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Bumble Bees (Hymenoptera: Apidae) of Montana

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Abstract

Montana supports a diverse assemblage of bumble bees (*Bombus* Latreille) due to its size, landscape diversity, and location at the junction of known geographic ranges of North American species. We compiled the first inventory of *Bombus* species in Montana, using records from 25 natural history collections and labs engaged in bee research, collected over the past 125 years, as well as specimens collected specifically for this project during the summer of 2015. Over 12,000 records are included, with 28 species of *Bombus* now confirmed in the state. Based on information from nearby regions, four additional species are predicted to occur in Montana. Of the 28 species, *Bombus bimaculatus* Cresson and *Bombus borealis* Kirby are new state records. The presence of *B. borealis* was previously predicted, but the presence of *B. bimaculatus* in Montana represents a substantial extension of its previously reported range. Four additional “eastern” bumble bee species are recorded from the state, and three species pairs thought to replace one another from the eastern to western United States are now known to be sympatric in Montana. Additionally, our data are consistent with reported declines in populations of *Bombus occidentalis* Greene and *Bombus suckleyi* Greene, highlighting a need for targeted surveys of these two species in Montana.

Key words: pollination, Apidae, natural history collection, museum, pollinator

Shrinking ranges and declining populations of wild and managed bees (Hymenoptera: Apoidea) have recently raised 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 and climate change, lack of high-quality forage, pathogens and parasites, pesticides, and competition with and pathogen transfer from nonnative or commercial bees (Winfree et al. 2009, Goulson et al. 2015, Kerr et al. 2015).

Bumble bees (*Bombus* spp.) are among the most recognizable bees due to their large size and colorful bodies. Because 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 having poricidal anthers, such as 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 (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 experienced drastic reductions in their historic ranges over the past 20–30 yr. Some estimates indicate that up to 25% of North American bumble bee species are facing some level of decline (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* Latreille 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. There may be as many as 250 bumble bee species worldwide (Williams 1998, Michener 2007), and though bumble bees are relatively well-known, some regions have been better studied than others. In the United States, checklists, range maps, and population-monitoring studies have been published on the

bumble bees of some states (e.g., Severin 1926, Thorp et al. 1983, Colla et al. 2011, Scott et al. 2011, Warriner 2012, Koch et al. 2012, Figueroa and Bergey 2015, Tripodi and Szalanski 2015), whereas other states have few published records.

In the United States, Montana is one of the least-studied areas with regards to bee species and distribution (Koch et al. 2015), partly because of a vast, sparsely populated area, much of which is difficult to access (Montana Wilderness Association 2015). Bumble bee range maps created using museum data and statistical models predicted that 25–30 species occur in Montana (Williams et al. 2014). Twenty-seven species have been reported in the literature (Franklin 1912; Frison 1923; Milliron 1971, 1973a,b; Koch et al. 2012; Williams et al. 2014), but some of these reports are based on a single locality. Furthermore, <500 specimens have been reported from the entire eastern half of the state, an area of ~190,000 km² (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, the state 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 habitat corridor 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 assemblage of bumble bee species that differs from surrounding states or provinces.

Habitat and landscape changes have been cited as one of the primary factors threatening bumble bee populations (Williams and Osborne 2009, Goulson et al. 2015). Montana's history includes disturbances associated with mining, logging, agriculture, transportation, and recreation (Burlingame and Toole 1957, Wyckoff 2006). However, before we can determine if and how bumble bee populations are changing in Montana, a baseline understanding of the fauna is necessary.

The literature includes records of 27 species of bumble bees collected in Montana since 1883 (Table 1). Four other species (*Bombus bohemicus* Seidl, *Bombus borealis* Kirby, *Bombus morrisoni* Cresson, and *Bombus ternarius* Say) are recorded close to the Montana border (Williams et al. 2014), and several additional species are predicted to be here, based on proximity of neighboring populations, climatic suitability (*sensu* Williams et al. 2014), and geographic considerations (Milliron 1973b; Table 1).

Our objectives were to 1) create an inventory of *Bombus* species in the state, 2) provide county-level distribution data for each of these species, 3) create a taxonomic key to make identifications easier and more accurate for those working on *Bombus* in Montana, and 4) generate a greatly expanded dataset on the history, occurrence, and temporal distribution of bumble bees in Montana. This study was not meant to include ecological or conservation assessments, but to provide baseline data to inform future research and conservation efforts.

Materials and Methods

Museum and Lab Collections

Our inventory is based on 12,067 specimens of *Bombus* species from 25 North American natural history collections or research labs and four databases (Supp. Table 1 [online only]). The total number of specimens examined ($N = 15,235$) was larger because duplicates from long series of the same species from the same date, place, and

time were examined to check for determination errors, but not every individual was databased (see Supp. Table 1 [online only]).

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* (F.) and *Bombus californicus* Smith, which we consider to be separate species (see discussion), and *Bombus kirbiellus* Curtis as separate from *Bombus balteatus* Dahlbom, following recent DNA evidence (Williams et al. 2015). New state records, rare species, and 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 (mtent.org) managed through The Ohio State University (hol.osu.edu). Additionally, *Bombus* specimens deposited in other labs at MSU (Supp. Table 1 [online only]) were examined, determined, and databased.

Records of *Bombus* specimens collected in Montana were obtained from the BLCU database, the American Museum of Natural History (AMNH) database, the Yale University Peabody Museum of Natural History (PMNH) database, and from Leif Richardson's (Williams et al. 2014) database. These records 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) questionable determinations, 4) range discrepancies, and/or 5) undetermined *Bombus* from Montana. Two large, historic collections, the National Museum of Natural History (NMNH) and the Academy of Natural Sciences, Philadelphia (ANSP), with specimen data not available electronically, were visited and Montana specimens were sorted, identified, and added to the database. For all specimens, we verified or updated historic determinations, identified undetermined specimens, and added the records to the database.

