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CONSERVATION GENETICS OF A DECLINING BUMBLE BEE IN WESTERN  
NORTH AMERICA; THE INFLUENCE OF GEOGRAPHY, DISPERSAL  
LIMITATION, AND ANTHOPOGENIC ACTIVITY

by

Ashley T. Rohde

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

DOCTOR OF PHILOSOPHY

in

Ecology

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2022

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## ABSTRACT

Conservation Genetics of a Declining Bumble Bee in Western North America; the  
Influence of Geography, Dispersal Limitation, and Anthropogenic Activity

by

Ashley T. Rohde, Doctor of philosophy

Utah State University, 2022

Major Professors: Dr. Karen Mock  
Department: Wildland Resources

Conservation biology addresses the problem of biological species loss and decline by identifying species in need of protection or recovery. Conservation biology has subfields to better address aspects of biodiversity loss, including conservation genetics, phylogenomics, and sociology. In this dissertation, I used genetic and phylogenomic approaches to assess the conservation status of a bumble bee species of concern, *Bombus occidentalis*, and a sociological approach to measure conservationists' interest in genetics methods for conservation studies.

*Bombus occidentalis* is a widespread North American bumble bee species that is decreasing in abundance in portions of its range. It is currently under consideration for listing under the Endangered Species Act in the United States and is listed as endangered in parts of its Canadian distribution through the Species At Risk Act. To complicate the problem further, there is debate about whether *Bombus occidentalis* is one species or two. Recent genetic analyses of the mitochondrial *cytochrome oxidase I* (COI) gene indicate



that the group may consist of a northern species (*B. mckayi*) and a southern species (*B. occidentalis*).

I used nuclear (ultraconserved elements, UCE) and mitochondrial (COI) phylogenomic methods to infer maximum likelihood (ML) and Bayesian (BI) phylogenies of the relationship between the two taxa. I used seven species delimitation methods to conduct the most thorough test of the species status of these taxa yet performed. The species delimitation analyses sometimes contradicted one another, but *B. occidentalis mckayi* was consistently recovered as a monophyletic group in both UCE and COI phylogenetic analyses. This analysis provided sufficient evidence to elevate *B. occidentalis mckayi* to the level of species.

I used landscape genetic methods to measure patterns of genetic diversity and structure in *B. occidentalis* and *B. mckayi* from 1960 through 2020, and tested associations with potential environmental drivers of genetic diversity across the landscape. *B. occidentalis* showed patterns of decreasing genetic diversity and increasing genetic structure, but *B. mckayi* did not. The genetic diversity in both species were most strongly influenced by springtime minimum temperatures and proximity to known infections of the fungal parasite *Vairimorpha bombi*.

Finally, I surveyed 974 conservationists from diverse backgrounds to measure their level of understanding, trust, and motivation from conservation genetic studies. The results indicate that lack of understanding, but not trust, may inhibit increased use of molecular methods in conservation.

## PUBLIC ABSTRACT

Conservation Genetics of a Declining Bumble Bee in Western North America; the  
Influence of Geography, Dispersal Limitation, and Anthropogenic Activity

Ashley T. Rohde

Conservation biology addresses the problem of species loss by identifying species in need of protection. Conservation biology has subfields to address different aspects of biodiversity loss, including genetics and sociology. I used genetic approaches to assess the conservation status of western bumble bees, a bumble bee species of conservation concern.

The western bumble bee is a bumble bee species that ranges from Alaska to New Mexico and as far east as Wyoming and Colorado. This species is disappearing in some places. It may soon be listed as endangered in the United States and is already listed as endangered in parts of its Canadian distribution. To complicate the problem further, the western bumble bee might really be two cryptic species. Recent genetic analyses indicate that there might be a northern species (Mckay's bumble bee) and a southern species (the western bumble bee).

I used DNA from specimens collected across the range and ran genetic analyses to estimate the relationships between western bumble bees and Mckay's bumble bees. This study provided enough evidence to conclude that they are, in fact, two species.

Next, I compared patterns of genetic diversity in the two species to environmental variables to determine how the environment influences how the bees to move across the landscape. I compared patterns of genetic diversity in bees that were collected between

1960 through 2020. Western bumble bees showed patterns of slightly decreasing genetic diversity through time from 1960 to 2019, but McKay's bumble bee did not. For both species, nighttime temperatures during the spring and proximity to a native fungal parasite were important predictors of differences in genetic diversity among samples. The distance from parasites is probably important because specimens that are near infections are more likely to be infected themselves. Although we found decreases in genetic diversity for western bumble bees, there is still enough genetic diversity in present-day populations for the species to recover if the effects of the drivers of the declines are managed.

Finally, I surveyed 974 conservationists from diverse backgrounds to measure their understanding, trust, and motivation to action from conservation genetic studies. This is important because molecular methods provide important insight into the conservation status of at-risk species, but they are not used very often when land managers make conservation decisions. The results indicate that lack of understanding, but not trust, may be a barrier to increased use of molecular methods in conservation actions.

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The projects that make up this dissertation are the results of collaborations between multiple agencies. Thanks to the USDA-ARS Insect Pollinating Unit, the USGS Forest and Rangeland Ecosystem Science Center, the US Fish and Wildlife Service, and the Utah State University Ecology Center, who all funded my progress through these projects at one time or another. Thanks to the Wildland Resources Department at Utah State University, especially to the graduate student advisor, Marsha Bailey, who kept my proverbial ducks in a row.

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Ashley T. Rohde

## CONTENTS

	Page
ABSTRACT.....	iii
PUBLIC ABSTRACT .....	v
ACKNOWLEDGMENTS .....	vii
LIST OF TABLES.....	xiii
LIST OF FIGURES .....	xvi
CHAPTER I: INTRODUCTION.....	1
References.....	10
CHAPTER II: GENOME-WIDE MARKERS TEST THE STATUS OF TWO PUTATIVE SPECIES OF NORTH AMERICAN BUMBLE BEES.....	16
Abstract.....	16
Introduction.....	17
Materials and Methods.....	22
Acquisition and management of <i>Bombus occidentalis</i> tissue samples.....	22
DNA extraction, UCE enrichment, and sequencing.....	22
UCE processing and analysis.....	24
COI processing and analysis.....	27
Species delimitation.....	29
Results.....	32
Phylogenetic reconstruction.....	33
SODA analysis.....	34
PTP and mPTP analysis.....	34
ABGD analysis.....	34
ASAP analysis.....	35
GMYC analysis.....	35
Discussion.....	36
Species delimitation methods disagree on the species status of <i>Bombus occidentalis mckayi</i> .....	36
Comparison of results among methods and to previous studies.....	37
Species status.....	40

Conservation implications .....	40
Future work - genetic differentiation of <i>Bombus occidentalis</i> within a biogeographical context .....	42
References.....	43
Tables.....	55
Figures.....	58
CHAPTER III: THE INFLUENCE OF GEOGRAPHY, DISPERSAL LIMITATION, AND ANTHROPOGENIC CHANGE ON THE POPULATION GENETIC CHARACTERISTICS OF TWO BUMBLE BEE SPECIES OF CONSERVATION CONCERN ( <i>BOMBUS OCCIDENTALIS</i> AND <i>BOMBUS MCKAYI</i> ) IN WESTERN NORTH AMERICA .....	62
Abstract.....	62
Introduction.....	63
Methods.....	69
Study area.....	69
Acquisition and management of tissue samples .....	70
DNA extraction and microsatellite amplification .....	70
<i>Bombus occidentalis</i> and <i>Bombus mckayi</i> location records.....	71
Population genetic analyses .....	72
I. Definition of populations .....	72
II. Population structure analyses .....	74
Environmental data for occupancy and resistance modeling.....	76
I. Elevation .....	76
II. Weather.....	76
III. Land cover (Habitat Quality) .....	77
IV. Distance to cropland .....	79
Environmental data for structural equation modeling .....	79
I. Environmental predictors.....	79
II. Parasitism .....	79
Landscape genetic analyses .....	80
I. Genetic distance matrices .....	80
II. Resistance rasters .....	81
III. Cost-distance matrices .....	81
IV. Structural equation modeling.....	82
Results.....	85
Microsatellite amplification and group assignments .....	85
Population genetic analyses .....	85

Landscape resistance.....	88
Environmental influences on genetic differentiation.....	89
Discussion.....	92
Measurements of heterozygosity within populations indicate inbreeding in most geographic clusters.....	93
Measurements of genetic structure among populations indicate lower levels of gene flow among populations than previously detected .....	94
The influence of environmental variables on maximum entropy models of <i>B. mckayi</i> and <i>B. occidentalis</i> .....	98
Assessment of structural equation model fit to determine suitability for interpretation .....	101
The influence of environmental variables on the genetic variation of <i>B. mckayi</i> and <i>B. occidentalis</i> across the landscape (i.e. resistance).....	103
Conclusions and implications for conservation .....	105
References.....	106
Data Accessibility .....	119
Benefit-sharing Statement.....	119
Author Contributions .....	119
Tables.....	120
Figures.....	130
CHAPTER IV: MEASUREMENTS OF ATTITUDES AMONG STAKEHOLDERS TOWARD MOLECULAR TECHNIQUES IN BIOLOGICAL CONSERVATION STUDIES .....	139
Abstract.....	139
Introduction.....	140
Methods.....	145
Creation of a survey questionnaire .....	145
Solicitation of respondents.....	145
Questionnaire design.....	146
Data analyses .....	146
Results.....	147
Survey respondent demographics .....	147
Learning, interests, and actions taken by respondents.....	149
Influence of understanding and motivation on conservation actions.....	152
Discussion.....	152



Respondents experience with molecular and traditional conservation studies .....	152
Methods for learning about conservation .....	154
Conservation priorities among conservationists .....	155
Trust in the results of conservation science .....	157
Relationships among understanding, trust, and motivation in conservation .....	157
Recommendations for improving understanding of molecular methods .....	159
References .....	161
Figures .....	168
CHAPTER V: DISCUSSION .....	174
References .....	177
APPENDICES .....	179
APPENDIX A: Chapter II supplemental tables and figures .....	180
APPENDIX B: Chapter III supplemental tables and figures .....	299
APPENDIX C: Chapter IV supplemental tables and figures .....	307
CURRICULUM VITAE .....	329

## LIST OF TABLES

	Page
Table 2.1. The species delimitation tests used on each dataset included in this study and whether or not the delimitation method identified <i>B. occidentalis occidentalis</i> and <i>B. occidentalis mckayi</i> as separate species. Speciation tests included Poisson Tree Process (PTP), multi-rate Poisson Tree Process (m-PTP), monophyly within the phylogenetic tree, generalized mixed Yule-coalescent model (GMYC), Automatic Barcode Gap Discovery (ABGD), Automated simultaneous analysis phylogenetics (ASAP), and Species bOundary Delimitation using ASTRAL (SODA). Asterisk indicates that the method identified each taxa as multiple species.....	55
Table 2.2. The number of potential species identified by Automatic Barcode Gap Discovery (ABGD) using the COI barcoding dataset with variable assigned values of P, the prior limit to the expected intraspecific diversity, and X, the minimum gap size between sequence clusters to identify a group (the sensitivity of the analysis.....	56
Table 2.3. The number of potential species identified by Automated Simultaneous Analysis Phylogenetics (ASAP) using the COI barcoding dataset. The ASAP score indicates the level of support for the grouping, p indicates the likelihood that the taxa are actually part of one large panmictic population, and W indicates the size of the diversity ‘gap’ between the current partition and the one before it.....	57
Table 3.1. The listed status of North American bumble bees of conservation concern. Bumble bees with an asterisk are parasitic bees from the subgenus <i>Psytherus</i> , whose declines parallel the decline of their host species, bumble bees from the subgenus <i>Bombus sensu stricto</i> .....	120
Table 3.2. Fifteen microsatellite primers were identified for use from previously published literature.....	121
Table 3.3. The measured and adjusted units of variables included in the structural equation models .....	122
Table 3.4. $X^2$ test of genotypic disequilibrium and rarefied allelic richness in the fifteen microsatellite loci used to genotype bumble bee specimens.....	123
Table 3.5. Results of AMOVA analysis of genetic structure among geographic clusters for both species, including analyses using uncorrected Nei’s genetic distance matrices and matrices corrected for time between sample collection. <i>p</i> is the significance of the relationship as described by a Monte-Carlo randomization test .....	124

Table 3.6. Percent contribution of the measured environmental variables to the occupancy likelihood of <i>Bombus mckayi</i> and <i>Bombus occidentalis</i> . Only variables that contributed a minimum of one percent are listed.....	125
Table 3.7. Percent contribution of the measured environmental variables to the occupancy likelihood of <i>Bombus occidentalis</i> in two time categories, 1960 to 1994 and 1995 to 2019. Only variables that contributed a minimum of one percent are listed.....	126
Table 3.8. Scores of goodness of fit for each of the four structural equation models used in this analysis .....	127
Table 3.9. Indirect influences of predictor variables on Nei's genetic differentiation. Paths from predictors through latitude and through elevation and latitude were measured. Variables with values of NA were not included in the model, variables with values in gray were not significant at $p = 0.05$ .....	128
Table 3.10. Factor loadings of measured variables on latent variables in the model of <i>Bombus occidentalis</i> 1960 to 2020.....	129
Table A1. Collection and institutional information associated with the bumble bee specimens (1 of 4 .....	180
Table A2. Collection and institutional information associated with the bumble bee specimens (2 of 4 .....	185
Table A3. Collection and institutional information associated with the bumble bee specimens 3 of 4.....	190
Table A4. Collection and institutional information associated with the bumble bee specimens (4 of 4 .....	198
Table A5. UCE summary statistics (1 of 2).....	203
Tables A6. UCE summary statistics (2 of 2) .....	247
Table A7. PTP, mPTP, ABGD and ASAP group assignments for maximum likelihood COI barcoding sequences four, five, six and seven species are identified. PTP and mPTP found solutions for five species. ABGD found solutions for four, five and seven species, with four as the most likely. ASAP found solutions for four, five, six, and seven species, with four identified as the most likely .....	290
Table A8. mPTP and GMYC species assignments based on the Bayesian COI barcoding phylogeny.....	293

Table A9. SODA species assignments based on the maximum likelihood UCE phylogeny.....	296
Table B1. The geographical clusters included in the population genetics analyses. GeoCluster is the cluster number, N is the number of specimens included in the cluster, N no siblings is the number of individuals in the cluster after all but one sibling from each sibling set was removed, SibSets is the number of sibling sets within each geographic cluster, and Species is the species that the cluster represents .....	299
Table B2. Weighted ranks of Land cover values used to create habitat quality values .....	304
Table C1. The questions and response options included in the questionnaire.....	307
Table C2. The number of respondents from each organization that participated in the survey .....	310
Table C3. Self-identified conservation roles of respondents that selected “other” on their questionnaire.....	320
Table C4. The pairwise correlations associated with the Pearson’s rank correlations reported in the main text. A) Role in conservation, B) training in conservation, C) type of experience, D) conservation topic of interest, E) type of experience, F) way of learning about conservation (respondents with graduate degrees included), G) way of learning about conservation (respondents with graduate degrees excluded), H) conservation decisions based on molecular studies, I) conservation decisions based on traditional studies.....	321

## LIST OF FIGURES

	Page
Figure 2.1. The distribution of <i>Bombus occidentalis occidentalis</i> (green) and <i>B. occidentalis mckayi</i> (yellow) samples included in A) the UCE dataset and B) the COI barcoding dataset.....	58
Figure 2.2. Estimate of the species-level maximum likelihood phylogeny based on 1683 UCE loci including <i>Bombus occidentalis</i> (green) and <i>B. mckayi</i> (gold). Branch lengths represent nucleotide substitutions. Vertical black bars represent the species assignments based on each delimitation method. Some delimitation methods represented here were conducted on the COI barcode dataset.....	59
Figure 2.3. Estimate of maximum likelihood phylogeny of the COI genes of five closely related species within the subgenus <i>Bombus sensu stricto</i> . Branch lengths represent nucleotide substitutions. Numbers at clade nodes represent bootstrap values. Species are color coded: <i>B. lucorum</i> (purple), <i>B. jacobsoni</i> (orange), <i>B. hypocrita</i> (blue), <i>B. terricola</i> (black), <i>B. occidentalis</i> (green) and <i>B. mckayi</i> (gold). Names of taxa include the length of the barcode sequence, the institutional ID number and the species name, according to the Genbank record. Samples of <i>B. occidentalis</i> and <i>B. mckayi</i> also include sampling state or province .....	60
Figure 2.4. Estimate of Bayesian phylogeny of the COI genes of five closely related species within the subgenus <i>Bombus sensu stricto</i> . Posterior probabilities of well supported clades are shown at the clade nodes. Species as defined by their GenBank records are color coded: <i>B. lucorum</i> (purple), <i>B. jacobsoni</i> (orange), <i>B. hypocrita</i> (blue), <i>B. terricola</i> (black), <i>B. occidentalis</i> (green) and <i>B. mckayi</i> (gold). Names of taxa include the length of the barcode sequence, the institutional ID number and the species name. Samples of <i>B. occidentalis</i> and <i>B. mckayi</i> also include sampling state or province .....	61
Figure 3.1. The historical ranges and recorded observations of <i>Bombus mckayi</i> (yellow range, grey observation records) and <i>Bombus occidentalis</i> (green range, black observation records). Photo credits: <i>Bombus mckayi</i> Alistair Fraser, <i>Bombus occidentalis</i> Joyce Knoblett .....	130
Figure 3.2. The number of microsatellite loci that successfully amplified in specimens of A) <i>Bombus occidentalis</i> and B) <i>Bombus mckayi</i> collected between 1904 and 2020. Small gray circles represent individual specimens, variably-sized black circles represent the mean number of loci amplified for all of the specimens from the year, the solid blue line represents the linear relationship between the number of loci amplified and the collection year, and the dashed red line is the cutoff of seven successfully amplified loci that was determined to represent a useful genotype for downstream analyses. The red n value is the number of specimens that had seven or more amplified loci .....	131

Figure 3.3. Rarefied allelic richness of geographic clusters of *Bombus occidentalis* and *Bombus mckayi* throughout time. A and B) samples from 1960 to 2020 included in the linear regression. C and D) regressions from 1960 to 1994 (blue) and 1995 to 2020 (red).....132

Figure 3.4. The geographic distribution of genotyped specimens with seven or more microsatellite loci amplified, grouped into clusters (populations). Each pie represents a single cluster. Color divisions within pies represent the proportion of the clusters that was derived from one of two identified likely lineages. Top: *Bombus mckayi* (blues) and bottom: *Bombus occidentalis* (oranges). The *B. occidentalis* cluster framed in black had an excess of heterozygotes. Sizes of the pies are scaled to the average rarefied allelic richness across all loci within each cluster. Also included are bar graphs of the lineage assignments of individuals, each bar represents the likely lineages of an individual. Gray lines on the graphs demarcate clusters. Clusters were arranged from north to south (top to bottom) for *B. occidentalis* and from west to east (left to right) for *B. mckayi* .....133

Figure 3.5. A and B)  $F_{IS}$  values of clusters of *Bombus occidentalis* and *Bombus mckayi* averaged across all loci and distributed throughout time from 1960 to 2020. C and D) global  $F_{ST}$  values of *B. occidentalis* and *B. mckayi* averaged across all loci among groups of clusters that were sampled within similar years. Samples were compared by single-tailed one sample t-tests, red points represent clusters ( $F_{IS}$ ) or groups of clusters ( $F_{ST}$ ) that had values significantly higher than expected and black points represent clusters or groups of clusters with values that are not significantly different than expected for  $\alpha = 0.05$ . The black lines,  $R^2$  values, and  $p$  values represent linear regressions of values throughout time for each statistic and species. Only populations that were represented with samples greater than one individual were able to be included in these analyses (*B. occidentalis* N = 48, *B. mckayi* N = 36) .....135

Figure 3.6. Resistance distributions based on distribution of *Bombus mckayi* and *Bombus occidentalis* across elevation and averaged weather variables from 1960 through 2019. These time categories roughly represent before and after the observed decrease in abundance and range of *B. occidentalis*.....136

Figure 3.7. Resistance distributions based on the distribution of *Bombus occidentalis* across elevation and averaged weather variables in two time categories, 1960 to 1944 and 1995 to 2019. These time categories roughly represent before and after the observed decrease in abundance and range of *B. occidentalis* .....137

Figure 3.8. Graphical representation of the structural equation models used to quantify the relative influences of environmental variables on genetic divergence among individuals across the range of *Bombus mckayi* (top) and *Bombus occidentalis* (bottom). Variables in boxes are measured and variables in ovals are latent. Thin black lines moving from latent variables to measured variables represent confirmatory factor analyses to define latent variables, thick solid black lines represent direct regressions, dotted gray lines represent non-significant direct regressions, colored dashed lines

represent path analyses, and colored dotted lines represent non-significant indirect regressions. Colors of the indirect paths correlate with the labels in Table 9. Direct regressions onto variables other than genetic differentiation are provided in the supplemental materials.....	138
Figure 4.1. The locations of individuals who submitted a questionnaire .....	168
Figure 4.2. Measures of the diversity of experience of the respondents in the survey. A) The conservation role that the respondents reported holding, and B) the highest level of conservation or biological science training that the respondents reported having. Each bar is proportionately filled with the type of experience that the respondents reported .....	169
Figure. 4.3. The primary way that conservationists learn about conservation issues.....	170
Figure 4.4. Respondents' opinions of the importance of species characteristics in determining their conservation value.....	171
Figure 4.5. Taxonomic groups of organisms that were included in respondents' descriptions of conservation studies in which they had participated.....	172
Figure 4.6. Spearman's rank correlation of understanding and motivation to action of a) molecular and B) traditional conservation studies. Bubble size corresponds to the number of respondents with the same response (largest = 228 smallest = 1 .....	173
Figure B1. The Delta K values reported for each tested value of K for the three Structure analyses. Asterisks highlight values of K that had relatively high probabilities of representing the true structure within each analysis. The value of K with the highest support was accepted for these analyses, but the other highlighted values may represent within-species hierarchical structure.....	306

# CHAPTER I

## INTRODUCTION

Biological species loss and decline have been documented in many taxonomic groups around the world and rates of extinction continue to increase in most groups (Spooner et al. 2018, Falaschi et al. 2019, Fisher and Garner 2020, Noske and Briggs 2020, Zattara and Aizen 2020, Bali and Kaleka 2021). Conservation biology addresses this problem by identifying species in need of protection or recovery. Conservation biology is a relatively new field that was formally developed in the mid 1980s, combining resources from many previously established fields to address the apparent world-wide loss of biodiversity in a systematic way (Meine et al. 2006). Of course, the imperative to protect biodiversity is much older than that. In 1863 Alfred Russel Wallace warned that if species were not protected, future generations would “charge us with having culpably allowed the destruction of some of those records of Creation which we had it in our power to preserve; and while professing to regard every living thing... with a strange inconsistency, seeing many of them perish irrecoverably from the face of the earth, uncared for and unknown.” (Wallace 1863).

Since its formal conception, conservation biology has developed subfields by incorporating innovative methods and applications to improve the protection of biodiversity. Notably, during the nascent years of conservation biology, genetic methods were developed concurrently with traditional ecological approaches. In particular, the invention of polymerase chain reaction in 1983 allowed for quick and relatively inexpensive amplification of DNA samples (Mullis 1990), initiating an explosion in methods development to quantify evolutionary relationships among species and



population dynamics within species. The co-occurring developments of molecular genetics and conservation biology led to the formation of conservation genetics, a field defined by the application of “genetic principles and methods to advance the preservation of biodiversity” (Kardos 2021) which continues to develop with the increasing use of genomic methods (Allendorf et al. 2010, Véron et al. 2019). Conservation biology also benefited from recognition of the roles of sociology and psychology in conservation actions (Machlis 1992, Saunders 2003, Dunlap 2018). The inherently political nature of conservation decisions to protect biodiversity necessitates wide societal consent. Support for biological conservation is increased by overcoming barriers to understanding and motivation to action among stakeholders (Mascia et al. 2003, Schultz 2007).

Bees (Hymenoptera: Apoidea: Anthophila) pollinate more plant species than any other taxa of pollinators (Ollerton 2017), including approximately 75% of the world’s food crops (Klein et al. 2007). There are nearly 20,000 known bee species worldwide (Michener 2000), and more yet to be described, especially in the Neotropics of Central and South America (Freitas et al. 2009) and in parts of Asia (Teichroew et al. 2017). However, bees worldwide are decreasing in abundance and range (Goulson et al. 2015). Bumble bees (*Bombus*) are among the most studied bee genera, largely due to their use as pollinators in agriculture, their relatively large size and characteristic appearance, and their high abundance throughout their distribution. Bumble bees are often the dominant pollinators in cold climate regions, especially early in the active season when nighttime temperatures are relatively low (Goulson 2003). Decreases in abundance and range have been observed in bumble bee species around the world (Goulson et al. 2008, Colla et al. 2012, Cameron and Sadd 2020, Graves et al. 2020).

There are approximately 260 described bumble bee species worldwide, one third of which are under threat of extinction to some extent (Abertman et al. 2017). Bumble bee species in North America are decreasing in abundance and genetic diversity at alarming rates (Cameron et al. 2011, Colla et al. 2012, Abertman et al. 2017). Within the United States several species have been petitioned for listing as endangered through the Endangered Species Act (ESA). In 2016, *Bombus affinis* Cresson 1863 was listed as endangered. This was the first bumble bee species to be listed as endangered in the United States. *Bombus franklini* Frison 1921 was most recently listed as endangered by the ESA in September of 2021 and may already be extinct (<https://www.federalregister.gov>, accessed 11:05 a.m., 10/11/2019). Finally, *Bombus occidentalis* Greene 1858 is currently under review for listing as endangered through the ESA (<https://ecos.fws.gov/ecp/>, accessed 1:39 p.m., 8/13/2018), with a listing decision expected in 2023. This species is also listed as threatened or endangered by the Species At Risk Act (SARA) in portions of its Canadian distribution. Several additional species have been identified as endangered or at risk of decline by SARA and the International Union for Conservation of Nature and Natural Resources (IUCN, [www.iucnredlist.org](http://www.iucnredlist.org), accessed 11:36 a.m., 8/13/18).

Species in the bumblebee subgenus *Bombus sensu stricto* (s.s.) are economically important for crop pollination and are dominant native pollinators in many ecosystems across the Holarctic region of the world (Goulson 2003, Hines 2008). There are up to 23 identified species in the subgenus worldwide, with as many as eight species native to North America (Williams 2021). However, population distributions and abundances of many *Bombus s.s.* species are decreasing. These species include *B. affinis*, *B. occidentalis*

and *B. franklini* (Cameron et al. 2011, Colla et al. 2012, Abertman et al. 2017). *Bombus occidentalis*, in particular, is the focus of renewed interest among wildlife managers and conservationists due to unresolved taxonomic questions that may influence the upcoming ESA listing decision in the United States. Understanding the genetics and conservation status of *B. occidentalis* are the focus of chapters 2 and 3 of my dissertation.

*Bombus occidentalis* has a large geographical range. It is found throughout western North America from Alaska to New Mexico and as far east as Wyoming and Colorado, with distributions restricted to high-elevation sites in the southern portion of the range. Regional morphological variation in pyle color historically led to several proposed delimitations of species and subspecies status within *B. occidentalis*, with some taxonomists suggesting that it is conspecific with *B. terricola* Kirby 1837 (Milliron 1971, Poole 1996) and others defining several subspecies (see Sheffiend et al. 2016 for a thorough review). The most recent, and most widely accepted, delimitation indicates two taxa (*B. occidentalis occidentalis* and *B. occidentalis mckayi*), broadly based on the presence or absence of a yellow band of hairs on the abdominal terga. The “un-banded” group extends from the southern edge of the species’ range to approximately 55 degrees latitude (though specimens in some parts of this range do have a weak band), and the “banded” group extends from 55 degrees latitude to the northern edge of the range. Whether these taxa represent species or subspecies is a debated topic (Williams et al. 2012, Sheffield et al. 2016, Williams 2021). Identification of the morphotypes within the taxon is challenging, because their definitions are mostly based on pyle color, which is variable among and within geographical regions of the species range (Carolan et al. 2012, Sheffield et al. 2016) and specimens often exhibit intermediate characteristics among the

morphotypes. Geographic collection locations are often used to help define subspecies (Sheffield et al. 2016).

In this dissertation, I integrated methods from across conservation genetics and sociology to contribute to a growing body of literature on the conservation status of bumble bees in North America (Cameron et al. 2011, Colla et al. 2012, Abertman et al. 2017). I focused my genetic research on a widespread but imperiled species native to western North America, *Bombus occidentalis*. In chapter 2 I used phylogenomic methods to clarify the species status and distribution. In chapter 3 I used landscape genetic methods to identify the environmental drivers of diversity loss among populations of the species throughout its geographic range. Finally, in chapter 4 I assessed conservation practitioners' level of understanding and motivation to act on conservation issues in response to the results of conservation genetics studies and conservation biology studies based on more intuitive measurements, such as abundance or fecundity.

In chapter 2, I aimed to resolve the species status of *B. occidentalis* using an integrative approach that combines morphological identification with phylogenetic analysis of nuclear and mitochondrial markers, and automated species delimitation methods. This was the first study to use nuclear markers to address this question. I greatly expanded geographical sampling and used more species delimitation methods than any previous analysis of these taxa. I concluded that these two taxa represent true species and, therefore, recommend elevation of *B. occidentalis mckayi* to a species (from here forward referred to as *B. mckayi*). This finding is in agreement with the findings of Williams (2021).

In chapter 3, I used landscape genetic methods to ... Landscape genetics is an interdisciplinary field that combines aspects of population genetics, landscape ecology, and spatial statistics to measure genetic discontinuities and diversity patterns across landscapes and to correlate them with environmental features (Manel et al. 2003, Storfer et al. 2007). Landscape genetic techniques can provide insight into questions about potential threats to bumble bees and identify actions that can be taken to protect populations. Measurements of population structure, genetic diversity, and gene flow among populations are important indicators of current conservation status for species. Landscape genetic studies that measure environmental variables as well as gene flow, genetic structure and diversity can indicate which environmental changes have negative effects on bumble bees.

Genetic data and occupancy data are complementary tools for assessing the conservation status of *B. occidentalis* and *B. mckayi*. While patterns of occupancy may indicate where gene flow barriers exist, these patterns are insufficient to predict the causes of gene flow barriers (Roffler et al. 2016). The relationship between occupancy and gene flow could be particularly messy for bumble bees because of their eusocial life history, which dictates that most individuals in the census populations are not reproductive, so they do not contribute directly to gene movement across the landscape. The higher likelihood of observing sterile workers skews occupancy models to identify sites that are adequate or inadequate for colony establishment, rather than gene flow. Therefore, measures of occupancy alone are not enough to determine if gene flow is restricted.

I used microsatellite genetic data from museum specimens to predict current and past genetic structure (samples were collected between 1960 and 2020), genetic diversity, and gene flow patterns in *B. occidentalis* and *B. mckayi*. I used observation data and spatial environmental predictors to predict the influence of environmental variables on occupancy in the two species and to make associations between potential environmental barriers to gene flow and genetic isolation. This is the first landscape genetic study to measure the influence of environmental predictors on occupancy likelihood of *B. mckayi* separately from *B. occidentalis*. This is the first study to identify environmental predictors to gene flow patterns in either species. I detected clear patterns of decreasing genetic diversity and increasing genetic structure in *B. occidentalis*. Patterns of decline were not as strong in *B. mckayi*, but indicate that this species may also be at risk. Springtime minimum temperatures were the most important predictors of occupancy for both species. Proximity to known infections of the fungal parasite *Vairimorpha bombi* was a reliable predictor of genetic differentiation (restricted gene flow). Although decreases in allelic diversity and increases in inbreeding and population structure have been documented in these species, substantial genetic diversity remains in extant populations, which indicates a good opportunity for recovery of the species if the effects of the drivers of the declines are mitigated.

Lastly, in chapter 4 I focus on conservation sociology and use survey methods to determine how different stakeholders feel about molecular methods and results in conservation. Molecular techniques are being used increasingly commonly and to great effect in conservation studies (Abdul-Muneer 2014, Kress 2015, Shafer et al. 2015, Thomsen and Willerslev 2015, Corlett 2017, Holdregger et al. 2019, chapter 1 and 2).

However, these studies are not intuitively easy to understand for practitioners and stakeholders who are not specifically trained to interpret their results. As such, many conservation partners are left out of conversations about these types of studies and the appropriate conservation actions that their results indicate (Keller et al. 2015, Taylor et al. 2017, Sandström et al. 2019, Klütsch and Laikre 2021). A lack of detailed understanding of the results of genetic conservation studies may lead to a sense of helplessness that undermines motivation for action in some groups. The results of traditional studies more easily overcome the barriers to conservation action than the results of molecular studies (Hoban et al. 2013a, Keller et al. 2015, Shafer et al. 2015, Hoffman et al. 2015, Richardson et al. 2016, Taylor et al. 2017). As a result, the insights provided by genetic studies into distribution and population structure of the target species are not often used to inform conservation decisions (Keller et al. 2015, Shafer et al. 2015, Hoffman et al. 2015, Taylor et al. 2017). This phenomenon is widely known as the conservation genetics gap (Taylor et al. 2017, Britt et al. 2018, Sandström et al. 2019, Klütsch and Laikre 2021). The conservation genetics gap is widely acknowledged and discussed (Cook et al. 2013, Hoban et al. 2013a, Hoban et al. 2013b, McMahon et al. 2014, Hoffman et al. 2015, Keller et al. 2015, Shafer et al. 2015, Haig 2016, Taylor et al. 2017, Aurelle et al. 2018, Britt et al. 2018, Funk et al 2019, Mazel et al. 2019, Sandström et al. 2019, Klütsch and Laikre 2021), but few studies have directly measured the differences in perception of conservationists between genetic and traditional types of conservation surveys (However see Taylor et al. 2017 and Sandström et al. 2019).

