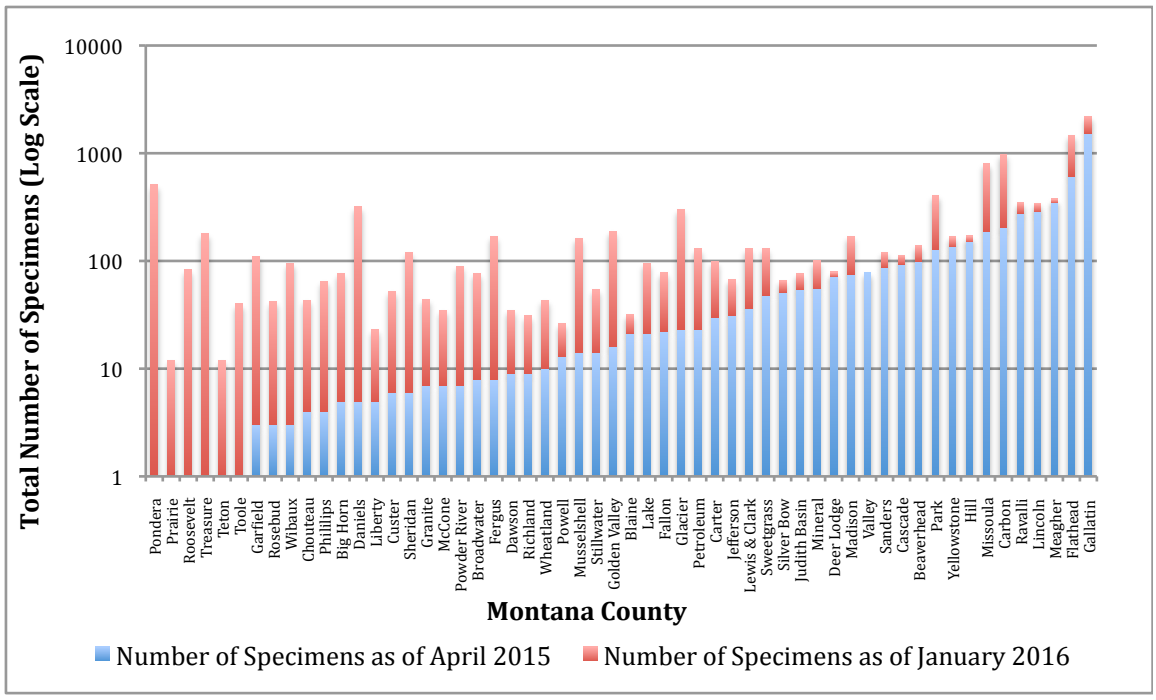


Figure 11. Number of *Bombus* Specimens per County, April 2015 and January 2016.

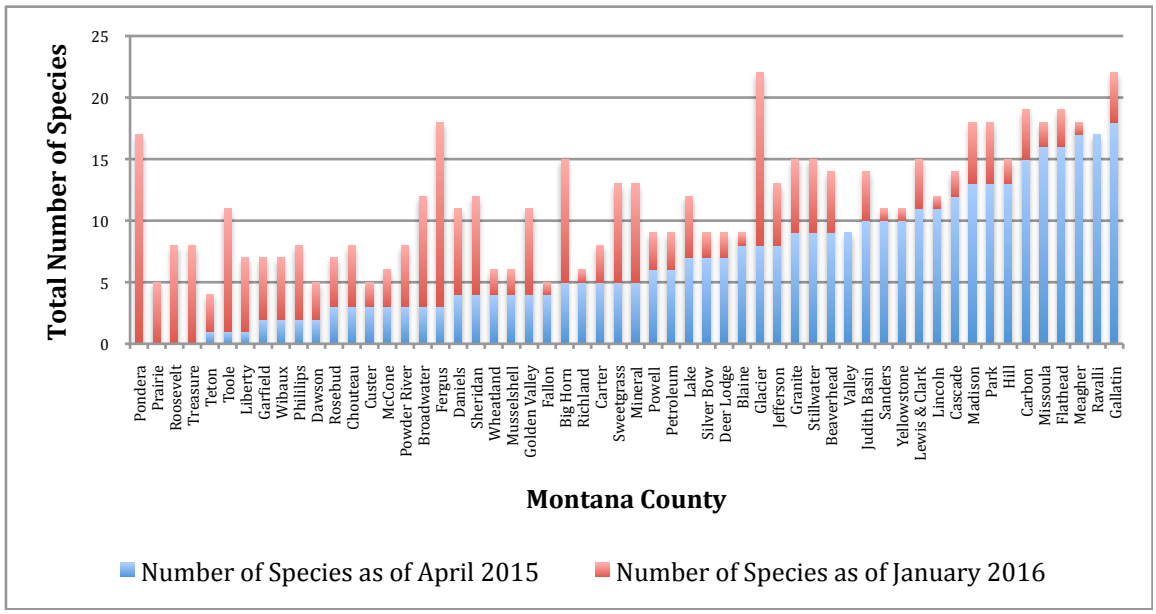


Figure 12. Number of *Bombus* Species per County, April 2015 and January 2016.

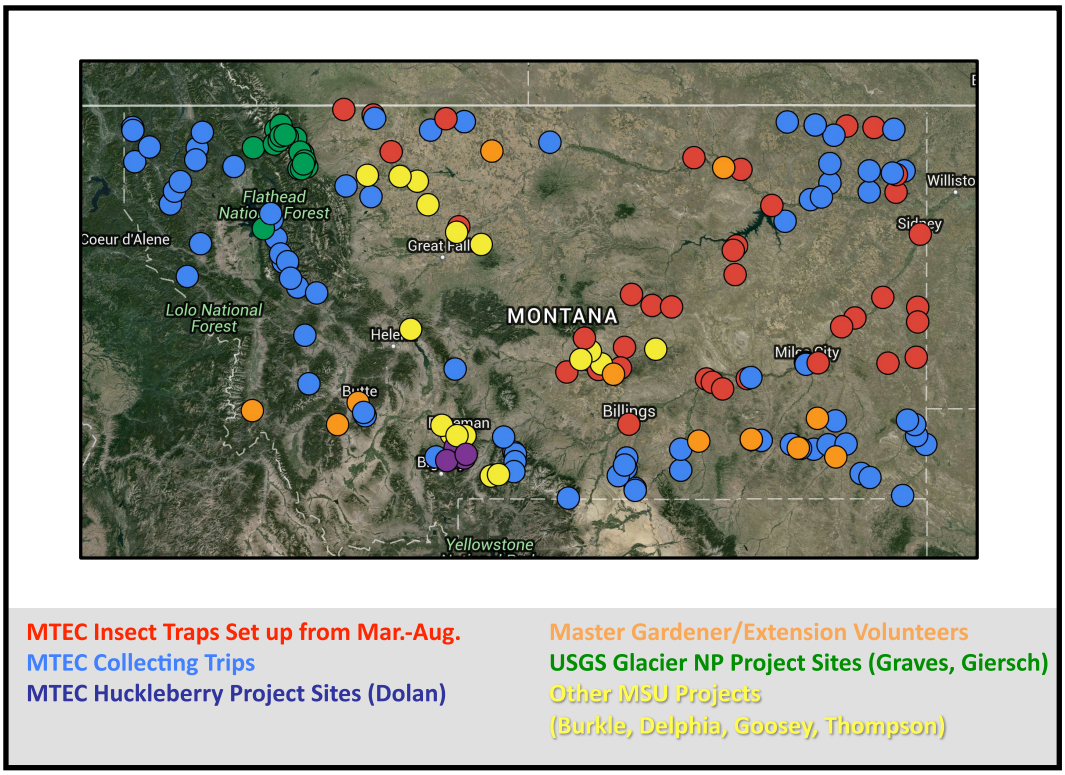


Figure 13. Summer 2015 *Bombus* Collecting Sites.

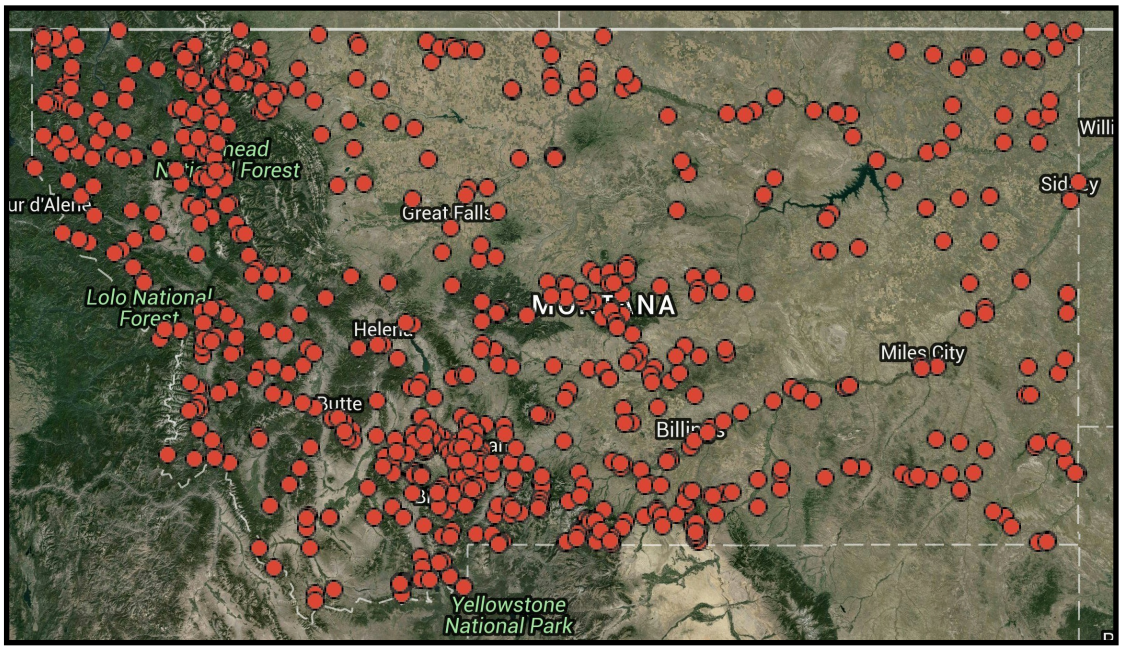


Figure 14. Montana *Bombus* Collecting Localities (1883-2015).

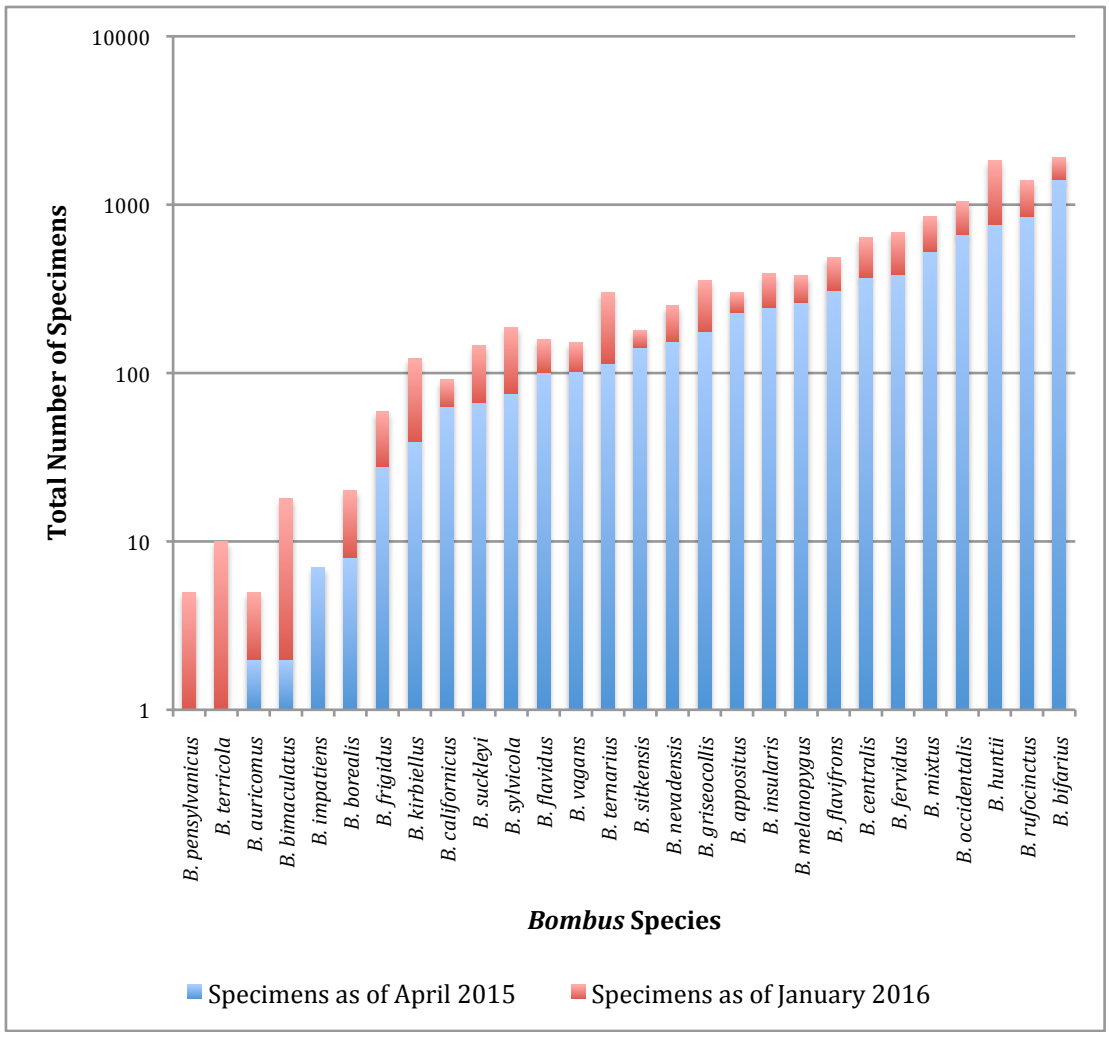


Figure 15. Number of Specimens per *Bombus* Species, April 2015 and January 2016.