Field Sampling

Historical data on *Bombus* from museum specimens revealed that Montana has been unevenly sampled, with especially low coverage in the eastern half of the state (Figs. 1–2). In April 2015, the database showed 4 of 56 counties with no *Bombus* records and 7 others with <3 species documented. To help remedy this, collecting was undertaken in the 2015 field season and focused on unsampled or undersampled regions of Montana. 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 U.S. 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 from various localities in the state.

Specimens were processed using standard procedures (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.

Table 1. Summary of literature records of *Bombus* from Montana

Citation	<i>Bombus</i> species documented
Morrill 1903	Recorded: <i>Bombus atrifasciatus</i> Morrill ^a , <i>Bombus cooleyi</i> Morrill ^b , <i>Psithyrus</i> ^c <i>latitarsus</i> Morrill ^d , <i>Psithyrus insularis</i>
Franklin 1912	Recorded: <i>B. appositus</i> , <i>B. centralis</i> , <i>Bombus edwardsii</i> Cresson ^e , <i>B. fervidus</i> , <i>B. flavifrons</i> , <i>B. huntii</i> , <i>B. kirbyellus</i> ^f , <i>B. mixtus</i> , <i>B. nevadensis</i> , <i>B. occidentalis</i> , <i>B. rufocinctus</i> , <i>Bombus separatus</i> Cresson ^g , <i>B. vagans</i> , <i>Psithyrus consultus</i> Franklin ^h , <i>P. insularis</i> , <i>P. latitarsus</i> ^d Predicted: <i>B. californicus</i> , <i>B. frigidus</i> , <i>B. melanopygus</i> , <i>B. pensylvanicus</i> , <i>B. sitkensis</i> , <i>Psithyrus tricolor</i> Franklin ⁱ
Franklin 1915	Recorded: <i>B. californicus</i>
Anonymous 1920	Recorded: <i>B. bifarius</i> , <i>B. centralis</i> , <i>B. occidentalis</i> , <i>B. rufocinctus</i> (Species not listed in publication, but specimens are deposited at the Academy of Natural Sciences, Philadelphia)
Frison 1923	Recorded: <i>B. ternarius</i> , <i>B. terricola</i> , <i>B. vosnesenskii</i> ^j
Kral 1955	Recorded: <i>B. edwardsii</i> ^e , <i>B. occidentalis</i> , <i>B. ternarius</i> , <i>B. terricola</i> ^k
Milliron 1971	Recorded: <i>B. nevadensis</i> , <i>B. occidentalis</i> Predicted: <i>B. auricomus</i> , <i>B. terricola</i>
Milliron 1973a	Recorded: <i>B. appositus</i> , <i>B. fervidus</i> <i>fervidus</i> Predicted: <i>B. fervidus californicus</i> , <i>B. kirbyellus</i> ^f , <i>B. pensylvanicus</i>
Milliron 1973b	Recorded: <i>B. griseocollis</i> Predicted: <i>B. morrisoni</i>
Hurd 1979	Recorded: <i>B. nevadensis auricomus</i> , <i>B. sitkensis</i> , <i>B. ternarius</i> , <i>B. terricola terricola</i> , <i>B. vagans vagans</i>
Bauer 1983	Recorded: <i>B. appositus</i> , <i>B. bifarius nearcticus</i> , <i>B. flavifrons</i> , <i>B. frigidus</i> , <i>B. kirbyellus</i> ^f , <i>B. melanopygus</i> , <i>B. mixtus</i> , <i>B. nevadensis nevadensis</i> , <i>B. occidentalis</i> , <i>B. sylvicola</i> , <i>P. insularis</i>
O'Neill et al. 1991	Recorded: <i>B. griseocollis</i> , <i>B. nevadensis nevadensis</i> , <i>B. rufocinctus</i>
Fultz 2005	Recorded: <i>B. appositus</i> , <i>B. californicus</i> , <i>B. edwardsii</i> ^e , <i>Bombus fernaldae</i> (Franklin) ⁱ , <i>B. fervidus</i> , <i>B. flavifrons</i> , <i>B. impatiens</i> ^j , <i>B. insularis</i> , <i>B. melanopygus</i> , <i>B. mixtus</i> , <i>B. occidentalis</i> , <i>B. rufocinctus</i> , <i>B. suckleyi</i>
Pearce et al. 2012	Recorded: <i>B. centralis</i> , <i>B. fervidus</i> , <i>B. griseocollis</i> , <i>B. huntii</i> , <i>B. rufocinctus</i> , <i>B. sp.</i>
Koch et al. 2012	Recorded: <i>B. appositus</i> , <i>B. bifarius</i> , <i>B. californicus</i> , <i>B. centralis</i> , <i>B. fernaldae</i> ⁱ , <i>B. fervidus</i> , <i>B. flavifrons</i> , <i>B. frigidus</i> , <i>B. griseocollis</i> , <i>B. huntii</i> , <i>B. insularis</i> , <i>B. melanopygus</i> , <i>B. mixtus</i> , <i>B. nevadensis</i> , <i>B. occidentalis</i> , <i>B. rufocinctus</i> , <i>B. sitkensis</i> , <i>B. suckleyi</i> , <i>B. sylvicola</i> , <i>B. vagans</i> Predicted: <i>Bombus balteatus</i> Dahlbom ^a , <i>B. morrisoni</i> , <i>B. ternarius</i> , <i>B. terricola</i>
Simanonok and Burkle 2014	Recorded: <i>B. appositus</i> , <i>B. balteatus</i> ^a , <i>B. bifarius bifarius</i> , <i>B. bifarius nearcticus</i> , <i>B. centralis</i> , <i>B. fernaldae</i> ⁱ , <i>B. flavifrons</i> , <i>B. frigidus</i> , <i>B. insularis</i> , <i>B. melanopygus</i> , <i>B. mixtus</i> , <i>B. nevadensis</i> , <i>B. sylvicola</i>
Williams et al. 2014	Recorded: <i>B. appositus</i> , <i>B. balteatus</i> ^a , <i>B. bifarius</i> , <i>B. centralis</i> , <i>B. fervidus</i> , <i>B. flavidus</i> , <i>B. flavifrons</i> , <i>B. frigidus</i> , <i>B. griseocollis</i> , <i>B. huntii</i> , <i>B. insularis</i> , <i>B. melanopygus</i> , <i>B. mixtus</i> , <i>B. nevadensis</i> , <i>B. occidentalis</i> , <i>B. pensylvanicus</i> , <i>B. rufocinctus</i> , <i>B. sitkensis</i> , <i>B. suckleyi</i> , <i>B. sylvicola</i> , <i>B. terricola</i> ^k , <i>B. vagans</i> Recorded Near Montana Border: <i>B. bohemicus</i> , <i>B. borealis</i> , <i>B. morrisoni</i> , <i>B. ternarius</i> Predicted ^l : <i>B. bohemicus</i> , <i>B. borealis</i> , <i>B. cryptarum</i> , <i>B. fraternus</i> , <i>B. morrisoni</i> , <i>B. ternarius</i> , <i>B. vosnesenskii</i>