I used a survey to measure the relative understanding, trust, and motivation to action of conservationists from multiple demographics in response to the results of

molecular and traditional conservation studies. I received responses from 974 conservationists from diverse backgrounds. This is the largest and most diverse sample of conservationists ever surveyed to assess attitudes toward conservation genetics. The results indicate that lack of understanding, but not trust, may be a barrier to increased use of molecular methods in conservation actions. However, comparisons of the data presented here to previous studies (Taylor et al. 2017, Sandström et al. 2019) are hopeful that a shift in perception and increased use of molecular studies may be underway. Previous studies have indicated that increased and improved outreach events among conservation geneticists and other conservation practitioners help to improve understanding of conservation genetics studies among all demographics of conservationists. Also, inclusion of authors who are not genetics experts on publications that include genetics increases the likelihood that those studies will be used to support conservation policy or action, presumably because they ensure the publications contain language that is accessible to a broad audience (Britt et al. 2018).

Taken as a whole, the research presented in this dissertation contributes new information to scientists' growing understanding of the conservation needs of *B. occidentalis* and *B. mckayi* by applying novel methods to the question. I present the first analysis of species status using the nuclear genome of the species, as well as a more robust analysis of the mitochondrial COI barcoding gene than has ever been conducted, and a greater variety of automated speciation methods than has ever been applied. I conducted the first population genetics study of the taxa that treats the two species separately, and used novel methods to associate changes in genetic diversity to changes in environmental conditions. Although my analysis of conservation practitioners'



perceptions of conservation genetics does not directly address the problem of the conservation status of *B. occidentalis* and *B. mckayi*, it does inform the choices researchers, policy-makers and conservationists of any background should make to be most effective in communicating the conservation needs of these and any other species.

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CHAPTER II  
GENOME-WIDE MARKERS TEST THE STATUS OF TWO PUTATIVE SPECIES  
OF NORTH AMERICAN BUMBLE BEES

**Abstract**

*Bombus occidentalis* Greene is one of at least three North American bumble bee species within the genus *Bombus* that is decreasing in abundance and range. The historical range of this species extends through western North America from Alaska to New Mexico and as far east as South Dakota (Black Hills) and western Nebraska, with populations restricted to high-elevation sites in the southern portion of the range. Two recent studies used mitochondrial *cytochrome oxidase I* (COI) barcode sequencing and automated species delimitation methods to identify two evolutionarily unique taxa, *B. occidentalis occidentalis* and *B. occidentalis mckayi* within *B. occidentalis*, but the species delimitation used in the studies disagreed on the species status of *B. occidentalis mckayi*. We used nuclear (ultraconserved elements) and mitochondrial (COI) markers to infer maximum likelihood (ML) and Bayesian phylogenies of the relationship between *B. occidentalis occidentalis* and *B. occidentalis mckayi*. We used seven species delimitation methods to conduct the most thorough test of the species status of these taxa yet performed. The phylogenies from our analyses agree that *B. occidentalis mckayi* is a monophyletic clade, but our ML phylogenies (UCE and COI) placed that clade within *B. occidentalis* while our Bayesian phylogeny (COI) resolved the taxa as reciprocally monophyletic. Similarly, the automated species delimitation analyses disagreed between ML and Bayesian phylogenies, with ML analyses lumping the taxa together and Bayesian analyses separating them. Species delimitation analyses based on diversity gaps among

sequences, rather than phylogenies, grouped *B. occidentalis occidentalis* and *B. occidentalis mckayi* together with their sister species *B. terricola*. Despite mixed results from species delimitation methods, we believe that the consistent monophyletic assignment of *B. occidentalis mckayi* specimens represents sufficient evolutionary divergence to elevate *B. occidentalis mckayi* to the level of species.

## Introduction

Species in the bumblebee subgenus *Bombus sensu stricto* (s.s.) are economically important for crop pollination and are dominant native pollinators in many ecosystems across the Holarctic region of the world (Goulson 2003; Hines 2008). There are up to 23 identified species in the subgenus worldwide, with as many as eight species native to North America (Williams 2021). However, population distributions and abundances of many *Bombus s.s.* species are decreasing, including at least three species in North America: *Bombus affinis* Cresson 1863, *Bombus franklini* Frison 1921, and *Bombus occidentalis* Greene 1858 (Cameron et al. 2011; Colla et al. 2012; Abertman et al. 2017). *Bombus affinis* was the first bumble bee species to be listed as endangered by the Endangered Species Act (ESA) in the United States. *Bombus franklini* has not been observed since 2006, is listed as endangered throughout its range in northern California and southern Oregon (Thorp 2005), and is suspected to be extinct. *Bombus occidentalis* is listed as threatened or endangered by the Species At Risk Act (SARA) in portions of its Canadian distribution and is under consideration for listing by the ESA in the United States. *Bombus occidentalis*, in particular, is the focus of renewed interest among wildlife managers and conservationists due to unresolved taxonomic questions that may influence the upcoming ESA listing decision in the United States. Resolution of the taxonomic



status of *B. occidentalis* could influence the listing decision in the United States by altering the definition of the species boundary, which would influence where land-use restrictions with potential economic repercussions could be enforced (Haig et al. 2006).

*Bombus occidentalis* currently has a large geographical range. It is found throughout western North America from Alaska to New Mexico and as far east as the Black hills in South Dakota and western Nebraska, with distributions restricted to high-elevation sites in the southern portion of the range. Regional morphological variation in pyle color historically led to several proposed delimitations of species and subspecies status within *B. occidentalis*, with some taxonomists suggesting that it is conspecific with *B. terricola* Kirby 1837 (Milliron 1971; Poole 1996) and others defining several subspecies (see Sheffield et al. 2016 for a thorough review). The most recent, and most widely accepted, delimitation indicates two taxa (*B. Occidentalis occidentalis* and *B. occidentalis mckayi*, Williams et al. 2012), broadly based on the presence or absence of a yellow band of hairs on the abdominal terga. The “un-banded” group extends from the southern edge of the species’ range to approximately 55 degrees latitude (though specimens in some parts of this range do have a weak band), and the “banded” group extends from 55 degrees latitude to the northern edge of the range. Whether these taxa represent species or subspecies is still unclear (Williams et al. 2012; Sheffield et al. 2016; Williams 2021). Identification of the morphotypes within the taxon is challenging, because their definitions are mostly based on pyle color, which is variable among and within geographical regions of the taxa’s ranges (Carolan et al. 2012; Sheffield et al. 2016) and specimens often exhibit intermediate characteristics among the morphotypes.

Geographic collection locations are often used to help define subspecies (Sheffield et al. 2016).

Given that morphology has proven unreliable to delimit species in *Bombus s.s.*, molecular data are needed to test and refine species boundaries. Molecular data have helped resolve boundaries in a variety of *Bombus* species groups (Lecocq et al. 2015; Lecocq et al. 2019; Williams et al. 2012; Williams et al. 2019; Williams et al. 2020; Ghisbain et al. 2020; Williams 2021), but few studies to date have examined species in *Bombus s.s.* and all have relied upon the single mitochondrial marker *cytochrome oxidase I* (COI), the barcoding gene (Williams et al. 2012; Williams 2021). Using COI data, Williams et al. (2012) found support that *B. occidentalis* is a separate species from *B. Terricola* and that *B. occidentalis* comprises two subspecies, *B. occidentalis occidentalis* in the southern portion of the range and *B. occidentalis mckayi* in the northern portion of the range, possibly with an overlapping distribution between 55 and 60 degrees latitude. Most recently, re-analysis of the same COI barcoding dataset using an alternate molecular delimitation method found support for raising *B. occidentalis mckayi* to species status (Williams 2021). Sharp decreases in geographic range and abundance have been observed primarily in the southern portion of the species range of *B. occidentalis occidentalis* (Evans et al. 2008; Cameron et al. 2011; Graves et al. 2020), with no evidence that populations of *B. occidentalis mckayi* in the northern portion of the range are unstable (Koch and Strange 2012; Pampell et al. 2015). In this case, the species status of *B. occidentalis mckayi* could have a strong influence on policy decisions regarding the conservation of *B. occidentalis* into the future.

Although COI data can be useful for differentiating and identifying species (Williams et al. 2012; Williams et al. 2019; Williams et al. 2020; Nneji et al. 2020; Williams 2021), there are some cases in which the evolution of the mitochondrial COI gene does not concur with the multi-locus nuclear phylogeny (i.e. mito-nuclear discordance, Toews and Brelsford, 2012; Achurra and Eréus 2013; Guening et al. 2020), including some examples in bumble bees (Williams 2021). Reasons for this discordance include incomplete lineage sorting caused by the dramatically smaller effective population sizes of mitochondrial than nuclear genomes within census populations (Funk and Omland 2003; Després 2019), asymmetrical introgression of the two types of genomes across a geographic range after a period of isolation among groups of populations (Després 2019), cytoplasmic bacterial infections (e.g. *Wolbachia*) that may drive fixation of mitotypes in populations (Hurst and Jiggins, 2005), and dissimilarities in how the mitochondrial and nuclear markers are dispersed across the landscape due to sex-based dispersal (mitochondrial genomes are often maternally inherited while nuclear genomes are biparental, Rheind and Edwards 2011). Due to the challenge presented by mito-nuclear discordance, use of multiple nuclear and mitochondrial markers along with multiple species delimitation methods (each with their own strengths and weaknesses), and morphological analysis for species delimitation are necessary to confidently delimit potentially cryptic species (Dupuis et al. 2012; Fujita et al. 2012; Carstens et al. 2013; Hurtado-Burillo et al. 2016; Lukhtanov 2019; Després 2019), with the final delimitation informed by the majority consensus of the markers (Pedraza-Marrón et al. 2019; Després 2019; Gueuning et al. 2020).

*Bombus sensu stricto*, and the species status of *B. occidentalis* in particular, has proven a difficult group to disentangle using mitochondrial barcoding (Williams 2012), though the recent re-analysis of available mitochondrial data has added some clarity (Williams 2021). The particular difficulties of resolving these species emphasizes the need for both mitochondrial and nuclear markers for species delimitation in this group. The addition of phylogenies based on nuclear markers will greatly improve the confidence of species or subspecies delimitations between *B. occidentalis occidentalis* and *B. occidentalis mckayi* and will contribute substantially to future conservation decisions (Hines et al. 2006; Cameron et al. 2007; Gueuning et al. 2020; Sun et al. 2021).

In this study we tested the taxonomic status of *B. occidentalis occidentalis* and *B. occidentalis mckayi* by analyzing a genome-scale dataset composed of thousands of nuclear ultraconserved element markers and a complementary COI dataset. For both, we tested species boundaries using a variety of species delimitation methods. Ultraconserved elements (UCEs) are highly conserved regions of nuclear DNA found throughout the genome of most eukaryotic species, and many recent studies have used these markers to successfully resolve phylogeny and test species boundaries (Musher and Cracraft 2018; Prebus 2020, Guening et al. 2020; Branstetter and Longino 2022), including in bees and other Hymenoptera. We used next generation sequencing and phylogenomic analyses to build phylogenomic trees representing the relationships among sampled individuals. Additionally, we were able to extract full COI barcodes from our UCE sequences. We used these samples and publicly available COI barcode sequences from the Barcode of Life Database (BOLD) (<https://www.boldsystems.org/index.php>) to build a gene tree that expands on the geographic sampling of the tree presented in Williams (2012, 2021). We

used the UCE and COI datasets to assess the current species status of *B. occidentalis occidentalis* and *B. occidentalis mckayi*.

## **Materials and Methods**

### *Acquisition and management of Bombus occidentalis tissue samples*

We obtained tissue samples from 102 specimens from across the range of *B. occidentalis occidentalis* and *B. occidentalis mckayi* (Fig. 2.1). Samples were provided by six institutions: the U.S. National Pollinating Insect Collection, the Royal Museum of British Columbia, the University of Alaska Museum of the North, the Essig Museum of Entomology, the University of Calgary Zoology Museum, and the Canadian National Collection. All tissue samples collected for this study were frozen and stored at USDA-ARS Pollinating Insect-Biology, Management, Systematics Research Laboratory (PIRU) in Logan, Utah, USA. DNA extracts were frozen and stored at USDA-ARS PIRU. Specimens owned by each of the respective collections were assigned unique identifiers by those institutions and are permanently stored in those collections (Tables A1, A2, A3, A4).

### *DNA extraction, UCE enrichment, and sequencing*

Methods generally followed those in Branstetter et al. 2021. We extracted DNA from the mid and hind legs of specimens using a Zymo Quick-DNA Miniprep Plus extraction kit and stored extracts in -80°C freezers at the PIRU. Specimens were collected between 1956 and 2017, with one specimen from 1920.

We used a TapeStation 4150 automated electrophoresis system (Agilent, 5301 Stevens Creek Blvd. Santa Clara, CA 95051, USA) to measure the size of DNA

fragments extracted from the specimens and Qubit 3.0 to quantify DNA concentrations. The size of fragments varied among specimens due to their variable ages, collection methods, and storage histories. We sheared the DNA fragments to target fragment sizes of 400 to 600 base pairs using a Q800R2 acoustic sonicator (Qsonica, Newtown, CT, U.S.A.). We varied shearing times from 0 seconds to 120 seconds with a 10 seconds on, 10 seconds off pulsing pattern. Samples with small fragment sizes were sheared for less time and samples with large fragment sizes were sheared for more time. Once sonicated, we purified the DNA samples using a homemade paramagnetic bead solution (Rohland and Reich 2012).

We captured and sequenced UCE loci from our sample specimens following the methods described in Branstetter et al. (2021). We prepared Illumina sequencing libraries using Kapa Hyper prep kits and custom 8 bp dual indexing adapters (Glenn et al. 2019). We amplified the libraries using 12 cycles of PCR, cleaned the amplified DNA using 1.0 to 1.2x SPRI beads to remove contaminants and fragments smaller than 200 bp, and quantified the DNA using Qubit. Samples with low measured volumes of DNA were re-amplified for 14 to 16 PCR cycles from an aliquot of the pre-PCR library.

We enriched the samples using an existing UCE bee-ant specific baitset (bee-ant-specific Hym-v2, Branstetter et al. 2017; Grab et al. 2019) identified and optimized for use in the order Hymenoptera. The baitset was developed using seven genomes from hymenopteran species, including two species from the bee families Apidae and Halictidae. We enriched the pooled libraries following a combination of the Arbor Biosciences v3.02 protocol (enrichment day 1) and a protocol based on Blumenstiel et al. (2010, available at [ultraconserved.org](http://ultraconserved.org)). We pooled up to ten samples per library at

equimolar concentrations for enrichment. Finally, we repeated the PCR amplification, purification, and quantification steps previously described for the pooled enriched samples. Enriched pools were combined into a final sequencing pool and sent to Novogene Inc. for sequencing on an Illumina HiSeq X instrument (PE150).

### *UCE processing and analysis*

We demultiplexed and converted the raw sequences to fasta files using BCL2FASTQ (Illumina, San Diego, CA, USA). In addition to the *B. occidentalis* samples we included one *B. terricola* sequence as an outlier that was extracted and sequenced using the same methods for a previous study. *B. terricola* is the sister species to *B. occidentalis*. We used PHYLUCE version 1.7.1 software (Faircloth 2016) and the associated programs to process the UCE dataset and to generate sequence alignments using the method described by Branstetter et al. (2021). Within the PHYLUCE environment, we used ILLUMIPROCESSOR (Faircloth 2013) to batch process sequences and trim for adaptor contamination using TRIMMOMATIC (Bolger et al. 2014), and assembled contigs *de novo* using SPADES (Bankevich et al. 2012). We used PHYLUCE programs to extract, clean, and align the sequences. We used the `match_contigs_to_probes` program, which uses LASTZ (Harris 2007), to match the contig sequences to probe sequences and create a database of the fasta files. Finally, we used the `get_fastas_from_match_counts` program to create a monolithic fasta file. Per the recommendation of Branstetter et al. (2021), we set the min-identity and min-coverage to 70 and 75, respectively, to recover the highest number of UCE loci possible. We aligned the UCE loci using MAFFT within the PHYUCE program `align_seqcap_align`. We removed poorly aligned regions using GBLOCKS (Talavera and Castresana 2007) within

the PHYLUCE program `align_get_gblocks_trimmed_alignments_from_untrimmed` with settings of  $b1 = 0.5$ ,  $b2 = 0.5$ ,  $b3 = 12$ , and  $b4 = 7$ . Finally, we filtered the alignments to include only those alignments that contained at least 75% of the samples using the PHYLUCE program `align_get_only_loci_with_min_taxa` program and concatenated the alignments into one phylip file using the `align_concatenate_alignments`.

A preliminary UCE tree was inferred using IQ-TREE version 2.0 (Nguyen et al. 2015) and visualized using FIGTREE version 1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/>). This tree showed that many of the older samples had terminal branches that were longer than expected, potentially skewing their positions in the tree. This is likely due to alignment issues caused by aligning smaller DNA fragments to longer ones. To remove poorly aligned sequences, we used the program SPRUCEUP version 2020.2.19, which is designed to remove outlier sequences from multiple sequence alignments (Borowiec 2019) by removing base pairs on a per sample basis, rather than entire alignment columns. We used an uncorrected distance method with a window size of 20 and an overlap of 15. We iteratively trimmed sequences using user-defined cutoffs for individual samples and compiled intermediate trees until most samples had appropriate branch lengths. Samples that still had exaggerated branch lengths after trimming with SPRUCEUP had relatively short average fragment sizes (<1000 bp), and were removed from the analysis.

After poorly aligned sequences were removed, the concatenated loci were separated back into genes using AMAS (Borowiec 2016) and empty columns were removed from each gene matrix using the custom script `remove_empty_columns.py` ([https://github.com/marekborowiec/remove\\_empty\\_columns](https://github.com/marekborowiec/remove_empty_columns)). The loci were filtered for



taxon completeness at 75%, 90%, 95%, and 100% using the `get_fastas_from_match_counts` program in PHYLUCE. The matrix that required 75% completeness was selected for further analysis. The taxa included in the analysis are very closely related, so there were many loci that were uninformative (had no site differences). The required level of completeness was kept relatively low to include more informative loci. Assessments of the influence of missing data on phylogenomic analyses have produced conflicting results (Phillippe et al. 2004; Thomson and Shaffer 2010; Roure et al. 2012; Sayyari et al. 2017), but careful selection of evolutionary models and inclusion of thousands of genes in analyses likely help to mitigate incorrect taxon placement on phylogenetic trees caused by missing data (Roure et al. 2012; Sayyari et al. 2017) and datasets that contained 30% or less of missing data have been shown to resolve phylogenies correctly (Shah et al. 2021).

We ran a partitioned analysis in IQTREE to produce a final maximum likelihood (ML) species tree. Partitioning creates an analysis that accommodates different substitution patterns in DNA based on the site. We used the general time reversible substitution model with the rate of variation across sites incorporated (GTR + G, Tavaré 1986; Yang 1994). The partitions were derived from the directory of aligned nexus files (one for each locus) produced in PHYLUCE and the best-fit partition scheme was determined using the TESTMERGE option, which uses the greedy algorithm of PartitionFinder (Lanfear et al. 2012) and immediately reconstructs the tree using the best partitioning scheme. We optimized our analysis (sped it up) by choosing some model parameters *a priori*, in place of the model default which runs multiple analyses for each parameter and chooses the best fit. We used the fast relaxed clustering algorithm in place

of the slow greedy algorithm with ten percent of the partition pairs to find the best-fit partitions (Lanfear et al. 2017). We also specified AICc (corrected Akaike information criterion) as our optimality criterion, in place of the default of also considering AIC and BIC (Bayesian information criterion). AICc corrects for bias in AIC when sample sizes are small. The correction disappears when sample sizes are large (Hurvich and Tsai 1989; Susko and Roger 2020). We used 1000 replicates of ultrafast bootstrapping (UFB) optimized with nearest neighbor interchange to generate bootstrap supports for the final tree. Additionally, we used 1000 replicates of an approximate likelihood ratio test (Guindon et al. 2010) to provide supports for single branches. We used FigTree to visualize the final species tree.

We used IQTREE to infer gene trees for each locus within the directory of aligned nexus files, which were used in downstream species delineation analyses. We used model testing to select the best substitution model and the -S option in IQTREE to loop through the aligned locus sequences and used 1000 replicates of ultrafast bootstrapping over trees to generate bootstrap support values for the nodes on the gene trees.

### *COI processing and analysis*

We extracted COI barcodes from the *B. occidentalis* and *B. terricola* UCE targeted sequences using the PHYLUCE program `assembly_match_contigs_to_barcodes` and a sequence downloaded from BOLD as a bait sequence (BBHYL247). We aligned the COI sequences using MAFFT within the PHYLUCE program and visually inspected the alignments using the program Mesquite version 3.7.0.

The species delimitation method we used with the COI data (see below) requires equivalent sampling of multiple closely-related species (Taravera et al. 2013) and a less

closely related outgroup species to train the model (as well as the unresolved taxa) to perform reliably. We downloaded all publicly available COI barcode sequences from genbank (Sayers et al. 2022) for *B. occidentalis*, *B. terricola*, *B. hypocrita* Pérez 1905, and *B. jacobsoni* Skorikov 1912, which are closely related, and *B. lucorum* Linnaeus 1761, which is not as closely related but still within the sub-genus, as an outgroup. We combined the sequences with the complete COI barcodes extracted from our samples and re-aligned the entire dataset using PHYLUCÉ tools as described above.

We performed a partitioned analysis in IQTREE to produce a preliminary ML COI barcoding tree. We used all available *B. occidentalis occidentalis* and *B. occidentalis mckayi* specimens from our sequences and from publicly available sequences in BOLD, plus all publicly available sequences from the closely-related species in BOLD. We used the ModelFinder substitution model (Lanfear et al. 2012) to automatically determine the best-fit model for the data. We used 1000 ultrafast bootstrap replicates and 1000 replicates of an approximate likelihood ratio test to generate bootstrap supports for the tree. We removed all but one specimen that shared the same haplotypes from the *B. occidentalis occidentalis* and *B. occidentalis mckayi* groups and reran the analysis to produce a final ML gene tree. We visualized the final gene tree using FigTree.

We created a Bayesian gene tree using the COI barcoding dataset for use with a downstream species delimitation analysis. We used BEAUti version 1.10.4 (Drummond et al. 2012) to prepare an input file and BEAST version 1.10.4 (Drummond et al. 2012) to infer the tree. We defined taxon sets *a priori* as the previously described species, including *B. occidentalis occidentalis* and *B. occidentalis mckayi* separately. We used the GTR + G substitution model (Hasegawa et al. 1985) with three partitions and a strict

clock (Drummond and Suchard 2010). We set the tree prior to a Yule Process (Drummond et al. 2010). We ran the analysis for 70,000,000 MCMC steps and visualized the resulting traces in TRACER version 1.7.2 (Rambaut et al. 2018) to ensure that the model coalesced. We used TreeAnnotator version 1.10.4 (Drummond et al. 2012) to summarize the data from the replicated trees onto a single target tree. We used 10% of the dataset (2,500 trees) as burn-in, calculated the median of the support values, and mapped them onto the target tree. We visualized the final gene tree in FigTree.

### *Species delimitation*

We tested species boundaries in *Bombus occidentalis* using seven molecular delimitation approaches applied to ML and Bayesian estimates (Table 2.1). These included consideration of species monophyly within phylogenetic reconstructions, Species bOundary Delimitation using ASTRAL (SODA, Rabiee and Mirarab 2020), the Poisson Tree processes (PTP, Zhang et al. 2013), multi-rate PTP (mPTP, Kapli et al. 2017), generalized mixed Yule-coalescent models (GMYC, Pons et al. 2006), Automatic Barcode Gap Discovery (ABGD, Puillandre et al. 2012), and Automated simultaneous analysis phylogenetics (ASAP, Sarkar et al. 2008). PTP, mPTP, ABGD, and ASAP are methods based on the phylogenetic species concept (Baum and Shaw 1995) while SODA analyses are based on the multi-species coalescent model (MSC), which uses the discordance among gene trees to estimate the species tree (Pamilo and Nei 1988; Rannala et al. 2020).

SODA (Rabiee and and Mirarab 2020, <https://github.com/maryamrabiee/SODA>) was used to delimit species for the UCE dataset. This method is based on the multispecies coalescent model and is similar to the popular program BPP (Yang 2015). It compares

discordance among gene trees which is useful with datasets that contain information from many genes. Genes with no informative sites were removed from species delimitation analyses.

PTP and mPTP use gene or species trees (based directly on sequence substitutions rather than time since divergence) to estimate the number of species in the tree based on branch lengths (Zhang et al. 2013). mPTP is a modification of PTP which incorporates a new algorithm and model to accommodate varying levels of intraspecific genetic diversity among closely related species and sampling bias. PTP was used with COI datasets by Williams (2021) to delimit bumble bee species within the subgenus *Bombus* sensu stricto and by Williams et al. (2020) to delimit bumble bee species within the subgenus *Melanobombus*. We applied both PTP and mPTP to our COI barcode dataset in this study. We did not apply these methods to the UCE dataset because they require a minimum of five well-sampled, related species to train their algorithms (similar to GMYC as described by Taravers et al. 2013). COI sequences for species closely related to our taxa of interest were publicly available via BOLD, but we did not have a comparable dataset for our UCE analyses (UCE data for closely related but non-target species). We filtered haplotypes of the COI barcodes of our target taxa (*B. occidentalis occidentalis* and *B. occidentalis mckayi*) per the recommendation of Williams et al. (2020), to avoid uneven sampling. One sample from groups with identical haplotypes was chosen to represent that group in the tree based on the length of the haplotypes. If all haplotypes were full barcodes (658 bp), representative samples were chosen to maximize the geographic sampling of the dataset. COI barcodes from the closely-related but non-target taxa were not filtered for haplotypes. Instead, we selected sequences based on

length and included equivalent numbers of sequences from each species where possible. In the case of *B. jacobsoni*, only three COI barcode sequences were available. PTP species delineations were analyzed using the online PTP web server (<https://species.hits.org/ptp/>, Zhang et al. 2013) with 500,000 MCMC generations thinned by 100 with a burn-in of 0.1. mPTP species delineations were analyzed using the program mPTP (Kapli et al. 2017, <https://github.com/Pas-Kapli/mptp>).

GMYC classifies the branches of an ultrametric gene or species phylogenetic tree by maximizing the likelihood of a GMYC model; speciation rates held constant among species without extinction, and panmixia within species (Taravers et al. 2013). GMYC is the only analysis included in this study that requires an ultrametric phylogenetic tree in which the branches represent time, rather than nucleotide substitutions. Due to this requirement, this analysis was only performed on the Bayesian COI barcoding tree. The GMYC analysis was performed using the *splits* version 1.0-20 package.

ABGD sorts aligned barcode sequences (not appropriate for datasets that include multiple genes) into groups based on the ratio of divergence within and among groups. This analysis assumes that genetic divergence among species is greater than genetic divergence within species. The difference between the within-group and among-group diversity is called the ‘barcode gap’. It requires two user inputs: P, the prior limit to the expected intraspecific diversity, and X, the minimum gap size between sequence clusters to identify a group (the sensitivity of the analysis). We did not have *a priori* knowledge of the range of intraspecies diversity or gap size among species, so we ran the analysis with a minimum P of 0.001 and a maximum P of 0.1 with steps of 10 at each of four gap

widths, 1, 1.5, 2, 2.5, and compared the results. We used a simple distance measurement for each analysis.

ASAP is similar to ABGD in that it uses a clustering method to sort aligned barcode sequences into groups based on intra- and interspecies diversity and does not build a phylogeny to identify those groups. However, it is different from ABGD in that it uses an updated scoring system that does not require any user defined input estimating the intraspecific diversity. We used a simple distance measurement with this analysis.

## Results

We sequenced 102 samples that ranged in age from 3 to 65 years with one sample that was 101 years old. We removed 57 samples because the mean alignment length was below 1,000 bp. The final UCE dataset contained 23 *B. occidentalis occidentalis* specimens and 32 *B. occidentalis mckayi* specimens (Figure 2, Table A5 and A6). The final 75% taxon matrix included 2233 UCE loci (mean sequence length:  $1346 \pm 334.7$ ), of which 1683 had at least one informative site. Loci with 0 informative sites were removed from the analysis (Table S2). There was a large gap in the geographical coverage of sampling for our UCE dataset in the southern half of British Columbia, Canada. This is partially due to an actual paucity of sampling in that region of the range, but also because the samples we did have for that area had low mean alignment lengths and, therefore, were removed from the analysis.

We mined 34 *B. occidentalis occidentalis* COI barcodes that represented 14 unique haplotypes and 32 *B. occidentalis mckayi* COI barcodes that represented 12 unique haplotypes from our sequences. We also included 12 *B. occidentalis occidentalis*

COI barcode sequences and nine *B. occidentalis mckayi* COI barcode sequences from BOLD that represented unique haplotypes.

#### *Phylogenetic reconstruction*

The UCE-based phylogenetic tree inferred with IQ-Tree recovered *B. occidentalis mckayi* as reciprocally monophyletic to *B. occidentalis occidentalis* (Table 2.1, Fig. 2.2). However, the support for this relationship was very low, indicating that *B. occidentalis mckayi* is likely a subclade within *B. occidentalis*. Within each group, we examined the results for any evidence of geographic clustering that might indicate phylogeographic structure and did not find any clear patterns. Except for the monophyly of *B. occidentalis mckayi*, samples were generally randomly placed within clades.

The final ML COI barcoding tree indicated that *B. jacobsoni* and *B. hypocrita* were sister species and *B. terricola* was sister to *B. occidentalis* (Table 2.1, Fig. 2.3). All of these relationships were strongly supported, and agree with previous analyses (Cameron et al. 2007; Williams et al. 2012). We found strong support for *B. occidentalis mckayi* as a monophyletic clade, nested within a paraphyletic clade that also included multiple clades of *B. occidentalis occidentalis*, matching the UCE results above (Fig. 2.3).

The topology of the Bayesian COI barcoding tree agreed with the ML tree for all relationships except for *B. occidentalis occidentalis* and *B. occidentalis mckayi*, which it resolved as reciprocally monophyletic with strong support (Table 2.1, Fig. 2.4).



### *SODA analysis*

SODA analyses identified 22 species using the UCE phylogeny (Fig. 2.2, Table A7). The analysis correctly identified the *B. terricola* specimen as a separate species and the potential species that it identified were always composed of either *B. occidentalis occidentalis* or *B. occidentalis mckayi*, never mixed (Table 2.1, Table A4).

### *PTP and mPTP analysis*

PTP and mPTP analyses both agreed that the ML COI phylogeny contained five species, with *B. occidentalis occidentalis* and *B. occidentalis mckayi* grouped as a single species and all other previously identified species separated (Table A8, Fig. 2.3).

However, mPTP found 7 species using the Bayesian COI phylogeny (Table A9). It split one specimen of *B. hypocrita* into a separate species, but otherwise grouped the species into monophyletic clades and separated *B. occidentalis* and *B. mckayi* (Table A8, Fig. 2.2, Fig. 2.4).

### *ABGD analysis*

ABGD analyses were fairly consistent across the four sensitivity levels. Analyses with X (the minimum gap size that identifies a group) = 1 and 1.5 organized the samples into sets of one, four, five, or seven potential species, depending on the assigned intraspecies diversity, and analyses with X = 2 and 2.5 found organized samples into sets of four, five, and seven potential species (Table 2.2, Table A8). Analyses that delimited four species grouped *B. terricola* with *B. occidentalis occidentalis* and *B. occidentalis mckayi* (Table 2.1, Fig. 2.2), but identified *B. lucorum*, *B. hypocrita*, and *B. jacobsoni* as separate groups. Analyses that delimited five species separated *B. terricola* from *B.*

*occidentalis* and *B. occidentalis mckayi*, but left the latter two taxa as a single species.

Analyses that delimited seven species separated *B. occidentalis occidentalis* and *B. occidentalis mckayi*, but they also identified one specimen of *B. occidentalis occidentalis* from Idaho, USA (BLX2160) as a separate species.

#### *ASAP analysis*

ASAP analysis grouped the taxa in the COI barcoding dataset into groups of four, five, six, and seven species. The group of five species agreed with ABGD, PTP, and mPTP (Table A8). The groups of four and seven species agreed with those described by ABGD (Table 2.3, Table A8). The group of six species was identical to the group of seven species except for the specimen *B. occidentalis occidentalis* BLX2160, which was placed into the species with the other *B. occidentalis occidentalis* specimens (it was identified as its own species in the ABGD analysis, Table A8). The support ranking indicated that the four species solution was the most likely (Fig. 2.2), followed by the five species solution, seven species solution, and six species solution. The P value for the partition that includes four species is by far the lowest, which can be interpreted to indicate that it is favored as the most likely number of species. Note that P in the ABGD analysis and p in the ASAP analysis are different metrics.