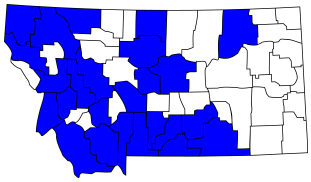


Figure 16a: *Bombus appositus* in MT
302 records from 25 counties

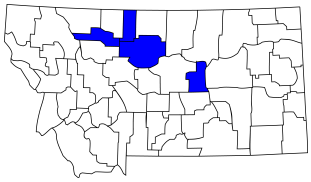


Figure 16b: *Bombus auricomus* in MT
5 records from 4 counties

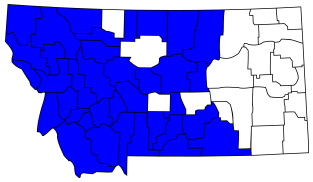


Figure 16c: *Bombus bifarius* in MT
1,911 records from 37 counties

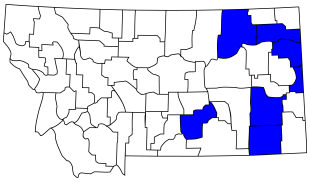


Figure 16d: *Bombus bimaculatus* in MT
18 records from 7 counties

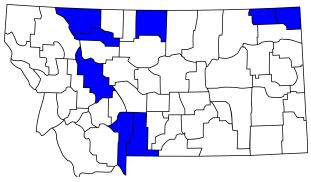


Figure 16e: *Bombus borealis* in MT
20 records from 8 counties

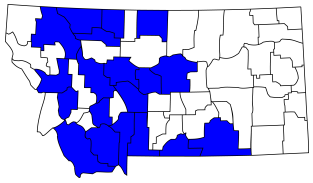


Figure 16f: *Bombus californicus* in MT
91 records from 19 counties

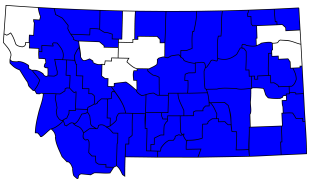


Figure 16g: *Bombus centralis* in MT
641 records from 47 counties

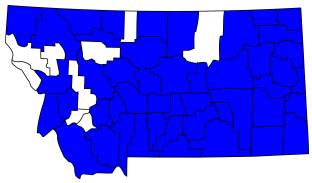


Figure 16h: *Bombus fervidus* in MT
688 records from 47 counties

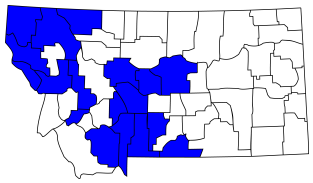


Figure 16i: *Bombus flavidus* in MT
158 records from 19 counties

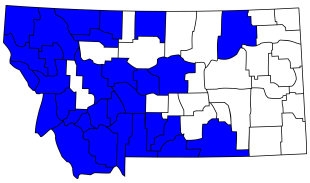


Figure 16j: *Bombus flavifrons* in MT
488 records from 30 counties

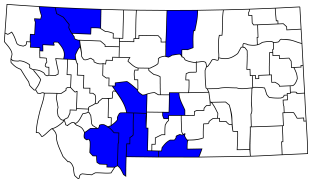


Figure 16k *Bombus frigidus* in MT
59 records from 9 counties

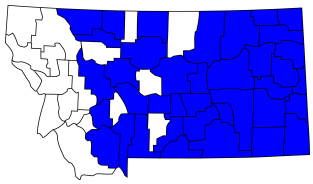


Figure 16l: *Bombus griseocollis* in MT
357 records from 38 counties

Figure 16. County-Level Distribution Maps for Montana's 28 *Bombus* Species.

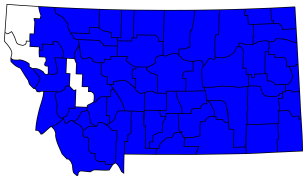


Figure 16m: *Bombus huntii* in MT
1,840 records from 53 counties

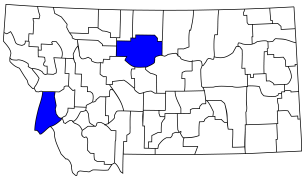


Figure 16n: *Bombus impatiens* in MT
7 records from 2 counties

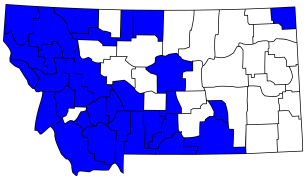


Figure 16o: *Bombus insularis* in MT
389 records from 30 counties

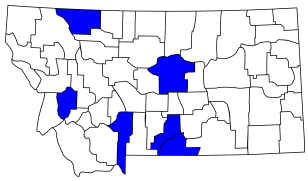


Figure 16p: *Bombus kirbiellus* in MT
122 records from 6 counties

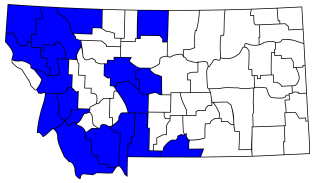


Figure 16q: *Bombus melanopygus* in MT
379 records from 19 counties

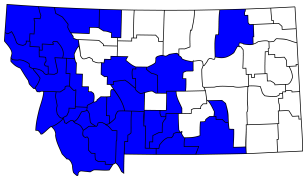


Figure 16r: *Bombus mixtus* in MT
855 records from 30 counties

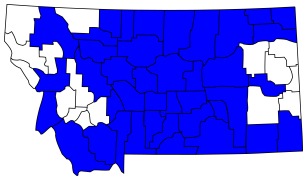


Figure 16s: *Bombus nevadensis* in MT
252 records from 41 counties

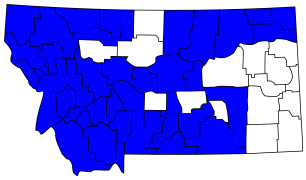


Figure 16t: *Bombus occidentalis* in MT
1,046 records from 41 counties

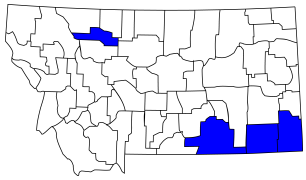


Figure 16u: *Bombus pensylvanicus* in MT
5 records from 4 counties

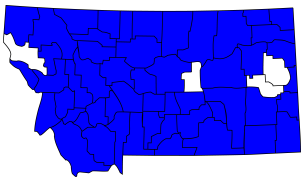


Figure 16v: *Bombus rufocinctus* in MT
1,391 records from 52 counties

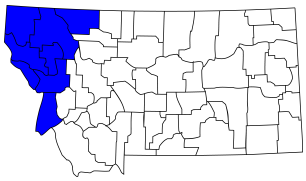


Figure 16w: *Bombus sitkensis* in MT
180 records from 8 counties

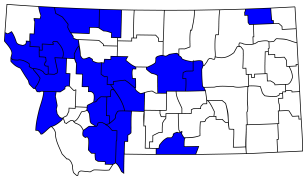


Figure 16x: *Bombus suckleyi* in MT
146 records from 19 counties

Figure 16 Continued.

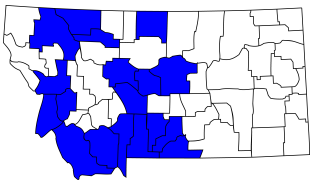


Figure 16y: *Bombus sylvicola* in MT
187 records from 18 counties

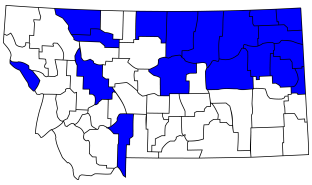


Figure 16z: *Bombus ternarius* in MT
301 records from 18 counties

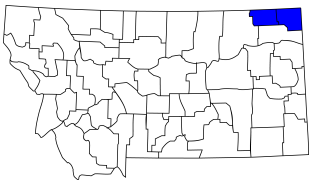


Figure 16aa: *Bombus terricola* in MT
10 records from 2 counties

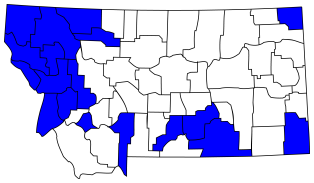


Figure 16ab: *Bombus vagans* in MT
152 records from 18 counties

Figure 16 Continued.

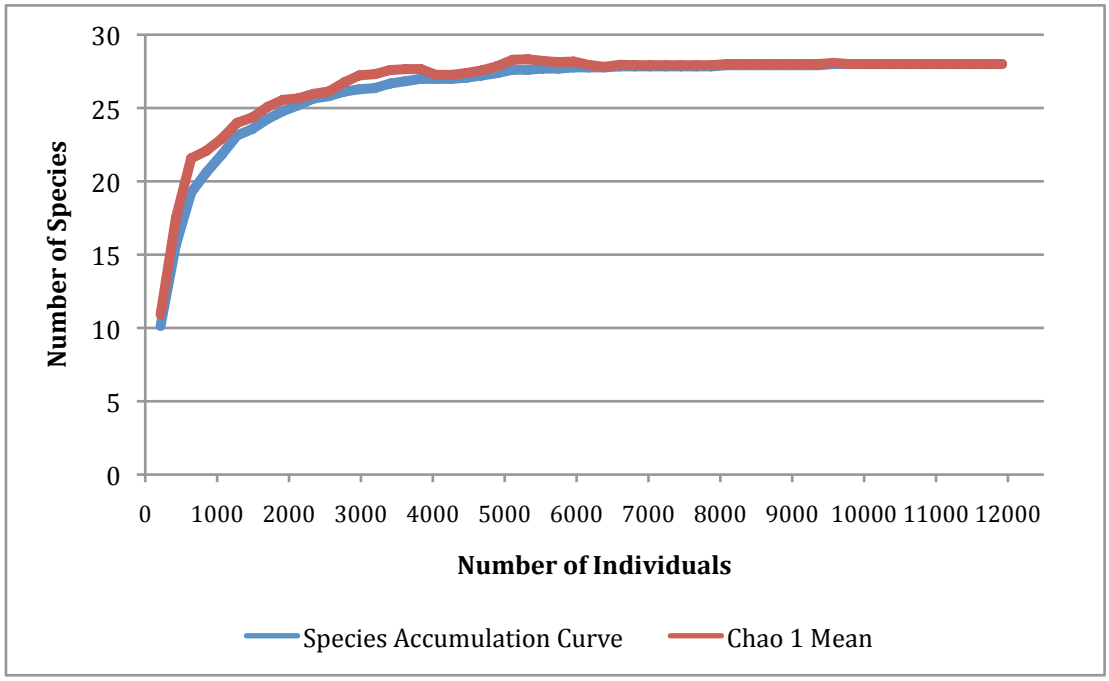


Figure 17. Montana *Bombus* Species Accumulation Curve. The curve shows the species accumulation and the Chao 1 mean prediction. Each county was considered a sample, and samples were randomized 50 times to create the mean accumulation curve.