^a *B. atrifasciatus* = *B. balteatus* (sensu Hurd 1979, sensu Williams et al. 2014) = *B. kirbiellus* Curtis (Williams et al. 2015).

^b *B. cooleyi* = *B. bifarius* (Hurd 1979).

^c The genus *Psithyrus* is considered to be a subgenus of *Bombus* (Williams 1998).

^d *P. latitarsus* = *B. suckleyi* (Hurd 1979).

^e *B. edwardsii* = *B. bifarius* (Frison 1923) or *B. melanopygus* (Owen et al. 2010).

^f *Bombus kirbyellus* is an unjustified emendation of *B. kirbiellus* Curtis (Williams et al. 2015).

^g *B. separatus* = *B. griseocollis* (Hurd 1979).

^h *P. consultus* = *B. insularis* (Williams et al. 2014).

ⁱ *P. tricolor* = *B. fernaldae* (sensu Hurd 1979) = *B. flavidus* (sensu Williams et al. 2014).

^j This record is not verified, see discussion.

^k Likely *B. occidentalis*, see discussion.

^l Predicted via climatic suitability maps.

Data Analysis

Data were extracted from MTEC XBio:D database into Excel for analysis. County-level maps were created using a vector graphic from Wikipedia's U.S. Counties Map. The vector graphic code was edited in Adobe Dreamweaver and transferred to Adobe Illustrator using SVG Crowbar 2 plugin for final editing. The topographical map was created using Google My Maps. The map was saved as a PDF and copied into Adobe Photoshop for final editing.

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 species richness 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). It is a lower bound estimate, and often underestimates the true parameter (Chao 1984), but is considered a good 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 MTEC XBio:D database. After sampling in all 56 counties (Fig. 3), 28 *Bombus* species are now known to occur in Montana (Table 2; Fig. 4). These species include two new state records, *Bombus bimaculatus*

Fig. 1. Number of *Bombus* specimen records per Montana county in April 2015 (A) and January 2016 (B). White = 0; light gray = 1–10; medium gray = 11–100; dark gray = 101–1,000; black >1,000.

Fig. 2. Number of *Bombus* species records per Montana county in April 2015 (A) and January 2016 (B). White = 0–3; light gray = 4–8; medium gray = 9–12; dark gray = 13–17; black = 18–22.

Cresson and *B. borealis*. Seven of the 28 are typically considered to have “eastern” United States ranges (Koch et al. 2012): *Bombus auricomus* (Robertson), *B. bimaculatus*, *B. borealis*, *B. pensylvanicus*, *B. ternarius*, *B. terricola*, and *Bombus impatiens* Cresson. The last is an

eastern species that is reared for commercial purposes (see discussion for more details about its presence in Montana). *Bombus vosnesenskii* Radoszkowski is not included in our species list because no specimen from Montana could be found to verify Frison’s (1923) literature record.

The mean species accumulation curve generated with the EstimateS program (Colwell 2013) reaches an asymptote at 28 species (Fig. 5). Additional analysis with the EstimateS program (Colwell 2013) yielded a Chao1 mean prediction of 28 species of *Bombus* for Montana (SD = 0.12; 95% confidence interval = 28.0–28.2 species). The variation in sampling methodology by many individuals over the past 130 yr, as well as the uneven spatial and temporal distributions of sampling prevents quantitative analyses of diversity and abundance comparisons by region. Nevertheless, the distribution maps (Fig. 4) and numbers of specimens per species presented here (Table 2) can provide insights into the relative abundance and ranges of *Bombus* species in Montana. It seems clear that species vary in abundance in the state as a whole. Of the 28 species, just 4 are represented by >1,000 specimens (Table 2). For another 16, >100 specimens are in the database, but just 10 or fewer specimens were available for 4 species.

The oldest Montana specimens in the dataset were collected in 1883 (four individuals, NMNH). Sixty-three percent of the records in the database were collected between 1990 and 2015. The greatest accumulation of specimens (over 3,000) came in 2015, mostly from the current project. For a full discussion of the history of *Bombus* collecting in Montana, see Dolan (2016).