#### *GMYC analysis*

GMYC analyses identified six species using the Bayesian COI barcoding phylogeny. It grouped all of the species as monophyletic groups, including *B. occidentalis occidentalis* and *B. occidentalis mckayi* (Fig. 2.2, Table 2.1, Table A9).

## Discussion

Our analysis of the relationship between *B. occidentalis occidentalis* and *B. occidentalis mckayi* is the most thorough yet produced. We conducted the first analyses of nuclear markers to address this question. We expanded geographical sampling and applied more species delimitation methods than any previous analysis of the taxonomic status of the group (Williams et al. 2012; Williams 2021). We compared methods based on the phenic (Michener 1970), monophyletic (Donoghue 1985), diagnosable (Cracraft 1983), diagnosable phylogenetic (Nixon and Wheeler 1990), and multi-species coalescent (Pamilo and Nei 1988) concepts.

### *Species delimitation methods disagree on the species status of Bombus occidentalis mckayi*

Our ML and Bayesian analyses did not agree on the phylogenetic relationship between *B. occidentalis occidentalis* and *B. occidentalis mckayi*. The ML UCE phylogeny found weak support for reciprocal monophyly between *B. occidentalis occidentalis* and *B. occidentalis mckayi*, indicating that *B. occidentalis mckayi* is probably a subclade within the larger group. SODA analysis of the ML UCE phylogeny split the two taxa into 22 species, which is far more than have been previously suggested (Sheffield et al. 2016). The ML COI phylogeny and the automated species delimitation analyses associated with it agree that *B. occidentalis mckayi* is a monophyletic clade within *B. occidentalis occidentalis*. However, the Bayesian COI phylogeny and the automated species delimitation analyses performed on that dataset strongly support reciprocal monophyly between the taxa. Although reciprocal monophyly is strong evidence for speciation, it is not required (Rieseberg and Brouillet 1994; Knowles 2001;

Hörandl and Stuessy 2010). If *B. occidentalis mckayi* is accepted as a monophyletic species, our ML analyses indicate this would create a paraphyletic species in *B. occidentalis occidentalis*.

The most likely solutions from ABGD and ASAP (not dependent on any phylogeny) not only grouped *B. occidentalis occidentalis* and *B. occidentalis mckayi* together, but also included *B. terricola* as the same species. This is a relationship which has been previously analyzed and discounted (Williams et al. 2012; Williams et al. 2012) and which is not supported by any other analyses in this study. ABGD and ASAP both ranked a five species solution in which *B. terricola* is recognized as a separate species as second-most likely, but they ranked it far below the first-choice four species solution.

#### *Comparison of results among methods and to previous studies*

The topology of our ML UCE species tree and the ML COI barcode tree agreed that *B. occidentalis mckayi* is a well-supported monophyletic subclade within *B. occidentalis occidentalis*. However, SODA analysis of the ML UCE data based on the gene trees split the samples into over 20 species, very likely over splitting them. An important aspect of MSC is that individuals of the same species are assumed to have no structure within the species, so their alleles coalesce randomly (Rabiee and Mirarab 2020). SODA exploits this feature by creating a species tree in its sister program ASTRAL (Mirarab et al. 2014) and uses heuristic patterns of quartet trees (unrooted trees that include four taxa, Reaz et al. 2014) to identify areas of the species tree where there is complete coalescence (Rabiee and Mirarab 2020). However, if species do contain substantial structure, SODA may identify that intraspecies structure as species delimitations. UCEs are, as advertised, highly conserved, so one might expect to detect

little within-species genetic diversity using these markers. However, our ML phylogeny of the dataset indicates many highly supported bifurcating nodes within the clades that define *B. occidentalis occidentalis* and *B. occidentalis mckayi*, which is indicative of genetic structure within the taxa, though no geographic pattern of that structure was detected. Although more computationally intensive, Bayesian methods that use an MCMC chain to assign species based on gene trees may be more appropriate for datasets in which intraspecies genetic structure is detected or suspected because plausible species membership can be incorporated into the model based on previous work, geographic distribution, or morphology (e.g. Bayesian Phylogenetics and Phylogeography, Yang and Rannala 2010, Yang 2015).

The results of our Bayesian analyses disagree with the findings of Williams et al. (2012), who found that *B. occidentalis mckayi* is likely an evolutionarily unique taxon within *B. occidentalis* using GMYC modeling. This contradiction is likely due to characteristics inherent to GMYC modeling and the respective datasets. An increase in the number of specimens or haplotypes included in GMYC models is likely to increase the proportion of lineage splits detected (Pentinsaari et al. 2016). Our analysis included 14 haplotypes of *B. occidentalis occidentalis* and 12 haplotypes of *B. occidentalis mckayi* while Williams et al. (2012) included five haplotypes of *B. occidentalis occidentalis* and four haplotypes of *B. occidentalis mckayi*. Also, previous studies indicate that the performance of GMYC increases with the number of species and depth of subclade (Taravers et al. 2013). Our analysis included only six species from the subgenus *Bombus s.s.* (separating *B. occidentalis occidentalis* and *B. occidentalis mckayi*), while Williams et al. (2012) included many more morphologically identified taxa from among the entire

genus *Bombus*. Likely for these reasons, GMYC was not consistent between the two studies. The sensitivity of GMYC to differences in model parameters and input has contributed to its less frequent use in recent years, with PTP succeeding it in popularity for single gene tree and species tree analyses (Zhang et al. 2013; Simon 2020).

In a follow-up analysis, Williams (2021) re-analyzed the same Bayesian COI barcoding phylogeny using PTP analysis, which does not require dating for an ultrametric tree, and determined *B. occidentalis occidentalis* and *B. occidentalis mckayi* to represent two good species. This result agrees with the results of our Bayesian GMYC and mPTP analyses, but contradicts our ML analyses. Bayesian methods have been alternately praised for the easily interpreted support values of posterior probabilities, which describe the proportion of trees that return a clade in an MCMC chain, and criticized for inflated support values and sensitivity to the evolutionary models selected for the analyses (Suzuki et al. 2002; Simon 2020). Likewise, the bootstrap supports associated with ML analyses have been criticized for their unclear definition. They have been described as measures of “precision not accuracy” (Page and Holmes 1998) among other suggested interpretations (Simon 2020). Berry and Gascuel (1996) suggested that 1 minus the bootstrap value is the equivalent to a  $p$ -value associated with the test of the null hypothesis that a split (branching event) is not really present. The differences in the topology of our ML and Bayesian COI barcode phylogenies may be attributable to relatively inflated support for a split in the Bayesian analysis that was not supported in the ML analysis. As such, the ML and Bayesian analyses may be considered as conservative and liberal estimations respectively of the species status of *B. occidentalis mckayi*.

### *Species status*

Although our analyses provided some mixed support for the independence of *B. occidentalis mckayi* as a separate species, we conclude that the consistent monophyly of the taxa and the support of the species delimitation analyses of the Bayesian phylogeny are adequate to acknowledge *B. occidentalis mckayi* as a distinct species from *Bombus occidentalis*, *Bombus mckayi*. This result is in agreement with the conclusions of Williams (2021), and will encourage continued research into the conservation status of both species.

### *Conservation implications*

The rank of subspecies is not as clearly defined as higher taxonomic levels, and has been applied inconsistently in the past (Haig et al. 2006; Phillimore and Owens 2006). Subspecies within *B. occidentalis* have previously been described based on morphology (Sheffield et al. 2016) and phylogenies (Williams et al. 2012; Williams 2021), with variable results. Our study confirms the monophyletic status of *B. mckayi* with a robust analysis of the COI barcoding gene and 1683 nuclear genes, though it is still unclear if that clade is within *B. occidentalis* (thereby rendering *B. occidentalis* a paraphyletic species) or if it represents a reciprocally monophyletic sister clade to *B. occidentalis*.

Recognition of these two well-defined taxa has implications for conservation policy in the United States and Canada. Within the bounds of the United States, *B. occidentalis* is found within the contiguous western states and is decreasing dramatically in abundance and range (Graves et al. 2020). *B. mckayi* is found in Alaska where populations appear to be stable at this time (Koch and Strange 2012; Pampell et al. 2015).

The Endangered Species Act of the United States allows listing of subspecies (Haig et al. 2006; Waples et al. 2018), which makes it possible to list *B. occidentalis* as endangered without listing *B. mckayi* regardless of species status. Endangered species listings are contentious in the United States, as the restrictions placed on habitat often limit use of public and private lands (Haig et al. 2006; Sims and Palikhe 2019). Flexibility to list only the taxa of concern, regardless of species status, eases the burden of such restrictions at the national level. However, protections at the state and municipal level are variable in their taxonomic requirements and subspecies of conservation concern may not garner the attention or resources granted to species. Identification of evolutionarily distinct taxa as species provides a clear and easily understood delimitation for which to create conservation policy.

Both taxa exist within the bounds of Canada and the cryptic morphology and geographical overlap of the taxa make monitoring of population abundances tricky in some regions (Sheffield et al. 2016). Legislation under the Species at Risk Act varies among provinces and territories, which provides flexibility to protect populations in regions where they are in decline. However, this political structure for species protection has also been criticized for inconsistency in standards for listing and compliance with required actions for listed species among provinces and territories (Turcotte et al. 2021). Treatment of the taxa as a single species where their boundaries overlap would provide misleading information about the abundance of the separate taxa and add to confusion about conservation needs for the species. Species delimitation for *B. occidentalis* and *B. mckayi* will help to clarify the need for monitoring of the taxa separately. Continued sampling to monitor abundance and genetic viability of populations at risk is critical to



maintain the species in the Canadian portion of their ranges where they may be confounded.

*Future work - genetic differentiation of Bombus occidentalis within a biogeographical context*

All of our phylogenies agree that *B. mckayi* is at least a monophyletic group. Historical biogeography may help to explain this observed pattern of differentiation.

The ancestors to extant species of *Bombus sensu stricto* in North America likely entered the continent by crossing the Bering Land Bridge less than five million years ago (Hines 2008). Due to their evolutionary history, these taxa were likely to have been adapted to cold or temperate climates and could have migrated south along the coastal mountain ranges of western North America relatively quickly (Hines 2008). However, approximately 2.6 mya the Cordilleran ice sheet began to form in the Alaskan Range and grew southward (Hidy et al. 2013). At its maximum, this ice sheet stretched as far south as the North Cascades (Seguinot et al. 2016).

Genomic signals within *B. occidentalis* and *B. mckayi* may provide more information about how the two taxa evolved during the development and recession of this ice sheet across their ranges. If the current distributions of *B. occidentalis* and *B. mckayi* are predictive of the range of the most recent common ancestor before the formation of the Cordilleran ice sheet, that range likely would have been affected by the development of the ice sheet in one of two ways: first, by splitting and reducing the distribution of the ancestor species into isolated northern and southern distributions, or second, by reducing the range completely to a relatively small southern distribution. The ice sheet advanced and receded several times over the course of its existence, likely only receding

sufficiently to allow migration to resume along the pacific coast of North America 20,000 to 17,000 years ago (Pitulko and Pavlova 2020). If there were northern and southern relict populations, such a long separation would have permitted genetic divergence between them. Time since divergence could be estimated using single nucleotide polymorphisms (SNPs) called from the UCE dataset presented in this study (Gutenkunst et al. 2009; Everson et al. 2019) to estimate if the taxa diverged before or after the maximum extent of the ice sheet was established. Additionally, patterns of genetic diversity across the range estimated from the SNPs could indicate if there were two refugia or one that repopulated the previously glaciated portion of the range after the ice sheet retreated (Eckert et al. 2008; Swaegers et al. 2013).

Increased sampling in the geographic region where the subspecies ranges' overlap would provide data that could test the biological speciation concept (Wright and Huxley 1940) for these taxa by detecting (or not detecting) hybrid specimens and testing for reinforcement or introgression between the taxa (Butlin and Smadja; Garner et al. 2018). These analyses would provide additional information about the evolutionary history of the two species.

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## Tables

**Table 2.1.** The species delimitation tests used on each dataset included in this study and whether or not the delimitation method identified *B. occidentalis occidentalis* and *B. occidentalis mckayi* as separate species. Speciation tests included Poisson Tree Process (PTP), multi-rate Poisson Tree Process (m-PTP), monophyly within the phylogenetic tree, generalized mixed Yule-coalescent model (GMYC), Automatic Barcode Gap Discovery (ABGD), Automated simultaneous analysis phylogenetics (ASAP), and Species bOundary Delimitation using ASTRAL (SODA). Asterisk indicates that the method identified each taxa as multiple species.

Data Type	Phylogenetic Analysis	Speciation Test	<i>B. occidentalis</i> and <i>B.</i>
			<i>mckayi</i> separate species?
COI	Maximum likelihood	PTP	No
COI	Maximum likelihood	mPTP	No
COI	Maximum likelihood	Monophyly	No
COI	Bayesian	mPTP	Yes*
COI	Bayesian	GMYC	Yes*
COI	Bayesian	Monophyly	Yes
COI	None	ABGD	No
COI	None	ASAP	No
UCE	Maximum likelihood	SODA	Yes*
UCE	Maximum likelihood	Monophyly	No

**Table 2.2.** The number of potential species identified by Automatic Barcode Gap Discovery (ABGD) using the COI barcoding dataset with variable assigned values of P, the prior limit to the expected intraspecific diversity, and X, the minimum gap size between sequence clusters to identify a group (the sensitivity of the analysis).

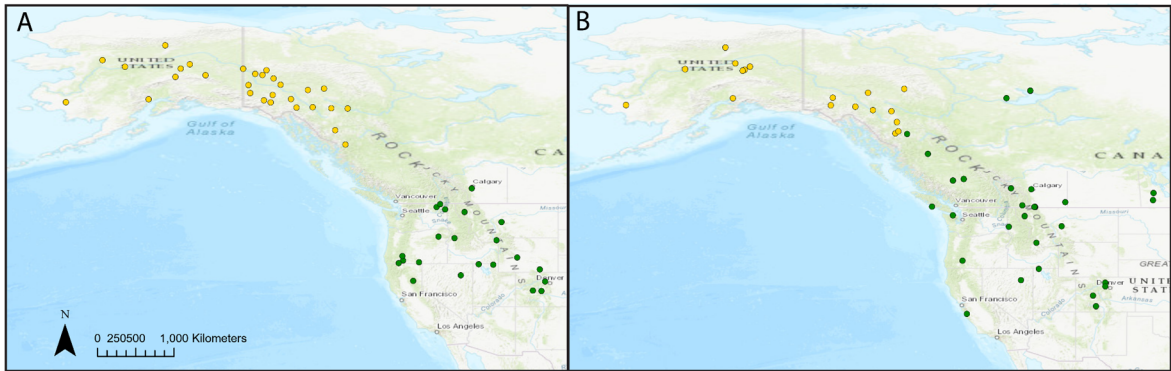
P	X = 1	X = 1.5	X = 2	X = 2.5
0.001	7	7	7	7
0.001668	7	7	7	7
0.002783	5	5	5	5
0.004642	5	5	5	5
0.007743	5	5	4	4
0.012915	4	4	4	4
0.021544	1	1	NA	NA

**Table 2.3.** The number of potential species identified by Automated Simultaneous Analysis Phylogenetics (ASAP) using the COI barcoding dataset. The ASAP score indicates the level of support for the grouping, p indicates the likelihood that the taxa are actually part of one large panmictic population, and W indicates the size of the diversity ‘gap’ between the current partition and the one before it.

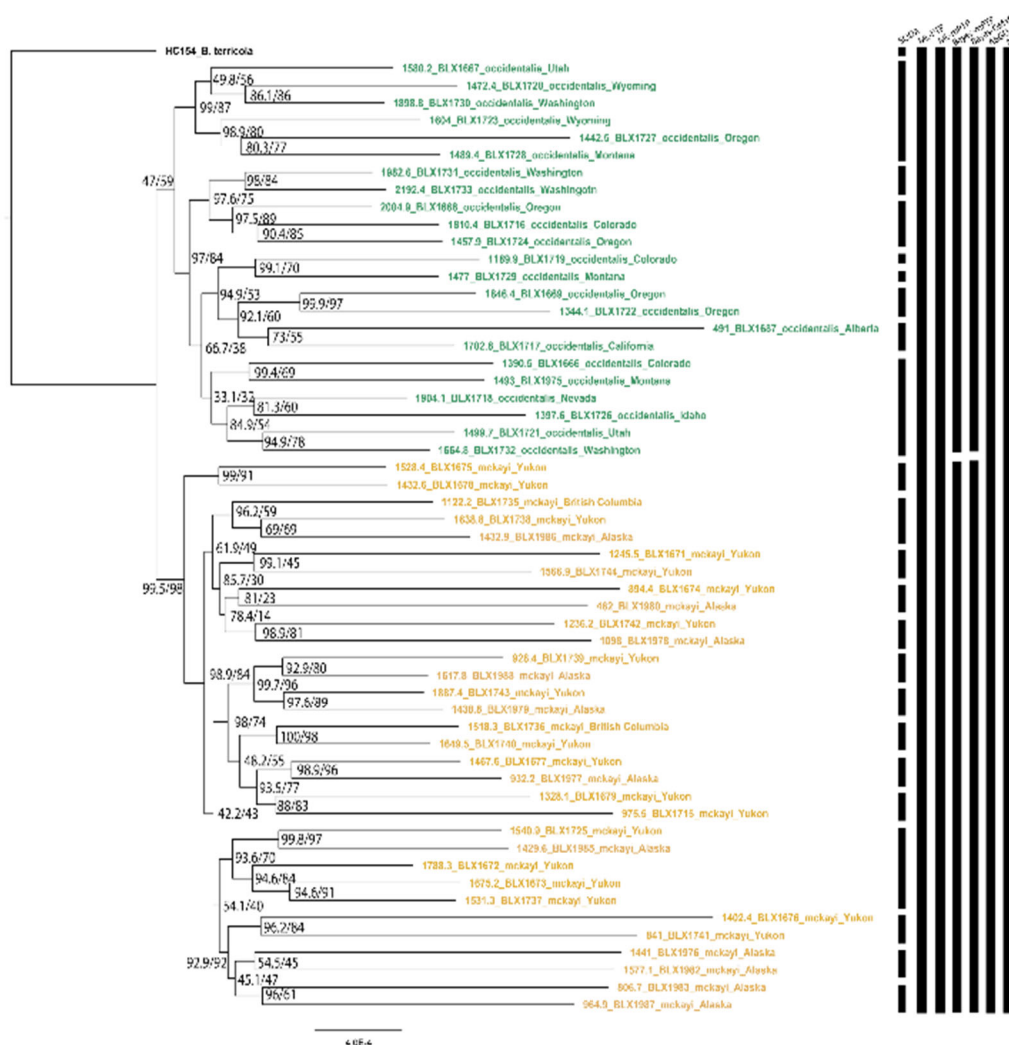
Number of Species	ASAP score	p (rank)	W (rank)
4	1	0.00157 (1)	0.0000383 (1)
5	3	0.733 (4)	0.00366 (2)
6	5.5	0.81 (7)	0.000266 (4)
7	5	0.747 (5)	0.0000234 (5)



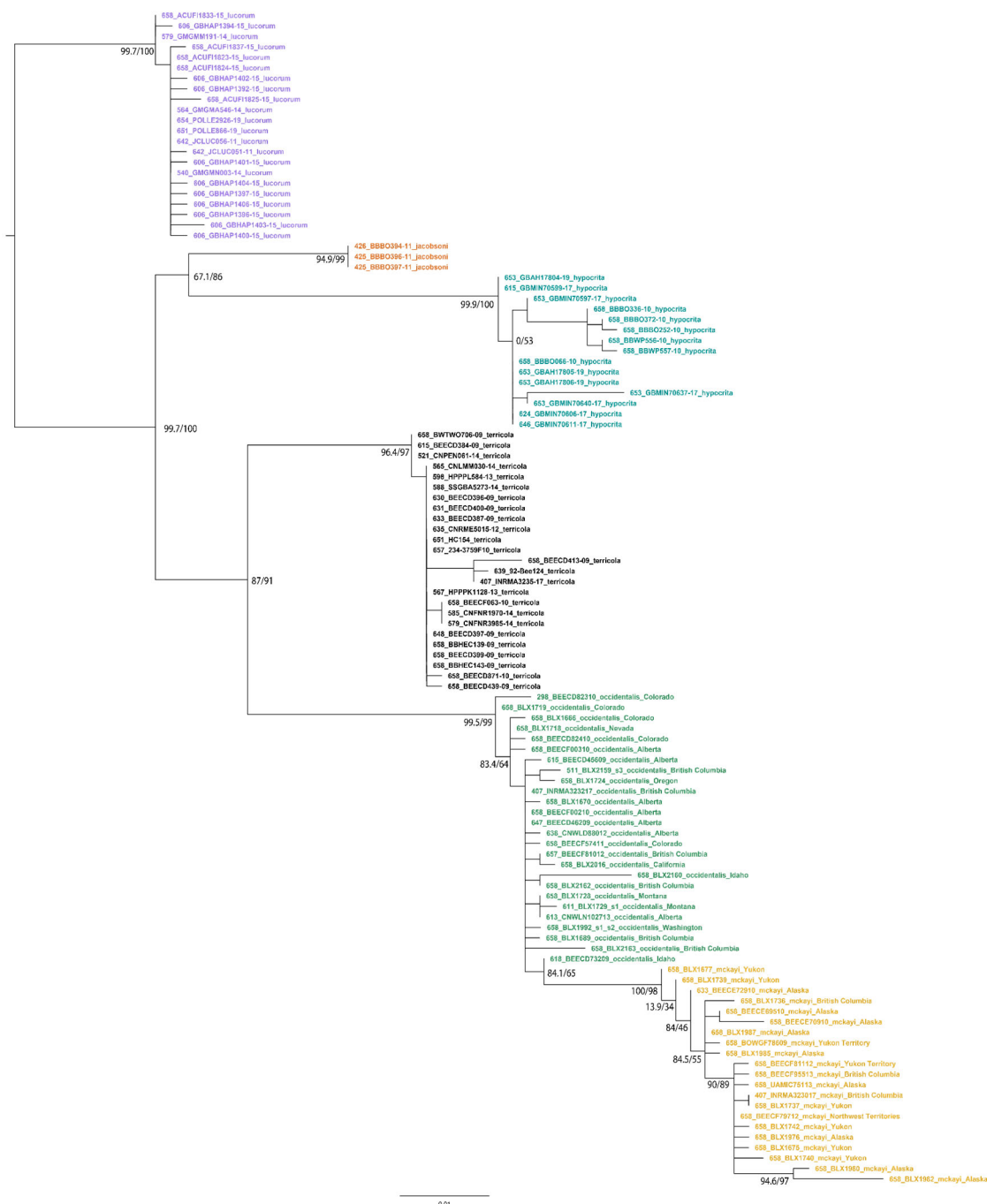
## Figures



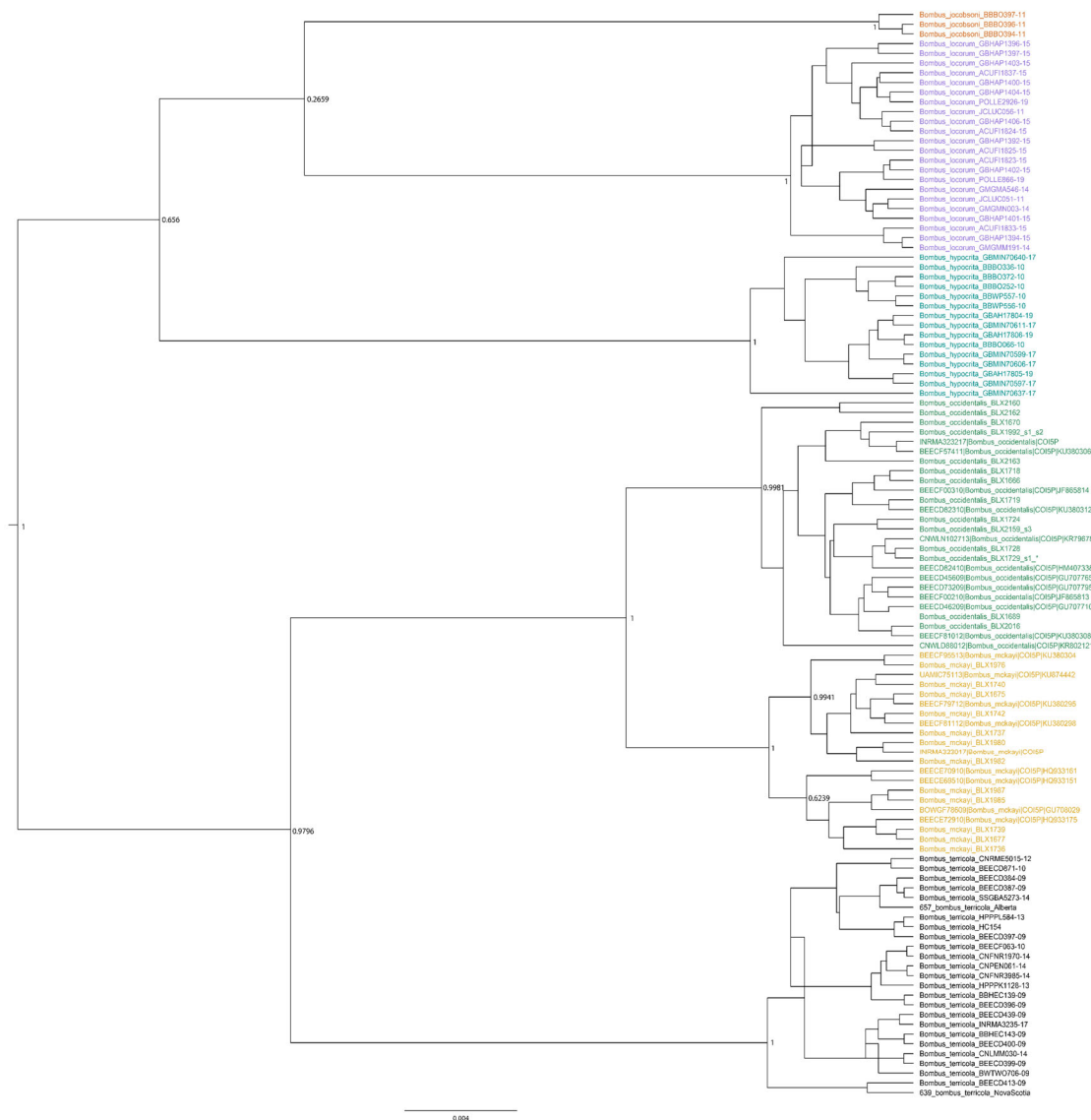
**Figure 2.1.** The distribution of *Bombus occidentalis occidentalis* (green) and *B. occidentalis mckayi* (yellow) samples included in A) the UCE dataset and B) the COI barcoding dataset.



**Figure 2.2.** Estimate of the species-level maximum likelihood phylogeny based on 1683 UCE loci including *Bombus occidentalis* (green) and *B. mckayi* (gold). Branch lengths represent nucleotide substitutions. Vertical black bars represent the species assignments based on each delimitation method. Some delimitation methods represented here were conducted on the COI barcode dataset.



**Figure 2.3.** Estimate of maximum likelihood phylogeny of the COI genes of five closely related species within the subgenus *Bombus sensu stricto*. Branch lengths represent nucleotide substitutions. Numbers at clade nodes represent bootstrap values. Species are color coded: *B. lucorum* (purple), *B. jacobsoni* (orange), *B. hypocrita* (blue), *B. terricola* (black), *B. occidentalis* (green) and *B. mckayi* (gold). Names of taxa include the length of the barcode sequence, the institutional ID number and the species name, according to the Genbank record. Samples of *B. occidentalis* and *B. mckayi* also include sampling state or province.



**Figure 2.4.** Estimate of Bayesian phylogeny of the COI genes of five closely related species within the subgenus *Bombus sensu stricto*. Posterior probabilities of well supported clades are shown at the clade nodes. Species as defined by their GenBank records are color coded: *B. lucorum* (purple), *B. jacobsoni* (orange), *B. hypocrita* (blue), *B. terricola* (black), *B. occidentalis* (green) and *B. mckayi* (gold). Names of taxa include the length of the barcode sequence, the institutional ID number and the species name. Samples of *B. occidentalis* and *B. mckayi* also include sampling state or province.

CHAPTER III

THE INFLUENCE OF GEOGRAPHY, DISPERSAL LIMITATION, AND  
ANTHROPOGENIC CHANGE ON THE POPULATION GENETIC  
CHARACTERISTICS OF TWO BUMBLE BEE SPECIES OF CONSERVATION  
CONCERN (*BOMBUS OCCIDENTALIS* AND *BOMBUS MCKAYI*) IN WESTERN  
NORTH AMERICA

**Abstract**

Bumble bees are often the dominant insect pollinator species in arctic and high-elevation Nearctic ecosystems. *Bombus mckayi* and *B. occidentalis* are two species of montane bumble bees in western North America which were considered a single species until a recent revision of their status. Populations of *B. occidentalis* have been in decline, with decreasing abundance and range, since the mid 1990's, while populations of *B. mckayi* appear to have remained stable. Understanding patterns of population structure and isolation, as well as the environmental factors that drive them, is critical to aid ongoing efforts to provide federal, state, and provincial protections for these species. Here, we examine genetic structure and diversity in *B. mckayi* and *B. occidentalis*, treating them as separate species in a population genetic analysis for the first time. Patterns of genetic diversity and genetic structure in *B. mckayi* and *B. occidentalis* were measured using microsatellite markers and specimens collected between 1960 and 2020. Associations between genetic structure and potential environmental drivers, including weather, distribution, habitat change, and exposure to parasites, were tested using structural equation models. *Bombus occidentalis* showed significant but weak patterns of decreasing genetic diversity and increasing genetic structure through time. Detected

patterns of decline were not as strong for *B. mckayi*, but may indicate that this species is also at risk. Historical specimens indicate populations of the two species contained similar levels of allelic richness and structure ( $F_{ST}$ ) prior to recent declines, though the patterns of gene flow across the landscape were not similar between the species. For both species, springtime minimum temperatures were the most important predictor of occupancy likelihood, and proximity to known infections of the fungal parasite *Vairimorpha bombi* was a reliable predictor of genetic differentiation (restricted gene flow). Although decreases in allelic diversity and increases in inbreeding and population structure have been documented in these species, substantial genetic diversity remains in extant populations relative to historical populations, which indicates a good opportunity for recovery of the species if the effects of the drivers of the declines are mitigated.

## **Introduction**

Bees (Hymenoptera: Apoidea: Anthophila) pollinate more plant species than any other taxa of pollinators (Ollerton 2017), including approximately 75% of the world's food crops (Klein et al. 2007). There are nearly 20,000 known bee species worldwide (Michener 2000), and more yet to be described, especially in the Neotropics of Central and South America (Freitas et al. 2009) and in parts of Asia (Teichroew et al. 2017). However, bees worldwide are decreasing in abundance and range (Goulson et al. 2015). Bumble bees (*Bombus*) are among the most studied bee genera, largely due to their use as pollinators in agriculture, their relatively large size and characteristic appearance, and their high abundance throughout their distribution. Bumble bees are often the dominant pollinators in cold climate regions, especially early in the active season when nighttime temperatures are relatively low (Goulson 2003). Decreases in abundance and range have

been observed in bumble bee species around the world (Goulson et al. 2008; Colla et al. 2012; Cameron and Sadd 2020).

There are approximately 260 described bumble bee species worldwide, one third of which are under threat of extinction to some extent (Abertman et al. 2017). At least three bumble bee species in North America are decreasing in abundance and genetic diversity at alarming rates (Cameron et al. 2011; Colla et al. 2012; Abertman et al. 2017). In 2016, *Bombus affinis* was listed as endangered by the U.S. Fish and Wildlife Service through the Endangered Species Act (ESA). This was the first bumble bee species to be listed as endangered in the United States. *Bombus franklini* was most recently listed as endangered by the ESA in September of 2021 and may already be extinct (<https://www.federalregister.gov>, accessed 11:05 a.m., 10/11/2019). Finally, *Bombus occidentalis* is currently under review for listing as endangered through the ESA (<https://ecos.fws.gov/ecp/>, accessed 1:39 p.m., 8/13/2018), with a listing decision expected in 2023. Several additional species have been identified as endangered or at risk of decline by the Species at Risk Act (SARA) and the International Union for Conservation of Nature and Natural Resources (IUCN, [www.iucnredlist.org](http://www.iucnredlist.org), accessed 11:36 a.m., 8/13/18; COSEWIC 2014; Table 3.1).

Bumble bees are often the dominant insect pollinator species in arctic and high elevation Nearctic ecosystems because they have hairy and robust bodies and they perform a buzzing behavior that vibrates flight muscles to produce heat. These adaptations allow them to tolerate colder temperatures than many other insect species (Heinrich and Kammer 1973; Goulson 2010). Recent distributional changes may limit population sizes and gene flow among populations, especially at the relatively low

elevation portions of their ranges. Distributions of some European bumble bee species have retracted to high-elevation and high-latitude portions of their historical ranges due to changes in land use and climate (Ploquin et al. 2013). The status of North American bumble bees is less well studied than their European counterparts. However, (low) elevational barriers have been shown to limit or direct gene flow in some North American species (Jackson et al. 2018; Koch et al. 2018), indicating that they may be most vulnerable to reductions in abundance and gene flow at the relatively low-elevation portions of their ranges, similar to the patterns found in European species.