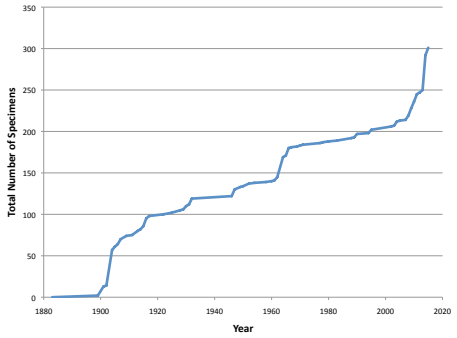


Figure 18a: Accumulation of *Bombus appositus*

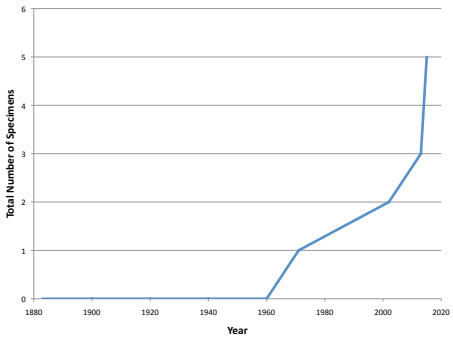


Figure 18b: Accumulation of *Bombus auricomus*

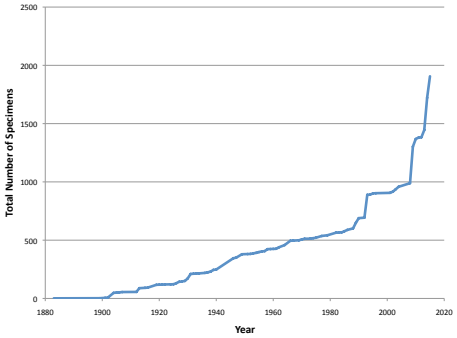


Figure 18c: Accumulation of *Bombus bifarius*

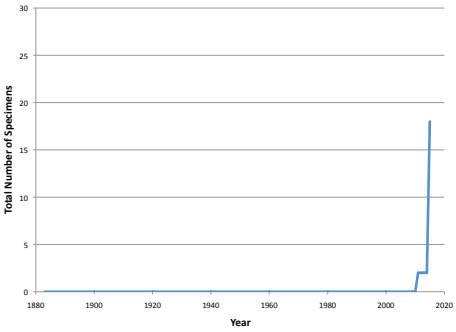


Figure 18d: Accumulation of *Bombus bimaculatus*

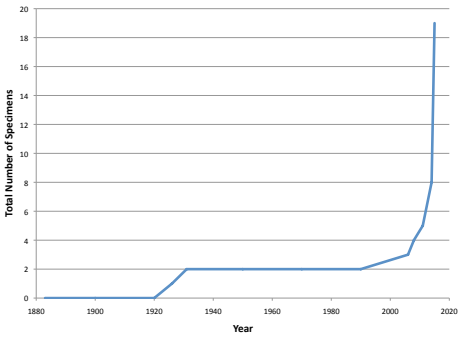


Figure 18e: Accumulation of *Bombus borealis*

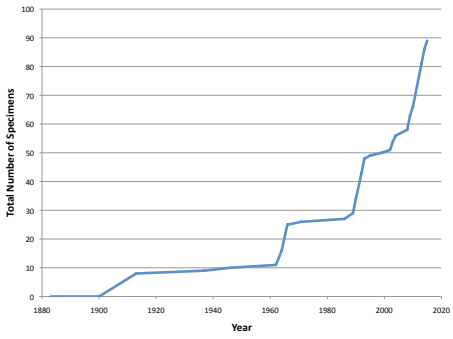


Figure 18f: Accumulation of *Bombus californicus* in MT

Figure 18. Accumulation Graphs for Montana's 28 *Bombus* Species.

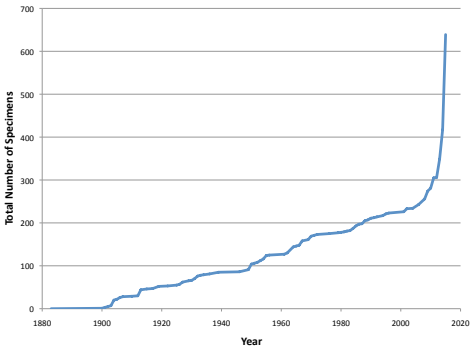


Figure 18g: Accumulation of *Bombus centralis*

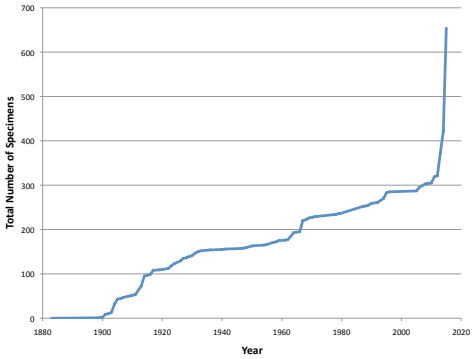


Figure 18h: Accumulation of *Bombus fervidus*

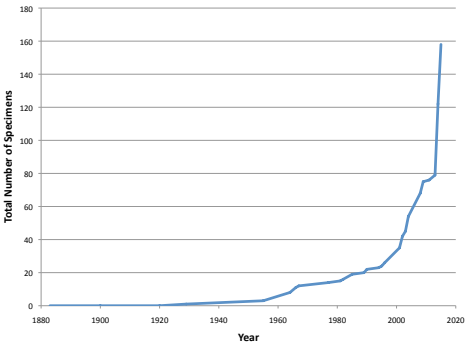


Figure 18i: Accumulation of *Bombus flavidus*

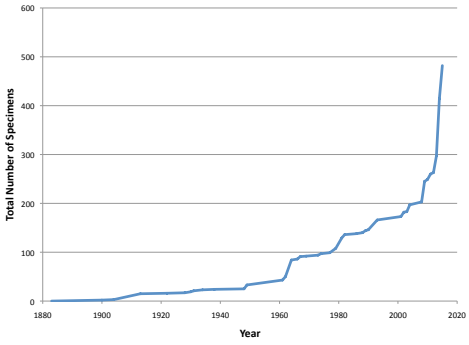


Figure 18j: Accumulation of *Bombus flavifrons*

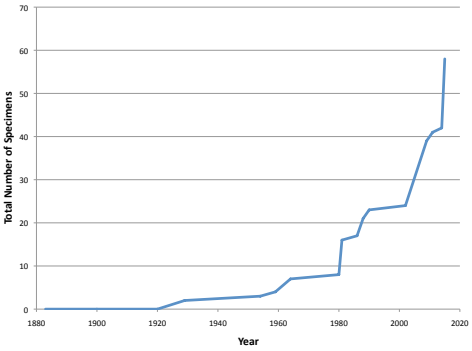


Figure 18k: Accumulation of *Bombus frigidus*

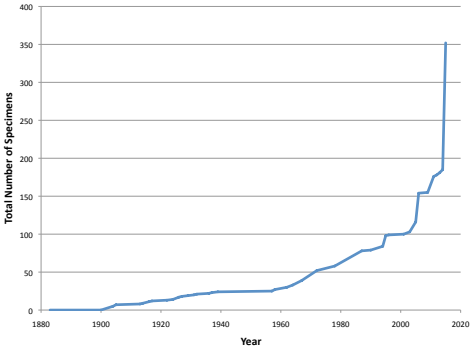


Figure 18l: Accumulation of *Bombus griseocollis*

Figure 18 Continued.

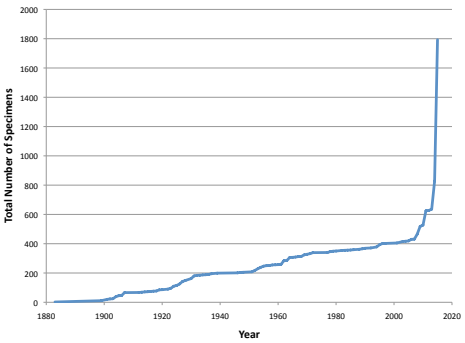


Figure 18m: Accumulation of *Bombus huntii*

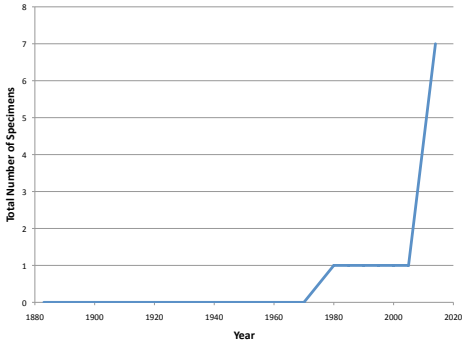


Figure 18n: Accumulation of *Bombus impatiens*

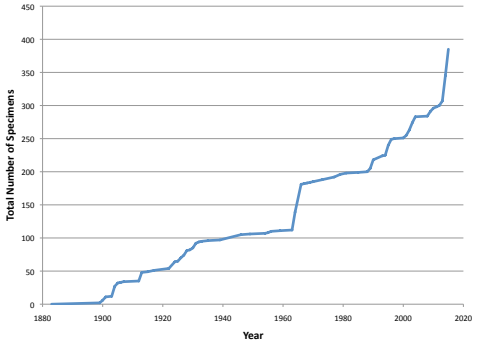


Figure 18o: Accumulation of *Bombus insularis*

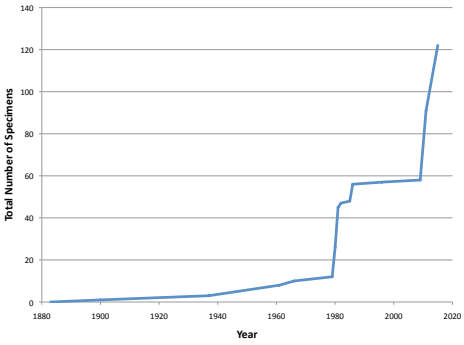


Figure 18p: Accumulation of *Bombus kirbiellus*

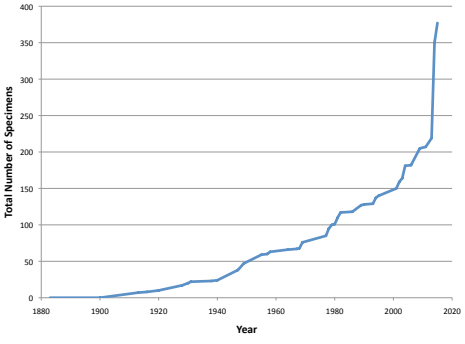


Figure 18q: Accumulation of *Bombus melanopygus*

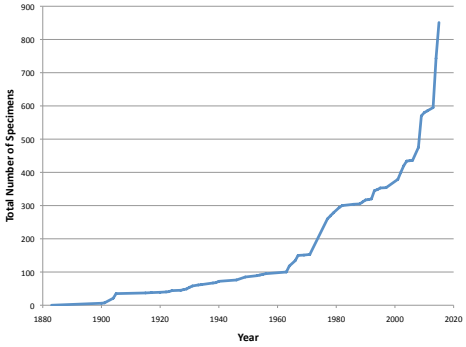


Figure 18r: Accumulation of *Bombus mixtus*

Figure 18 Continued.