The intensive 2015 sampling did not uncover any new state records. There were, however, 113 new county records. Moreover, sampling in 2015 increased sample sizes and added species records for previously undersampled localities (Figs. 1–2). Excluding new records (where the divisor would be zero), increase in specimens per species from April 2015 to January 2016, ranged from 0% for the special case of the introduced *B. impatiens* and 27% for native species *B. sitkensis*, to 900% for *B. terricola*, with a mean increase of 146% for the 27 native species.

Discussion

Bumble bee records are now available for 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 in Montana over the past 15 yr (e.g., Fultz 2005, Cameron et al. 2011, Pearce et al. 2012, Simanonok and Burkle 2014). With the exception of two species, *B. occidentalis* and *Bombus suckleyi* Greene, all species have experienced at least a 49% increase in the number of specimens known from Montana since 2000.

Of the two new state records, *B. borealis* had previously been documented in Alberta and Saskatchewan, just north of Montana’s border and just east of the state in North Dakota. Its presence in Montana was predicted, but never confirmed (Williams et al. 2014). The presence of *B. bimaculatus* is of special note because this species had previously not been documented or even predicted to be west of the eastern Dakotas and Nebraska (Williams et al. 2014). The discovery of this species in Montana represents a substantial westward extension of its known range.

Additional sampling is still needed to fully document the range and diversity of *Bombus* species in Montana since >50% of Montana’s counties (29/56) currently have <100 *Bombus* records

Fig. 3. Map of localities where *Bombus* specimens in Montana have been collected from 1883–2015. Map data 2016 Google, INEGI Imagery 2016 TerraMetrics.

(Table 2) 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 and might also reveal the presence of additional species.

The Influence of Sampling Effort

Geographic variation in past sampling effort is certainly a factor in interpreting the data presented here. The counties where entomologists have conducted research projects not necessarily focused on survey work (e.g., Gallatin, Flathead, Carbon, and Meagher) have the most species (Fig. 2). Additionally, the map of collection sites in Montana (Fig. 3) 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 our relative abundance data for their targeted species. O'Neill et al. (1991) preferentially collected *Bombus griseocollis* (DeGeer), *Bombus nevadensis* Cresson, and *Bombus rufocinctus* Cresson. Cameron et al. (2011) did the same for *Bombus bifarius* Cresson and *B. occidentalis*. Thus, the number of these species in our data set may not accurately reflect their actual relative abundance in the communities sampled. 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 2016). Bumble bees were only collected in specific habitats from *V. globulare*, so these counties in northwest Montana almost certainly have more *Bombus* species than the data suggest.

Unrecorded *Bombus* Potentially Present in Montana

The Chao1 mean prediction of 28 *Bombus* species in Montana (Fig. 5) indicates that we are unlikely to find more species than we have already documented. However, based on proximity of neighboring populations, climatic suitability (*sensu* Williams et al. 2014), and geographic considerations (Milliron 1973b), there are four *Bombus* species not yet recorded from Montana that may still

be found. One of these is *Bombus cryptarum* (F.), whose range is recorded as the tundra/taiga regions of the northern Rocky Mountains 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*. Records from Canada show this species has been collected within 20 km of Montana's northern border near Milk River, Alberta (Ashton Sturm, personal communication, specimens in Jessamyn Manson Lab Collection, University of Alberta).

Predictive habitat suitability maps extend the possible range of *B. morrisoni* from the deserts in the southwestern United States to the dry scrubland regions of southwestern Montana (Williams et al. 2014). There are records of this species in parts of Idaho near Montana, including one from Salmon, ID, just 17 km southwest of the border (Discover Life 2016). There are also records of *B. morrisoni* in southern Wyoming (Williams et al. 2014, Discover Life 2016); thus, it is possible that the range of *B. morrisoni* extends into southwest Montana (e.g., Beaverhead County).

Bombus bohemicus has been recorded from New England across the Midwestern United States 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 just to the north in Alberta and Saskatchewan, Canada (Williams et al. 2014). This species is very similar to *B. suckleyi*, which is also in the subgenus *Psithyrus* and is thought to replace *B. bohemicus* in parts of the West (R. Thorp, personal communication). Montana, especially northeastern Montana, is a place where the ranges of these two species may overlap, though both of these species are apparently 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 (Williams et al. 2014), and we added a record from Calgary, 225 km north of the Montana border (Museum of Zoology, University of Calgary (BDUC) #MTEC 019296). This distribution pattern, which is similar to *B. borealis*

Table 2. The 28 *Bombus* species occurring in Montana, organized alphabetically by species