A species of particular conservation concern in North America is *Bombus occidentalis*. *B. occidentalis* was once abundant in western North America, with a range that extended from Alaska in the north to New Mexico in the south and as far east as western Nebraska and the Black Hills of South Dakota (Rao and Stephen 2007; Williams et al. 2014). This species was and is an important pollinator in high elevation and high latitude ecosystems in the region. Comparisons of early museum records and studies from before 1997 against recent museum records and collections indicate that populations of *B. occidentalis* have declined dramatically along the west coast and in the Rocky Mountains and Intermountain West since the mid 1990's (Evans et al. 2008; Cameron et al. 2011; Graves et al. 2020). Although a pattern of decrease in abundance for *B. occidentalis* was clearly demonstrated, the cause of the decline remains uncertain (Cameron et al. 2016) and new studies are required to determine if the decline is ongoing.

In addition to declines in abundance and range, the species status of *B. occidentalis* has recently changed. Two morphologically identified subspecies, *B. occidentalis mckayi* and *B. occidentalis occidentalis* have been supported as distinct



clades and species in recent analyses of the mitochondrial *cytochrome oxidase I* (COI) barcode region (Williams et al 2012; Williams 2021) and nuclear ultraconserved elements (UCEs). These taxa (hereafter *B. occidentalis* and *B. mckayi*) are geographically separated within the historical range, with *B. mckayi* dominant north of 55° latitude and *B. occidentalis* dominant south of 55° latitude. There is a region of likely overlap in distribution between the species (possibly a hybrid zone?) near the boundary where differentiating species has proven challenging using morphology (Williams et al. 2012; Sheffield et al 2016; McHugh and Sikes 2016; Williams 2021, Fig. 3.1). Phylogenies based on mitochondrial and nuclear genes clearly group *B. mckayi* specimens into a monophyletic clade, but sampling in the overlapping portions of the ranges is poor (Williams et al. 2012; Williams 2021). The two taxa are likely to be treated as separate species in future conservation decisions (Williams 2021), so we treat each taxon separately throughout the rest of this manuscript. Although there is ample evidence of decreases in population abundance and range within the southern species, *B. occidentalis* (Evans et al. 2008; Cameron et al. 2011; Graves et al. 2020), previous studies indicate that populations and the distribution of the northern species, *B. mckayi*, have remained stable (Koch and Strange 2012; Pampell et al. 2015). However, several years have passed since these data were collected and there has been a call for additional study of the conservation status of both species (McHugh and Sikes 2016; personal correspondence with Jeffery Everett, U.S. Fish and Wildlife Service) to update knowledge of their current distributions, densities, and genetic resiliency.

In assessing conservation status of *Bombus* species, genetic data are an important adjunct to location records. While patterns of occupancy may indicate where gene flow

barriers exist, these patterns are insufficient to predict the causes of gene flow barriers (Roffler et al. 2016). The relationship between occupancy and gene flow could be particularly messy for bumble bees because of their eusocial life history, which dictates that most individuals in the census populations are not reproductive, so they do not contribute directly to gene movement across the landscape, although they are vital to the survival of their colonies. Reproductive individuals require different resources and are active at different times during the season from non-reproductives. The higher likelihood of observing sterile workers skews maximum entropy models to identify sites that are adequate or inadequate for colony establishment, rather than gene flow. Therefore, measures of occupancy alone are not enough to determine if gene flow is restricted.

Landscape genetics is an interdisciplinary field that combines aspects of population genetics, landscape ecology, and spatial statistics to measure genetic discontinuities and diversity patterns across landscapes and to correlate them with environmental features (Manel et al. 2003; Storfer et al. 2007). This field of study has applications in many aspects of evolution and ecology. Applications in conservation ecology include determinations of population boundaries (Safner et al. 2011), estimates of dispersal ability (Cayuela et al. 2018), estimates of population structure (Jost et al. 2018; Masuda 2018), genetic rescue of high risk and inbred populations (Whiteley et al. 2015; Forsman 2014; Frankham 2015; Hendrick and Garcia-Dorado 2016; Ralls et al. 2017), estimation of metapopulation dynamics (Hand et al. 2015; Salisbury et al. 2016; Hanski et al. 2017), and measurements of the temporal and spatial scale of evolutionary processes (Ellegren and Galtier 2016). Accurate estimates of gene flow and genetic

structure within and among populations are the basic tools needed for land managers to use landscape genetics methods for any of these applications.

Landscape genetic techniques can provide insight into questions about potential threats to bumble bees and identify actions that can be taken to protect populations. Measurements of population structure, genetic diversity, and gene flow among populations are important indicators of current conservation status for species. Landscape genetic studies that measure environmental variables as well as gene flow and genetic structure and diversity can indicate which environmental changes have negative effects on bumble bees. Interest in this work has been piqued in the United States in recent years, especially since the Pollinator Partnership Action Plan (2016) was released by the federal Pollinator Health Task Force, as mandated by President Barack Obama via a presidential memorandum. This plan has increased awareness of decreases in pollinator abundances and ranges and encouraged interest in research into pollinators to inform environmental policy and management.

Here we use observation records, microsatellite genetic data from museum specimens, and spatial environmental data to predict current and past genetic structure, genetic diversity, and gene flow patterns in *B. occidentalis* and *B. mckayi*. We used these data to test two hypotheses: (1) genetic structure among populations has increased and genetic diversity within populations has decreased for *Bombus occidentalis* over time. These population characteristics have remained relatively stable for *Bombus mckayi*, (2) changes in environmental drivers, such as climate, habitat fragmentation, and increased parasite pressures drive genetic diversity and structure in *Bombus occidentalis* and *Bombus mckayi*. We used specimens captured from across the historical range of the

species to measure genetic structure within and among populations and genetic distance among individuals. We used maximum entropy modeling to build resistance landscapes using measured environmental variables and observation records across the range of the species. We used genotypes from museum specimens to estimate gene flow across the resistance landscapes. We used structural equation modeling to quantify the relative influences of the measured environmental variables included in the resistance landscapes on the genetic distances among the genotyped individuals (Wang et al. 2013). We found significant but weak patterns of decreasing genetic diversity and increasing genetic structure in *Bombus occidentalis* through time. Detected patterns of decline were not statistically significant for *B. mckayi*, but may indicate that this species is also at risk. Historical specimens indicate populations of the two species contained similar levels of allelic richness and structure ( $F_{ST}$ ) prior to recent declines, though the patterns of gene flow across the landscape were not similar between the species. For both species, springtime minimum temperatures were the most important predictor of occupancy likelihood, and proximity to known infections of the fungal parasite *Vairimorpha bombi* was a reliable predictor of genetic differentiation (restricted gene flow).

## **Methods**

### *Study area*

Samples used in this study extended across the full extent of the historical range of the target species, *Bombus occidentalis* Greene including *Bombus mckayi* (Williams et al. 2014; Hatfield et al. 2015, Fig. 3.1). This broad area includes two mountain ranges, over 8,000 miles of coastline, and intermountain habitat across 35 degrees of latitude.

### *Acquisition and management of tissue samples*

*Bombus occidentalis* and *Bombus mckayi* tissue samples were obtained from field-captured bumble bees and museum specimens. Specimens were provided by the U.S. National Pollinating Insect Collection, the Royal Museum of British Columbia, the University of Alaska Museum of the North, the University of Alberta E.H. Strickland Entomological Museum, the University of Calgary Zoology Museum, Montana State University Entomology Collection, the Canadian National Collection, The University of California Berkeley Essig Museum of Entomology, the University of Alberta, the U.S. Forest Service, and the U.S. Geological Survey.

Mid-legs of specimens collected in the field specifically for this study (not museum specimens) were frozen and stored at the U.S. Department of Agriculture, Agricultural Research Service Pollinating Insect Research Unit (PIRU). Extracted DNA was frozen at -80°C and stored on-site at PIRU. Specimens owned by each of the respective collections were assigned unique identifiers by those institutions and are permanently stored in those collections.

### *DNA extraction and microsatellite amplification*

For DNA extraction, one mid-leg or two fore-legs were removed from each specimen and placed into a single well of a 96-well plate. DNA was extracted from tissue samples using a Chelex(R) extraction method (Strange et al. 2009): 150  $\mu\text{L}$  of 5% Chelex® solution was added to each well with 5  $\mu\text{L}$  of Proteinase K solution (10 mg/mL) and incubated in a thermocycler at 55°C for 60 minutes, 99°C for 15 minutes, 37°C for 1 minute, 99°C for 15 minutes, and cooled to 15°C.

Fifteen microsatellite loci were targeted for amplification using fluorescently tagged primers and amplified using PCR as described by Koch et al. (2017). The loci were identified from the literature (Table 3.2). PCR amplifications were performed in a thermocycler in two multiplex reactions (plex A and plex B), determined by the melting points of the primers (Table 3.2). The heating and cooling cycle for plex A was 95°C for 3 minutes 30 seconds for the initial denaturation, followed by 30 cycles of 95°C for 30 seconds, 55°C for 1 minute 15 seconds, and 72°C for 45 seconds for replication, followed by 72°C for fifteen minutes for final extension before a final chill at 15°C. The heating and cooling cycle for plex B was the same as plex A, except the 55°C step in replication was adjusted to 58°C. Fragment sizes were measured through capillary electrophoresis using an ABI PRISM™ 3730 DNA Analyzer. Fragment sizes were scored using Geneious v. 7.1. Specimens that successfully amplified seven or more loci were included in downstream analyses.

#### *Bombus occidentalis and Bombus mckayi location records*

Location records for *B. occidentalis* from 1960 to 2020 were downloaded from the Global Biodiversity Information Facility (GBIF, September 8, 2020, 2:23 pm). Records were composed of human observations (N = 543), material records (N = 123), and museum specimens (N = 17,895). Erroneous identification is unlikely from material records and museum specimens, as these records were verified by experts and samples are retained in institutions. The records from in-situ human observations, however, are more likely to be erroneous. The white setae on the terminal abdominal terga of *B. occidentalis* are an easily identifiable and diagnostic character for the species throughout most of its geographic range because it is the only species with this characteristic.

However, portions of the geographic range that overlap with the range of other bumble bees with white setae on the terminal abdominal terga (i.e. *Bombus terricola* in the southeastern portion of the range and *Bombus cryptarum* in the northern portion of the range) could contain records that were mis-identified. These records represent a very small portion of the records for this species ( $N < 100$ ) and if they are incorrectly identified, they are likely to have a negligible influence on the outcome of our analyses. These records were named prior to the recent phylogenetic work that indicates the taxa is actually two species (Williams 2021, Chapter 1) and consist of both *B. occidentalis* and *B. mckayi*, without differentiation between the taxa. Therefore, all specimens collected north of 55° latitude (per the likely range boundary identified by Sheffield et al. 2016) were treated as *B. mckayi* and all specimens collected south of 55° latitude were treated as *B. occidentalis*. Only records associated with geographic coordinates were included for these analyses.

### *Population genetic analyses*

#### *I. Definition of populations*

The *Buffer* tool in ArcGIS Pro was used to draw a 10 km buffer around the collection location of each genotyped specimen, to define an area slightly larger than the largest expected foraging range for that specimen (Osborne et al. 2001; Westphal et al. 2006; Greenleaf et al. 2007). All specimens that had overlapping buffers were grouped and these groups were defined as geographic clusters for downstream analyses (Table B1). The probability of sibship was analyzed within the geographic clusters in Colony version 2.0.6.7 (Jones and Wang 2010). Sibship analyses were run twice, with different initiation seed numbers (1234 and 4321). All but one specimen from each sibling set

identified by Colony with a probability higher than 0.7 were removed for all downstream analyses, because multiple siblings of eusocial insects in a dataset can lead to underestimates of allelic richness and overestimates of structure at the population level (Table B2). Structure version 2.3.4 (Pritchard et al. 2000) was used to identify genetic structure within each of the species. Admixture models were used and included the geographic clusters as location priors to identify lineages within the species. Location priors in Structure are defined by integers representing groups of samples that were collected at geographically close locations. In this case, where the true number of populations is unknown, the geographic cluster definitions are biologically meaningful. Location priors are useful in analyses when there is population structure in the dataset, but the signal is too weak for standard Structure models to detect (Hubisz et al. 2009). Inclusion of location priors does not tend to cause Structure to find population structure where none is present and, in datasets where population structure is strong, it does not influence population assignments (Hubisz et al. 2009). Initial values for  $\lambda$  (a measure of the independence of markers from one another) and  $\alpha$  (the relative admixture levels among populations) were left at the recommended values ( $\lambda = 1.0$  and  $\alpha = 1.0$ ) for all Structure analyses. Thirty replicates were run (Porrás-Hurtado et al. 2013) for every value from  $K = 1$  through the total number of geographic clusters identified for each species, plus ten (*B. mckayi* = 51 and *B. occidentalis* = 90), per the recommendation of Pritchard et al (2009). The initial burn-in length and run length was set to 200,000 and the convergence of summary statistics included in the output of the initial analyses was verified to confirm that the burn-in was long enough to reach convergence.



Structure\_threader version 1.3 (Pina-Martins et al. 2017) was used to parallelize the computation of the replicate runs of Structure. Structure\_threader also wraps Structure Harvester version 6.94 (Earl and vonHoldt 2012) which automates the summarization of the data and conducts analyses to choose the most likely value of K. The most likely values of K for each dataset were selected based on the output values of Delta K with guidance provided by Porras-Hurtado et al. (2013). Structure Harvester also reformats the data from the Structure output files to Clumpp (Jakobsson and Rosenberg 2007) input files for each value of K. Clumpp version 1.1.2b was used to permute the 30 replicate runs of each of the values of K that were most likely to be real (as determined by the analyses from Structure Harvester), making the values from each replicate run as similar as possible for each value of K, and to derive the median values into a single output matrix. The *Greedy* algorithm was used for values of K = 15 and smaller and the *LargeKGreedy* algorithm for values of K larger than 15. These analyses were conducted using the Ceres high performance computing cluster, part of USDA-ARS SCINet (<https://scinet.usda.gov>)

## II. Population structure analyses

GENEPOP version 4.7 was used to test for Hardy-Weinberg equilibrium (HWE) and pairwise genotypic disequilibrium (exact G test) for all loci in all populations. The exact G test tests the null hypothesis that “genotypes are drawn from the same distribution in all populations” (Raymond and Rousset 1995). Rejection of this null hypothesis is an indication of genotypic differentiation among the populations. HP-Rare version 1.0 was used to estimate mean allelic richness across all loci for each population (Kalinowski 2005). The mean allelic richness from all measured loci is often used to

estimate the amount of genetic diversity within populations. However, comparisons of estimates of allelic richness are sensitive to differences in sample size among populations (El Mousadik and Petit 1996; Leberg 2002; Foulley and Ollivier 2006), which are exaggerated in this study due to our dependence on availability of museum specimens (Table B1). HP-Rare uses rarefaction to estimate true allelic diversity in populations with uneven population sizes. Geographic clusters were standardized to 10 individuals for rarefaction. FSTAT version 2.9.4 (Goudet 1995) was used to perform analyses to measure the amount of inbreeding ( $F_{IS}$ ) within populations. A one-sample t-test was used to identify populations with significantly higher than expected  $F_{IS}$  values (Callahan et al. 2013). Pairwise genetic structure ( $F_{ST}$ ) was measured among populations that were sampled at similar times (within six years, five time groups total) and global  $F_{ST}$  values were estimated within groups of temporally similar populations using GENEPOP.

An analysis of molecular variance (AMOVA) was performed using the `poppr.amova` function in the *poppr* package version 2.9.3 (Kamvar et al. 2014) in R to measure the extent of genetic differentiation among geographic clusters and among samples within geographic clusters for both species. Because the populations were sampled in different years, the pairwise genetic differentiation matrix (Nei's genetic distance, Nei 1972) used in the analysis was weighted by subtracting a pairwise matrix of the average number of mutations expected at microsatellite loci ( $10^{-4}$  per generation, Estoup and Angers 1998) times the number of loci (15) times the number of years between the pair of populations times two, because there are two populations in each comparison (equation 1).

adjusted genetic distance = (calculated genetic distance \* 0.001) \* 15 \* pairwise  
 difference in years \* 2 [1]

This adjustment estimates the genetic differentiation among samples not accounted for by time since sampling if the loci mutate at the predicted average rate for microsatellite markers. The same adjusted genetic differentiation matrix was used in a Mantel test to measure the relationship between genetic distance and geographical distance of the populations.

### *Environmental data for occupancy and resistance modeling*

#### *I. Elevation*

The publicly available world elevation GMTED raster was downloaded from the U.S. Geological Survey (Danielsen and Gesch 2011) through the Living Atlas of the World feature of ArcGIS Pro (version 2.8.2). This raster has a resolution of 250 m<sup>2</sup> and was used for maximum entropy modeling and structural equation modeling (see below). Additionally, least cost distances were calculated using the R package *leastcostpath* (Lewis 2021) which uses a DEM (digital elevation model) in addition to a continuous landscape resistance raster (McRae 2007; Spear et al. 2010) in this case generated by MaxEnt, see below) to estimate least-cost resistance distance.

#### *II. Weather*

Monthly modeled data of maximum, minimum, and mean temperatures and precipitation from across the historical range of *B. occidentalis* from 1960 through 2019 were gathered from PRISM (PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, created 24 August 2021) using the ClimateNA tool (Wang et al. 2016b). The elevation raster described above was resampled to 10 km<sup>2</sup> cells using

the *Resample* tool in ArcGIS Pro version 2.4 and was clipped to the extent of the species range (Hatfield et al. 2015) using the *Clip Raster* tool in ArcGIS Pro. The resulting raster was converted to a table including columns for the latitude, longitude, and cell values using the *Generate Table from Raster Function* tool and the table was exported as a CSV file. This CSV was used as an input for the ClimateNA tool to calculate the monthly weather variables. The results from the ClimateNA tool were exported as one large CSV file including columns for each modeled weather variable at each of the locations (same latitude and longitude values as the input CSV generated from the elevation DEM) during each month of each year. R for Windows version 4.1.1 and R Studio version 1.3.1 were used to extract the data generated for months included in the active season (April through September) and to create monthly tables of maximum temperature, minimum temperature, average (mean) temperature, and precipitation for each location during these months for each year. Additionally, tables of means and standard deviations for all years (1960-2019), approximate years prior to the measured decline in abundance of *B. occidentalis* (1960-1994), and years since the decline (1995-2019) by each month of the active season were created. These tables were exported as CSV files to ArcGIS Pro where the *XY Table to Points* tool and the *Point To Raster* tool were used to create new rasters with the same cell size and orientation for each of the datasets (monthly for each year separately, mean for the entire time frame, standard deviation for the entire time frame) for use with the software MaxEnt (version 3.4.1) in downstream analyses.

### III. Land cover (Habitat Quality)

Annual land cover data from 1992 to 2015 were modeled at 300 m<sup>2</sup> resolution across the globe by the European Space Agency (ESA) Climate Change Initiative (Wei et

al. 2018) with annual updates at <https://www.esa-land-cover-cci.org/?q=node/197>) and classed into 22 land cover types. Reliable land cover data from across the entire range of this species was not available before 1992. Therefore, analyses for these models do not include land cover data from before 1992. Land cover data was downloaded for each year individually and clipped to the extent of the historical *B. occidentalis* and *B. mckayi* ranges using the *Extract by Mask* tool in ArcGIS Pro.

Land cover data was converted to estimated habitat quality. The *Calculate Combined Table of Raster Values that Intersect Points* tool (Welty et al. 2021) was used with the point locations of all known records of *B. occidentalis* and *B. mckayi* from 1992 to 2015 (GBIF) to extract the land cover types where each record was collected. A weighted rank of habitat quality was calculated by dividing the percentage of the *B. occidentalis* and *B. mckayi* observations that were found within each land cover type by the number of specimens counted in that land cover type. The weighted habitat quality values were finally rescaled from 1 to 100 using the *rescale* function in R. Any Land cover types where *B. occidentalis* or *B. mckayi* have never been collected were assigned a value of zero (Table B2). The rangewide annual land cover layers were reclassified to the weighted and scaled habitat quality values using the *Reclassify* tool in ArcGIS Pro (values were rounded to whole integers). The *Resample Raster* tool was used to resample the resulting rasters from their native cell size of 300 m<sup>2</sup> to 10 km<sup>2</sup>, so they would match the resolution of the elevation and weather rasters. Finally, the *Raster Calculator* tool was used to calculate the change in habitat quality from 1992 to 2015.

#### IV. *Distance to cropland*

Data on the density of honey bee hives and pesticide use across the landscape are difficult to obtain and often unreliable from year to year. As a surrogate for these environmental factors, we measured the distance from the collection locations of the genotyped specimens to the nearest croplands, where domesticated bees and pesticides are most likely to be used. Raster cells that represented croplands were extracted from the annual ESA land cover rasters using the *Extract by Attributes* tool and converted to polygons with the *Raster to Polygon* tool in ArcGIS Pro. Euclidean distance between sampling points and the nearest croplands was calculated using the *Near* tool in ArcGIS Pro. As with habitat quality, data was only available for this variable from 1992 to 2015.

#### *Environmental data for structural equation modeling*

##### I. *Environmental predictors*

The *Calculate Combined Table of Raster Values that Intersect Points* tool (Welty et al. 2021) was used to extract mean, minimum, maximum, and standard deviation temperature and precipitation information from the monthly PRISM rasters described above for the precise collection locations and times of each of the genotyped specimens. Additionally, the habitat quality values, elevations, and latitudes of each specimen's sampling location were extracted from the appropriate rasters using the *Extract Values to Points* tool in ArcGIS Pro.

##### II. *Parasitism*

Data on the presence of *Vairimorpha bombi* (*V. bombi*, Tokarev et al. 2020) were provided by bumble bee researchers from published and unpublished datasets (Cameron et al. 2011; Strange and Tripodi, unpublished data). The species was recently moved from

the genus *Nosema* into *Vairimorpha*, and previously published literature refers to it as *Nosema bombi*. *Vairimorpha bombi* is an important species of internal parasite that causes lethargy and death in non-reproductive bumble bees, and reduced fecundity in reproductive castes of bumble bees throughout the range (Gegear et al. 2006; Cameron et al. 2011). *V. bombi* is native in the range of *B. occidentalis*, but frequency of infections in wild-caught *B. occidentalis* specimens increased as population density decreased through time, indicating at least a negative correlation between infection rates and population density (Cameron et al. 2011), and possibly a causative one. Euclidean distance between genotyped bumble bee samples and nearest known *V. bombi* infections from that same year or before was calculated using the *Near* tool in ArcGIS Pro. Any *V. bombi* infections that were detected in specimens collected prior to the sampling year of the genotyped specimens were assumed to be part of a persistent population, and were therefore retained in analyses of bees collected in subsequent years. This sampling scheme is not systematic and likely underestimates the prevalence of *V. bombi* throughout the range of *B. occidentalis* and *B. mckayi*. However, this dataset represents the most complete distribution information currently available for these parasites.

### *Landscape genetic analyses*

#### *I. Genetic distance matrices*

The R function *nei.dist* in the package *poppr* (Kamvar et al. 2014) was used to calculate pairwise Nei's standardized genetic distances among sampled individuals from across the species ranges. This statistic describes the pairwise number of nucleotide substitutions between two specimens and is measured on a scale of 0 to 1.

## II. *Resistance rasters*

The elevation, weather, and land cover rasters described above were used along with the location records to create maximum entropy models for both species in the software MaxEnt (version 3.4.0). Twenty-five percent of the data was used as training sets and 75% of the data as the test sets with a logistic output (cell values represent likelihood of occupancy and range from 0 to 1). The monthly and annual weather predictors were likely highly correlated, but these variables were not removed from the analyses because recent empirical and simulation studies found that collinearity (correlation) among predictor variables in training datasets does not influence the outcome of MaxEnt models (De Marco et. al 2018; Feng et al. 2019). However, these studies did indicate an influence of collinearity shift, in which the relationships among predictor variables within geographically separated training and testing datasets were not similar. The training data for each model in this study was taken from across the entire range of the test dataset. Therefore, collinearity shift among predictor correlations for the training and test datasets is not a concern. Most historical records of *B. occidentalis* do not differentiate between *B. mckayi* and *B. occidentalis*, so we were dependent on the ranges described in previously published literature to estimate the likely species identification of the GBIF observation records. The continuous occupancy likelihood raster produced by MaxEnt was inverted using the *Raster Calculator* tool in ArcGIS Pro to estimate a resistance landscape, as described by Wang et al. (2013).

## III. *Cost-distance matrices*

Cost-distance measurements describe the cost to organisms of moving across a landscape, and have been shown to represent the influence of distance on organisms'



movements better than Euclidean distance (McRae 2006; Graves et al. 2014). The *create\_FETE\_lcps* function in the R package *leastcostpath* was used with the resistance rasters to create least-cost distance matrices. *Circuitscape* version 4.0.5 (McRae et al. 2013) was used with the resistance rasters to create input files that were used in *Circuitscape.jl* version 0.27 (Anantharman et al. 2020) to calculate pairwise random walk cost-distance matrices. Least-cost and random walk distance measurements mimic the paths traveled by an individual that seeks the route of least resistance across the landscape and an individual that is directed by stochastic movements across the landscape, respectively. These distance measurements represent conservative and liberal estimates of the influence of environmental resistance on the movement of individuals (Marrotte and Bowman 2017).

#### *IV. Structural equation modeling*

Structural equation modeling (SEM) can be used to differentiate between the effects of multiple predictor variables on response variables within a complex system using a combination of confirmatory factor analysis (CFA, measurement mode) and path analysis (structural model) to improve the fit of multiple regression models (Grace 2006; Bauer and Curran 2020). An advantage of CFA is that it uses latent variables, which are the variables of interest but are not measured directly. Latent variables are informed using one or more observed variables (Grace 2006). An advantage of path analysis is that it allows the effects of some variables to be mediated by others, which improves the fit of the model to complex hypotheses. Four SEMs were created. Two models measured the relative influences of resistance distance and the measured environmental variables on the pairwise genetic distances among the *B. occidentalis* and the *B. mckayi* samples from

across the entire sampling period. Two additional models used the same predictor variables among samples in subsets of *B. occidentalis* from 1960 to 1994 and 1995 to 2020 to compare the relative influences of the predictor variables before and after the initial observed decrease in abundance and range in the species (Cameron et al. 2011).

SEMs must be overidentified, meaning that there are more variables with known values than variables with unknown values (Grace 2006; Bauer and Curran 2020). In models such as ours, which contain both latent variables and directed paths (hybrid models), the measured model and the structural model can be tested for identification separately. If the two components of the model are identified, the model is identified. The models were estimated using a maximum likelihood estimator in the *Lavaan* package (Yves 2012). Maximum likelihood estimation of SEMs assumes a continuous normal distribution of the endogenous variables. Measurements of distance from *V. bombi* infections, distances from agricultural lands, and latitude of the samples' collection locations were not normally distributed. However, our response variable is the pairwise genetic differentiation among samples, so the predictors had to be pairwise comparisons among samples also (Wang et al. 2013). The pairwise differences of the values of all of the predictor variables except for distance from *V. bombi* infections and distance from agricultural lands were calculated. For distance from *V. bombi* infections and agricultural lands, pairwise sums were used instead of differences. This way, pairs of two specimens that were both far from *V. bombi* infections or agricultural lands had a higher score than pairs with one specimen that was far but one that was close, or two specimens that were close. The values of these pairwise comparisons were normally distributed. Our predictor variables were measured on different scales, which sometimes produced absolute values

that were orders of magnitude different from each other. In order to allow the model to measure differences in variance among the variables, the measured units were adjusted to reduce the disparity between absolute values among variables (Table 3.3) and the standardized regression relationships were reported. This means that each regression value reported indicates the number of units of change in the response variable (genetic differentiation) per (adjusted) unit of change in the predictor variable, under the conditions described by the model.

Direct and indirect regression values were standardized, so the values indicate one unit of change in the predictor resulted in the reported number of units of change in the response. Only regressions for which the response is Nei's genetic differentiation are reported (all other relationships are available in the supplement), so the values are in units of Nei's genetic differentiation (0 to 1, hereafter D). We evaluated the fit of the models using a mix of absolute and relative goodness-of-fit tests, following the recommendations of Bauer and Curran (2020) for fit requirements. To define a model fit as good, we required a non-significant  $p$  value from a  $Chi^2$  test, values of 0.9 or higher from the comparative fit index (CFI) and Tucker-Lewis index (TLI), and values less than 0.08 from the root mean square error of approximation (RMSEA) and the standardized root mean square residual (SRMR). We used inferential tests of indirect effects with bootstrapped confidence intervals to infer mediation effects. Significant links in mediational pathways is not sufficient to infer the whole relationship (Bauer and Curran 2020). We used 1000 bootstrapped samples and calculated bias-corrected confidence intervals to infer mediation effects.

## Results

### *Microsatellite amplification and group assignments*

We genotyped 1790 *B. mckayi* specimens and 1541 *B. occidentalis* specimens from across their ranges. The number of loci that amplified varied considerably among specimens and was significantly negatively correlated with the age of the specimens in both taxa (*B. occidentalis*  $t = 6.8$ ,  $p < 0.0001$ , *B. mckayi*  $t = 4.5$ ,  $p < 0.0001$ , Fig. 3.2). Three hundred ninety-two specimens of *B. occidentalis* collected between 1963 and 2020 and 568 specimens of *B. mckayi* collected between 1967 and 2019 amplified seven or more loci.

We analyzed 99 geographic clusters of *B. occidentalis* and 55 geographic clusters (representing possible populations, hereafter clusters) of *B. mckayi* specimens with overlapping foraging ranges for sibship. Sample sizes for each cluster (treated as discrete populations) of *B. occidentalis* ranged from one to 45 and *B. mckayi* ranged from 1 to 93. Obviously, we could not perform population genetic analyses on clusters represented by a single specimen, but the mean number of specimens in the clusters that were included in those analyses was 6.1 (standard error = 0.9,  $N = 50$ ) for *B. occidentalis* and 14.6 (standard error = 2.4,  $N = 37$ ) for *B. mckayi*. Within clusters, we identified seven likely *B. occidentalis* and four likely *B. mckayi* sibling sets (Table B1). We removed 37 *B. occidentalis* specimens and nine *B. mckayi* specimens from downstream analyses.

### *Population genetic analyses*

We detected significant genotypic disequilibrium (from the G-test) across populations in every locus in the analysis of *B. mckayi* and in every locus except two in

*B. occidentalis* (BTERN02 and BTMS0083). We detected significant divergence from expected heterozygosity (Hardy Weinberg Equilibrium, HWE) across populations at every locus for both species. These rangewide differences indicate structure among the sampled clusters. However, average heterozygosity within clusters diverged from HWE in only one population of *B. occidentalis*, which had a measured excess of heterozygosity (sampled in 2018). The cluster was represented by two individuals (Fig. 3.1) and this result is likely due to sampling error associated with the small sample size. No *B. mckayi* populations diverged from HWE. Mean rarefied allelic richness for each locus ranged from 1.62 to 2.41 in *B. occidentalis* and 2.23 to 6.27 in *B. mckayi* (Table 3.4). Rarefied mean allelic richness for all loci in each population of *B. occidentalis* ranged from 2.27 to 43.13 (mean = 16.88, standard error = 1.70) and in *B. mckayi* ranged from 1.67 to 37.93 (mean = 17.79, standard error = 2.40, Fig. 3.3). Linear regressions of rarefied allelic richness through time indicated a significant decline in allelic richness in *B. occidentalis* ( $F_{1,96} = 5.95, p = 0.02$ ), and a non-significant trend of decline in *B. mckayi* ( $F_{1,52} = 2.67, p = 0.11$ ). Linear regressions of subsets of the datasets from 1960 to 1994 and from 1995 to 2020 were not significant for *B. occidentalis* (before:  $F_{1,24} = 0.58, p = 0.45$ , after:  $F_{1,70} = 0.16, p = 0.73$ ). However, *B. mckayi* showed a slight significant increase in allelic richness from 1995 to 2020 (before:  $F_{1,3} = 2.20, p = 0.23$ , after:  $F_{1,47} = 5.36, p = 0.02$ ). Despite statistically significant relationships, the  $R^2$  values for these relationships indicate that sampling year was a poor predictor of allelic richness.

We identified two as the most likely number of lineages in the Structure analysis of *B. mckayi* (Fig. 3.4). The distribution of these specimens across Alaska and northern Canada indicate an eastern lineage and a western lineage with some overlap in central

and eastern Alaska. Similarly to *B. mckayi*, analyses of *B. occidentalis* specimens indicated that two lineages were most likely (Figure S1). Unlike *B. mckayi*, the members of these two lineages were more geographically mixed and this dataset contained many samples that had mixed ancestry from both lineages (Fig. 3.4). Although the two lineages identified for *B. occidentalis* were quite mixed, geographic groups of clusters dominated by lineage two (Fig. 3.4) are discernable in Wyoming and in southern British Columbia. The strongest support was for two lineages within each taxon, however there was some support for eight lineages within *B. mckayi* and for nine lineages within *B. occidentalis* (Figure B1). This result may indicate that there is hierarchical population structure within the lineages.