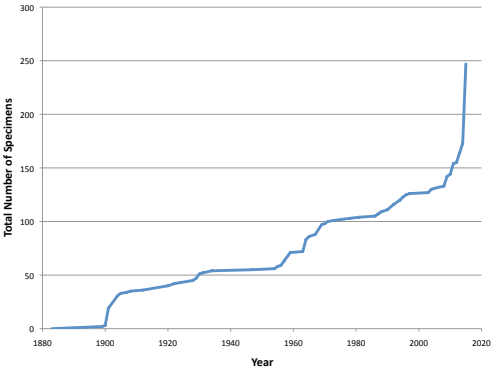


Figure 18s: Accumulation of *Bombus nevadensis* in MT

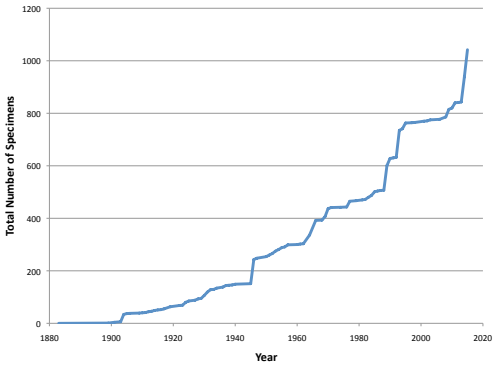


Figure 18t: Accumulation of *Bombus occidentalis* in MT

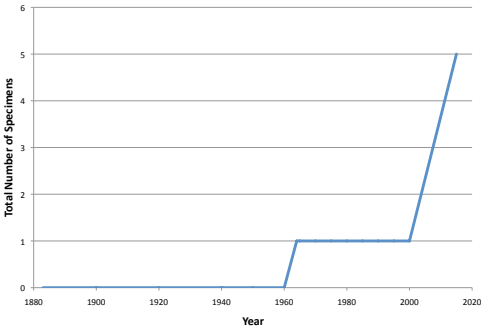


Figure 18u: Accumulation of *Bombus pensylvanicus* in MT

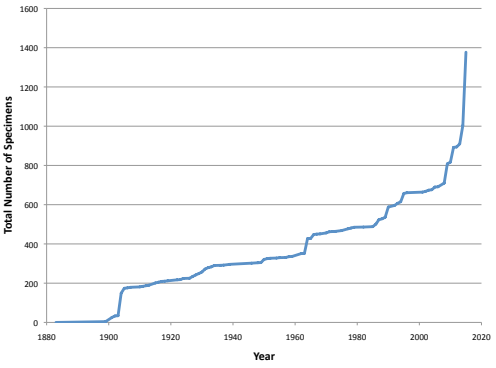


Figure 18v: Accumulation of *Bombus rufocinctus* in MT

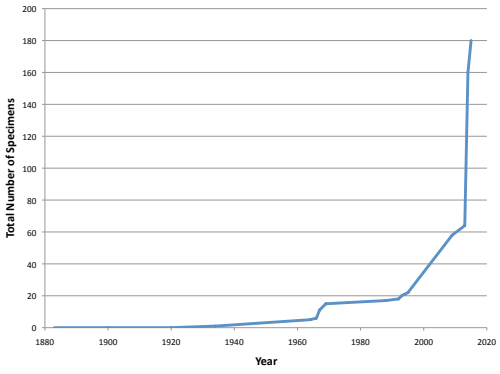


Figure 18w: Accumulation of *Bombus sitkensis* in MT

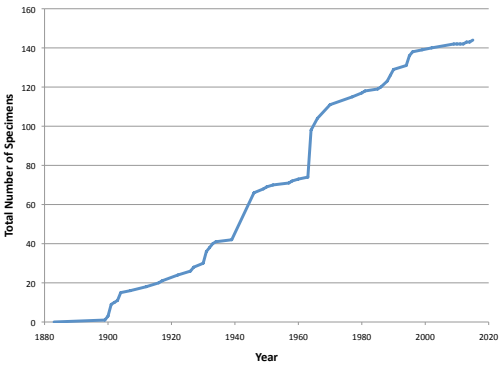


Figure 18x: Accumulation of *Bombus suckleyi* in MT

Figure 18 Continued.

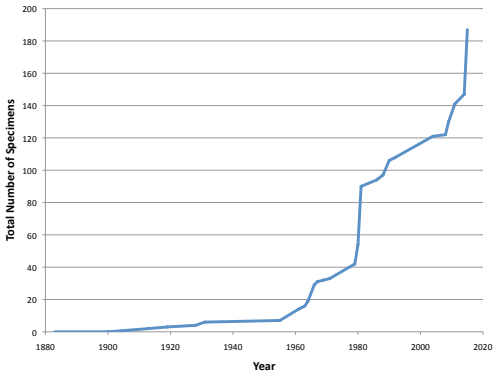


Figure 18y: Accumulation of *Bombus sylvicola* in MT

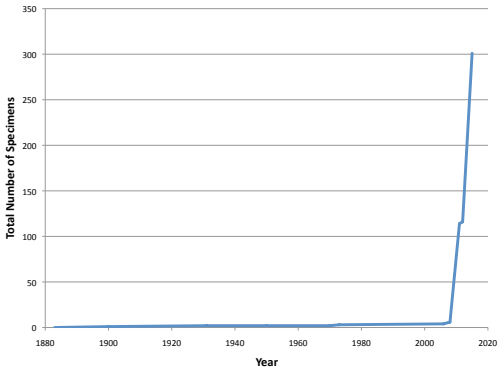


Figure 18z: Accumulation of *Bombus ternarius* in MT

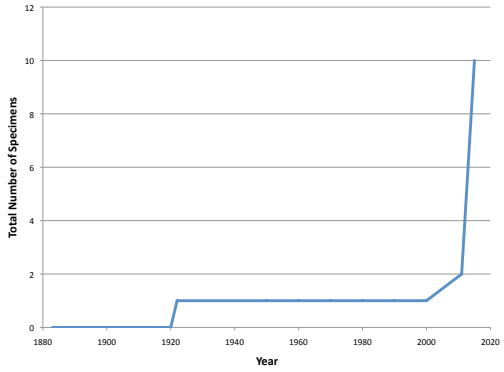


Figure 18aa: Accumulation of *Bombus terricola* in MT

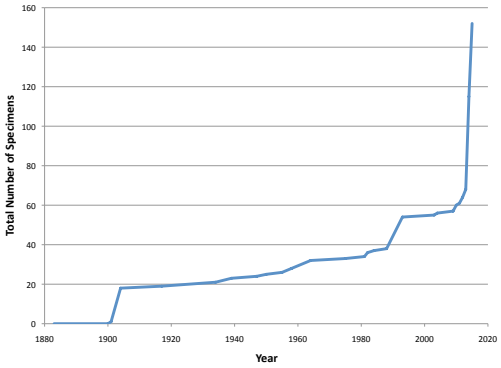


Figure 18ab: Accumulation of *Bombus vagans* in MT

Figure 18 Continued.

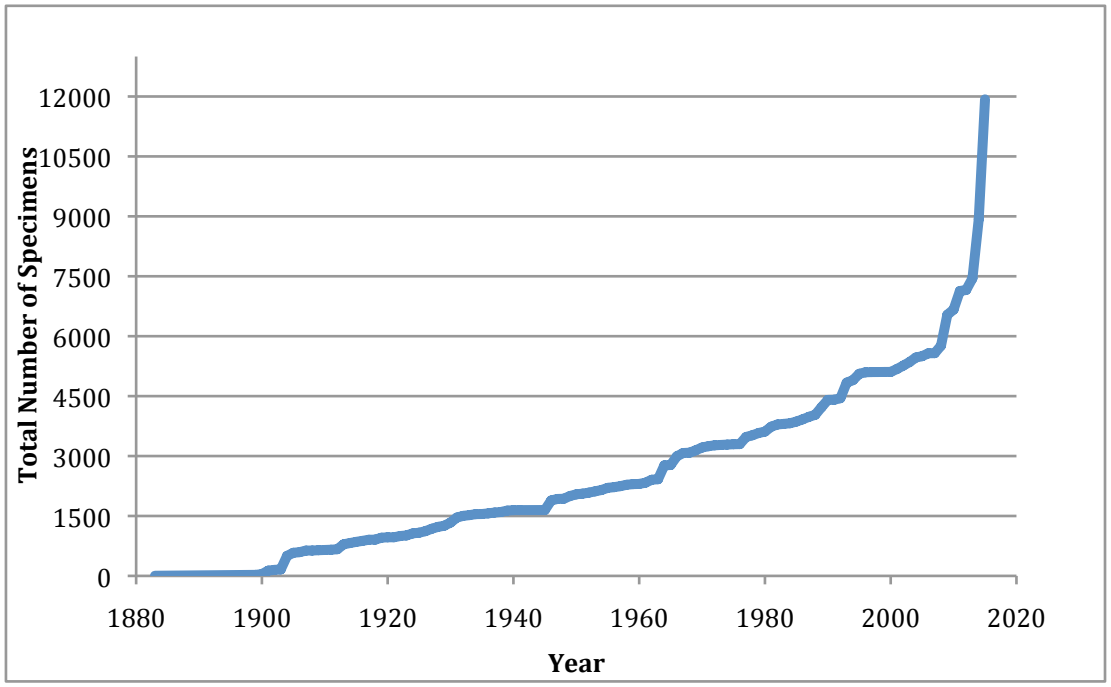


Figure 19. Total Accumulation of *Bombus* Specimens by Year.

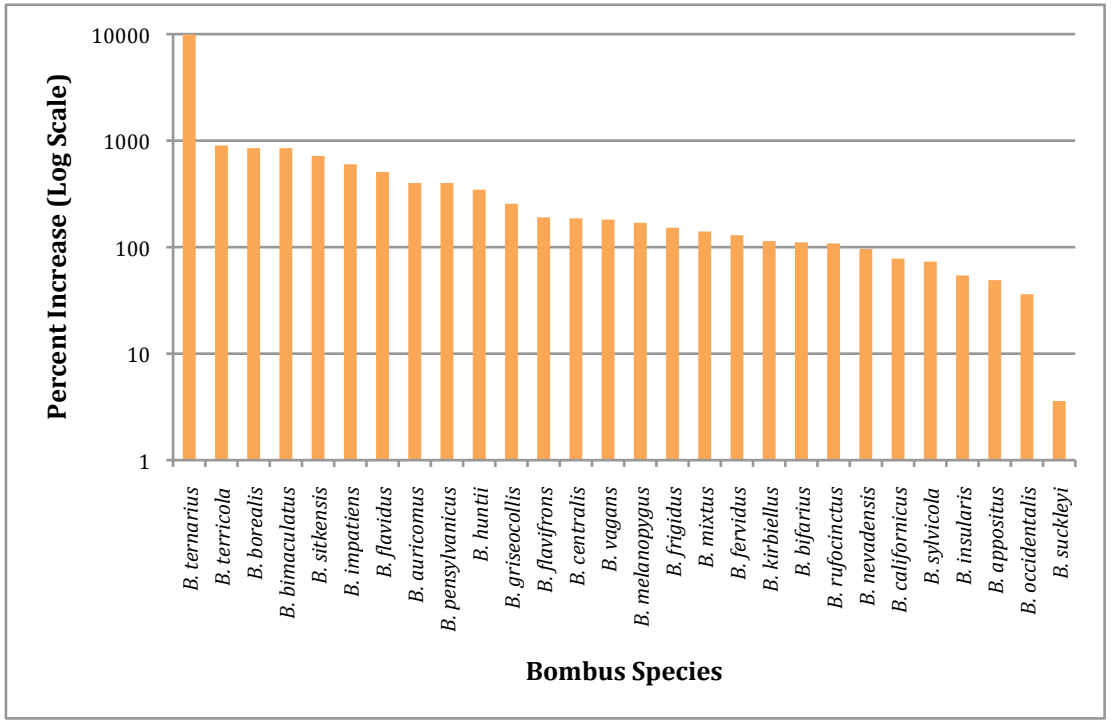


Figure 20. Percent Increase in the Number of *Bombus* Specimens Since 2000. The year 2000 was when sampling efforts in Montana substantially increased.