Species	Earliest specimen (Year)	First literature record	Total no. of specimens	Total no. of counties
<i>Bombus (Subterraneobombus) appositus</i> Cresson, 1878	1899	Franklin 1912	302	25
<i>Bombus (Bombias) auricomus</i> (Robertson, 1903)	1971	Hurd 1979	5	4
<i>Bombus (Pyrobombus) bifarius</i> Cresson, 1878	1883	Morrill 1903	1,911	37
<i>Bombus (Pyrobombus) bimaculatus</i> Cresson, 1863	2011	New State Record	18	7
<i>Bombus (Subterraneobombus) borealis</i> Kirby, 1837	1926 ^a	New State Record ^b	20	8
<i>Bombus (Thoracobombus) californicus</i> Smith, 1854	1913	Franklin 1915	91	19
<i>Bombus (Pyrobombus) centralis</i> Cresson, 1864	1901 ^a	Franklin 1912	641	47
<i>Bombus (Thoracobombus) fervidus</i> (F., 1798)	1899 ^a	Franklin 1912	688	47
<i>Bombus (Psithyrus) flavidus</i> Eversmann, 1852	1929 ^b	Fultz 2005	158	19
<i>Bombus (Pyrobombus) flavifrons</i> Cresson, 1863	1900	Franklin 1912	488	30
<i>Bombus (Pyrobombus) frigidus</i> Smith, 1854	1929	Bauer 1983	59	9
<i>Bombus (Cullumanobombus) griseocollis</i> (DeGeer, 1773)	1904	Franklin 1912	357	38
<i>Bombus (Pyrobombus) huntii</i> Greene, 1860	1883 ^a	Franklin 1912	1,840	53
<i>Bombus (Pyrobombus) impatiens</i> Cresson, 1863	1980	Fultz 2005 ^c	7	2
<i>Bombus (Psithyrus) insularis</i> (Smith, 1861)	1899	Morrill 1903	389	30
<i>Bombus (Alpinobombus) kirbiellus</i> Curtis, 1835	1900	Morrill 1903	122	7
<i>Bombus (Pyrobombus) melanopygus</i> Nylander, 1848	1913	Franklin 1912	379	19
<i>Bombus (Pyrobombus) mixtus</i> Cresson, 1878	1900	Franklin 1912	855	30
<i>Bombus (Bombias) nevadensis</i> Cresson, 1874	1899 ^a	Franklin 1912	252	41
<i>Bombus (Bombus) occidentalis</i> Greene, 1858	1899 ^a	Franklin 1912	1,046	41
<i>Bombus (Thoracobombus) pensylvanicus</i> (DeGeer, 1773)	1964	Williams et al. 2014	5	4
<i>Bombus (Cullumanobombus) rufocinctus</i> Cresson, 1863	1899	Franklin 1912	1,391	52
<i>Bombus (Pyrobombus) sitkensis</i> Nylander, 1848	1934 ^b	Hurd 1979	180	8
<i>Bombus (Psithyrus) suckleyi</i> Greene, 1860	1899	Morrill 1903	146	19
<i>Bombus (Pyrobombus) sylvicola</i> Kirby, 1837	1913	Bauer 1983	187	18
<i>Bombus (Pyrobombus) ternarius</i> Say, 1837	1931 ^a	Frison 1923	301	18
<i>Bombus (Bombus) terricola</i> Kirby, 1837	2011 ^a	Frison 1923 ^d	10	2
<i>Bombus (Pyrobombus) vagans</i> Smith, 1854	1901	Franklin 1912	152	18

^a 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 (J. Weintraub personal communication).

^b This species was predicted, but not confirmed, by earlier literature to be in Montana.

^c This record of *B. impatiens* could not be verified. See text.

^d The specimen recorded by Frison (1923) is likely *B. occidentalis*. See text.

Figure 4a: *Bombus appositus* in MT
302 records from 25 counties.

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

Figure 4c: *Bombus bifarius* in MT
1,911 records from 37 counties.

Figure 4d: *Bombus bimaculatus* in MT
18 records from 7 counties.

Figure 4e: *Bombus borealis* in MT
20 records from 8 counties.

Figure 4f: *Bombus californicus* in MT
91 records from 19 counties.

Figure 4g: *Bombus centralis* in MT
641 records from 47 counties.

Figure 4h: *Bombus fervidus* in MT
688 records from 47 counties.

Figure 4i: *Bombus flavidus* in MT
158 records from 19 counties.

Figure 4j: *Bombus flavifrons* in MT
488 records from 30 counties.

Figure 4k: *Bombus frigidus* in MT
59 records from 9 counties.

Figure 4l: *Bombus griseocollis* in MT
357 records from 38 counties.

Figure 4m: *Bombus huntii* in MT
1,840 records from 54 counties.

Figure 4n: *Bombus impatiens* in MT
7 records from 2 counties.

Figure 4o: *Bombus insularis* in MT
389 records from 30 counties.

Fig. 4. (a–ab). County-level distribution maps for the 28 *Bombus* species known to occur in Montana. Note that the map of *B. impatiens*, Figure 4n, is documenting 1) the presence of bees introduced for research in Chouteau County and 2) a distribution outlier in Ravalli County. See text for details.

Figure 4p: *Bombus kirbiellus* in MT
122 records from 7 counties.

Figure 4q: *Bombus melanopygus* in MT
379 records from 19 counties.

Figure 4r: *Bombus mixtus* in MT
855 records from 30 counties.

Figure 4s: *Bombus nevadensis* in MT
252 records from 41 counties.

Figure 4t: *Bombus occidentalis* in MT
1,046 records from 41 counties.

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

Figure 4v: *Bombus rufocinctus* in MT
1,391 records from 52 counties.

Figure 4w: *Bombus sitkensis* in MT
180 records from 8 counties.

Figure 4x: *Bombus suckleyi* in MT
146 records from 19 counties.

Figure 4y: *Bombus sylvicola* in MT
187 records from 18 counties.

Figure 4z: *Bombus ternarius* in MT
301 records from 18 counties.

Figure 4aa: *Bombus terricola* in MT
10 records from 2 counties.

Figure 4ab: *Bombus vagans* in MT
152 records from 18 counties.

Fig. 5. Species accumulation curve and Chao 1 mean for *Bombus* in Montana. Figure was generated using EstimateS (Colwell 2013). Each county was considered a sample and samples were randomized 50 times to create the mean accumulation curve.

and *B. ternarius*, may suggest the presence of *B. perplexus* in the northeastern part of Montana.