AMOVA analyses indicated significant partitioning of genetic variation among geographic clusters for *B. occidentalis* and *B. mckayi* (Table 3.5). Mantel tests indicated a weak but significant positive correlation between Euclidean and genetic distance in *B. occidentalis* ( $r = 0.07$ ,  $p = 0.01$ ) and a stronger relationship in *B. mckayi* ( $r = 0.23$ ,  $p = 0.0002$ ). The Mantel test using the corrected genetic distance matrices slightly weakened the relationships in both species, but remained significant (*B. occidentalis*:  $r = 0.05$ ,  $p = 0.04$ , *B. mckayi*:  $r = 0.19$ ,  $p = 0.002$ ).

Single-tailed one sample t-tests of  $F_{IS}$  values indicated that some clusters in both species had significantly higher than expected levels of inbreeding (Fig. 3.5 a and b). Single-tailed one-sample t-tests of global  $F_{ST}$  values for groups of clusters sampled in similar years indicated that some clusters had higher than expected genetic structure. However, linear regressions of neither species indicated a significant increase in  $F_{ST}$  over time (Fig. 3.5 c and d), and linear regression indicated no significant relationship between

sampling year and relatively high  $F_{ST}$  (*B. occidentalis*:  $t = 0.367$ ,  $p = 0.738$ , *B. mckayi*:  $t = 1.525$ ,  $p = 0.225$ ), though non-significant trends are observable in the data.

### *Landscape resistance*

We included 10,814 GBIF records of *B. occidentalis* (including *B. mckayi*) observations and collections in the MaxEnt analysis. Maximum entropy produced good fitting models (*B. occidentalis* AUC = 0.857, standard deviation = 0.008, *B. mckayi* AUC = 0.948, standard deviation = 0.008). Resistance rasters generated from the maximum entropy models indicated that *B. occidentalis* was historically most common along the west coast and in the intermountain west, mostly excluding the Great Basin and Mojave desert, which are arid relative to the rest of the region. *B. mckayi* was most likely to be detected in two general clumps, one in eastern Alaska and one in northern British Columbia and southern Yukon Territory (Fig. 3.6).

The likelihoods of occupancy of *B. occidentalis* and *B. mckayi* across their ranges were most strongly predicted by different variables (Table 3.6). Springtime precipitation and variability in springtime temperatures were strongly influential for *B. occidentalis*, accounting for 63.3% of total variation in that model. Variation in springtime temperature was also an important predictor for *B. mckayi*, but temperature at the end of the active season and variability in temperatures throughout the active season were also influential for that species. Only 3.2% of the variation in the *B. mckayi* model was predicted by variables that measured precipitation. Elevation was not an important predictor for either species in these models.

Resistance rasters generated from the maximum entropy models for *B. occidentalis* in the two time-categories before and after the observed beginning of its

decrease in abundance indicate that resistance increased in some portions of the range in the later time category, notably along the coast of California and on the eastern side of the distribution (Fig. 3.7). However, the models also indicate that resistance is lower in more recent years in the intermountain west region of the United States and southwestern Canada.

Analyses of the likelihood of occupancy of *B. occidentalis* before (1960 to 1994) and after (1995 to 2019) the observed decrease in abundance and range indicated that the variability in temperatures in April remains a very important predictor throughout time (Table 3.7). Surprisingly, elevation was an important predictor prior to 1995, but was ranked as one of the least important predictors in more recent years. Additionally, temperature variables at the beginning of the active season and the end of the active season (April and September) explained the most variation in the model from 1960 to 1994, 58.2%. Variation in temperature in the early season remained very important in the 1995 to 2019 time-category, but temperature at the beginning and end of the active season was less influential overall, with a total contribution of 32.5%, while temperatures during mid-season months were more influential during the later time category.

#### *Environmental influences on genetic differentiation*

With the help of modification indices built into the Lavaan package, we identified well-fitting SEMs to describe the relationships among our predictor and response variables for *B. mckayi* and *B. occidentalis* from 1960 to 2020 (Table 3.8). We achieved good relative measures of fit, but the one test of absolute fit, the  $\chi^2$  test, never achieved non-significance. The  $\chi^2$  test compares the variance in the model covariance matrix to the population covariance matrix. If the matrices are not significantly different, this is an



indication that the model describes all of the variance in the dataset (Bauer and Curran 2020). Since the  $\chi^2$  test never achieved non-significance, this is an indication that there is variance in the dataset that is not explained by the model.  $\chi^2$  tests are sensitive to sample size, and datasets with large samples are often rejected even when they describe relationships well (Schermelele-Engel and Moosbrugger 2003). My datasets are exceptionally large (*B. mckayi* n = 153735 and *B. occidentalis* All Years n = 56953, *B. occidentalis* 1960 to 1994 n = 2016, *B. occidentalis* 1995 to 2020 n = 37401), because we used pairwise comparisons of predictor variables for each genotyped specimen. In both cases, the  $\chi^2$  statistic was reduced by more than an order of magnitude from the baseline model (*B. mckayi* baseline: 54,769.419, *B. occidentalis* baseline: 354497.631, Table 3.8 for model statistic), but the  $\chi^2$  statistic remained significant. However, the relative tests of fit indicate that the predictors in the models do improve model fit and, therefore, are useful to describe changes in the response variables. We was not able to generate models for the datasets that included only data from *B. occidentalis* from 1960 to 1994 and *B. occidentalis* from 1995 to 2020 that fit well enough to be interpreted with any confidence. Therefore, results are only presented for the models with the full datasets (1960 to 2020).

Measurements of habitat quality, maximum monthly temperature, and mean monthly temperature did not improve the model fit to the data when they were included in models for either species, so they were removed from the analyses completely. Temperature was represented in the models by monthly minimum temperatures.

Of all the variables we measured, only distance from a known infection of *V. bombi* had a significant relationship to D in *B. mckayi* (Fig. 3.8). For every 1 kilometer

that a pair of specimens was farther away from known *V. bombi* infections, they were 0.067 D units more closely related (the value in Figure 6 is negative, indicating that genetic distance is decreased). This relationship accounts for the geographic distance between the pair of specimens. This indicates that specimens that were farther from *V. bombi* infections were more likely to exchange genes (have gene flow) than specimens that were closer to *V. bombi* infections, even if the pairs of specimens were the same geographic distance apart.

The variable that had the greatest impact on the D of *B. occidentalis* was geographic distance, which is a latent variable that is composed of two variables with different units. The standardized CFA indicates that least cost distance (the more conservative measure) accounted for roughly twice as much variance as random walk distance (the more liberal measure, Table 3.10). For every one standardized unit of geographic distance that a pair of specimens was farther away from each other, they were 0.075 D units less closely related (accounting for the geographic distance of the specimens from each other). Distance from known *V. bombi* infections also influenced genetic differentiation for this species. For every 1 kilometer that a pair of specimens was farther away from *V. bombi* infections, they were 0.027 D units more closely related. Indirect analyses of precipitation and temperature also had significant relationships with D (Table 3.9). The influence of precipitation on D was relatively small, and was primarily driven by precipitation in May, June, and July (Table 3.10). One centimeter increase in the difference in precipitation between the collection locations of the specimens in a pair indicated a decrease of 0.003 D units (more closely related) when mediated by latitude alone and an additional 0.002 D units when mediated by latitude and

elevation. Temperature also had a relatively small effect on D. Only springtime minimum temperatures improved the fit of the model, so minimum temperatures from July, August, and September were not included. One degree Celsius increase in the difference in temperature between the collection locations of the specimens in a pair indicated an increase of 0.002 D units (less closely related). However, when mediated by elevation and latitude, that relationship was weakened by 0.009 D units per degree Celsius. Precipitation and temperature had no significant direct effect on D, they were only influential when contextualized by latitude and elevation.

## **Discussion**

*B. occidentalis* and *B. mckayi* are important and historically abundant pollinators within their geographic ranges (Goulson 2003; Cameron et al. 2011; Koch and Strange 2012). We tested two hypotheses using landscape genetic methods to assess the current and historical genetic diversity and genetic structure within these species: (1) genetic structure among populations has increased and genetic diversity within populations has decreased for *B. occidentalis* over time; these population characteristics have remained relatively stable for *B. mckayi*; and (2) changes in environmental drivers, such as climate, habitat fragmentation, and increased parasite pressures drive patterns of genetic diversity and structure in *B. occidentalis* and *B. mckayi*. Through testing my first hypothesis, we built on the previously published literature that describes the conservation status of these species (Rao and Stephen 2007; Evans et al 2008; Lozier et al. 2011; Colla et al. 2012; Koch and Strange 2012; Williams et al. 2012; Hatten et al. 2015; Pampell et al. 2015; McHugh and Sikes 2016; Sheffield et al. 2016; Graves et al. 2020; Williams 2021), and we presented the first population genetics study to treat these taxa as separate species

(Williams et al 2021, Chapter 1). Through testing my second hypothesis, we used SEMs to directly measure the influence of environmental variables and isolation by distance on the genetic distances between pairs of geographically separated specimens.

*Measurements of heterozygosity within populations indicate inbreeding in most geographic clusters*

We measured significant genetic disequilibrium in most loci and significantly higher than expected inbreeding in most geographic clusters in both species. However, there was no evidence that populations from recent years were more likely to be inbred than populations from earlier sampling years. We detected higher rarefied allelic richness within most populations of both species than was previously reported for *B. occidentalis* or other North American *Bombus* species within the continental U.S.A. (Lozier et al. 2011). Despite relatively high absolute values of rarefied allelic richness within geographic clusters, we detected a weak statistically significant decline in allelic richness through time in *B. occidentalis* and a non-significant trend of decline in *B. mckayi*. The measured loss in allelic richness is not likely to be biologically meaningful, but signals a need for ongoing monitoring, in case the trend continues. These results may indicate that geographic clusters have been isolated from each other for many generations (at least several generations before 1960), but that genetic diversity within them was slow to decrease. These results may reflect a lag in the loss of allelic diversity due to inbreeding. A simulation study found that in some species (trees), populations with more than 500 (reproductive) individuals had elevated  $F_{IS}$  values after only 5 generations, but did not incur substantial decreases in allelic richness until several generations later (Stefenon et al. 2012).

An alternative explanation is that allelic richness and inbreeding are not associated in this dataset. Although we detected statistically significant genetic disequilibrium, the magnitude of the effect may not reflect strong genetic isolation. Allelic richness decreases in inbreeding populations, but it also decreases with reductions in abundance, which are not necessarily associated with reduced gene flow. For example, allelic richness would be expected to decrease suddenly in response to a pathogenic outbreak or large disturbance event that removes many individuals from a population. Such events would not necessarily prevent gene flow among the surviving populations. The detected decrease in allelic richness from 1960 to 2020 was gradual in both species, and did not coincide with the observed sudden decrease in abundance for *B. occidentalis*. Although the allelic richness was lower in the time frame after the decline, it increased slightly during that time for both species (statistically significantly only for *B. mckayi*). Continued monitoring is necessary to determine if *B. occidentalis* or *B. mckayi* will continue to gain allelic diversity in future generations.

*Measurements of genetic structure among populations indicate lower levels of gene flow among populations than previously detected*

Our analyses of genetic structure among populations of *B. mckayi* and *B. occidentalis* indicate that populations within both species may be more isolated than previous studies have indicated. Cameron et al. (2011) measured the abundance and genetic structure of *B. occidentalis* within the contiguous U.S.A. (CONUS) from 2009 to 2011 and Lozier et al (2011) measured the same characteristics within CONUS and Alaska. While both of these studies found a severe decrease in relative abundance in CONUS, they reported low global  $F_{ST}$  values (0.032 from Cameron et al. (2011) and

0.035 from Lozier et al., including Alaskan populations). Our reported  $F_{ST}$  values were much higher than those previously reported, which may indicate less gene flow among populations of *B. occidentalis* and similarly low gene flow among populations of *B. mckayi*. However, there are several other factors that may have inflated our measurements of genetic structure relative to other studies.

One possible explanation for the higher  $F_{ST}$  values is that the samples included in our study were taken from across many generations. Microsatellite markers are neutral (not under selection) and have relatively high mutation rates (Estoup and Angers 1998; Gemayel et al. 2012; Vieira et al. 2016) compared to other genetic markers (especially other nuclear markers), which makes them useful for measuring genetic changes within and among populations over short time-scales due to genetic drift. However, this characteristic also means that genetic structure among populations due to population isolation (reduced gene flow) and time (genetic drift) are confounded. To accommodate this limitation, population genetic studies that use microsatellite markers are often conducted using specimens that were collected in the same generation (bumble bees are annual species, so one generation is one year), or as close to the same generation as possible (Cameron et al. 2011; Koch et al. 2017; however see Rosche et al. 2022). This limitation often prevents sampling from across the entire range of widespread species due to the practical limitations of conducting field work across a large geographical area in one or a few years. A goal of this study was to leverage the resource of museum specimens collected from across time to compare population genetic characteristics within and among populations across time. We used a correction to account for genetic differentiation due to time, rather than population isolation, which reduced the amount of

among-population variance detected by AMOVA considerably in both species. To test the change in genetic structure through time, we measured global  $F_{ST}$  among populations from similar years (at most seven years per analysis). Although the relationship was not significant, there was an observable increase in  $F_{ST}$  values through time, and we suspect that a larger dataset (more populations sampled within each year) may have resulted in statistical significance. Additionally, the global  $F_{ST}$  value for *B. occidentalis* populations collected from 2007 to 2009 was 0.13, still higher than that reported by Cameron et al. (2011) or Lozier et al. (2011).

A second possible reason for the higher detected genetic structure values in this study could be small sample sizes (largest  $n$  for *B. occidentalis*: 45, largest  $n$  for *B. mckayi*: 93), although samples of 4 to 6 individuals have been shown to be sufficient to accurately estimate genetic structure using  $F$  statistics when the number of loci used for genotyping is high (Willing et al. 2012). Cameron et al. (2011) did not report the number of specimens included in each sampling group and Lozier et al. (2011) collected between 7 and 34 specimens per site (average 17.69 standard error 2.60). Both studies used the same microsatellite loci for genotyping as we did. They amplified between eight and ten loci for each *B. occidentalis* specimen, which is similar to our amplification success. Although the small sample sizes of some of the geographic clusters in our study may have inflated our  $F_{ST}$  values relative to those reported by previous studies, that statistical artifact does not account for the magnitude of difference between the measured genetic structure in the studies. Our results indicate that gene flow is lower among populations in *B. occidentalis* and *B. mckayi* than is expected based on results from previous studies.

Finally, the analysis conducted by Cameron et al. (2011) focused on *B. occidentalis* populations from a much smaller portion of the species range, mostly from the intermountain west of the United States of America. The subsequent study by Lozier et al. (2011) expanded this data set to include populations from Alaska (now *B. mckayi*) but did not include many Canadian specimens. This difference in sampling range is likely to influence estimates of  $F_{ST}$  because isolation by distance increases those estimates (van Strien et al. 2015).

No other population genetic study has specifically focused on *B. mckayi* to date (however see Lozier et al. 2011 for a study that includes *B. mckayi* specimens sampled from Alaska), but abundance surveys indicate that it had a stable abundance and distribution as of 2015 (Koch and Strange 2012; Pampell et al. 2015; Sheffield et al. 2016). Structure analyses and the Mantel test both indicated that the structure in *B. mckayi* was more strongly associated with geographic distance than *B. occidentalis*. Also, the relationship of increasing  $F_{ST}$  values throughout time that we observed in *B. occidentalis* was not as strong in *B. mckayi* (neither relationship was statistically significant). These measurements indicate that populations of *B. mckayi* are exchanging more genes than populations of *B. occidentalis* and more of the genetic structure detected in *B. mckayi* may be associated with natural environmental barriers to gene flow rather than recent population declines. Recent studies indicate that population structure is not necessarily similar across bumble bee species, with some species indicating an effect of isolation by distance (IBD) and other species exhibiting no such patterns, even species that have broadly overlapping ranges (Koch et al. 2017). This finding indicates that population structure may be dependent on species specific niche characteristics. If more



of the genetic structure in *B. mckayi* can be described by natural IBD, the elevated  $F_{ST}$  values detected in this study may be less of a conservation consideration for *B. mckayi* than they are for *B. occidentalis*, and more of an indication of local adaptation among populations across a heterogeneous landscape.

*The influence of environmental variables on maximum entropy models of B. mckayi and B. occidentalis*

Until the recent split of *B. mckayi* from *B. occidentalis*, the relationships between the species and their environments were likely confounded, because they were treated as a single species. This study presents the first assessment of a *B. mckayi* ecological niche model and compares the environmental predictors of that species to those of *B. occidentalis*.

*Bombus mckayi* and *B. occidentalis* were influenced by different environmental predictors in the MaxEnt models. Precipitation was important for *B. occidentalis*, but not *B. mckayi*. This may be because the range of *B. occidentalis* extends into semi-arid and arid habitats, whereas precipitation is relatively abundant throughout the range of *B. mckayi* (Lemmen and Warren 2004; Kharin et al. 2013; Westra et al. 2014). The impact of precipitation (or lack thereof) on *B. occidentalis* is likely to increase into the future, particularly along the southern and eastern edges of the range, as projected climate change for those regions includes hotter, drier summers and longer, more variable springs. While temperature is projected to increase dramatically across the range of *B. mckayi*, precipitation is predicted to remain stable or increase slightly (Lemmen and Warren 2004; Kharin et al. 2013; Westra et al. 2014; IPCC 2018; IPCC 2019).

Variability in springtime temperature was an important predictor for both species. Spring is the time when new queens forage and establish nests. Increased stressors associated with variable springtime temperatures, or potential climatic release of predators or parasites associated with warmer springs (Clare et al. 2016; Gehman et al. 2018; Turner et al. 2020) may have strong impacts on the success or failure of nests. Springs and autumns are predicted to get longer and more variable in temperature and precipitation in the intermountain west of the USA and southern Canadas, and temperatures throughout all seasons are predicted to increase across the range of *B. mckayi* (Cayan et al. 2001; Lemmen and Warren 2004; Melaas et al. 2018).

The ranges of both *B. mckayi* and *B. occidentalis* include mountain ranges throughout, but elevation was an important predictor for only *B. occidentalis*. This is likely because elevation is associated with a greater shift in temperature and precipitation at low latitudes than it is at high latitudes (Minder et al. 2018). *Bombus occidentalis* is more likely to be captured at high elevation sites at the southern end of its range (Fig. 3.1), because high elevation sites have lower temperatures and higher precipitation (Cameron et al. 2011; Notarnicola 2020). However studies indicate that these habitat refugia are warming and drying faster than lower elevation sites (Minder et al. 2018; Notarnicola 2020) indicating that some populations isolated on high elevation sites in the southwestern USA are at highest risk of encountering unsuitable habitat. High elevation sites at northern latitudes are too cold for many bee species, but *B. mckayi* is evolved to thrive in temperate and arctic habitats, and has not been found to be limited by low temperatures within its range (Koch and Strange 2012). However, the short growing season and presence of year-round ice at high elevations at northern latitudes likely

provides some limits, even if elevation is not a factor, and future warming and ice loss may result in a net gain of suitable habitat.

Changes in the drivers of *B. occidentalis* occupancy between the two time-frames (1960 to 1994 and 1995 to 2019) reaffirm the importance of springtime minimum temperatures for this species. This association may be driven in part by minimum thermal tolerance, but is more likely to be associated with changes in vegetation phenology, particularly bloom timing (Cayan et al. 2001), and with competitive pressures due to ecological release (Clare et al. 2016; Gehman et. al 2018; Turner et al. 2020). However, maximum thermal thresholds seem to influence bumble bee movement (Oyen et al. 2016), and temperatures during the hottest time of the year were more influential in the later time frame. Additionally, there was a shift in the importance of elevation, from being ranked as the second most important variable in the early time frame to one of the least important variables in the later time frame. This seems counter-intuitive, because as temperatures change species are expected to move upward in elevation (Pyke et al. 2016) or poleward in latitude (Kerr et al. 2015) to track suitable climate, and some bumble bee species have been shown to do that (Kerr et al. 2015; Pyke et al. 2016). However, *B. occidentalis* has always been a montane species, and it may have already maximized potential elevation gain within the most vulnerable portions of its range (southern edge, Cameron et al. 2011). There is evidence that bumble bees are not shifting their ranges north in latitude to track suitable climate (Kerr et al. 2015; Soroye et al. 2020). If all of these trends hold for *B. occidentalis*, it is possible that elevation is less influential for contemporary populations than it once was, because warming springs have reduced the suitability of high elevation habitat, so that it is no longer optimal.

A possible stressor that was not included in this model was wildfire. Although wildfire has not been identified as a direct stressor to any North American bumble bee species to date, increased fire frequency and size across ranges of both *B. mckayi* and *B. occidentalis* are changing the composition of vegetation on the landscape and are predicted to continue to have major impacts on vegetation in western North America into the future (Kasischke et al. 2010; Wang et al. 2016a; Stralberg et al. 2018; Wotton et al. 2017; Holden et al. 2018; Fusco et al. 2019; Rogers et al. 2020). Such changes may alter or limit the quality and quantity of nesting sites for ground nesting bumble bees, including *B. mckayi* and *B. occidentalis*, in the future. Impacts of wildfire on bumble bee nesting under these changing conditions is an area that needs further study.

*Assessment of structural equation model fit to determine suitability for interpretation*

There is no single statistical significance test that measures the fit of SEMs, so all goodness-of-fit measures have to be taken together (Bauer and Curran 2020). The only measure associated with a significance test is the  $\chi^2$  test (Bauer and Curran 2020), which did not achieve non-significance for any of our models. This result indicates that there is variance in the dataset that is not explained by the model, despite indications of good fit from the other (relative) fit measures. Due to our large datasets, which are known to prevent statistically significant  $\chi^2$  results (Schermelleh-Engel and Moosbrugger 2003), and good-fitting relative measures, we accepted the models for *B. mckayi* and *B. occidentalis* from 1960 to 2020 as good-fitting models and interpreted them with confidence. However, we could not identify good-fitting models for *B. occidentalis* from the time frames that roughly represent relationships before (1960-1994) and after (1995-2020) the observed decrease in abundance and range. The poor fit of these models is

perplexing because they represent subsets of the larger dataset which are represented well by the models. Additionally, even as subsets of the full data, the size of the datasets for these analyses were still quite large (1960 to 1994,  $N = 2016$ ; 1995 to 2020,  $N = 37401$ ).

The most likely explanation for this lack of fit is simply that relationships among samples from these shorter time frames were not strong enough to explain the datasets. Variance within the data was quite high for most predictors, and was exaggerated by the fact that each datapoint represented a comparison of measurements between two points, rather than a single point (though this is also true in Wang et al. 2013). One possible solution to this problem may be to use  $F_{IS}$  rather than  $D$  as the genetic response variable in models.  $F_{IS}$  is a measure of inbreeding derived from measurements of heterozygosity within populations rather than a ratio of amino acid substitutions among individuals (Wright 1951; Holsinger and Weir 2009), so it is not a direct measurement of genetic differentiation. However,  $F_{IS}$  increases in populations that are genetically isolated and can be used as an indicator of a lack of gene flow into those populations (Holsinger and Weir 2009). The benefit of using  $F_{IS}$  is that it is not a pairwise measurement, so the relationships between the predictor and response variables are more straightforward, and may have lower variance. The drawback of using  $F_{IS}$  rather than  $D$  is that sampling units become populations (geographic clusters), rather than individuals, which limits sample sizes considerably; in this study *B. mckayi*  $N = 36$  and *B. occidentalis*  $N = 48$ . Additionally, using population genetic measures excludes samples that were not collected as part of a series (that come from geographic clusters with only one specimen). A second possible solution to this problem may be to use a different type of model (in place

of an SEM) to describe genetic differentiation along the genetic gradient, Milligan et al (2018) suggests the spatial  $\Lambda$ -Flemming-Viot model.

*The influence of environmental variables on the genetic variation of B. mckayi and B. occidentalis across the landscape (i.e. resistance)*

This study is the first attempt to determine relationships between environmental variables and gene flow (or resistance to gene flow) in *B. mckayi* or *B. occidentalis* using SEMs. The loadings for each regression were reported in units of D (0 to 1) and represent the average amount of change in D within pairs of specimens per unit of change in the predictor.

The largest effect was geographic distance. The relationship of distance was significant within *B. occidentalis*, but not within *B. mckayi*, despite being stronger. This is likely due to a high amount of variance in the RandomWalk and LeastCost distance datasets. If the relationship with geographic distance for *B. mckayi* is cautiously interpreted, the strength of the relationship indicates that *B. mckayi* is more strongly influenced by IBD than *B. occidentalis*, which agrees with the results of the Mantel test.

The second most influential relationship for *B. occidentalis* and the most influential statistically significant relationship for *B. mckayi* was with distance from *V. bombi* infections. In both cases, specimen pairs that were collected closer to the locations of known *V. bombi* infections were less genetically differentiated, indicating that they were more closely related. This relationship could be confounded with geographic distance, if the specimens driving the relationship are geographically close to the same detected *V. bombi* infection, and therefore close to each other, but the fit of the model decreased when geographic distance and distance from *V. bombi* infections were allowed

to correlate. The correlation between geographic distance within the pair of specimens and distance from a known *V. bombi* infection had to be removed to improve the model fit, indicating that geographic distance was likely not a confounding factor. Koch and Strange (2012) detected similarly high *V. bombi* infection rates in *B. mckayi* and *B. occidentalis* in 2010. Cameron et al. (2016) measured an increase in infection rates in *B. occidentalis* that began in the mid 1990's, but did not report *B. mckayi* separately from *B. occidentalis*. Cameron et al (2016) reported that the four North American *Bombus* species included in the study with high *V. bombi* infection rates were decreasing in abundance and range. It is possible that the effect of the drivers of the reported decline in the four measured species is having the same effect in *B. mckayi*, but later than in the other species or to a moderated extent because of the relative isolation of the species range from other drivers with potentially compounding effects (e.g., agricultural lands, dense urban areas).

Finally, the indirect relationships of precipitation and temperature on the genetic differentiation of *B. occidentalis* were statistically significant. However, the influences were so small, it is likely that they are not biologically meaningful. Habitat quality and distance from agricultural fields were poor predictors that did not improve the fit of any of our models, but may fit better in a model that does not include pairwise comparisons.

Some variables that were not included in the model but that may be barriers to gene flow for these species include competitive interactions with other species, such as domestic honey bees, and density of roads across the landscape. Sufficient data to inform analyses of these variables is not currently available, but there is some evidence to suggest that they have an impact on colony success and reproductive bumble bee

movement across the landscape (Thomson 2004; Keilshon et al. 2018; Fitch and Vaidya 2021), and they merit additional study.

For this system, a combination of SEMs that measure variable influences on  $D$  and  $F_{IS}$  may be best to resolve relationships between environmental predictors and gene flow. Comparisons of geographic distance to  $D$  among pairs of samples is a biologically meaningful way to assess the relative influence of IBD on species. However, measuring the differences of the effect of temperature and precipitation as mediated by elevation and latitude, the differences in habitat quality at collection sites, or combined distance from agricultural lands are regressions that may be too convoluted to describe the true relationships between the variables. Also, significant relationships between distance from *V. bombi* infections and  $D$  that were detected in the models presented here may prove to be even stronger when regressed with  $F_{IS}$ . Sample size is a concern for models that use populations rather than specimens as sampling units because a lack of degrees of freedom may limit the power of the model. However careful design could mitigate these issues.

#### *Conclusions and implications for conservation*

The results of the population genetics analyses partially support my first hypothesis. Both *B. mckayi* and *B. occidentalis* have sustained reductions in genetic diversity over time and currently have moderate levels of genetic structure. Although decreases in allelic diversity, and some evidence of inbreeding have been documented in these species, substantial genetic diversity (Holsinger et al. 2009 for interpretation of  $F$  statistics) remains in extant populations, which indicates a good opportunity for recovery of the species if the effects of the drivers of the decline are mitigated.



The results of the SEMs supported my second hypothesis, if somewhat weakly. Improvements on the model design may reveal relationships that were not detected in this study. My results indicated that the two species were influenced by different environmental variables, and were influenced by IBD to different extents. The range of *B. mckayi* is at a higher latitude and has less urban and agriculturally developed land than the range of *B. occidentalis*, characteristics which may buffer *B. mckayi* against some of the factors that drive the decline of *B. occidentalis*. However, the strongest ecological driver of genetic differentiation that I detected was distance from known *V. bombi* infections, a surrogate for the likelihood of infection in our samples, which had a stronger relationship to D in *B. mckayi* than in *B. occidentalis*. Despite more dramatic decreases in abundance in *B. occidentalis*, our results indicate that *B. mckayi* may also be facing increased environmental pressures. Additional monitoring is necessary to ensure populations of *B. mckayi* maintain sufficient population sizes and genetic diversity. Additionally, changes in the importance of environmental variables to predict *B. occidentalis* occupancy reaffirm the influence of changing climate on this montane bumble bee species. Future conservation work should focus on mitigating the impacts of increasing parasite loads and increasing temperatures within the ranges of *B. mckayi* and *B. occidentalis*.

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**Data Accessibility**

All data generated for this study will be submitted for publication through the US Geological Survey. When the publication is complete, it will be assigned a DOI number and will be publicly available.

**Benefit-sharing Statement**

This study contributes to the body of information that will inform the upcoming Endangered Species Act listing decision in the USA. It is imperative that this decision is based on the best available science, as it is likely to have ecological and economic impacts throughout the range of the species.

This study would not have been possible without the generosity of the institutions in the USA and Canada who shared their *Bombus occidentalis* specimens with us. This study is an example of the powerful datasets that can be produced through such collaborations. Additionally, this study is a clear example of the value of developing and maintaining museum collections of biological specimens.

**Author Contributions**

Ashley Rohde conceived of the study, collected samples, analyzed data, and wrote the manuscript as part of her dissertation research. James Strange, Michael Branstetter, Karen Mock and Thomas Edwards provided guidance during the development and execution of the project through their roles on the dissertation committee. James Strange and Michael Branstetter secured funding for the support of Ashley Rohde and for research materials.

## Tables

**Table 3.1.** The listed status of North American bumble bees of conservation concern. Bumble bees with an asterisk are parasitic bees from the subgenus *Psitherus*, whose declines parallel the decline of their host species, bumble bees from the subgenus *Bombus sensu stricto*.

Species	U.S. Endangered Species Act	Canadian Species at Risk Act	IUCN Red List
<i>Bombus affinis</i>	endangered	endangered in portion of range	critically endangered
<i>Bombus brachycephalus</i>			endangered
<i>Bombus bohemicus</i> *		endangered	decreasing
<i>Bombus crotchii</i>			endangered
<i>Bombus franklini</i>	endangered		decreasing
<i>Bombus fraternus</i>			endangered
<i>Bombus haueri</i>			endangered
<i>Bombus occidentalis</i>	under review for endangered listing	threatened in portion of range	vulnerable
<i>Bombus pensylvanicus</i>	petitioned for listing		decreasing
<i>Bombus steindachneri</i>			endangered
<i>Bombus suckleyi</i> *			critically endangered
<i>Bombus terricola</i>		species of special concern	decreasing
<i>Bombus variabilis</i> *			critically endangered

**Table 3.2.** Fifteen microsatellite primers were identified for use from previously published literature.

Plex A		Plex B	
Locus	Source	Locus	Source
B124	Estoup et al. 1995	B126	ü et al. 1995
B96	Estoup et al. 1996	BL13	Reber-Funk et al. 2006
BT30	Reber-Funk et al. 2006	BTERN02	Reber-Funk et al. 2006
BT28	Reber-Funk et al. 2006	BTMS0062	Stolle et al. 2009
BTERN01	Reber-Funk et al. 2006	BTMS0066	Stolle et al. 2009
BT10	Reber-Funk et al. 2006	BTMS0086	Stolle et al. 2009
BTMS081	Stolle et al. 2009	BTMS0059	Stolle et al. 2009
		BTMS0083	Stolle et al. 2009



**Table 3.3.** The measured and adjusted units of variables included in the structural equation models.

Variable	Measured Unit	Adjusted Unit
Random Walk distance	Cumulative resistance scores across 10 km raster cells	x 10
Least Cost Distance	meters	/ 10,000
Precipitation	millimeter	centimeter
Temperature	° Celcius	° Celcius
Genetic Distance	Nei's standard genetic distance	Nei's standard genetic distance
Habitat Quality	standardized index units	10 standardized index units
Elevation	meters	/ 100
Latitude	decimal degrees	decimal degrees
Distance to <i>V. bombi</i> infection	meters	/ 10,000

**Table 3.4.**  $\chi^2$  test of genotypic disequilibrium and rarefied allelic richness in the fifteen microsatellite loci used to genotype bumble bee specimens.

Locus	<i>Bombus occidentalis</i>			<i>Bombus mckayi</i>		
	$\chi^2$	<i>p</i>	AR	$\chi^2$	<i>p</i>	AR
B124	178.89	<0.0001	2.59	231.1	<0.0001	2.83
BTERN01	163.81	<0.0001	3.41	146.82	<0.0001	4.99
BT28	150.39	<0.0001	2.1	207.39	<0.0001	2.23
BT10	209.92	<0.0001	2.98	109.16	<0.0001	3.36
B96	53.35	0.005	2.01	51.71	0.044	2.9
BT30	172.46	<0.0001	2.22	168.32	<0.0001	2.02
BTMS081	158.75	<0.0001	2.12	86.66	0.021	2.65
BTMS0066	118.79	<0.0001	3.18	149.91	<0.0001	4.47
BTMS0083	75.43	0.007	2.98	83.24	<0.0001	3.52
B126	171.22	<0.0001	2.81	144.03	<0.0001	3.95
BTMS0062	223.35	<0.0001	3.27	260.19	<0.0001	6.27
BTERN02	177.5	<0.0001	3.4	195.23	<0.0001	5.11
BTMS0086	141.59	<0.0001	1.62	218.73	<0.0001	2.38
BL13	88.52	<0.0001	1.76	233.41	<0.0001	3.19
BTMS0059	86.87	<0.0001	2.5	178.88	<0.0001	3.65

**Table 3.5.** Results of AMOVA analysis of genetic structure among geographic clusters for both species, including analyses using uncorrected Nei's genetic distance matrices and matrices corrected for time between sample collection.  $p$  is the significance of the relationship as described by a Monte-Carlo randomization test.