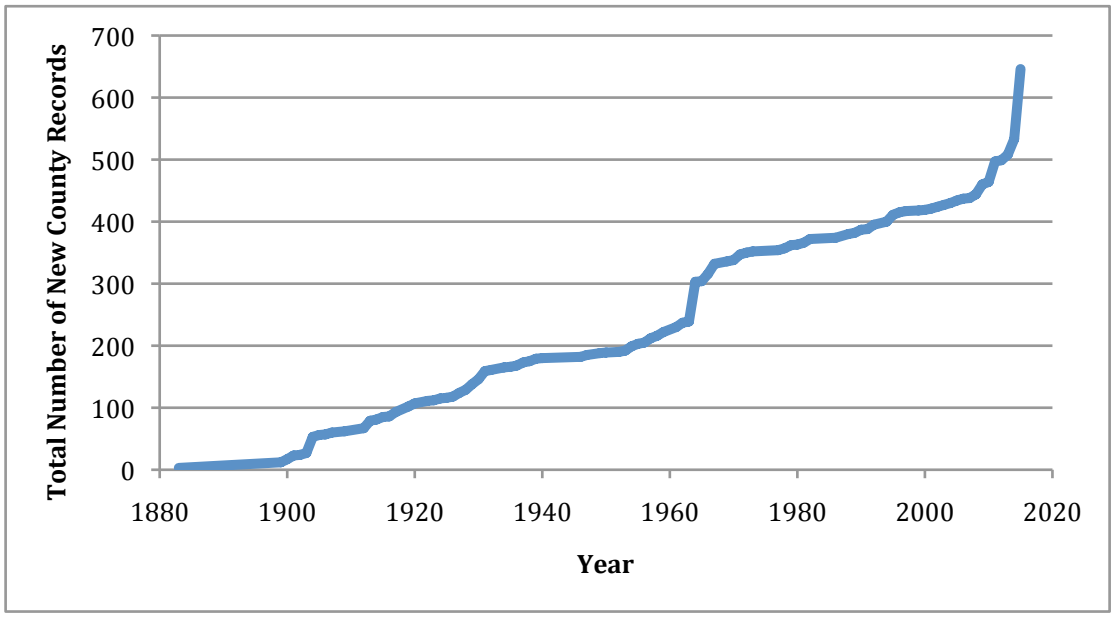


Figure 21. Accumulation of New *Bombus* County Records. A new county record is defined as the first time one of the 28 *Bombus* species known to be in Montana was first recorded in one of the 56 Montana counties.

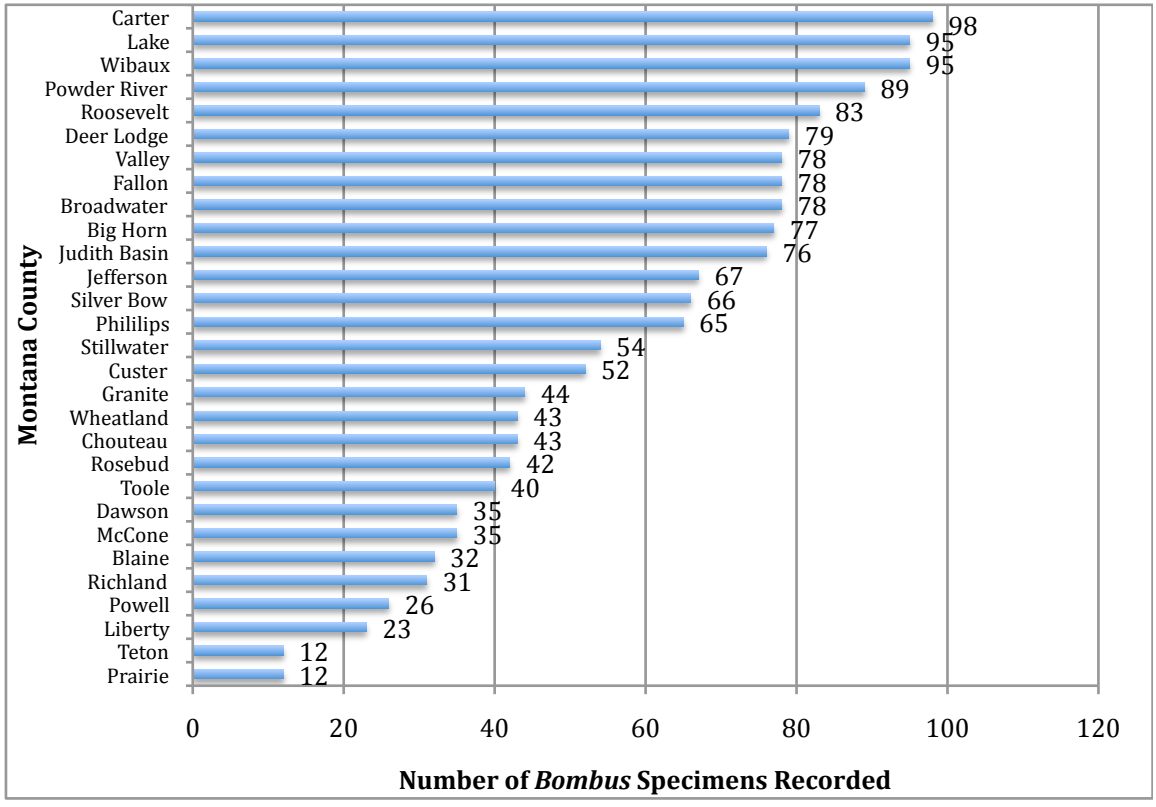
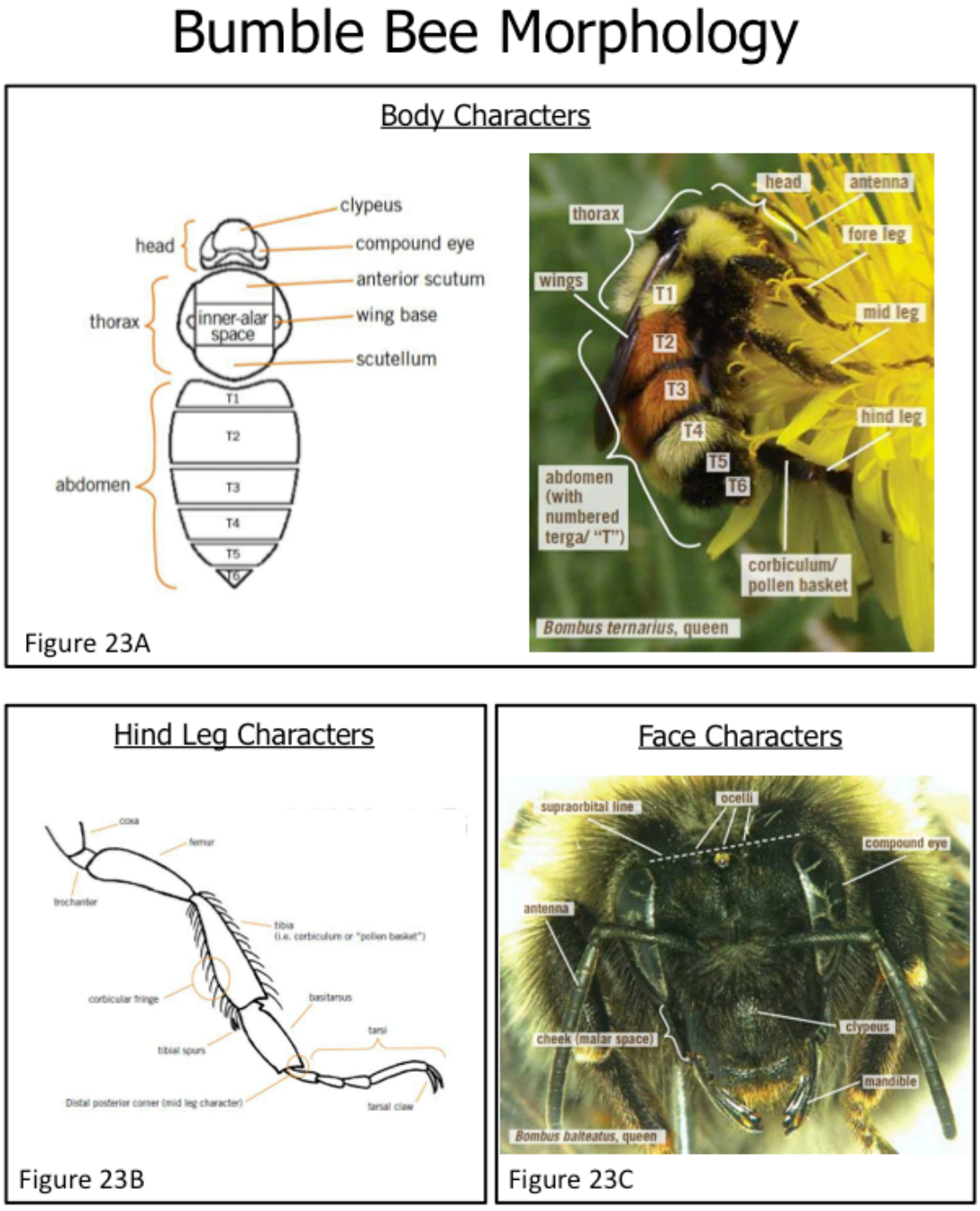


Figure 22. Montana Counties with Less than 100 *Bombus* Records.



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Figure 23. Morphological Characters Used to Key out *Bombus* Females to Species.

Bumble Bee Morphology

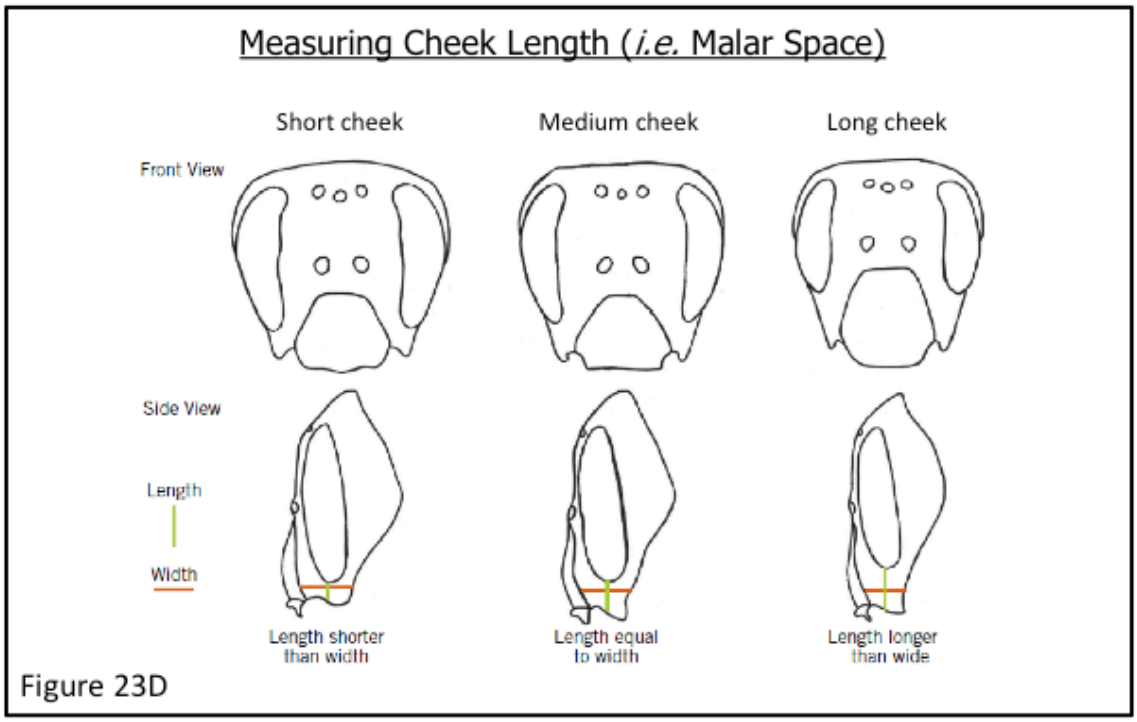


Figure 23D

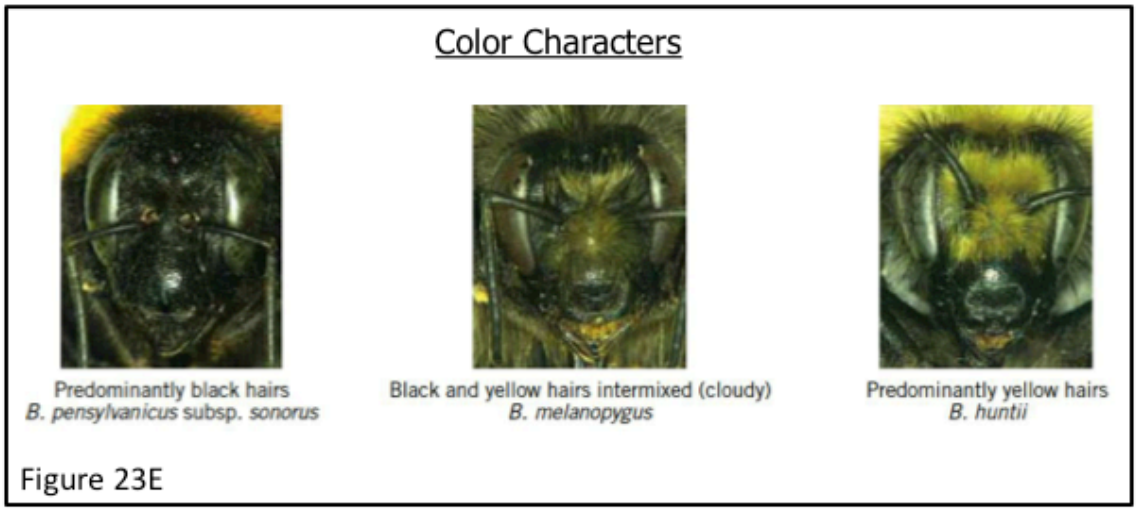


Figure 23E

Used with permission from Koch *et al.* 2012

Figure 23 Continued.