Sympatry of Eastern/Western Species Pairs

In North America, there are several morphologically similar species thought to have ranges that are geographically distinct (i.e., one species is said to be “eastern”, the other “western”; Colla et al. 2011, Koch et al. 2012, Williams et al. 2014). This geographic distinction is often used to aid in species diagnosis. The division between eastern and western North America is often split at the 100th meridian, but that separation is relatively arbitrary. Because Montana’s eastern border is near the 100th meridian, eastern Montana is one area where eastern and western species ranges may overlap. This project has confirmed the sympatric occurrence of three of these species pairs: *B. auricomus*/*B. nevadensis*, *Bombus huntii* Greene/*B. ternarius*, and *B. occidentalis*/*B. terricola*.

Bombus auricomus/*Bombus nevadensis*

Throughout their taxonomic histories, *B. nevadensis* and *B. auricomus* have been considered either separate species or subspecies (Hurd 1979). Currently, they are considered separate species, with *B. nevadensis* occurring in western North America and *B. auricomus* in the East (Williams et al. 2014). *Bombus nevadensis* is considered common throughout its range (Koch et al. 2012) and is widespread in Montana (252 specimens in 41 counties; Fig. 4s). On the other hand, the presence of *B. auricomus* in Montana was uncertain prior to this study, though its occurrence here was predicted by Milliron (1971). *Bombus auricomus* is a common eastern species known to occur throughout eastern temperate forests west to the Great Plains (Williams et al. 2014). We documented five specimens of *B. auricomus* in four Montana counties reaching as far west as Pondera County (Fig. 4b). These records extend the known range of *B. auricomus* west to the foothills of the Rocky Mountains (111.506° W), and suggest an extensive area of *B. auricomus*/*B. nevadensis* sympatry across the eastern two-thirds of Montana (compare Fig. 4b and Fig. 4s).

Bombus huntii/*Bombus ternarius*

Bombus huntii and *B. ternarius* are morphologically similar, but they have been thought to be geographically distinct. *Bombus huntii* is said to replace *B. ternarius* in the interior western United States, while *B. ternarius* replaces *B. huntii* in the North (Williams et al. 2014). Across much of Montana, however, these two species occur sympatrically (compare Fig. 4m and Fig. 4z). In Montana, *B. huntii* is one of the most common and widespread species. The earliest specimen was collected in 1883, and it has been consistently collected since that time across the entire state (Fig. 4m). Conversely, only six specimens of *B. ternarius* were collected before 2008 and added to the database. However, since 2011, when the Montana Department of Agriculture began using bucket traps to monitor for invasive pests in eastern Montana, many more individuals of *B. ternarius* have been collected, and it has become one of the most commonly collected species in the northeastern portion of the state (Fig. 4z).

Bombus occidentalis/*Bombus terricola*

The range of *B. occidentalis* is extensive across western North America (Williams et al. 2014), and this species was once one of the most common bees in the West. However, since the 1990s, some populations have experienced sharp declines (Cameron et al. 2011, Williams et al. 2014). *Bombus terricola* is an eastern and northern North American species (Williams et al. 2014), known to be in the Black Hills area of South Dakota (Koch et al. 2012) and 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). These two species are thought to be geographically distinct with *B. occidentalis* replacing *B. terricola* in the West. Literature records placed *B. terricola* in multiple locations across 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 (Fig. 4aa). There is one more verified *B. terricola* specimen determined by Franklin in 1922 (ANSP), but it lacks a date or specific locality. *Bombus occidentalis* has been collected in 41 Montana counties (Fig. 4t), but has not yet been collected in the southeastern-most region of Montana, where *B. terricola* is also likely to be found. However, we now have records of these two species being sympatric, at least in the two northeastern-most counties of Montana (compare Fig. 4t and Fig. 4a).

Taxonomic Challenges

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). 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 (Williams 2007, Koch 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, A.C.D., unpublished data), making identification even more challenging. For the species pairs described below, characters used to distinguish between similar species are for females only. Male determination requires examination of genitalia (see Williams et al. 2014 for more information on identification of males).

Bombus auricomus/Bombus nevadensis

As discussed above, *B. auricomus* and *B. nevadensis* are morphologically similar species that were thought to be geographically distinct. Both occur in Montana, and distinguishing between them using morphological characters is extremely difficult. The main morphological character used to tell these species apart is the presence or absence of a black interalar band. *Bombus auricomus* typically has a strong black interalar band, while *B. nevadensis* usually has yellow hairs predominating dorsally on the mesosoma with only a circle of black hairs medially. Another diagnostic character used is the size and spacing of punctations between the eyes and the ocelli (Williams et al. 2014), but the very subtle spacing differences make this character difficult. Some individuals are especially difficult to distinguish because the circular patch of black hairs on *B. nevadensis* is expanded into a nearly complete interalar band, more closely resembling *B. auricomus*, though this color variant is most common on the West Coast of the United States. For this study, we relied on a complete black interalar band as diagnostic for *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, most of the hairs touching the wing bases were yellow, we determined it to be *B. nevadensis*.

Bombus huntii/Bombus ternarius

As discussed above, *B. huntii* and *B. ternarius* are morphologically similar species previously thought to be geographically distinct. However, because they occur sympatrically across much of Montana, geographic location cannot be used to aid determinations.

Key morphological characters, however, can be used to tell these two species apart. *Bombus ternarius* has black hairs on the face with yellow hairs located centrally near the antennal bases, and the yellow hairs on the scutellum are divided by a line or triangle of black hairs. Often there are also yellow hairs on the front coxae. In *B. huntii*, the yellow hairs of the scutellum are not divided by black, the hairs on the face are predominantly yellow, and the hairs on the coxae are completely black.