Species	Variation between clusters	Variation within clusters	$p$
<i>Bombus occidentalis</i>	25.82%	74.17%	0.001
<i>Bombus occidentalis</i> corrected for time	11.13%	88.87%	0.001
<i>Bombus mckayi</i>	20.64%	79.36%	0.001
<i>Bombus mckayi</i> corrected for time	11.84%	88.15%	0.001

**Table 3.6.** Percent contribution of the measured environmental variables to the occupancy likelihood of *Bombus mckayi* and *Bombus occidentalis*. Only variables that contributed a minimum of one percent are listed.

<i>Bombus mckayi</i>	Percent Contribution	<i>Bombus occidentalis</i>	Percent Contribution
mean max temp in September	25.7	mean precip in April	36.5
variation in min temp in April	18.5	variation in min temp in April	26.8
variation in max temp in September	12.9	mean precip in July	8
variation in max temp in June	12.5	variation in min temp in August	4.1
variation in min temp in May	6.3	variation in min temp in June	3.4
variation in max temp in May	5.1	variation in max temp in September	2.9
variation in precip in April	3.7	mean habitat quality	2.5
variation in precip in June	2.8	mean max temp in September	2.4
mean precip in July	2.1	elevation	2.1
mean precip in September	1.1	variation in min temp in September	1.7
elevation	1	variation in max temp in June	1.4
		variation in max temp in April	1.1
		variation in min temp in July	1
		mean precip in August	1
		mean average temp in July	1

**Table 3.7.** Percent contribution of the measured environmental variables to the occupancy likelihood of *Bombus occidentalis* in two time categories, 1960 to 1994 and 1995 to 2019. Only variables that contributed a minimum of one percent are listed.

<i>Bombus occidentalis</i> 1960 to 1994	Percent Contribution	<i>Bombus occidentalis</i> 1995 to 2019	Percent Contribution
variation in min temp in April	34.2	variation in min temp in April	26.4
elevation	12.9	max temp in June	20.8
max temp in September	8.6	variation in max temp in June	15.7
variation in mean temp in April	8.4	variation in mean temp in July	7.7
variation in max temp in September	8.3	variation in mean temp in June	6.1
max temp in July	7.9	variation in min temp in August	3.8
variation in min temp in September	7.1	variation in mean temp in April	3
variation in max temp in May	2.7	variation in min temp in September	2.7
Variation in max temp in July	1.2	variation in max temp in August	2
variation in min temp in May	1.1	max temp in September	1.8
variation in mean temp in August	1.1	variation in max temp in May	1.7
		variation in max temp in September	1.6
		variation in min temp in May	1.5
		elevation	1.1

**Table 3.8.** Scores of goodness of fit for each of the four structural equation models used in this analysis.

Model	$\chi^2 (p)$	CFI	TLI	RMSEA	SRMR
<i>Bombus mckayi</i>	2249.50 (<0.001)	0.960	0.933	0.067	0.044
<i>Bombus occidentalis</i> All Years	27805.4 (<0.001)	0.922	0.886	0.069	0.050
<i>Bombus occidentalis</i> 1960 to 1994	3174.377 (<0.001)	0.834	0.765	0.128	0.082
<i>Bombus occidentalis</i> 1995 to 2020	61785.502 (<0.001)	0.677	0.603	0.142	0.108

**Table 3.9.** Indirect influences of predictor variables on Nei's genetic differentiation. Paths from predictors through latitude and through elevation and latitude were measured. Variables with values of NA were not included in the model, variables with values in gray were not significant at  $p = 0.05$ .

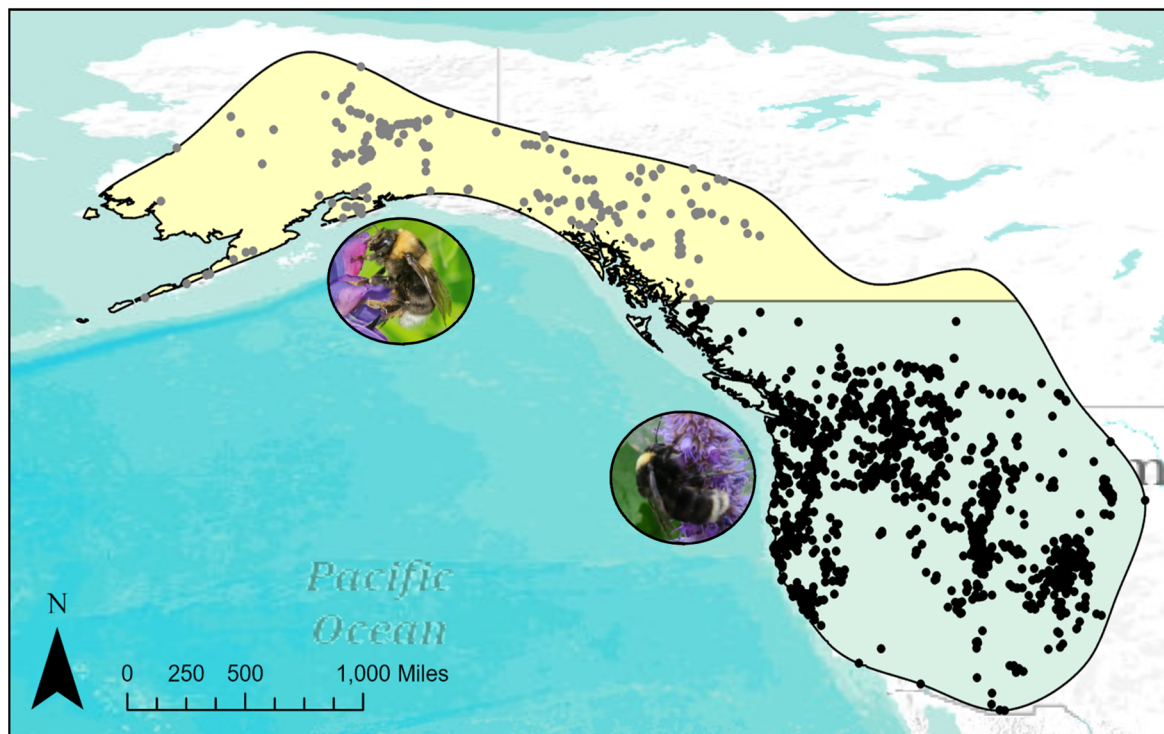
Mediating Variable	Latitude		Elevation and Latitude	
	Precipitation	Temperature	Precipitation	Temperature
<i>Bombus mckayi</i> 1960 to 2020	NA	-0.000013	NA	NA
<i>Bombus occidentalis</i> 1960 to 2020	-0.003	0.002	-0.002	-0.009

**Table 3.10.** Factor loadings of measured variables on latent variables in the model of *Bombus occidentalis* 1960 to 2020.

Geographic Distance		Precipitation		Minimum Temperature	
Variable	Value	Variable	Value	Variable	Value
Least Cost distance	0.4	April	0.567	April	1.158
Random Walk resistance	0.199	May	0.477	May	1.077
		June	0.508	June	0.917
		July	0.037		
		August	0.022		
		September	0.462		

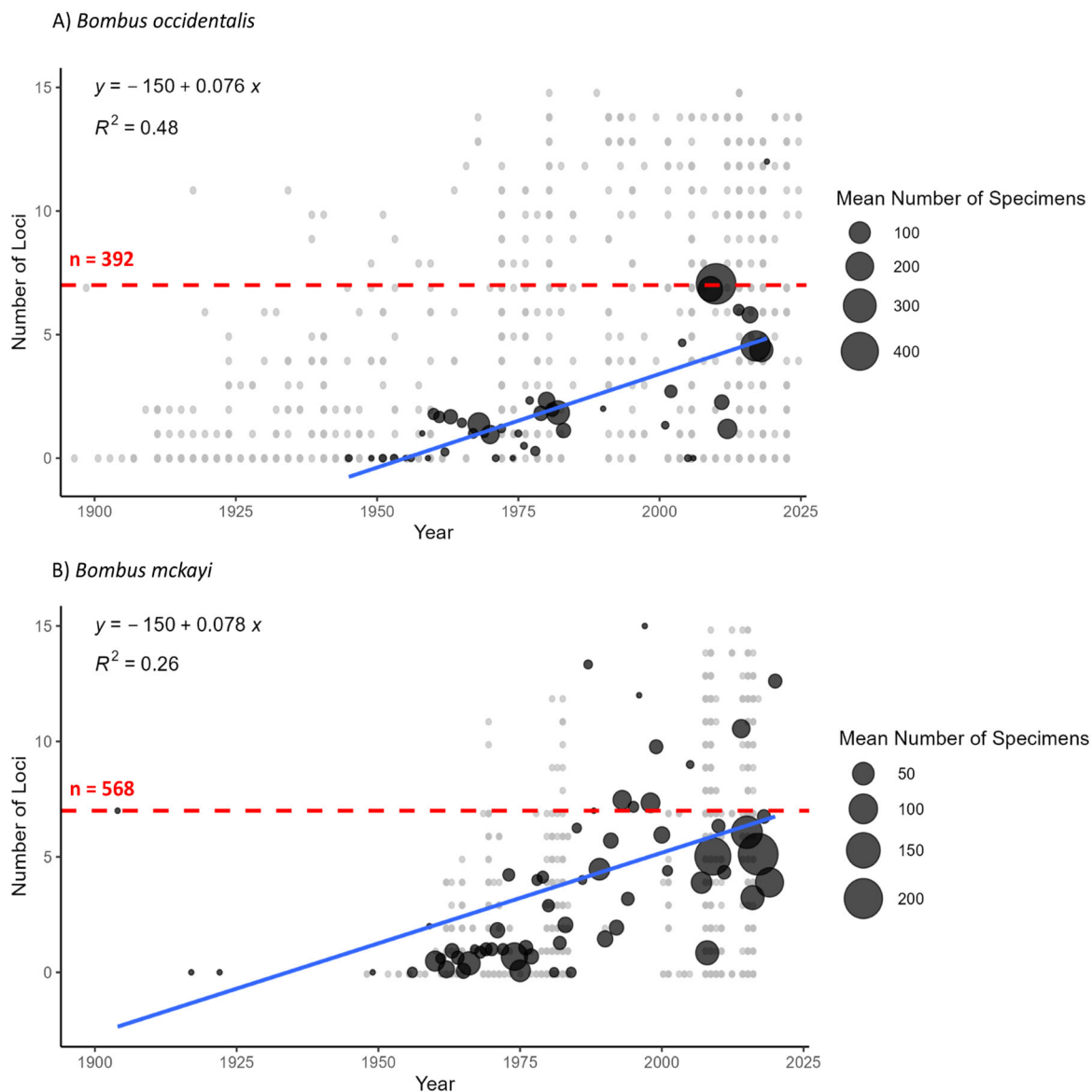


## Figures

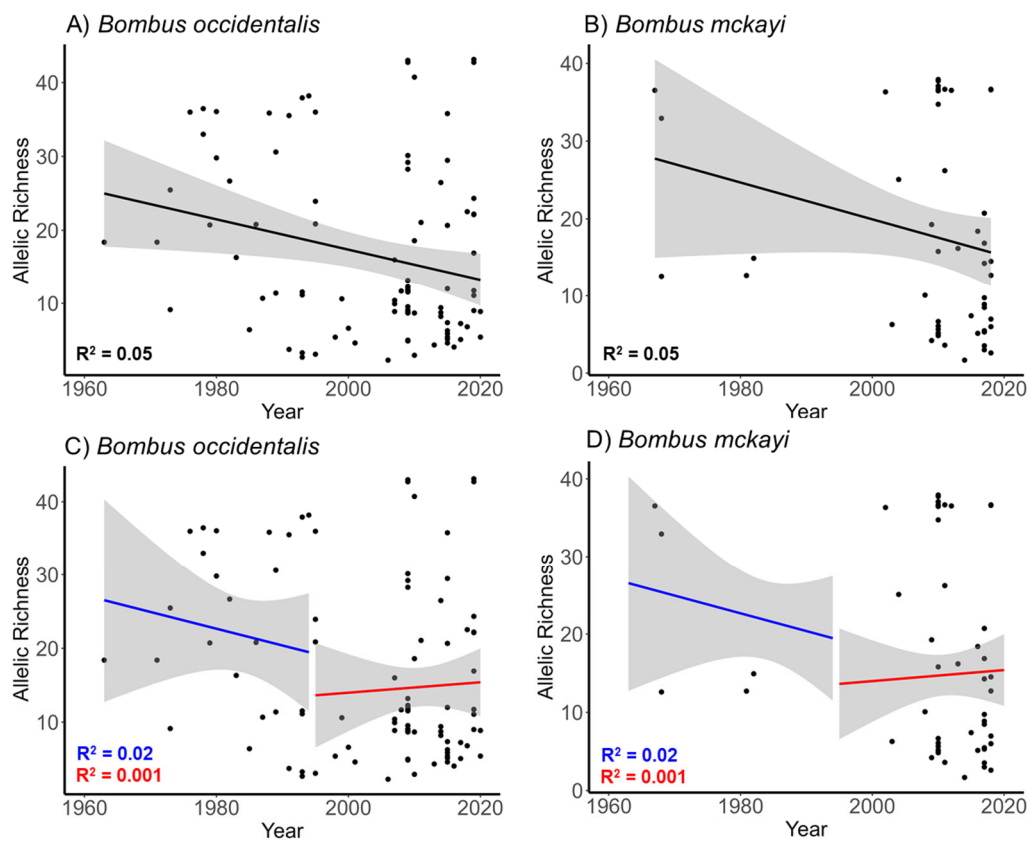


**Figure 3.1.** The historical ranges and recorded observations of *Bombus mckayi* (yellow range, grey observation records) and *Bombus occidentalis* (green range, black observation records).

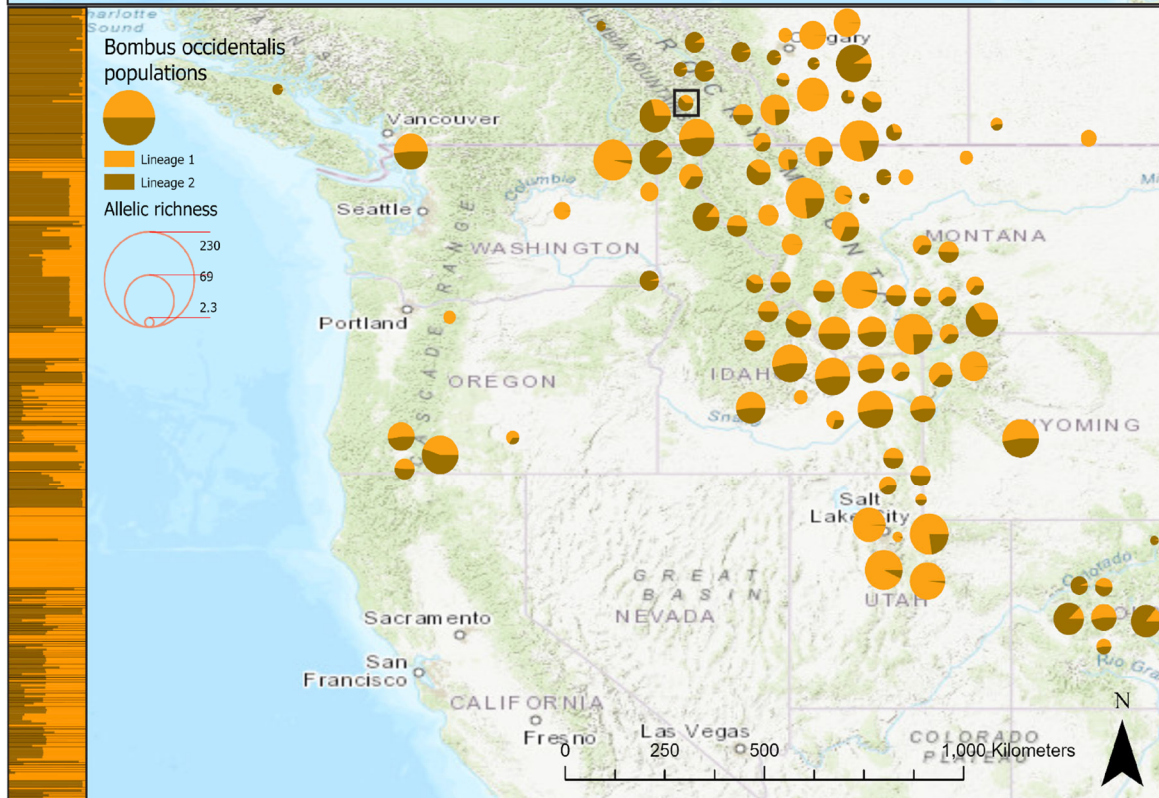
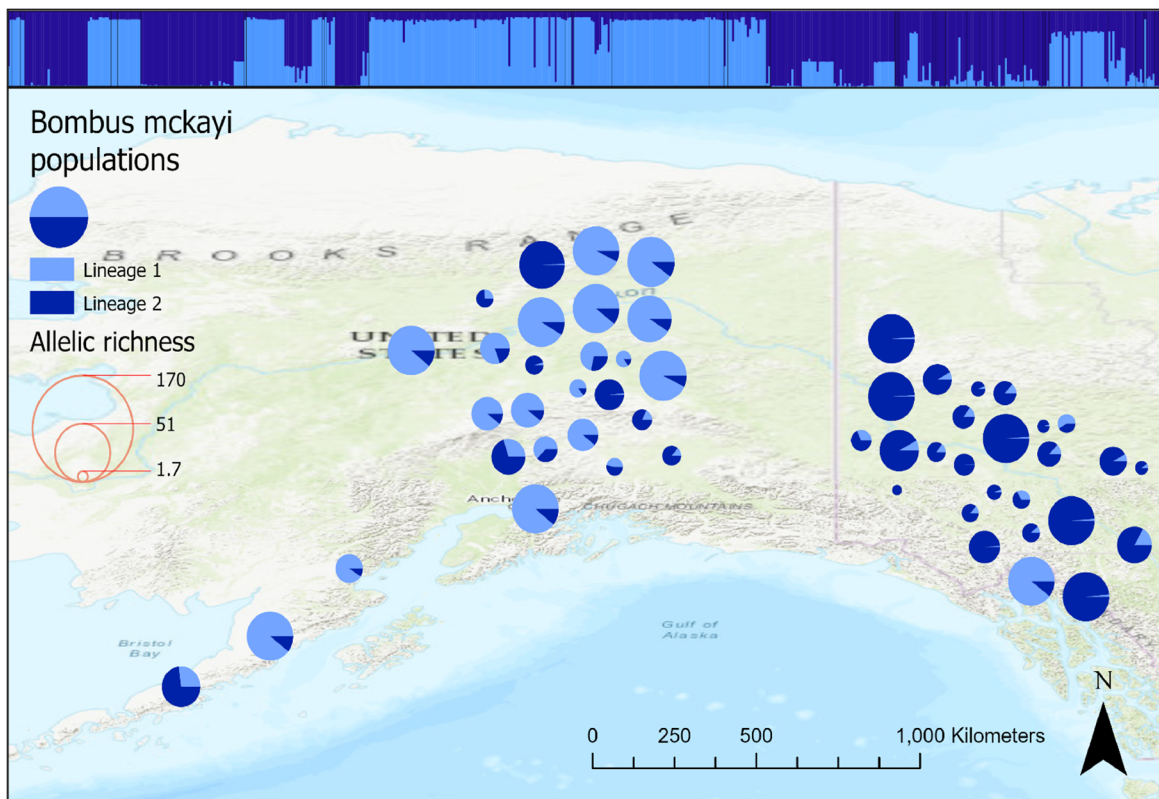
Photo credits: *Bombus mckayi* Alistair Fraser, *Bombus occidentalis* Joyce Knoblett.



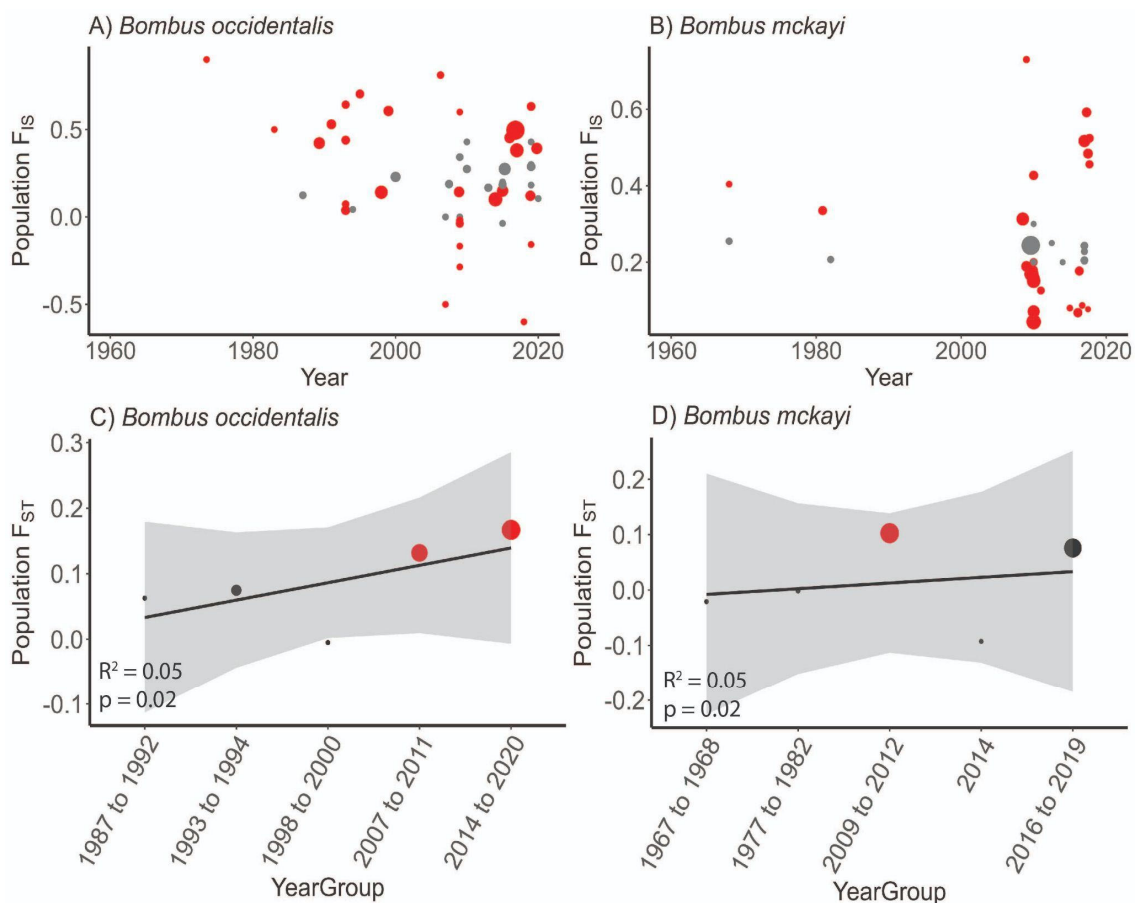
**Figure 3.2.** The number of microsatellite loci that successfully amplified in specimens of A) *Bombus occidentalis* and B) *Bombus mckayi* collected between 1904 and 2020. Small gray circles represent individual specimens, variably-sized black circles represent the mean number of loci amplified for all of the specimens from the year, the solid blue line represents the linear relationship between the number of loci amplified and the collection year, and the dashed red line is the cutoff of seven successfully amplified loci that was determined to represent a useful genotype for downstream analyses. The red n value is the number of specimens that had seven or more amplified loci.



**Figure 3.3.** Rarefied allelic richness of geographic clusters of *Bombus occidentalis* and *Bombus mckayi* throughout time. A and B) samples from 1960 to 2020 included in the linear regression. C and D) regressions from 1960 to 1994 (blue) and 1995 to 2020 (red).

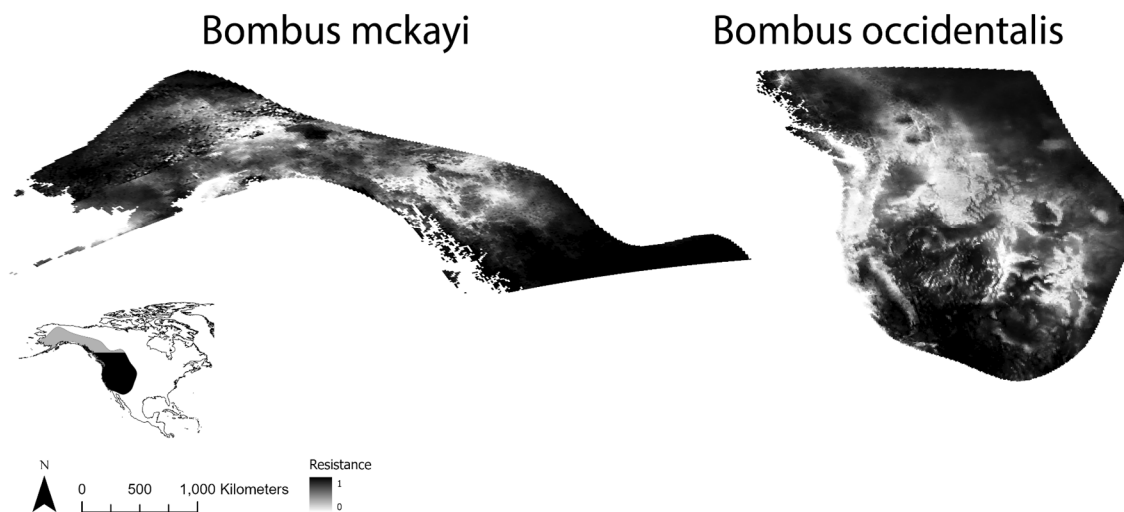


**Figure 3.4.** The geographic distribution of genotyped specimens with seven or more microsatellite loci amplified, grouped into clusters (populations). Each pie represents a single cluster. Color divisions within pies represent the proportion of the clusters that was derived from one of two identified likely lineages. Top: *Bombus mckayi* (blues) and bottom: *Bombus occidentalis* (oranges). The *B. occidentalis* cluster framed in black had an excess of heterozygotes. Sizes of the pies are scaled to the average rarefied allelic richness across all loci within each cluster. Also included are bar graphs of the lineage assignments of individuals, each bar represents the likely lineages of an individual. Gray lines on the graphs demarcate clusters. Clusters were arranged from north to south (top to bottom) for *B. occidentalis* and from west to east (left to right) for *B. mckayi*.

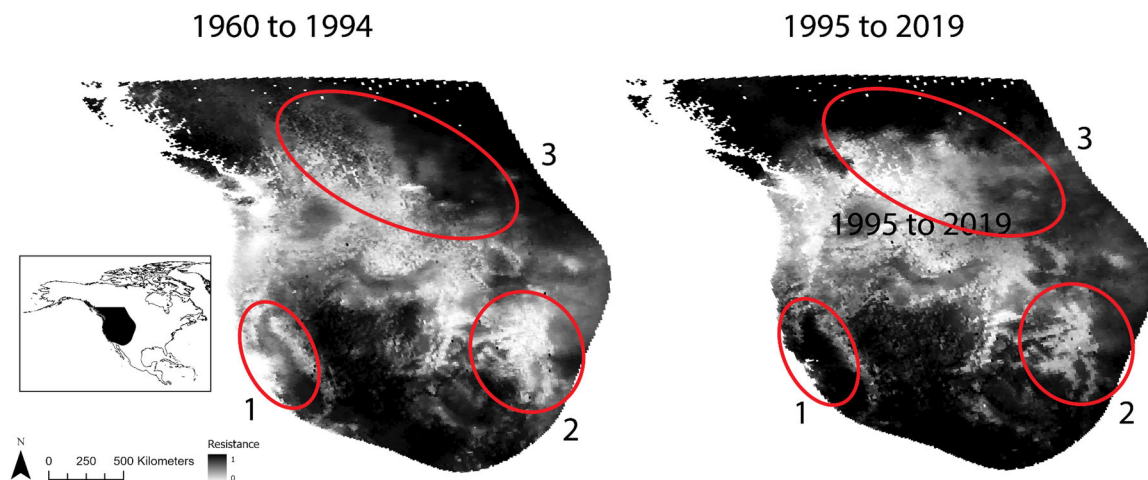


**Figure 3.5.** A and B)  $F_{IS}$  values of clusters of *Bombus occidentalis* and *Bombus mckayi* averaged across all loci and distributed throughout time from 1960 to 2020. C and D) global  $F_{ST}$  values of *B. occidentalis* and *B. mckayi* averaged across all loci among groups of clusters that were sampled within similar years. Samples were compared by single-tailed one sample t-tests, red points represent clusters ( $F_{IS}$ ) or groups of clusters ( $F_{ST}$ ) that had values significantly higher than expected and black points represent clusters or groups of clusters with values that are not significantly different than expected for  $\alpha = 0.05$ . The black lines,  $R^2$  values, and  $p$  values represent linear regressions of values throughout time for each statistic and species. Only populations that were represented with samples greater than one individual were able to be included in these analyses (*B. occidentalis*  $N = 48$ , *B. mckayi*  $N = 36$ ).



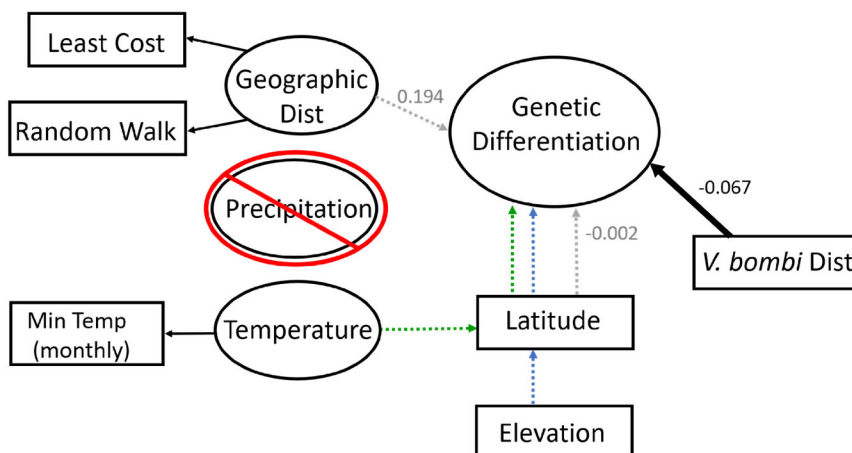
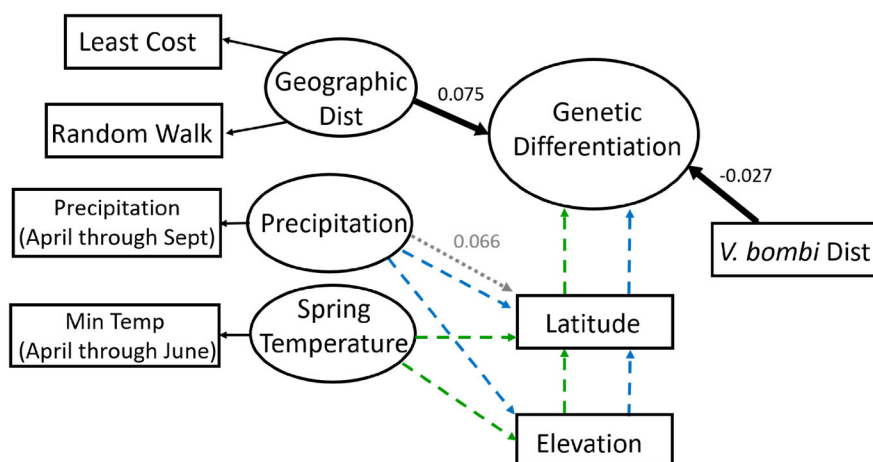


**Figure 3.6.** Resistance distributions based on distribution of *Bombus mckayi* and *Bombus occidentalis* across elevation and averaged weather variables from 1960 through 2019. These time categories roughly represent before and after the observed decrease in abundance and range of *B. occidentalis*.



**Figure 3.7.** Resistance distributions based on the distribution of *Bombus occidentalis* across elevation and averaged weather variables in two time categories, 1960 to 1944 and 1995 to 2019. These time categories roughly represent before and after the observed decrease in abundance and range of *B. occidentalis*.



*Bombus mckayi* 1960 to 2020*Bombus occidentalis* 1960 to 2020

**Figure 3.8.** Graphical representation of the structural equation models used to quantify the relative influences of environmental variables on genetic divergence among individuals across the range of *Bombus mckayi* (top) and *Bombus occidentalis* (bottom). Variables in boxes are measured and variables in ovals are latent. Thin black lines moving from latent variables to measured variables represent confirmatory factor analyses to define latent variables, thick solid black lines represent direct regressions, dotted gray lines represent non-significant direct regressions, colored dashed lines represent path analyses, and colored dotted lines represent non-significant indirect regressions. Colors of the indirect paths correlate with the labels in Table 3.9. Direct regressions onto variables other than genetic differentiation are provided in the supplemental materials.