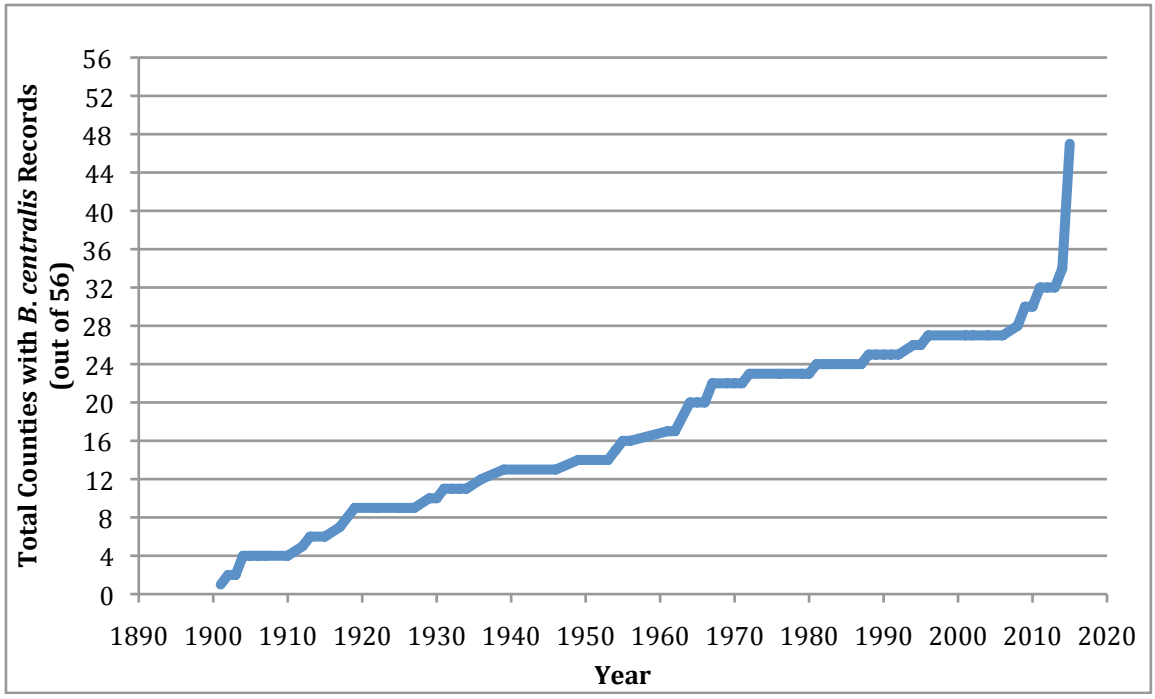


Figure 24. Accumulation of New County Records of *Bombus centralis.*

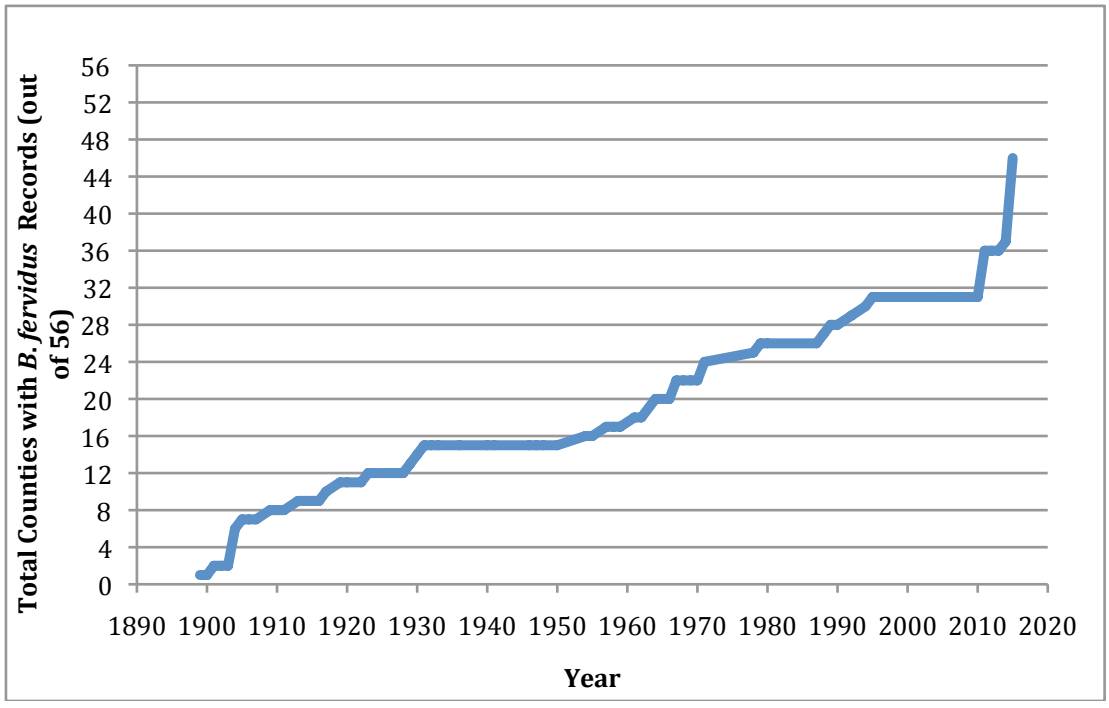


Figure 25. Accumulation of New County Records of *Bombus fervidus.*

CONCLUSION

This work on insects associated with huckleberry plants and on the bumble bee species known to occur in the state has increased our knowledge of the insect fauna of Montana. A total of 2,470 individual insects were collected and databased from flowers, leaves and stems, and fruits of the huckleberry plant. Additionally, over 12,000 bumble bee specimens collected in Montana and deposited in the MTEC and other U.S. collections since 1883 were identified and databased.

One goal of my thesis work was to not only learn more about insects, but also to share what I learn with others. All insects collected were databased and results have been made available to the public online through the MTEC website (www.mtent.org). This resource is meant for an audience that includes both the scientific community and the general public. Current technology makes it easy to share databased information to support future scientific work and basic information on insects to educate the general public.

The huckleberry project led to the discovery of a new sawfly species in the genus *Pristiphora*. New host plant records and many state/county records have been documented. These baseline data on insects associated with the huckleberry plant lay the foundation for future research including phenological studies, pollinator exclusion experiments, explorations of host plant resistance, or efforts to monitor the impact of native and non-native herbivores.

Twenty-eight bumble bee species are now known to occur in Montana, and four others are predicted to be here. New state records, new county records, and expansions of previously-documented ranges have resulted from this project. The baseline knowledge that now exists can inform future bumble bee work monitoring population trends, exploring responses to landscape changes, mapping diversity across an elevational gradient, or studies of behavior and natural history.

A great challenge to any entomologist undertaking an inventory project is attempting to identify individual insects to species. Insects are a phenomenally large and diverse group. Determining individuals to species often requires an expert, and for some taxa, experts do not exist. The value of insect taxonomists should not be underestimated, and the need for entomologists trained in taxonomy is great.

In addition to the need for baseline data, little is known about the natural history of many insect groups. For example, there is no documented knowledge of basic biological information like food choice or larval habits for at least one-third of the 34 Diptera families collected on the huckleberry plants. Similarly, little is known of the nesting habits of one of the vespid species, *D. norvegicoides,* commonly collected visiting huckleberry flowers. Insect subjects for natural history studies are abundant, and resources on methods and identification are readily available online. The opportunity for discovery associated with the study of insects needs to be communicated to the next generation of potential entomologists to inspire them to pursue work in this field.

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APPENDICES

APPENDIX A

ARTHROPOD TAXA REPORTED TO USE *VACCINIUM* AS A HOST PLANT

Appendix A. Arthropod Taxa Reported to Use *Vaccinium* as a Host. Records may be generic or refer to a species other than *V. globulare*. No published records for *V. globulare* were found.

Hymenoptera		
Family	***Genus/Species***	**Reference**
Pollen and Nectar Sources		
Andrenidae	*Andrena bradleyi*	Krombein *et al.* 1979
	Andrena carlini carlini	Krombein *et al.* 1979
	Andrena carolina	Krombein *et al.* 1979
	Andrena crataegi	Krombein *et al.* 1979
	Andrena forbesii	Krombein *et al.* 1979
	Andrena fulva	Poelen *et al.* 2014
	Andrena haemorrhoa	Poelen *et al.* 2014
	Andrena hippotes	Krombein *et al.* 1979
	Andrena imitatrix	Krombein *et al.* 1979
	Andrena kalmiae	Krombein *et al.* 1979
	Andrena melanochroa	Krombein *et al.* 1979
	Andrena miranda	Krombein *et al.* 1979
	Andrena nigroaenea	Poelen *et al.* 2014
	Andrena regularis	Krombein *et al.* 1979
	Andrena sayi	Krombein *et al.* 1979
	Andrena striatifrons	Krombein *et al.* 1979
	Andrena thaspii	Krombein *et al.* 1979
	Andrena transnigra	Krombein *et al.* 1979
	Andrena vicina	Krombein *et al.* 1979
	Andrena wilkella	Krombein *et al.* 1979
Apidae	*Anthophora ursina ursina*	Krombein *et al.* 1979
	Apis mellifera	Poelen *et al.* 2014
	Bombus affinis	Williams *et al.* 2014
	Bombus bimaculatus	Williams *et al.* 2014
	Bombus bohemicus	Williams *et al.* 2014
	Bombus calignosis	Williams *et al.* 2014
	Bombus flavifrons	Williams *et al.* 2014
	Bombus frigidus	Williams *et al.* 2014
	Bombus insularis	Williams *et al.* 2014
	Bombus jonellus	Williams *et al.* 2014
	Bombus melanopygus	Williams *et al.* 2014
	Bombus nevadensis	Williams *et al.* 2014
	Bombus polaris	Williams *et al.* 2014
	Bombus sandersoni	Williams *et al.* 2014
	Bombus sitkensis	Williams *et al.* 2014
	Bombus ternarius	Williams *et al.* 2014
	Bombus terricola	Williams *et al.* 2014
	Ceratina calcarata	Krombein *et al.* 1979
	Ceratina strenua	Krombein *et al.* 1979
	Emphoropsis laboriosa laboriosa	Krombein *et al.* 1979
	Nomada sp.	Poelen *et al.* 2014

Appendix A Continued.

Hymenoptera continued

Family	***Genus/Species***	**Reference**
Colletidae	*Colletes thoracicus*	Krombein *et al.* 1979
	Colletes validus	Krombein *et al.* 1979
Formicidae	*Formica spp.*	Poelen *et al.* 2014
	Myrmica spp.	Poelen *et al.* 2014
Halictidae	*Augochlora pura pura*	Krombein *et al.* 1979
	Augochlorella gratiosa	Krombein *et al.* 1979
	Augochlorella striata	Krombein *et al.* 1979
	Augochloropsis sumptuosa	Krombein *et al.* 1979
	Lasioglossum spp.	Poelen *et al.* 2014
	Sphecodes spp.	Poelen *et al.* 2014
Megachilidae	*Chalicodoma exilis parexilis*	Krombein *et al.* 1979
	Chalicodoma georgica	Krombein *et al.* 1979
	Chalicodoma rugifrons	Krombein *et al.* 1979
	Hoplitis truncata truncata	Krombein *et al.* 1979
	Megachile addenda	Krombein *et al.* 1979
	Megachile brevis pseudobrewvis	Krombein *et al.* 1979
	Megachile gemula gemula	Krombein *et al.* 1979
	Megachile ingenua	Krombein *et al.* 1979
	Megachile mendica mendica	Krombein *et al.* 1979
	Osmia atriventris	Krombein *et al.* 1979
	Osmia chalybea	Krombein *et al.* 1979
	Osmia inermis	Krombein *et al.* 1979
	Osmia inspergens	Krombein *et al.* 1979
	Osmia pumila	Krombein *et al.* 1979
	Osmia sandhouseae	Krombein *et al.* 1979
Melittidae	*Macropis nuda*	Krombein *et al.* 1979
Vespidae	*Dolichovespula spp.*	Poelen *et al.* 2014
	Vespula spp.	Poelen *et al.* 2014
Plant as a host		
Tenthredinidae	*Neopareophora litura*	Krombein *et al.* 1979
	Pristiphora banksi	Krombein *et al.* 1979
	Pristiphora cincta	Krombein *et al.* 1979
	Pristiphora mollis	Krombein *et al.* 1979
	Pristiphora reticulatus	Krombein *et al.* 1979
	Pristiphora macnabi	Wong 1968

Appendix A Continued.