Bombus occidentalis/Bombus terricola

As discussed above, *B. terricola* and *B. occidentalis* were thought to be geographically separated as eastern and western North American species, but both occur in Montana. For these two species, key morphological characters can be used for determination. *Bombus terricola* has metasomal T2 (T = tergite) entirely yellow while *B. occidentalis* always has at least some black on T2.

Bombus californicus/Bombus fervidus

Bombus fervidus is a widespread species that has been collected continentally in North America while *B. californicus* is a western species known from the Pacific Coast to the Rocky Mountains (Koch et al. 2012, Williams et al. 2014). 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, where the two species are sympatric, *B. fervidus* occurs mostly in the prairies, whereas *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 appear to be sympatric in the western counties, though our collection sites and observations support the 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 Fig. 4f and Fig. 4h).

Bombus californicus has several different color morphs, some more cryptic than others. Metasomal T4 is always yellow, as in *B. fervidus*, while T1–T3 are variable in color. 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 (Williams et al. 2014, Koch 2015). Based on our observations, *B. fervidus* in Montana have only yellow hairs on T1–T4.

Bombus centralis/Bombus flavifrons

Certain individuals of *B. centralis* are very similar to *B. flavifrons*. Both species have a longer-than-wide malar space and a hair pattern of metasomal T1: yellow, T2: yellow, T3: orange, and T4: orange. The key morphological character that separates these two is the amount of black hair intermixed with 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, A.C.D., unpublished data). 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 (Thorp et al. 1983; Fig. 4g and j;

A.C.D., unpublished data). Because these habitats often overlap in Montana, the species also occur in both habitats.

We used the amount of black hairs 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 identification of *B. centralis* or *B. flavifrons* was not obvious, we defaulted to an identification of *B. flavifrons*, following the recommendation of James Strange at the BLCU 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*.

Species Introduced to Montana

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 United States and the possible consequences for native bees if feral *B. impatiens* colonies become established outside of their native range (Xerces Society et al. 2013). Commercial hives contain queen excluders in order to prevent the escape of new queens and the establishment of feral colonies (Planet Natural 2016). 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, Graystock et al. 2016).

There was one record of this species in Montana from a 2005 study (Fultz 2005), but this record could not be validated because the specimen could not be located.

The database currently contains seven specimens of *B. impatiens* from Montana (Fig. 4n). 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 (Snow Entomological Museum Collection, University of Kansas, SEMC). The other six specimens of *B. impatiens* are from a 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 in case feral colonies of this species are detected in that region in the future. At the end of the summer 2014 field season, 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 (Graystock et al. 2016).

Species Possibly in Decline

The purpose of our project was to provide baseline data and general distribution data for *Bombus* species occurring in Montana. We did not attempt to use these data to form conclusions about population trends or changes in historic ranges. Still, our results show that, of the 28 species collected, records for all but two experienced an increase of $\geq 49\%$ since 2000 when sampling efforts in Montana substantially increased. The increase in records of *B. occidentalis* is just

36% since 2000, and only five individuals of *B. suckleyi* have been added to the database since 2000 (MTEC, BLCU, KMOC), representing only a 4% increase. These relatively low percentage increases are consistent with reported population declines for these species (Cameron et al. 2011; Hatfield et al. 2015a,b; Koch et al. 2015).

Changes in the prey composition of natural enemies over the past 50 yr may also be reflective of population declines in *B. occidentalis*. Armitage (1965) found *B. occidentalis* to be the most common prey (35% of 203 *Bombus* spp.) of the wasp *Philanthus bicinctus* Mickel at a site on the southern edge of Yellowstone National Park (50 km south of 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 remaining prey.

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. 2015b). 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 populations declining. Because of this, the low number of *B. suckleyi* collected in the past 15 yr initially seemed 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 both *B. suckleyi* and its primary host, *B. occidentalis*, in Montana.

Notes on Sampling Methods

Many of the bumble bees collected in Montana over the past 130 yr and examined for this project were captured using a net. However, other methods were also used to obtain specimens, including pan traps, pitfall traps, flight intercept traps, bucket traps, and Japanese beetle traps. In most cases, the bumble bees collected by these traps, excluding pan traps, would be considered "by-catch," because they are commonly used to sample non-Hymenopteran taxa. Typically, nontarget species collected in these traps are stored but not processed, or discarded. Even the small and biased samples of nontarget bee species collected by nontraditional trapping methods provide valuable insights when added to larger specimen and literature databases (Hung et al. 2015, Spears and Ramirez 2015). In our study, by-catch provided samples from a variety of localities throughout Montana that may not otherwise have been represented (e.g. Ivie et al. 1998, Winton 2010).

Because bucket and Japanese beetle traps are extremely effective at attracting bumble bees, their use is very enticing. We advise that anyone utilizing these traps in the future should exercise caution and deploy them at very low densities 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 May and left up throughout the summer. Consequently, all castes of bees were collected, including a large number of queens. We would caution against using these traps early in the spring or summer and late in the summer when queens are active, since the capture of queens compared to workers potentially has a much greater impact on colony establishment. In addition, because the yellow color and floral scents used as lures in Japanese beetle and bucket traps make them highly attractive to bees, we encourage the development of alternative trap colors and lures that effectively collect target species while avoiding the unnecessary capture of nontarget 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 identify 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 6. When color is used in the key, it refers to the color of the hair-like setae (referred to as “hairs”) unless otherwise stated.

Fig. 6. (A–C). Morphological characters used to identify female *Bombus* to species.