CHAPTER IV  
MEASUREMENTS OF ATTITUDES AMONG STAKEHOLDERS TOWARD  
MOLECULAR TECHNIQUES IN BIOLOGICAL  
CONSERVATION STUDIES

**Abstract**

Molecular methods are important tools for addressing biodiversity loss by identifying species and populations within species that have low or decreasing genetic diversity. However, adoption of molecular methods to inform conservation decisions has been slow in some areas, while traditional, often abundance-based, methods are used more frequently. This disparity is often called the conservation genetics gap. In order to bridge the gap, practitioners must overcome barriers to understanding and use of molecular methods in conservation studies and policy decisions. In this study, 974 conservationists from diverse backgrounds were surveyed to determine their levels of understanding and trust in molecular and traditional conservation studies that may represent barriers (or motivation) to action. This is the largest and most diverse sample of conservationists ever surveyed to assess attitudes toward conservation genetics. The results indicate that lack of understanding, but not trust, may be a barrier to increased use of molecular methods in these types of studies. However, comparisons of the data presented here to previous studies are hopeful that a shift in perception and increased use of molecular studies may be underway. Establishment of additional centralized conservation genetic research centers in underserved regions of the world, increased incentivization for conservation genetic researchers to communicate their science to

practitioners, and research targeting regionally important topics would improve understanding and utilization of molecular studies in conservation.

## **Introduction**

Conservation science is an amalgamation of data-driven biological studies and social actions that attempt to address degradation in the conservation status of taxa or habitats, which is often caused by human activities (Robertson and Hull 2002; Mascia et al. 2003). However, in order to bridge the gap between data and action, practitioners must overcome three barriers: **understanding** of the results of studies, **trust** that the results are reliable, and **motivation** to change the current conservation status of the target taxa (Mascia et al. 2003; Schultz 2007).

Molecular techniques are being used increasingly often and are gaining impact in conservation studies by providing vital information about the standing genetic diversity within and gene flow among populations of at-risk species (Abdul-Muneer 2014; Kress et al. 2015; Shafer et al. 2015; Thomsen and Willerslev 2015; Corlett 2017; Holdregger et al. 2019). However, these studies are not intuitively easy to understand for practitioners and stakeholders who are not specifically trained to interpret their results. As such, many conservation partners are left out of conversations about these types of studies and the appropriate conservation actions that their results indicate (Keller et al. 2015; Taylor et al. 2017; Sandström et al. 2019; Klütsch and Laikre 2021). A lack of detailed understanding of the results of genetic conservation studies may lead to a sense of mistrust or helplessness that undermines motivation for action in some groups (Taylor et al. 2017; Sandström et al. 2019).

Applications of genetic tools have been shown to be under-utilized in conservation decisions (Hoban et al. 2013a and b; Shafer et al. 2015; Taylor et al. 2017; Sandström et al. 2019; Klütsch and Laikre 2021), especially outside of the United States (Taylor et al. 2017; Sandström et al. 2019) and despite the fact that conservation genetic studies are published at similar rates for all continents except Antarctica (Klütsch and Laikre 2021). Shafer and colleagues (2015) described categories of conservation applications for genetic tools and their relative level of use for conservation activities. They indicated that genetic tools are often used to measure population history, taxonomic identification, inbreeding detection, population census (abundance estimates), and kinship. However, studies of adaptive and quantitative genetic variation, population viability and genetic monitoring are rarely used for conservation studies (Shafer et al. 2015). These latter applications are most relevant to landscape-scale genetic questions that might inform species-level conservation decisions. Hoban et al. (2013a) found that only 24.8% of articles published in the scientific journal *Conservation Genetics* between 2000 and 2013 contained the word “management” and only 0.8% contained the word “policy.” Taylor et al. (2017) found that genetics are only mentioned in conservation policy documents 50% of the time in Australia, 30% of the time in Canada, and 18% of the time in South Africa. Also, when genetics are mentioned in conservation policy documents, genetic diversity is the most commonly mentioned concept, and it is described so generically that it is effectively meaningless (Taylor et al. 2017). Similarly, Sandström et al. (2019), found that genetics were often mentioned in international and national policies on biodiversity conservation in the Baltic Sea, but were rarely mentioned in regional documents. Regional managers in the area indicated that

insufficient explanation of the policies, insufficient resources to implement them, and ambivalence toward the results of genetic studies were all barriers to their implementation.

Measurements of genetic diversity, gene flow or effective population size are less intuitively understandable than traditional studies of conservation status, which often involve simple counts of individuals or populations. Additionally, conservation practitioners who do not have experience with molecular studies or who have had experience with only poorly executed molecular studies may not trust the results of studies that use these methods for conservation. A possible lack of trust in molecular methods has been implied in previous studies, but never directly measured (Taylor et al. 2017; Sandström et al 2019; Klütsch and Laikre 2021). The results of traditional studies more easily overcome the barriers to conservation action than the results of molecular studies (Hoban et al. 2013a; Keller et al. 2015; Shafer et al. 2015; Hoffman et al. 2015; Richardson et al. 2016; Taylor et al. 2017). As a result, the insights provided by genetic studies into the likelihood of recovery and best recovery actions for the target species are not often used to inform conservation decisions (Keller et al. 2015; Shafer et al. 2015; Hoffman et al. 2015; Taylor et al. 2017). This phenomenon is widely known as the conservation genetics gap (Taylor et al. 2017; Britt et al. 2018; Sandström et al. 2019; Klütsch and Laikre 2021). While many studies acknowledge the conservation genetics gap (Haig et al. 2016; Britt et al. 2018; Klütsch and Laikre 2021) and offer suggestions for improving communication between researchers and other conservation practitioners, few actually measured the opinions of conservation practitioners about molecular and traditional methods (however see Taylor et al. 2017 and Sandström et al. 2019). Those

that did interview conservationists focused on professional resource managers in particular geographical regions or fields of interest; a small segment of the broader group represented by the broad category of conservationist. None addressed trust as a possible barrier to implementation separately from understanding (Taylor et al. 2017; Sandström et al. 2019).

The conservation genetics gap leaves practitioners with molecular results that are difficult to interpret and translate into action (Taylor et al. 2017; Sandström et al. 2019; Klütsch and Laikre 2021). This is opposed to traditional abundance or population counts, which are relatively easily interpreted and can be used to justify activities such as breeding programs (Harley et al. 2018), habitat protection (Dunk et al. 2019), or cessation of collection (Campbell et al. 2020) for rare species or lethal or non-lethal controls for invasive species (Fonner and Bohara 2017; Green and Grosholz 2020). Relatively abstract measurements of genetic diversity may decrease the understanding, trust, and motivation that are required to achieve conservation action within communities of stakeholders that actively participate in conservation actions or that are directly affected by conservation actions (Hoban et al. 2013a and 2013b; Keller et al. 2015; Funk et al. 2019, Holderegger et al. 2019; Klütsch and Laikre 2021). This disconnect between research and implementation in conservation is a great loss to conservation efforts, especially since the scientific community will undoubtedly continue to use and develop molecular techniques into the future (Hoban et al. 2013a and 2013b; Holderegger et al. 2019; Funk et al. 2019; Klütsch and Laikre 2021).

This study used a survey to measure the relative understanding, trust, and motivation to action of conservationists from multiple demographics in response to the

results of molecular and traditional conservation studies. It bypassed the question of whether or not the general public is interested in or motivated to act on conservation issues; that topic has been well-studied in other places (Fischer and Young 2007; Schultz 2007, Byg et al. 2017). Instead, only members of organizations that are directly involved in or affected by conservation decisions were included in the study. Participants included professional researchers and resource managers, as well as volunteer conservationists and industry professionals who are affected by conservation policy. In this way, the pool of respondents was limited to individuals who have already demonstrated the understanding and motivation necessary to participate in conservation decisions and activities. This study compared the understanding and resulting action response to molecular and traditional studies by the largest and most diverse group of conservationists ever sampled about their perceptions of the value of molecular and traditional methods for conservation science. Differences in the application of results between genetic and genomic studies was not measured, though genomic studies have been shown to be applied to conservation questions less frequently than genetic studies (McMahon et al. 2014; Taylor et al. 2017). I addressed two hypotheses: First, stakeholders with little understanding of molecular techniques trust the results of molecular studies more than they trust traditional studies. Stakeholders with training in molecular techniques are more critical of the results of molecular studies than stakeholders with little or no training. Second, stakeholders with little understanding of molecular techniques are less likely to be motivated to action based on the results of molecular studies than they would be by traditional studies because they do not understand them as well. Stakeholders with training in molecular techniques are more likely to act on the results of molecular studies than stakeholders

without molecular training based on their relatively strong understanding of the conclusions of these studies.

## **Methods**

### *Creation of a survey questionnaire*

The survey questions were drafted using the technique described by Dillman (1978; 2000). The survey was multi-mode (administered via tablets and online) and contained both quantitative and qualitative questions (Table C1). Qualtrics survey management software was used to create and format the questionnaire. The questionnaire was approved by the Utah State University Institutional Review Board as protocol # 9724.

### *Solicitation of respondents*

Organizations whose missions are directly affected by conservation actions and professionals who work in conservation science were contacted. Each identified organization representative was contacted twice by email, two weeks apart, or by telephone or social media if email was not available. The organization was not contacted again if there was no response after two attempts. If the organization representatives agreed to participate, they were asked to share the questionnaire with the members of their organization. The questionnaire was also submitted twice to potential participants, two weeks apart. Recommendations from the members of responsive organizations were requested for other groups that have an interest in conservation studies. Organization representatives were also encouraged to share the survey with anyone they thought might be interested in participating.



### *Questionnaire design*

Questionnaires were anonymous. However, respondents were asked to disclose their organizational affiliations. The survey consisted of 16 multiple choice questions, 1 short answer question, and one descriptive question (Table C1).

Question 2 on the survey assessed the accuracy of the assumption that members of the organizations included in the sampling pool are interested in conservation activities, regardless of study-type. Answers of “Not very important” and “I do not know” were interpreted as low interest, all other answers were interpreted as high interest. Only respondents that indicated high interest were included in downstream analyses. The remaining questions assessed the respondents’ opinions about the relative importances of species, their experience with molecular and traditional conservation studies, their formal education in conservation science, how they learn about conservation issues, and how they participate in conservation actions.

### *Data analyses*

All of the quantitative data collected in this survey were categorical. Binomial exact tests were used to compare binomial responses, always with a predicted success rate of 0.5 and a confidence level of 0.95. Pearson’s  $\chi^2$  tests were used to compare counts of response choices for nominal multiple-choice questions. A log-linear model was used to compare the levels of experience with molecular and traditional studies between respondents from the U.S.A. and from outside of the U.S.A. This was in response to a previous report which indicated that national policies in the U.S.A. promote the use of molecular methods more than other parts of the world (Taylor et al. 2017). Cochran’s  $Q$  test was used to compare counts of the proportional categorical ranked question.

Understanding of conservation studies was estimated by summing the ranked scores from two questions (for traditional and molecular studies separately): the type of experience and level of training. Trust in the studies was determined by if the respondent believes the studies should be used to make conservation decisions. Motivation to action was determined using the number of conservation studies and the number of conservation meetings the respondents participated in (Table C1). Our measurement of motivation to action may be confounded with opportunity to participate in actions (or lack thereof). By restricting our survey pool to conservationists who are members of conservation organizations we hoped to minimize the effect of restrictions from opportunities to participate in actions, but that restriction may still exist for some individuals. Spearman's rank correlation coefficient (Spearman's  $\rho$ ) was used to make correlations among variables to address the hypotheses.

## **Results**

### *Survey respondent demographics*

Overall, 974 respondents from 333 organizations returned surveys that contributed to this dataset (maximum from a single organization: 62, minimum: 1, mean: 2.5, standard deviation: 5.7). Surveys were collected primarily from organizations in the United States of America, which were targeted by the sampling scheme. However, respondents were encouraged to invite their collaborators to submit questionnaires, which resulted in 89 respondents associated with organizations from outside of the U.S.A (Figure 4.1, Table C2). Comparisons of the use of molecular and traditional conservation methods among countries was not the goal of this study, but previous literature have

indicated that national policies in the U.S.A encourage the use of molecular methods for conservation studies more strongly than policies in other countries (Taylor et al. 2017; Sandström et al. 2019). If this pattern existed in the dataset, uneven sampling between the U.S.A and other countries could produce misleading conclusions. However, a log-linear model indicated that frequencies of respondents reporting experience with different types of conservation studies (see Fig. 4.1 for options for types of experience) was not significantly different between the USA and all other countries ( $z = -0.975, p = 0.330$ ). Responses from all countries were analyzed together in downstream analyses.

Although our solicitation scheme targeted the leadership of organizations, who then disseminated our survey to members of their organizations, some respondents reported membership in organizations for which leadership did not explicitly agree to participate. Therefore, it is important to note that respondents were solicited to participate in this study through their memberships in conservation organizations because they are likely to have a stronger interest in biological conservation than the public at large, but their opinions are their own and do not represent the organizations with which they are associated. Response rates were consistently high for multiple-choice questions (max: 958, min: 882, mean: 921.8 standard deviation: 25.8). Eight hundred and seventy respondents answered the short answer question and 538 respondents answered the descriptive question.

Respondents to the survey were diverse in their experience and motivation for participating in conservation (Fig. 4.2). All respondents in the survey indicated that they were interested in biological conservation by rating it as very important ( $N = 916$ ) or somewhat important ( $N = 58$ ). Six hundred and thirty-eight respondents reported having

experience collecting data for traditional conservation studies (probability of an answer of yes: 0.67,  $p < 0.0001$ ) and 332 respondents reported having experience collecting data for molecular conservation studies (probability of an answer of yes: 0.35,  $p < 0.0001$ ). Respondents had variable levels of training and participated in variable roles within conservation (Figure 2). Respondents who chose “other” for this question listed general interest, private land-owner and science administrator most often (Table C3). Significant  $\chi^2$  tests of the number of respondents that identified different roles in conservation, and different levels of experience and training demographics indicated uneven sampling across the measured demographics (Type of Experience:  $\chi^2 = 254.4$ ,  $p < 0.0001$ , Training:  $\chi^2 = 413.7$ ,  $p < 0.0001$ , Conservation Role:  $\chi^2 = 167.6$ ,  $p < 0.0001$ , Figure 4.2, Table C4 for pairwise comparisons). In particular, many respondents had high levels of training in conservation or related biological sciences and few respondents participated in only molecular studies. One of the drawbacks of collecting data through voluntary surveys is that sampling is often uneven. Some respondents reported holding multiple roles in conservation. In this case, the first role reported was included in analyses.

#### *Learning, interests, and actions taken by respondents*

Most respondents reported that the primary way they learn about conservation science is through scientific papers ( $\chi^2 = 600.45$ ,  $p < 0.0001$ , Fig. 4.3). However, this statistic is skewed by the large group of respondents who hold graduate degrees. Training on how to access, read, and write scientific papers is often taught at the graduate level, and therefore is more likely to be an important source of information for respondents who hold a graduate degree. When respondents with graduate degrees were removed from the analysis ( $\chi^2 = 94.45$ ,  $p < 0.0001$ ), scientific papers, scientific presentations, and popular

science articles were ranked as the most common ways to learn about conservation and were not significantly different from one another (for pairwise comparisons see Table C4). Respondents who chose “other” for this question got their information through direct correspondences with scientists, land managers or, in one case, a conservation consultant.

Respondents expressed diverse values when they were asked what characteristics make a species valuable. Six hundred and ninety-one respondents (72.9%) indicated that some species are more valuable than others and 256 respondents (25.6%) indicated that all species are equally valuable (probability of an answer of yes: 0.73,  $p < 0.0001$ ). Respondents were asked to rank the importance of three characteristics in deciding which species to conserve, and most of them were in agreement that species that play an important role in their environments should be prioritized, followed by species that are unique. Most respondents did not think the value of species to humans should be the top priority for selecting species to conserve, but they did value it as second-most important in most cases (Fig. 4.4). The differences in the rankings of the importance of the three characteristics were significant ( $Q = 918.0$ ,  $p < 0.0001$ ).

Respondents were interested in conservation studies that focused on a wide variety of taxa (Fig. 4.5). Five hundred and eighty-six respondents described a conservation study in which they had participated. The most common taxa of interest by far were plants, while reported studies that focused on fungi and lichens were rare. The respondents' descriptions of the goals of the studies could be grouped into several classes based on life history characteristics of the taxa of interest. For example, some descriptions emphasized native or invasive species. However, 31 of the studies described

did not focus on any taxa in particular, but were landscape scale studies. Seven of those studies focused on habitat assessments, 11 focused on habitat restoration, 13 focused on water quality, and 15 were general biological diversity surveys (not included in Fig. 4.5). The differences in the number of studies that focused on each class of taxa (including landscape scale studies as a class) was significant ( $\chi^2 = 745.88, p < 0.0001$ ) including most of the pairwise comparisons (Table C4). The number of respondents that participated in studies that focused on different taxa characteristics was also significantly different ( $\chi^2 = 1437, p < 0.0001$ , Table C3), with rarity ranked as the most common characteristic of interest and medicinal value ranked as the least common characteristic of interest.

A large majority of respondents indicated that both molecular and traditional studies should be used to inform conservation decisions at least some of the time (molecular: 98.2%, traditional: 99.3%). Sixteen respondents indicated that molecular studies should never be used for conservation decisions and 6 indicated that traditional studies should never be used, which was significantly different from the counts recorded for the other two options (molecular:  $\chi^2 = 402.85, p < 0.0001$ , traditional:  $\chi^2 = 498.31, p < 0.0001$ ). Significantly more respondents answered “yes” than “sometimes” to whether or not traditional studies should be used (“Yes” N=518, “Sometimes” N = 374), indicating a relatively strong level of trust in this type of study. Fewer respondents answered “yes” than “sometimes” for molecular studies (“Yes N = 415 , “Sometimes” N = 461 ), but this relationship was not statistically significant (Table C4 for pairwise relationships).

*Influence of understanding and motivation on conservation actions*

Measures of understanding of traditional and molecular studies were positively correlated with respondents' level of motivation to participate in conservation actions (traditional:  $r = 0.33$ ,  $p < 0.0001$ , molecular:  $r = 0.17$ ,  $p = 0.002$ ), though the effect sizes were not strong, especially for molecular studies. The amount that respondents trusted the results of conservation studies was not correlated with understanding or motivation to action for either type of study. The distribution of data points driving the correlations indicate different relationships between understanding and motivation for the study types (Fig. 4.6). Respondents that had high scores for understanding molecular studies had variable levels of motivation to action, while respondents that had high scores for understanding of traditional studies had mostly high motivation to action.

## **Discussion**

### *Respondents experience with molecular and traditional conservation studies*

Respondents reported having participated in more molecular conservation studies than has been previously described. The most frequently reported type of experience was with traditional studies, but the second most reported option was experience with both types. Many respondents who identified as traditional researchers reported having experience working on molecular studies. Also, many of the respondents who self-identified as land managers indicated that they had worked with both molecular and traditional studies. These results indicate a shift in perception from previous studies, which found that the results of molecular research were far less likely to be implemented by managers or used by policy-makers than the results of traditional studies (Keller et al. 2015; Taylor et al. 2017; Sandström et al. 2019). The trends presented here may indicate

a shift away from the previously documented perception of molecular studies as financially out-of-reach, or unhelpful to address immediate conservation needs (Sandström et al. 2019; Klütsch and Laikre 2021) and towards normalization of the inclusion of molecular methods in conservation studies. However, previous studies included many fewer respondents and focused primarily on resource managers. Our results may simply indicate a different pattern in the broader conservation community that we sampled. Additionally, even respondents who reported the highest level of understanding of molecular studies reported mixed levels of motivation to action based on that understanding, which was in stark contrast to respondents with high levels of understanding of traditional studies, who reported being highly motivated to action (Fig. 4.6).

Most respondents who reported experience working on studies that use molecular methods held graduate degrees or 4-year degrees in conservation science. Almost no respondents with 2 years or fewer of formal training or who identified as non-professional conservationists had participated in molecular studies. It is possible that this contrast between professional and non-professional respondents' experience is driven by the necessity of training to work in genetics laboratories, which is often taught in 4-year programs and above. However, genetic studies require DNA samples from target taxa, which are collected using similar field methods to many traditional studies and can often be performed by technicians or volunteers with minimal training. For example, volunteers have been successfully deployed to collect environmental DNA in many studies (Julian et al. 2019; Larson et al. 2020; Meyer et al. 2021; Lavin 2022).



Respondents also indicated that they participated in conservation studies that focus on diverse taxa and various aspects of conservation (e.g. species rarity, invasive species, etc.). By far, the most commonly studied taxon that respondents mentioned was plants. Respondents were most likely to work on studies that focused on biological communities or rare species. Tissue or pollen samples could easily be collected from plants for use in molecular studies by conservationists with all levels of training. As the use of molecular methods in conservation science continues to grow, steps must be taken to overcome barriers to participation in these studies for conservationists from all backgrounds if the conservation genetics gap is to be closed. These steps may include ongoing education for conservationists without formal genetics training and including conservationists without genetics training at the sample collection stage of molecular studies, which is often similar to sample collection for traditional studies and also provides opportunity for communication and ongoing education about the uses of molecular methods.

#### *Methods for learning about conservation*

Unsurprisingly, most respondents with graduate degrees reported primarily learning about conservation research through scientific literature. However, when this group was removed from the analysis, scientific presentations and popular science articles became equally important sources of information as scientific papers. This result, taken in consideration with the finding that respondents with less than 4 years of formal training are unlikely to participate in molecular studies, indicates that diversification of the methods by which researchers disseminate their findings could improve understanding, especially for molecular studies.

Within professional science communities, a culture of “publish or perish” is pervasive (Moosa 2018; Kiai 2019; Coriat 2019; Chatterjee 2019; van Dalen 2021). However, the data presented here indicate that scientific papers may not be the only way or the best way to facilitate learning among all demographics of conservationists. A survey of science faculty at land grant universities across the U.S.A. indicated that academic researchers were interested in participating in science communication with diverse audiences (outside of their own colleagues), but that they were not encouraged and often felt indirectly discouraged from doing so by colleagues and administrators at their institutions (Rose et al. 2020). A call for a shift in academic culture to incentivize public science communication has been made and clearly documented (Bickford et al. 2012; Cook et al. 2013; Rose et al 2020), and we echo that call here. Also, including non-academic authors on scientific papers has been shown to increase the likelihood that studies provide direct solutions to conservation problems or advice to end-users (Britt et al. 2018). A combination of scientific papers that include authors with diverse experiences, publicly accessible scientific presentations (carefully crafted for a lay audience, Bullock et al. 2019), and increased exposure to novel scientific ideas in popular media may contribute to increased understanding and motivation among conservationists to participate in studies that use conservation genetics.

### *Conservation priorities among conservationists*

Even when respondents demonstrated a strong understanding of conservation methods, their motivation to action varied between molecular and traditional methods. This difference in response may be influenced by their personal values. The characteristics that respondents reported as important in species indicate a diversity of

values among them, which may present both challenges and opportunities to policy-makers whose decisions attempt to reflect those values. The characteristics that respondents valued when choosing species to conserve coincided with several conservation frameworks (van Eeden et al. 2020) that were previously defined. Twenty seven percent of respondents indicated that all species were equally important. This belief coincides with compassionate conservation (Wallach et al. 2018), which combines aspects of the animal rights movement with conservation. Sixty seven percent of respondents agreed that the importance of a species to its environment is its most valuable characteristic. This philosophy coincides with traditional conservation (Soulé 1985), which focuses on maintaining native ecosystems due to their inherent value. Twenty eight percent of respondents ranked the uniqueness of a species as the most valuable characteristic. This philosophy represents conservation based on critical faunas analysis (Vane-Wright et al. 1991; Diaz et al. 2013), which prioritizes conservation of species which are evolutionarily or functionally unique within their ecosystems. This framework is still being developed (Cadotte et al. 2011; Mazel et al. 2018; Mazel 2019), but is also being used with increasing frequency to identify species for conservation (Cadotte et al. 2011; Aurelle et al. 2018; Hoelzel et al. 2019). Very few respondents, 4%, ranked importance to humans as the most valuable characteristic. However, most respondents (81%) ranked it as the second most valuable characteristic, indicating that it is highly valued (but not the top concern) for most respondents. This option represents functionalist conservation (Callicott et al. 1999) which focuses on maintaining the function of ecosystems so humans can continue to use them.

Recognition of the diversity of worldviews and interests among conservationists requires a re-contextualization of conservation problems to a viewpoint that considers the plurality of values and objectives represented in conservation communities (Pascual et al. 2017). Incorporation of multiple worldviews into conservation learning, actions, and policy-making will encourage ongoing learning and participation in studies that include both traditional and novel (often molecular) methods.

#### *Trust in the results of conservation science*

Most of the respondents indicated that they think the results of both molecular and traditional studies should be used at least some of the time. Previous studies that measure the causes of the conservation genetics gap did not specifically measure the impact of conservationists' trust of molecular study results on their motivation to participate in the studies or to incorporate results from them into policy decisions (Taylor et al. 2017; Sandström et al. 2019; Klütsch and Laikre 2021). The relatively strong trust of the results of conservation research expressed by conservationists of diverse backgrounds and priorities in this study is an encouraging result, and provides a firm foundation from which to continue work toward closing the conservation genetics gap through continued education.

#### *Relationships among understanding, trust, and motivation in conservation*

Our results do not support hypothesis 1, that trust of molecular and traditional studies influences conservationists' motivation to action. They do, however, support hypothesis 2, that level of understanding of molecular and traditional studies influences motivation to action. The relationship was stronger for traditional studies than molecular

studies (higher  $r^2$  value, though neither was extremely high), indicating that there are still more barriers to motivating conservationists to participate in molecular studies than there are to motivating them to participate in traditional studies. One possible nuance that wasn't explored in this study is a differentiation between understanding of the meaning of the metrics used in molecular methods and understanding of the potential applications of those data to conservation issues. Previous studies found that one barrier to inclusion of the results of molecular studies in policy documents is the perception that the patterns documented in genetic studies are long-term, and therefore not relevant to immediate conservation decisions (Haig et al. 2006; Taylor et al. 2017; Klütsch and Laikre 2021). It is possible that respondents indicated a high level of understanding for molecular studies because they were familiar with the methods and metrics of genetics, but still did not understand the usefulness of these methods within the context of conservation. It is also possible that these people have a strong understanding of the methods, but prioritize relatively meager funds dedicated to conservation for other tasks over genetic work, such as habitat conservation or restoration. In subsequent surveys on this topic, direct measurement of conservationists' perceptions of the immediate applicability of the results of conservation genetics studies and their perceptions of the value of genetics studies relative to other conservation work when funding is limited would provide interesting insight into the drivers of the conservation genetics gap.

*Recommendations for improving understanding of molecular methods*

Suggestions have been made to improve understanding of conservation genetics tools in previous studies, and address similar themes. Taylor et al. (2017) suggest improved communication among conservation genetic researchers and policy-makers through networking events, improved scientific literacy among policy-makers through training events, and adjusted hiring practices to create a workforce of professional conservationists who are literate in the most current scientific methods. Sandström et al. (2019) recommended increased focus on integrating conservation genetics into regional conservation (as opposed to national or international policy), modifications to policy frameworks to specifically mandate conservation genetics, and financial resources specifically for implementation of conservation genetic studies. Both of these studies, as well as Haig et al. (2016) called for the creation of centralized units (e.g. conservation genetics hubs, national conservation genetics laboratories) where conservation genetics research is conducted and where managers and conservationists can easily obtain information (including raw genetic data and help understanding and interpreting results) that they need to use that research efficiently.

Taylor et al. (2017) and Sandström et al. (2019) identified the U.S.A. as the country most likely to employ molecular methods to make national conservation decisions. They credit this advancement to direct mandates from the U.S. Endangered Species Act to include the “best available science” in listing decisions, and to the U.S. Fish and Wildlife Service Conservation Genetics Laboratory. While it is true the U.S.A. has a strong national framework for including molecular data in conservation actions, international efforts in other parts of the world must not be discounted. Efforts through

the United Nations Convention on Biological Diversity (<https://www.cbd.int/>) call for political awareness of the value of genetic information for conservation, outline general applications for genetic information to conservation questions, and encourage international resource sharing. The European Molecular Biology Laboratory (<https://www.embl.org/>) conducts molecular biology, including research focusing on biodiversity, and researchers associated with the laboratory recently published a call for world-wide genetic data-sharing through a similar framework as their European Bioinformatics Institute (Scholz et al. 2022). Academic societies dedicated to conservation genetics exist and societies that focus on biodiversity more broadly often have subsections that focus on conservation genetics. Additionally, universities around the world host research programs that contribute directly to conservation genetics. All of these organizations fill the role of producing conservation research, possibly fulfilling the need for additional centralized conservation genetic research facilities in some places. However, these resources are not equitably distributed around the world (Culley et al. 2021; Titley et al 2021). If additional centralized conservation genetics research laboratories are to be established, as previous studies have recommended, resources should be focused on establishing them in underserved areas. Although there are many organizations that produce conservation research, they may not fill the role of providing a platform for interactions between researchers and conservationists who play different roles in conservation (e.g. managers, volunteers, private land-owners). Incentivizing these interactions at existing research institutions may help to improve understanding among diverse conservationists while leveraging resources available through those institutions and changing the perception among researchers that science communication is less

valuable than direct research. These interactions could also help researchers to identify species or ecosystems of particular interest to regional resource managers, which increases the likelihood that the results from those studies will be incorporated into on-the-ground conservation actions (Sandström et al. 2019).

This study concluded that understanding, and not trust, is likely to be the greatest barrier to the use of molecular information in conservation decisions. Ongoing efforts to narrow or close the conservation genetics gap should include improved education of conservation stakeholders about molecular methods. This improvement will require increased access to learning opportunities for decision-makers and conservation practitioners without molecular training, and increased incentivization for molecular researchers to engage in outreach.

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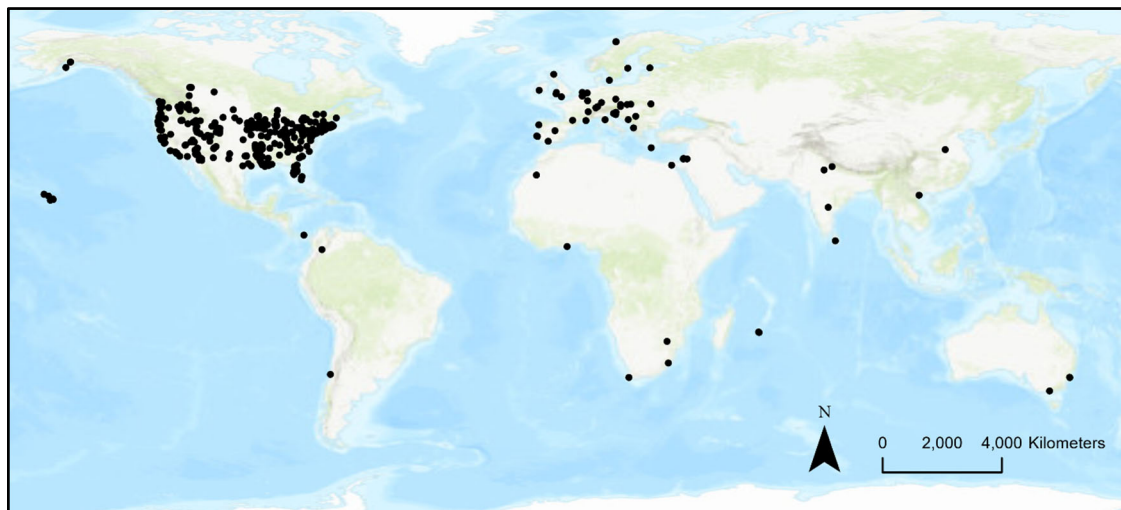
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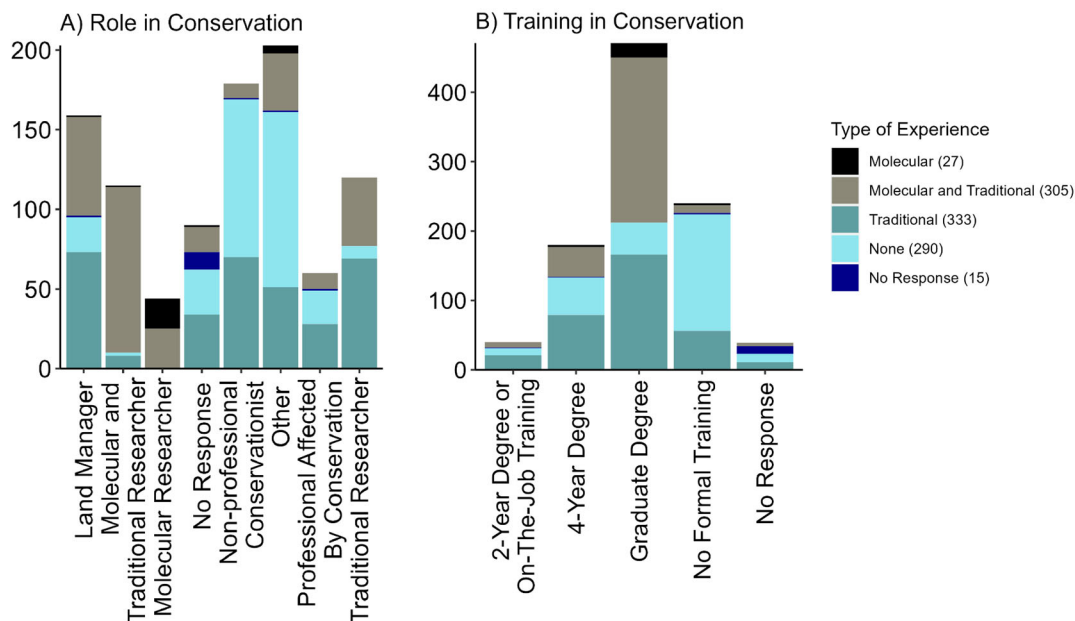
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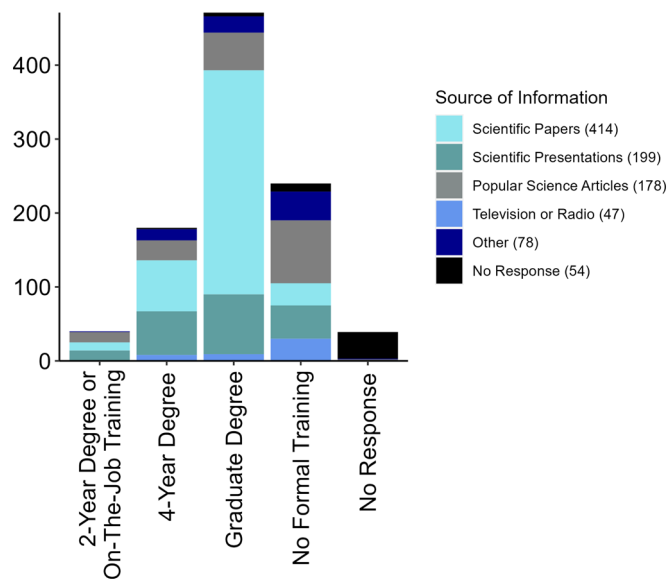
**Figures**

**Figure 4.1.** The locations of individuals who submitted a questionnaire.

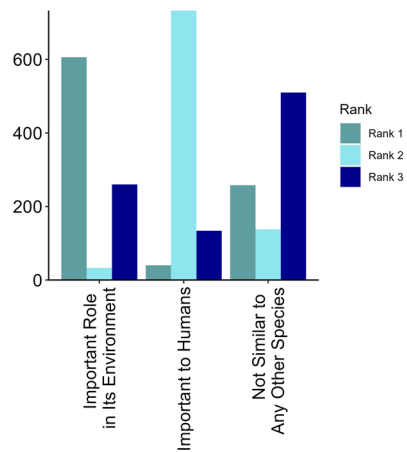


**Figure 4.2.** Measures of the diversity of experience of the respondents in the survey. A) The conservation role that the respondents reported holding, and B) the highest level of conservation or biological science training that the respondents reported having. Each bar is proportionately filled with the type of experience that the respondents reported.