Lepidoptera

Family	***Genus/Species***	**Reference**
Arctiidae sp.		Robinson *et al.* 2010
Copromorphidae sp.		Robinson *et al.* 2010
Gelechiidae spp.		Robinson *et al.* 2010
Geometridae	*Cingilia catenaria*	Johnson and Lyon 1991
	Macaria argillacearia Packard (NEA)	Smithsonian 2016
	Phigalia titea	Johnson and Lyon 1991
Geometridae spp.		Robinson *et al.* 2010
Gracillariidae spp.		Robinson *et al.* 2010
Heliozelidae	*Coptodisca sp.*	Johnson and Lyon 1991
Heliozelidae sp.		Robinson *et al.* 2010
Lasiocampidae	*Malacosoma disstria*	Robinson *et al.* 2010
Limacodidae sp.		Robinson *et al.* 2010
Limacodidae	*Limenitis*	Howe 1975
Lycaenidae spp.		Robinson *et al.* 2010
	Callophrys spp.	Howe 1975
	Celastrina spp.	Howe 1975
	Lycaena spp.	Howe 1975
	Plebeius spp.	Howe 1975
	Satyrium liparops	Howe 1975
Lymantriidae spp.		Robinson *et al.* 2010
Megalopygidae spp.		Robinson *et al.* 2010
Noctuidae spp.		Robinson *et al.* 2010
Notodontidae	*Datana major*	Johnson and Lyon 1991
	Schizura concinna	Johnson and Lyon 1991
	Schizura ipomoeae	Johnson and Lyon 1991
Notodontidae spp.		Robinson *et al.* 2010
Nymphalidae spp.		Robinson *et al.* 2010
Nymphalidae	Argynninae *Boloria* spp.	Howe 1975
	Limenitinae *Limenitis*	Howe 1975
Pieridae sp.		Robinson *et al.* 2010
	Colias spp.	Howe 1975
Psychidae sp.		Robinson *et al.* 2010
Pyralidae spp.		Robinson *et al.* 2010
Saturniidae spp.		Robinson *et al.* 2010
Sphingidae spp		Robinson *et al.* 2010
Tortricidae	*Amorbia humerosana*	Johnson and Lyon 1991
	Olethreutinae	Brown *et al.* 2008
	Rhopobota naevana	Johnson and Lyon 1991
	Sparganothis sulfureana	Johnson and Lyon 1991
	Tortricinae	Brown *et al.* 2008
Tortricidae spp.		Robinson *et al.* 2010
Yponomeutidae sp.		Robinson *et al.* 2010

Appendix A Continued.

Coleoptera		
Family	***Genus/Species***	**Reference**
Buprestidae	*Brachys aerosus*	Poelen *et al.* 2014
	Brachys floricola	Nelson *et al.* 2008
Cerambycidae	*Oberea myops*	Linsley and Chemsak 1997
	Oberea tripucntata	Johnson and Lyon 1991
	Prionus laticollis	Johnson and Lyon 1991
Chrysomelidae	*Altica Sylvia*	Clark *et al.* 2004
	Altica torquata	Clark *et al.* 2004
	Altica ulmi	Clark *et al.* 2004
	Altica vaccinia	Clark *et al.* 2004
	Bassareus formosus	Clark *et al.* 2004
	Capraita circumdata	Clark *et al.* 2004
	Capraita obsidiana	Clark *et al.* 2004
	Colaspis costipennis	Clark *et al.* 2004
	Colaspis flavocostata	Clark *et al.* 2004
	Cryptocephalus binominis	Clark *et al.* 2004
	Cryptocephalus gibbicollis	Clark *et al.* 2004
	Cryptocephalus incertus	Clark *et al.* 2004
	Cryptocephalus notatus	Clark *et al.* 2004
	Cryptocephalus quadruplex	Clark *et al.* 2004
	Cryptocephalus venustus	Clark *et al.* 2004
	Dibolia melampyri	Clark *et al.* 2004
	Epitrix cucumeris	Clark *et al.* 2004
	Neochlamisus chamaedaphnes	Clark *et al.* 2004
	Neochlamisus cribripennis	Clark *et al.* 2004
	Neochlamisus gibbosus	Clark *et al.* 2004
	Neochlamisus tuberculatus	Clark *et al.* 2004
	Rhabdopterus picipes	Clark *et al.* 2004
	Systena frontalis	Clark *et al.* 2004
	Systena hudsonias	Clark *et al.* 2004
	Timarcha cerdo	Clark *et al.* 2004
	Timarcha intricata	Clark *et al.* 2004
	Triachus atomus	Clark *et al.* 2004
	Tricholochmaea alni	Clark *et al.* 2004
	Tricholochmaea decora	Clark *et al.* 2004
	Tricholochmaea sablensis	Clark *et al.* 2004
	Tricholochmaea vaccinii	Clark *et al.* 2004
Nitidulidae	*Meligethes aeneus*	Poelen *et al.* 2014
Scarabaeidae	*Anomala orientalis*	Poelen *et al.* 2014
Scraptiidae	*Anaspis spp.*	Poelen *et al.* 2014

Appendix A Continued.

Hemiptera		
Family	***Genus/Species***	**Reference**
Acanthosomatidae	*Elasmucha ferrugata*	Poelen *et al.* 2014
Aphidoidea	*Acyrthosiphon brachysiphon*	Blackman and Eastop 2008
	Acyrthosiphon knechteli	Blackman and Eastop 2008
	Aphis vaccinii	Blackman and Eastop 2008
	Aulacorthum flavum	Blackman and Eastop 2008
	Aulacorthum pterinigrum	Blackman and Eastop 2008
	Aulacorthum rufum	Blackman and Eastop 2008
	Aulacorthum vaccinii	Blackman and Eastop 2008
	Brachycaudus helichrysi	Blackman and Eastop 2008
	Ericaphis latifrons	Blackman and Eastop 2008
	Ericaphis wakibae	Blackman and Eastop 2008
	Illinoia finni	Blackman and Eastop 2008
	Macrosiphum euphorbiae	Blackman and Eastop 2008
	Macrosiphum nasonovi	Blackman and Eastop 2008
	Myzus ornatus	Blackman and Eastop 2008
	Myzus persicae	Blackman and Eastop 2008
	Neomyzus circumflexus	Blackman and Eastop 2008
	Pachypappa myrtilli	Blackman and Eastop 2008
	Sitobion paludum	Blackman and Eastop 2008
	Smynthurodes betae	Blackman and Eastop 2008
	Wahlgreniella vaccinii	Blackman and Eastop 2008
Cicadellidae	*Aguriahana pictilis*	Dmitriev 2003
	Cuerna striata (Tettigonia septentrionalis)	Dmitriev 2003
	Dikraneura (Dikraneura) aridella	Dmitriev 2003
	Empoa (Empoa) spinosa	Dmitriev 2003
	Eratonerua cristata	Dmitriev 2003
	Eratonerua dumosa	Dmitriev 2003
	Eratoneura certa	Dmitriev 2003
	Eratoneura gemina	Dmitriev 2003
	Eratoneura mimica	Dmitriev 2003
	Eratoneura penesica	Dmitriev 2003
	Eratoneura restricta	Dmitriev 2003
	Eratoneura unica (Erythroneura quercalbae)	Dmitriev 2003
	Erythria aureola	Dmitriev 2003
	Erythridula jonesi	Dmitriev 2003
	Erythridula nitida	Dmitriev 2003
	Erythridula victorialis	Dmitriev 2003
	Clastoptera obtusa	Johnson and Lyon 1991
Coccidae	*Mesolecanium nigrofasciatum*	Johnson and Lyon 1991
	Pulvinaria ericicola	Johnson and Lyon 1991

Appendix A Continued.

Hemiptera continued		
Family	***Genus/Species***	**Reference**
Conchaspididae	*Conchaspis vaccinii*	Ben-Dov 2006
Coreidae	*Leptoglossus phyllopus*	Johnson and Lyon 1991
Diaspididae	*Aspidiotus nerii*	Johnson and Lyon 1991
	Diaspidiotus ancylus	Polavarapu *et al.* 2000
	Hemiberlesia rapax	Johnson and Lyon 1991
Flatidae	*Anormenis chloris*	Johnson and Lyon 1991
	Ormenoides venusta	Johnson and Lyon 1991
Miridae	*Campylomma collina*	Schuh 2013
	Campylomma fusca	Schuh 2013
	Closterotomus biclavatus	Schuh 2013
	Leptopterna dolabrata	Schuh 2013
	Plagiognathus fulvaceus	Schuh 2013
	Plagiognathus repetitus	Schuh 2013
	Pygovepres vaccinicola	Schuh 2013
Pentatomidae	*Halyomorpha halys*	Wiman *et al.* 2015
	Podisus modestus	Tostowaryk 1970
Pseudococcidae	*Phenacoccus aceris*	Johnson and Lyon 1991

Diptera		
Family	***Genus/Species***	**Reference**
Agromyzidae		Spencer 1990
Ceratopogonidae sp.		Poelen *et al.* 2014
Conopidae	*Sicus ferrugineus*	Poelen *et al.* 2014
Sarcophagidae spp.		Poelen *et al.* 2014
Syrphidae spp.		Poelen *et al.* 2014
Tachinidae spp.		Poelen *et al.* 2014

Mites		
Family	***Genus/Species***	**Reference**
Eriophyidae	*Acalitus caccinii*	Johnson and Lyon 1991
Tetranychidae	*Eotetranychus carpini*	Johnson and Lyon 1991

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APPENDIX B

VACCINIUM GLOBULARE BERRY DISSECTIONS NOTES

Appendix B. *Vaccinium globulare* Berry Dissection Notes. Three types of berries were dissected: green, undeveloped berries; white, fungus-filled "mummy berries;" and ripe but damaged berries.

Collection Site: Cottonwood Canyon; 19 July 2015
Type of Damage: Ripened but failed or pre-ripened, damaged
of Berries: 12
Observations:

- Most similar to berry observations above
- 1 filled with pellet-like frass, but no evidence of larva
- 1 filled with pellet-like frass, remains of what could have been a larva found
- 1 filled with pellet like frass
- 2 filled with dried pellet-like frass, a few seeds & a dead, blackened larva
- Cocoon-like structure found—dissected open—very long antennae that do not match either the adult sawfly or the braconid that emerged from other berries, 3 ocelli? Came apart & very liquidy
- Remains of one larva taken for DNA: MTEC 015753

Collection Site: Cottonwood Canyon; 19 July 2015
Type of Damage: Brown, undeveloped dried berries
of Berries: 9
Observations:

- 4 filled with dried pellet-like frass, a few seeds & a dead, blackened larva
- 3 with dried pellet-like frass, some seeds, no evidence of larvae
- 1 with dried seeds, no flesh remains
- 1 with some seeds, flesh dried and rubbery

Collection Site: Cottonwood Canyon; 19 July 2015
Type of Damage: Undeveloped, green berries
of Berries: 4
Observations:

- 3 with normal looking seeds of different sizes developing
- 1 with frass, but no larva

Collection Site: Cottonwood Canyon; 19 July 2015
Type of Damage: Mummy berries
of Berries: 10
Observations:

- 1 approx 50% filled with white fungus
- 4 approx. 75% filled with white fungus
- 4 approx 90% filled with white fungus
- 1 completely filled with white fungus

Collection Site: Lava Lake Trail; 20 July 2015
Type of Damage: Ripened but failed
of Berries: 24
Observations:

- Most similar to berry observations above
- 1 with only 3 seeds inside, the rest is flesh/juice; berry shrunken/shriveled

Collection Site: Lava Lake Trail; 20 July 2015
Type of Damage: Brown, dried up
of Berries: 5
Observations:

- 3 with some seeds and dried pellet-like frass. No evidence of larvae
- 2 with some seeds, some dried black fungus inside.