One of the most challenging characters used to identify bumble bees is the length of the malar space compared to its width. The length of the malar space is measured from the lower margin of the compound eye to the mandibular hinge. The width of the malar space is measured from the edge of the anterior mandibular hinge to the posterior hinge (Fig. 6b). This character is best viewed in profile. In general there are three malar-space 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.

Detailed species accounts, along with a summary of key diagnostic characters can be found on the Montana Entomology Collection website (Dolan et al. 2016) and in Dolan (2016).

1.	Female: antenna with 12 antennomeres; metasoma with six visible tergites.....	2
1'.	Male: antenna with 13 antennomeres; metasoma with seven visible tergites. No key provided. (To key males to species, use Williams et al. 2014.)	
2(1).	Outer surface of hind tibia concave and shiny; corbicula present; social species	3
2'.	Outer surface of hind tibia convex and hairy; corbicula absent; social parasites.....	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 basitarsus brownish-orange and often lighter than the tibia; corbicular fringes orange or brown.....	
	 <i>Bombus bifarius</i> Cresson	
5'.	T2 orange; hind tibia and basitarsus concolorous; corbicular fringes black, sometime with orange tips.....	
	 <i>Bombus melanopygus</i> Nylander	
6(4').	Malar space distinctly shorter than wide; face with predominantly black hairs	<i>Bombus rufocinctus</i> Cresson
6'.	Malar space as long as wide; face with yellow hairs, at least centrally	7
7(6').	Scutellum with yellow hairs only	<i>Bombus huntii</i> Greene
7'.	Scutellum with yellow or pale yellow hairs divided by a line or triangle of black hairs	8
8(7').	T2 color variable, but with black hairs at least medially; integument of hind leg basitarsus brownish-orange and often lighter than the tibia	<i>Bombus bifarius</i> Cresson
8'.	T2 predominately orange, lacking black hairs medially; integument of hind leg basitarsus and tibia concolorous.....	9
9(8').	T5 with yellow hairs on the lateral margins; hairs long and uneven; coxae with predominately black hairs.....	<i>Bombus sylvicola</i> Kirby
9'.	T5 black; hairs short and even; coxae often with yellow hairs	<i>Bombus ternarius</i> Say
10(3').	Malar space longer than wide (though sometimes only slightly longer than wide and appearing square).....	11
10'.	Malar space 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	<i>Bombus flavifrons</i> 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	<i>Bombus flavifrons</i> Cresson
14'.	Anterior scutum with predominantly yellow hairs... ..	<i>Bombus centralis</i> Cresson
15(13').	T5 yellow or brownish.....	<i>Bombus appositus</i> Cresson
15'.	T5 usually mostly black.....	<i>Bombus borealis</i> Kirby
16(11').	T5 and T6 with orange or pale orange hairs.....	
	 <i>Bombus kirbiellus</i> 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	<i>Bombus californicus</i> Smith
19(18).	T2 with yellow hairs medially and black hairs laterally (yellow often in the shape of a "W")	<i>Bombus bimaculatus</i> Cresson
19'.	T2 yellow	20
20(19').	Sides of the thorax with yellow hairs predominating.....	
	 <i>Bombus vagans</i> Smith	
20'.	Sides of the thorax usually with black hairs predominating	<i>Bombus perplexus</i> Cresson (possibly in MT)
21(17').	Interalar band completely or predominantly black	22
21'.	Interalar band predominantly yellow, if black hairs are present they form a small circle medially.....	
	 <i>Bombus nevadensis</i> 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.....	<i>Bombus pensylvanicus</i> (DeGeer)
23'.	T1 with black hairs, at least medially, sometimes with yellow hairs intermixed; surface of clypeus smooth and shiny.....	<i>Bombus auricomus</i> (Robertson)
24(22').	T2 yellow.....	<i>Bombus fervidus</i> (F.)
24'.	T2 with yellow hairs medially and black hairs laterally.....	<i>Bombus californicus</i> Smith
25(10').	Malar space shorter than wide.....	26
25'.	Malar space as long as or slightly longer than wide... ..	31
26(25).	Interalar band completely or predominantly black.....	
		27
26'.	Interalar band predominantly yellow; if black hairs are present they form a small circle medially	30
27(26).	T1 yellow	<i>Bombus rufocinctus</i> Cresson
27'.	T1 black	28
28(27').	T2 yellow	29
28'.	T2 with black hairs or, if some yellow, along posterior margin only	<i>Bombus occidentalis</i> Greene
29(28).	T3 black.....	<i>Bombus cryptarum</i> (F.) (possibly in MT)
29'.	T3 yellow.....	<i>Bombus terricola</i> Kirby
30(26).	T3 yellow, at least medially.....	
	 <i>Bombus morrisoni</i> Cresson (possibly in MT)	
30'.	T3 black	<i>Bombus griseocollis</i> (DeGeer)
31(25').	Scutellum with yellow or pale yellow hairs divided by a line or triangle of black hairs	<i>Bombus bifarius</i> Cresson
31'.	Scutellum not as above (with yellow hairs only, or yellow and black hairs intermixed throughout).....	32
32(31').	T2-6 black.....	<i>Bombus impatiens</i> Cresson (nonnative species 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 scutellum appearing lighter than the anterior scutum)
.....*Bombus mixtus* Cresson
- 35(2'). Occiput with predominantly black hairs; hairs of face predominantly black around bases of antennae; S6 with strong lateral ridges 37
- 35'. Occiput with predominantly yellow hairs; other characters variable..... 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 laterad beyond T6.....
.....*Bombus suckleyi* Greene
- 37'. Hairs on the side of the thorax predominantly black; T4 yellowish-white to white, at least medially; S6 lateral ridges barely extending laterad beyond T6
.....*Bombus bohemicus* Seidl (possibly in MT)

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