Collection Site: Lava Lake Trail; 20 July 2015
Type of Damage: Mummy berries
of Berries: 16
Observations:

- 6 approx 25% filled with white fungus; seeds fill the rest
- 3 approx. 50% filled with white fungus
- 6 approx 90% filled with white fungus
- 1 approx 75% filled with white fungus

Collection Site: Palisade Falls Trail; 22 July 2015
Type of Damage: Ripened but failed or pre-ripened, damaged
of Berries: 25
Observations:

- 5 filled with pellet like frass, but no evidence of larvae
- 1 filled with pellet-like frass that was really dried up, no evidence of larvae
- 3 filled with pellet like frass, tiny, maggot-like larvae found one with the tiny maggot-like larva and what looks like it might have been a larger larva of something else
- 2 filled with pellet like frass, dead larva found, one black (seems moldy?)
- the rest flesh & seeds as described above

Collection Site: Palisade Falls Trail; 22 July 2015
Type of Damage: Mummy berries
of Berries: 10
Observations:

- 2 approx 25% filled with white fungus
- 3 approx 75% filled with white fungus
- 4 approx 90% filled with white fungus
- 1 completely filled with white fungus

Collection Site: Hyalite Creek Trail; 24 July 2015
Type of Damage: Mummy berries
of Berries: 18
Observations:

- 1 filled with pellet like frass, but no evidence of larva
- 4 approx ½ filled with white fungus normally found in mummy berries
- 1 covered with mold—some bright orange fungus (spores?) inside
- 1 more dried out—normal flesh/juice replaced by thicker, waxier substance
- the rest actually mummy berries- completely filled with white fungus

Collection Site: Lava Lake Trail; 28 July 2015
Type of Damage: Ripened but damaged or shriveled
of Berries: 35
Observations:

- Lots of liquid (flesh turning to liquid), seeds look healthy, some outsides of the berries starting to have spots of mold; seeds look like small kernels of corn, flesh varies in color from dark purple to light pink to yellowish
- 2 berries had the flesh dried up and wax-like;
- 2 berries had the flesh in part of the berries replaced with pellet-like circles (frass?)- the remains of some sort of larvae were found amongst these pellets

Collection Site: Lava Lake Trail; 28 July 2015
Type of Damage: Undeveloped
of Berries: 1
Observations:

- Evidence of seed growth
- Flesh dried and hard

Collection Site: Lava Lake Trail; 28 July 2015
Type of Damage: Mummy berries
of Berries: 12
Observations:

- 1 with puncture wound, fungus filled whole fruit
- 1 with fungus only on outside, seeds inside look norma.l/healthy, flesh a little dry but not as hard as full fungus berries,
- 4 with developing seeds, flesh seems harder & more fibrous than normal—fungus starting to take over?
- 1 inside similar to previous observation, outside of berry has hair-like strands of fungus instead of the hard white mummy fungus
- 3- solid white through ~90% of berries, seeds there, started to develop
- 1 with puncture wound, white fungus = .75 of fruit, seeds fill the other .25
- 1 with evidence of frugivory on outside, nibble hole about 1/5 of surface area; approx ½ of inside of the fruit solid white (the half nearest the nibble hole)

Collection Site: Cottonwood Canyon; 29 July 2015
Type of Damage: Mummy berries
of Berries: 4
Observations:

- 1 solid white about 90% through the berry
- 1 evidence of frugivory on the outside, seeds directly below the nibble marks, other 2/3 of berry solid white
- 1 some small seeds inside, the rest of the flesh dried up and pellet like
- 1 about 50% solid white

Collection Site: Cottonwood Canyon; 29 July 2015
Type of Damage: Ripened but failed
of Berries: 12
Observations:

- Most same as similar lava lake berries described above
- 1 filled with pellet-like substance instead of normal flesh, remains of some larva, another oval, fibrous, cocoon-like structure found inside as well
- 1 more dried out—normal flesh/juice replaced by thicker, waxier substance
- 1- chewed hole, larger than other puncture holes, flesh dried up and replaced by small pellets, some of the seeds are black/rotted, only the head of a small larva found
- One small wasp found alive moving around in the petri dish of mixed, damaged berries

Collection Site: Lava Lake Trail; 03 August 2015
Type of Damage: Ripened but failed or pre-ripened, damaged
of Berries: 29
Observations:

- Most similar to berry observations above
- Several of the smaller, darker, more shriveled berries are more thick flesh than juicy flesh like the larger, lighter colored berries
- 2 with pellet-like frass replacing a small fraction of the flesh (~1/8), remains of a larva found in one; only the head of a larva found in the other
- 1 filled with pellet-like frass, remains of black, dead larva found
- 1 more dried out—normal flesh/juice replaced by thicker, waxier substance
- 1 approx ½ filled with white fungus normally found in mummy berries
- 1 with only 6 seeds inside, the rest is flesh/juice; berry shrunken/shriveled

Collection Site: Lava Lake Trail; 03 August 2015
Type of Damage: Yellowish-brown undeveloped berries
of Berries: 4
Observations:

- 2 with a few seeds, flesh dried and jelly-like
- 1 with pellet-like frass, remains of a dead larva
- 1 approx 25% filled with white fungus normally found in mummy berries

Collection Site: Lava Lake Trail; 03 August 2015
Type of Damage: Mummy berries
of Berries: 6
Observations:

- 2 approx 90% filled with white fungus
- 3 approx 75% filled with white fungus; seeds fill the other 25%
- 1 approx 25% filled with white fungus, seeds in the rest of the space

Collection Site: Hyalite Creek Trail; 04 August 2015
Type of Damage: Ripened but failed or pre-ripened, damaged
of Berries: 3
Observations:

- similar to berry observations above:
- Whitish pink-purple flesh & seeds that look like tiny corn kernels

Collection Site: Hyalite Creek Trail; 04 August 2015
Type of Damage: Yellowish-brown undeveloped berries
of Berries: 6
Observations:

- 4 with dried seeds, dried crumbly flesh
- 1 with dried out seeds, dried, jelly-like flesh
- 1 very small undeveloped, filled with blackened, dried frass

Collection Site: Hyalite Creek Trail; 04 August 2015
Type of Damage: Undeveloped, green berries
of Berries: 5
Observations:

- 1 with healthy looking seeds inside, just not ripened/developed
- 4 filled with frass, 1-2 small seeds, remains of sawfly larvae, 1 whole larva, not alive

Collection Site: Hyalite Creek Trail; 04 August 2015
Type of Damage: Mummy berries
of Berries: 7
Observations:

- 3 approx 90% filled with white fungus
- 2 approx 75% filled with white fungus
- 1 approx 50% filled with white fungus, the rest of the space with seeds
- 1 with some seeds and dried flesh

Collection Site: Kootenai National Forest Rd 2273 (Road to Ulm Peak); 05 August 2015
Type of Damage: Past ripe, ripened but failed/dried out
of Berries: 87
Observations:

- 2 thrips and 1 small wasp found alive walking around amongst damaged berries
- A live larva! Clear, approx 7mm long, "guts" have a purple tint (from eating berries?); took automontage photo
- 28 really dried out & rubbery
- 10 similar to berry observations above: whitish pink-purple flesh and seeds that look like tiny corn kernels
- 1 a little dried on outside, jelly-like flesh inside with a bunch of pellet-like frass and all starting to mold. No evidence of larva
- 3 a little dried on outside, jelly-like flesh inside with a bunch of pellet-like frass, no evidence of larva
- 1 a little dried on outside, pretty dry and rubbery on the inside with some pellet-like frass, no evidence of larva
- 2 with about 1/8 of inside filled with white-mummy-berry like fungus
- 1 with 2/3 of the entire berry eaten away by frugivore
- 1 a little dried on outside, jelly-like flesh inside with a bunch of pellet-like frass Also has a small chamber (pupation) directly below a small oval emergence hole on the outside of the berry
- 2 actually a mummy berry- completely filled with white fungus
- 23 really dried out and hard
- 1 outside of the berry more paper-like, seems more similar to a flower than a berry, opening near stem connection, completely filled with pellet-like frass; head only of a larva found
- 1 really light pink and small- inside with seeds much smaller than others
- 1 with frass and a maggot-like larvae inside
- 1 with frass starting to mold inside, obvious exit hole on berry
- 2 with approx. 25% of the outside of the berry chewed up, seeds inside exposed
- 1 actually a mummy berry—approx. 90% filled with white fungus
- The rest a little dried on outside, healthy seeds & jelly-like flesh inside

Collection Site: Kootenai National Forest Rd 2273 (Road to Ulm Peak); 05 August 2015
Type of Damage: Green & Undeveloped
of Berries: 35
Observations:

- 13 no seeds, lots of frass, clear remains of larvae
- 1 filled with frass, remains of larva in pieces found inside
- 6 with no seeds, filled with frass & molts, smaller larva found inside whole, 3 alive!, 3 not alive
- 3 filled with frass, only head capsule of larvae found
- 2 filled with frass, no evidence of larvae inside
- 2 with clear exit hole, filled with frass, no evidence of larvae inside
- 4 filled with frass, remains of small dead wasp found inside
- 1 filled with frass, small cocoon inside—moving, still alive! Placed in gelatin capsule in petri dish in cooler.
- Remains of one larva taken for DNA: MTEC 015754

Collection Site: Kootenai National Forest Rd 2273 (Road to Ulm Peak); 05 August 2015
Type of Damage: Mummy berries
of Berries: 52
Observations:

- 41 approx 75-90% filled with white fungus
- 6 approx 50% filled with white fungus
- 4 approx 25% filled with white fungus, the rest with seeds
- 1 with the beginnings of white fungus, filled with frass, no evidence of larva

Collection Site: Beulah Creek, Kootenai National Forest Rd 112; 06 August 2015
Type of Damage: Mummy berries
of Berries: 47
Observations:

- 43 approx. 75-90% filled with white fungus
- 3 approx 50% filled with white fungus; other 50% dried out seeds
- 1 approx 90% filled with white fungus; large hole in the side of berry exposed fungus

Collection Site: Beulah Creek, Kootenai National Forest Rd 112; 06 August 2015
Type of Damage: Ripe but dry and shriveled (past ripe)
of Berries: 47
Observations:

- 3 over 50% chewed up; seeds inside exposed
- 13 large, circular chew hole in the side of berry, near stem (~10-20% of surface area); inside of berry with seeds, flesh dried out
- 34 with about 50% of side of berry eaten away, seeds inside, very hard/dried
- 2 with approx. 75% of the berry eaten away, some seeds still inside
- 1 with large hole (~25% of surface area) inside of berry completely excavated
- 22 with seeds inside, berry dried and shriveled, flesh jelly-like
- 5 dried and very hard, seeds inside
- 2 with small chew hole near stem, approx 25% filled with fungus, seeds & rubbery flesh in the rest of the seed
- 2 with small chew hole near stem, seeds inside, flesh rubbery
- 1 not ripe (but pink), small chew hole in side of berry (~10% of surface area) seeds inside very dried out, a lot of dried out frass; no evidence of larvae

Collection Site: Whitetail Creek; 06 August 2015
Type of Damage: Undeveloped
of Berries: 1
Observations:

- Puncture wound through one side
- Seeds started to develop

Collection Site: Whitetail Creek; 06 August 2015
Type of Damage: Ripened but damaged or shriveled; collected past ripe
of Berries: 89
Observations:

- 21 Seeds present and whole, flesh seems healthy, outside shriveled and dried
- 42 small chew hole in the side (~10% surface area), seeds inside, flesh jelly-like
- 22 large chew hole in the side (~25% surface area), seeds inside, flesh jelly-like
- 3 most of the base of the berry chewed through (~50% of surface area, seeds inside, flesh jelly-like
- 1 with rasping-type damage (~25% surface area), hole doesn't go all the way through

Collection Site: Whitetail Creek; 06 August 2015
Type of Damage: Mummy berries
of Berries: 9
Observations:

- Some evidence of seeds. White fungus = solid through ~90-95% of the fruits;
- 3 fruits with obvious puncture wounds