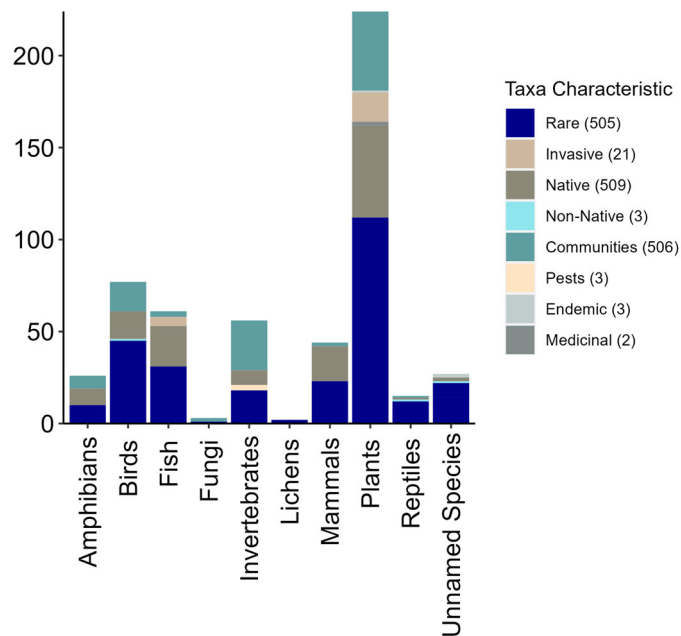




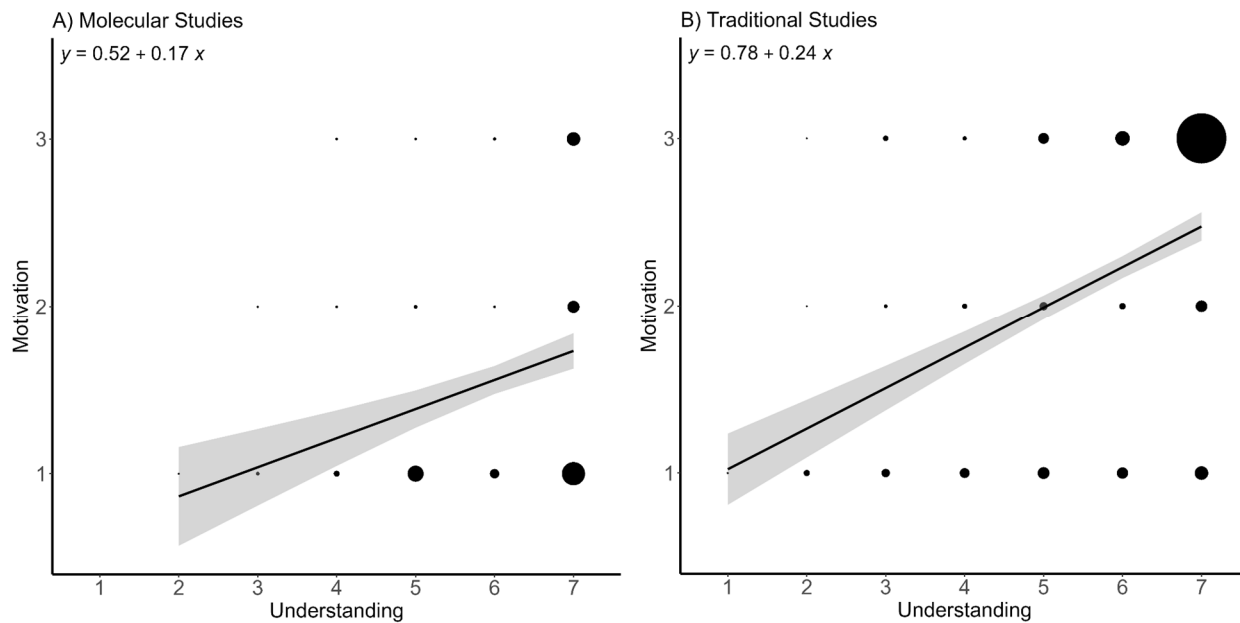
**Figure 4.3.** The primary way that conservationists learn about conservation issues.



**Figure 4.4.** Respondents' opinions of the importance of species characteristics in determining their conservation value.



**Figure 4.5.** Taxonomic groups of organisms that were included in respondents' descriptions of conservation studies in which they had participated.



**Figure 4.6.** Spearman's rank correlation of understanding and motivation to action of a) molecular and B) traditional conservation studies. Bubble size corresponds to the number of respondents with the same response (largest = 228 smallest = 1).

## CHAPTER V

### DISCUSSION

Bees are important pollinators world-wide and bumble bees in particular are important pollinators in high elevation and temperate biological communities. The importance of *Bombus occidentalis* as a pollinator within those communities is amplified by its expansive range and historically high abundance throughout that range. The observed decrease in abundance and range of *B. occidentalis* has the potential to cause cascading effects through the biological communities that it once inhabited (Tepedino 1979; Rollin et al. 2013; Parrey et al. 2021). The additional complexity associated with the unresolved taxonomic status of the species impedes attempts to assess the severity of the threat to the species continuation (Koch and Strange 2012; Williams et al. 2012; Sheffield et al. 2016; Williams 2021).

Through this dissertation, I contributed to the body of knowledge that informs ongoing attempts to conserve and protect *B. occidentalis* through four major findings: 1) *B. occidentalis* and *B. mckayi* are separate species, 2) genetic structure among populations of *B. occidentalis* has increased over time, but structure in *B. mckayi* remains stable, 3) minimum temperatures in the springtime and proximity to known infections from a fungal parasite influence genetic differentiation throughout the ranges of the two species, and 4) conservationists whose goal is to preserve these and other at-risk species require on-going education to make the best conservation and management decisions possible.

My finding that the taxa previously recognized as *B. occidentalis* are actually two separate species is in agreement with the findings of Williams (2021), who used

mitochondrial *COI* barcoding to revise the species delimitations in the subgenus *Bombus sensu stricto*. However, my addition of expanded geographic sampling for the mitochondrial analyses and use of ultraconserved elements (UCEs) to compare the nuclear genomes strengthened the evidence for the described relationship and improved the level of confidence in this conclusion. Previous publications have indicated that there may be a hybrid zone where the ranges of the two species overlap (Sheffield et al. 2016). There was no evidence of hybridization in my analyses, but this could be due to under-sampling of that geographic region. Unfortunately, sampling in that portion of the range is sparse, likely due to the relative remoteness of the region. Additional studies directly designed to search for hybridization of these closely-related species where the ranges overlap is an area of exciting research that could provide broad insights into the process of speciation in bumble bees.

My findings that genetic structure among populations of *B. occidentalis* is increasing over time, but that *B. mckayi* is currently relatively stable, is in agreement with previous studies (Lozier et al. 2011; Koch and Strange 2012). The task of tracking the gene flow among populations of an at-risk species requires ongoing sampling, and this study provided an update on previous findings. Additionally, this study expanded the geographic range of previous studies and compared measurements of genetic structure across a larger time frame than has been previously been included.

My findings that levels of genetic differentiation among specimens of both species were most strongly influenced by differences in springtime minimum temperatures and likelihood of exposure to the fungal parasite *Vairimorpha bombi* are supported by findings in previous studies (Cameron et al. 2016, Rohde and Pilliod 2021).

However, previous studies made associations between abundance and these environmental factors, not genetic differentiation. This is the first study to detect direct causal relationships between the environmental variables and genetic differentiation for either variable in these species.

Finally, my survey of conservationists from around the world indicated that conservationists require additional education and training to better understand conservation studies that use molecular methods. Contrary to my expectation, there was no significant difference in the amount of trust that the respondents feel for the results of studies that use molecular methods compared to more traditional, often abundance-based, studies. This result may seem to wander from the theme of the other work in this dissertation, but application of results is a crucial component of conservation science. Adoption of molecular methods, such as the ones used in chapters 2 and 3, to inform conservation decisions has been slow in some areas, while traditional, often abundance-based, methods are used more frequently. This disparity is often called the conservation genetics gap. This study is one of only few (Taylor et al. 2017; Sandström et al. 2019) that directly measured the opinions of conservation practitioners about their understanding of molecular methods. It is by far the largest ( $n = 974$ ), including people from diverse backgrounds and locations from around the world. It is also the first to measure the influence of trust, as well as understanding, on conservationists opinions of molecular studies.

The overarching goal of this dissertation was to assess the conservation status of *B. occidentalis* and *B. mckayi* using various molecular methods and to communicate the findings of that assessment to a community of interested conservation practitioners. My

research will contribute to an ever-growing body of literature that will, with a bit of luck, provide the knowledge and motivation needed to protect these important species.

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APPENDICES

## APPENDIX A

## Chapter II supplemental tables and figures

**Table A1.** Collection and institutional information associated with the bumble bee specimens (1 of 4).

<b>ExtractionID/ BOLD ID</b>	<b>COI or UCE dataset</b>	<b>Storing Institution</b>	<b>Institution ID</b>
632__mckayi_Alaska	COI	Research Collection of Paul H. Williams	B#92
657__mckayi_Alaska	COI	Research Collection of Paul H. Williams	B#234
657__mckayi_Alaska	COI	Research Collection of Paul H. Williams	B#93
ACUFI1823-15	COI	Finnish Museum of Natural History, Zoological Museum	GP.65583
ACUFI1824-15	COI	Finnish Museum of Natural History, Zoological Museum	GP.94694
ACUFI1825-15	COI	Finnish Museum of Natural History, Zoological Museum	GP.94695
ACUFI1833-15	COI	Finnish Museum of Natural History, Zoological Museum	GP.64851
ACUFI1837-15	COI	Finnish Museum of Natural History, Zoological Museum	GP.94702
BBBO066-10	COI	Research Collection of Paul H. Williams	6873F06
BBBO252-10	COI	Research Collection of Paul H. Williams	6875F02
BBBO336-10	COI	Research Collection of Paul H. Williams	6876000
BBBO372-10	COI	Research Collection of Paul H. Williams	6876H03
BBBO394-11	COI	Research Collection of Paul H. Williams	6878B02
BBBO396-11	COI	Research collection of Rifat Raina	6878B04
BBBO397-11	COI	Research collection of Rifat Raina	6878B05
BBHEC139-09	COI	Centre for Biodiversity Genomics	09BBEHY-0139
BBHEC143-09	COI	Centre for Biodiversity Genomics	09BBEHY-0143
BBWP556-10	COI	University of Kansas	1552G09
BBWP557-10	COI	University of Kansas	1552G10

BEECD384-09	COI	Royal Saskatchewan Museum	RSKM_ENT_E-125527
BEECD387-09	COI	Royal Saskatchewan Museum	RSKM_ENT_E-125532
BEECD396-09	COI	York University, Packer Collection	LRB-6471
BEECD397-09	COI	York University, Packer Collection	LRB-672
BEECD399-09	COI	York University, Packer Collection	LRB-662
BEECD400-09	COI	York University, Packer Collection	LRB-6493
BEECD413-09	COI	Royal Saskatchewan Museum	RSKM_ENT_E-125537
BEECD439-09	COI	Royal Saskatchewan Museum	RSKM_ENT_E-175887
BEECD45609	COI	Royal Saskatchewan Museum	RSKM_ENT_E-100508
BEECD73209	COI	York University, Packer Collection	CCDB-03759 F07
BEECD82410	COI	Royal Saskatchewan Museum	RSKM_ENT_E-163873
BEECD871-10	COI	York University, Packer Collection	USGS-DRO 119790
BEECE69510	COI	York University, Packer Collection	CCDB-06706 C06
BEECE70910	COI	York University, Packer Collection	CCDB-06706 D08
BEECE72910	COI	York University, Packer Collection	CCDB-06706 F04
BEECE823-10	COI	York University, Packer Collection	CCDB-06704 F03
BEECF00310	COI	York University, Packer Collection	CCDB-09869 A03
BEECF063-10	COI	York University, Packer Collection	CCDB-09869 F03
BEECF57411	COI	Royal Saskatchewan Museum	RSKM_ENT_E-100482
BEECF79712	COI	York University, Packer Collection	CCDB-15290 D01
BEECF81012	COI	York University, Packer Collection	CCDB-15290 E02
BEECF81112	COI	Royal Saskatchewan Museum	CCDB-15290 E03
BEECF95513	COI	Royal Saskatchewan Museum	CCDB-15254 A05
BLX1666	COI/UCE	USDA ARS US National Pollinating Insects Collection	BBSL744295
BLX1667	COI/UCE	USDA ARS US National Pollinating Insects Collection	BBSL746590
BLX1668	UCE	USDA ARS US National Pollinating Insects Collection	BBSL762078
BLX1669	UCE	USDA ARS US National Pollinating Insects Collection	BBSL762393

BLX1670	COI	University of Calgary	UC_OCCI_64
BLX1671	UCE	Royal British Columbia Museum	ENT017-010031
BLX1672	UCE	Royal British Columbia Museum	ENT017-011400
BLX1673	UCE	Royal British Columbia Museum	ENT017-013392
BLX1674	UCE	Royal British Columbia Museum	ENT012-000168
BLX1675	COI/UCE	Royal British Columbia Museum	ENT017-014560
BLX1676	UCE	Royal British Columbia Museum	ENT017-014391
BLX1677	UCE	Royal British Columbia Museum	Ent017-013381
BLX1678	UCE	Royal British Columbia Museum	Ent017-011263
BLX1679	UCE	Royal British Columbia Museum	Ent017-014160
BLX1687	UCE	University of Calgary	1117007
BLX1689	COI	University of Calgary	UC_OCCI_20
BLX1715	UCE	Royal British Columbia Museum	ENT012-000115
BLX1716	UCE	USDA ARS US National Pollinating Insects Collection	BBSL765548
BLX1717	UCE	USDA ARS US National Pollinating Insects Collection	BBSL747310
BLX1718	COI/UCE	USDA ARS US National Pollinating Insects Collection	BBSL748487
BLX1719	COI/UCE	USDA ARS US National Pollinating Insects Collection	BBSL765443
BLX1720	UCE	USDA ARS US National Pollinating Insects Collection	BBSL764695
BLX1721	UCE	USDA ARS US National Pollinating Insects Collection	BBSL749249
BLX1722	UCE	USDA ARS US National Pollinating Insects Collection	BBSL762297
BLX1723	UCE	USDA ARS US National Pollinating Insects Collection	BBSL764369
BLX1724	COI/UCE	USDA ARS US National Pollinating Insects Collection	BBSL762501
BLX1725	UCE	Royal British Columbia Museum	ENT015-007485
BLX1726	UCE	USDA ARS US National Pollinating Insects Collection	BBSL740482
BLX1727	UCE	USDA ARS US National Pollinating Insects Collection	BBSL754504
BLX1728	COI/UCE	USDA ARS US National Pollinating Insects Collection	BBSL764269
BLX1729	COI/UCE	USDA ARS US National Pollinating Insects Collection	BBSL764263
BLX1730	UCE	USDA ARS US National Pollinating Insects Collection	T34R40S11
BLX1731	UCE	USDA ARS US National Pollinating Insects Collection	D
BLX1732	UCE	USDA ARS US National Pollinating Insects Collection	J
BLX1735	UCE	Royal British Columbia Museum	ENT017-013555
BLX1733	UCE	USDA ARS US National Pollinating Insects Collection	M
BLX1736	COI/UCE	Royal British Columbia Museum	ENT017-012444
BLX1737	COI/UCE	Royal British Columbia Museum	ENT017-013562

BLX1738	UCE	Royal British Columbia Museum	ENT015-004025
BLX1739	COI/UCE	Royal British Columbia Museum	ENT017-014403
BLX1740	COI/UCE	Royal British Columbia Museum	ENT017-013863
BLX1742	COI/UCE	Royal British Columbia Museum	ENT013-001693
BLX1743	UCE	Royal British Columbia Museum	ENT017-012384
BLX1744	UCE	Royal British Columbia Museum	ENT015-006986
BLX1975	UCE	USDA ARS US National Pollinating Insects Collection	BBSL744967
BLX1976	COI	University of Alaska	UAM100430833
BLX1977	UCE	University of Alaska	UAM100026821
BLX1978	UCE	University of Alaska	UAM100040592
BLX1979	UCE	University of Alaska	UAM100250299
BLX1980	COI/UCE	University of Alaska	UAM100252948
BLX1982	COI/UCE	University of Alaska	UAM100430768
BLX1983	UCE	University of Alaska	UAM100260200
BLX1985	COI/UCE	University of Alaska	UAM100304704
BLX1986	UCE	University of Alaska	UAM100303236
BLX1987	COI/UCE	University of Alaska	UAM100303224
BLX1988	UCE	University of Alaska	UAM100363062
BLX1992	COI	Essig Museum of Entomology	JPS8915
BLX2016	COI	Essig Museum of Entomology	EMEC565478
BLX2159	COI	Canadian National Collection	8732
BLX2160	COI	Canadian National Collection	8685
BLX2162	COI	Canadian National Collection	8447
BLX2163	COI	Canadian National Collection	8684
BOWGF78609	COI	York University, Packer Collection	CCDB - 01565 C2
BWTWO706-09	COI	College of the North Atlantic, Carbonear	CCDB-03775 D05
CNFNR1970-14	COI	Centre for Biodiversity Genomics	BIOUG11382-B09
CNFNR3985-14	COI	Centre for Biodiversity Genomics	BIOUG11961-F08
CNLMM030-14	COI	Centre for Biodiversity Genomics	BIOUG13775-G08
CNPEN061-14	COI	Centre for Biodiversity Genomics	BIOUG10658-H04
CNRME5015-12	COI	Centre for Biodiversity Genomics	BIOUG03805-D05
CNWLD88012	COI	Centre for Biodiversity Genomics	BIOUG03602-A06
CNWLN102713	COI	Centre for Biodiversity Genomics	BIOUG06832-H01
GBAH17804-19	COI	Mined from GenBank, NCBI	MF361369

GBAH17805-19	COI	Mined from GenBank, NCBI	MF361370
GBAH17806-19	COI	Mined from GenBank, NCBI	MF361373
GBHAP1392-15	COI	Mined from GenBank, NCBI	LN714039
GBHAP1394-15	COI	Mined from GenBank, NCBI	LN714037
GBHAP1396-15	COI	Mined from GenBank, NCBI	LN714035
GBHAP1397-15	COI	Mined from GenBank, NCBI	LN714034
GBHAP1400-15	COI	Mined from GenBank, NCBI	LN714031
GBHAP1401-15	COI	Mined from GenBank, NCBI	LN714030
GBHAP1402-15	COI	Mined from GenBank, NCBI	LN714029
GBHAP1403-15	COI	Mined from GenBank, NCBI	LN714028
GBHAP1404-15	COI	Mined from GenBank, NCBI	LN714027
GBHAP1406-15	COI	Mined from GenBank, NCBI	LN714025
GBMIN70597-17	COI	Mined from GenBank, NCBI	MF361413
GBMIN70599-17	COI	Mined from GenBank, NCBI	MF361432
GBMIN70606-17	COI	Mined from GenBank, NCBI	MF361378
GBMIN70611-17	COI	Mined from GenBank, NCBI	MF361408
GBMIN70637-17	COI	Mined from GenBank, NCBI	MF361418
GBMIN70640-17	COI	Mined from GenBank, NCBI	MF361424
GMGMA546-14	COI	Zoologisches Forschungsmuseum Alexander Koenig	BIOUG16210-F04
GMGMM191-14	COI	Zoologisches Forschungsmuseum Alexander Koenig	BIOUG17297-H10
GMGMN003-14	COI	Zoologisches Forschungsmuseum Alexander Koenig	BIOUG17299-E0
HC154	COI	Cornell University Insect Collection	HTCH008906
HPPPK1128-13	COI	Centre for Biodiversity Genomics	BIOUG07703-F05
HPPPL584-13	COI	Centre for Biodiversity Genomics	BIOUG07818-D04
INRMA323017	COI	Royal British Columbia Museum	ENT012-013867
INRMA3232-17	COI	Royal British Columbian Museum	ENT012-013864
INRMA3235-17	COI	Royal British Columbian Museum	ENT013-006748
JCLUC051-11	COI	Natural History Museum, London	T691
JCLUC056-11	COI	Natural History Museum, London	T729
POLLE2926-19	COI	University of Orleans	MBF00290
POLLE866-19	COI	University of Orleans	MB00870
SSGBA5273-14	COI	Centre for Biodiversity Genomics	BIOUG14499-E01
UAMIC75113	COI	University of Alaska Museum	UAM Insects 187982

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**Table A2.** Collection and institutional information associated with the bumble bee specimens (2 of 4).

<b>ExtractionID/ BOLD ID</b>	<b>COI Sample Name</b>	<b>UCE Sample Name</b>
632__mckayi_Alaska	632__mckayi_Alaska	
657__mckayi_Alaska	657__mckayi_Alaska	
657__mckayi_Alaska	657__mckayi_Alaska	
ACUFI1823-15	658_ACUFI1823-15_lucorum	
ACUFI1824-15	658_ACUFI1824-15_lucorum	
ACUFI1825-15	658_ACUFI1825-15_lucorum	
ACUFI1833-15	658_ACUFI1833-15_lucorum	
ACUFI1837-15	658_ACUFI1837-15_lucorum	
BBBO066-10	658_BBBO066-10_hypocrita	
BBBO252-10	658_BBBO252-10_hypocrita	
BBBO336-10	658_BBBO336-10_hypocrita	
BBBO372-10	658_BBBO372-10_hypocrita	
BBBO394-11	426_BBBO394-11_jacobsoni	
BBBO396-11	425_BBBO396-11_jacobsoni	
BBBO397-11	425_BBBO397-11_jacobsoni	
BBHEC139-09	658_BBHEC139-09_terricola	
BBHEC143-09	658_BBHEC143-09_terricola	
BBWP556-10	658_BBWP556-10_hypocrita	
BBWP557-10	658_BBWP557-10_hypocrita	
BEECD384-09	615_BEECD384-09_terricola	
BEECD387-09	633_BEECD387-09_terricola	
BEECD396-09	630_BEECD396-09_terricola	
BEECD397-09	648_BEECD397-09_terricola	
BEECD399-09	658_BEECD399-09_terricola	
BEECD400-09	631_BEECD400-09_terricola	



BEECD413-09	658_BEECD413-09_terricola	
BEECD439-09	658_BEECD439-09_terricola	
BEECD45609	615_BEECD45609_occidentalis_Alberta	
BEECD73209	618_BEECD73209_occidentalis_Idaho	
BEECD82410	658_BEECD82410_occidentalis_Colorado	
BEECD871-10	658_BEECD871-10_terricola	
BEECE69510	658_BEECE69510_mckayi_Alaska	
BEECE70910	658_BEECE70910_mckayi_Alaska	
BEECE72910	658_BEECE72910_occidentalis_Alaska	
BEECE823-10	658_BEECE823-10_terricola	
BEECF00310	658_BEECF00310_occidentalis_Alberta	
BEECF063-10	658_BEECF063-10_terricola	
BEECF57411	658_BEECF57411_occidentalis_Colorado	
	658_BEECF79712_mckayi_Northwest Territories	
BEECF79712		
	657_BEECF81012_occidentalis_British Columbia	
BEECF81012		
BEECF81112	658_BEECF81112_mckayi_Yukon Territory	
BEECF95513	658_BEECF95513_mckayi_British Columbia	
BLX1666	658_BLX1666_occidentalis_Colorado	1390.5_BLX1666_occidentalis_Colorado
BLX1667	658_BLX1667_occidentalis_Utah	1580.2_BLX1667_occidentalis_Utah
BLX1668		2004.9_BLX1668_occidentalis_Oregon
BLX1669		1846.4_BLX1669_occidentalis_Oregon
BLX1670	658_BLX1670_occidentalis_Alberta	416.3_BLX1670_occidentalis_Alberta
BLX1671		1245.5_BLX1671_mckayi_Yukon
BLX1672		1788.3_BLX1672_mckayi_Yukon
BLX1673		1675.2_BLX1673_mckayi_Yukon
BLX1674		894.4_BLX1674_mckayi_Yukon
BLX1675	658_BLX1675_mckayi_Yukon	1528.4_BLX1675_mckayi_Yukon
BLX1676		1402.4_BLX1676_mckayi_Yukon
BLX1677		1467.6_BLX1677_mckayi_Yukon
BLX1678		1432.6_BLX1678_mckayi_Yukon
BLX1679		1328.1_BLX1679_mckayi_Yukon
BLX1687		491_BLX1687_occidentalis_Alberta

BLX1689	658_BLX1689_occidentalis_British Columbia	
BLX1715		975.5_BLX1715_mckayi_Yukon
BLX1716		1810.4_BLX1716_occidentalis_Colorado
BLX1717		1702.8_BLX1717_occidentalis_California
BLX1718	658_BLX1718_occidentalis_Nevada	1904.1_BLX1718_occidentalis_Nevada
BLX1719	658_BLX1719_occidentalis_Colorado	1189.9_BLX1719_occidentalis_Colorado
BLX1720		1472.4_BLX1720_occidentalis_Wyoming
BLX1721		1499.7_BLX1721_occidentalis_Utah
BLX1722		1344.1_BLX1722_occidentalis_Oregon
BLX1723		1604_BLX1723_occidentalis_Wyoming
BLX1724	658_BLX1724_occidentalis_Oregon	1457.9_BLX1724_occidentalis_Oregon
BLX1725		1540.9_BLX1725_mckayi_Yukon
BLX1726		1397.6_BLX1726_occidentalis_Idaho
BLX1727		1442.5_BLX1727_occidentalis_Oregon
BLX1728	658_BLX1728_occidentalis_Montana	1489.4_BLX1728_occidentalis_Montana
BLX1729	611_BLX1729_s1_occidentalis_Montana	1477_BLX1729_occidentalis_Montana
BLX1730		1898.8_BLX1730_occidentalis_Washington
BLX1731		1982.6_BLX1731_occidentalis_Washington
BLX1732		1664.8_BLX1732_occidentalis_Washington
BLX1735		1122.2_BLX1735_mckayi_British
BLX1733		2192.4_BLX1733_occidentalis_Washingotn
BLX1736	658_BLX1736_mckayi_British Columbia	
BLX1737	658_BLX1737_mckayi_Yukon	
BLX1738		1638.8_BLX1738_mckayi_Yukon
BLX1739	658_BLX1739_mckayi_Yukon	
BLX1740	658_BLX1740_mckayi_Yukon	
BLX1742	658_BLX1742_mckayi_Yukon	
BLX1743		1887.4_BLX1743_mckayi_Yukon
BLX1744		1566.9_BLX1744_mckayi_Yukon
BLX1975		1493_BLX1975_occidentalis_Montana
BLX1976	658_BLX1976_mckayi_Alaska	
BLX1977		932.2_BLX1977_mckayi_Alaska
BLX1978		1098_BLX1978_mckayi_Alaska
BLX1979		1438.8_BLX1979_mckayi_Alaska

BLX1980	658_BLX1980_mckayi_Alaska	462_BLX1980_mckayi_Alaska
BLX1982	658_BLX1982_mckayi_Alaska	1577.1_BLX1982_mckayi_Alaska
BLX1983		806.7_BLX1983_mckayi_Alaska
BLX1985	658_BLX1985_mckayi_Alaska	1429.6_BLX1985_mckayi_Alaska
BLX1986		1432.9_BLX1986_mckayi_Alaska
BLX1987	658_BLX1987_mckayi_Alaska	964.9_BLX1987_mckayi_Alaska
BLX1988		1617.8_BLX1988_mckayi_Alaska
BLX1992	658_BLX1992_s1_s2_occidentalis_Washington	
BLX2016	658_BLX2016_occidentalis_California	
	511_BLX2159_s3_occidentalis_British Columbia	
BLX2159		
BLX2160	658_BLX2160_occidentalis_Idaho	
BLX2162	658_BLX2162_occidentalis_British Columbia	
BLX2163	658_BLX2163_occidentalis_British Columbia	
BOWGF78609	658_BOWGF78609_mckayi_Yukon Territory	
BWTWO706-09	658_BWTWO706-09_terricola	
CNFNR1970-14	585_CNFNR1970-14_terricola	
CNFNR3985-14	579_CNFNR3985-14_terricola	
CNLMM030-14	565_CNLMM030-14_terricola	
CNPEN061-14	521_CNPEN061-14_terricola	
CNRME5015-12	635_CNRME5015-12_terricola	
CNWLD88012	638_CNWLD88012_occidentalis_Alberta	
CNWLN102713	613_CNWLN102713_occidentalis_Alberta	
GBAH17804-19	653_GBAH17804-19_hypocrita	
GBAH17805-19	653_GBAH17805-19_hypocrita	
GBAH17806-19	653_GBAH17806-19_hypocrita	
GBHAP1392-15	606_GBHAP1392-15_lucorum	
GBHAP1394-15	606_GBHAP1394-15_lucorum	
GBHAP1396-15	606_GBHAP1396-15_lucorum	
GBHAP1397-15	606_GBHAP1397-15_lucorum	
GBHAP1400-15	606_GBHAP1400-15_lucorum	
GBHAP1401-15	606_GBHAP1401-15_lucorum	
GBHAP1402-15	606_GBHAP1402-15_lucorum	
GBHAP1403-15	606_GBHAP1403-15_lucorum	

GBHAP1404-15	606_GBHAP1404-15_lucorum
GBHAP1406-15	606_GBHAP1406-15_lucorum
GBMIN70597-17	653_GBMIN70597-17_hypocrita
GBMIN70599-17	615_GBMIN70599-17_hypocrita
GBMIN70606-17	624_GBMIN70606-17_hypocrita
GBMIN70611-17	646_GBMIN70611-17_hypocrita
GBMIN70637-17	653_GBMIN70637-17_hypocrita
GBMIN70640-17	653_GBMIN70640-17_hypocrita
GMGMA546-14	564_GMGMA546-14_lucorum
GMGMM191-14	579_GMGMM191-14_lucorum
GMGMN003-14	540_GMGMN003-14_lucorum
HC154	651_HC154_terricola
HPPPK1128-13	567_HPPPK1128-13_terricola
HPPPL584-13	598_HPPPL584-13_terricola
INRMA323017	407_INRMA323017_mckayi_British Columbia
INRMA3232-17	407_INRMA323217_occidentalis
INRMA3235-17	407_INRMA3235-17_terricola
JCLUC051-11	642_JCLUC051-11_lucorum
JCLUC056-11	642_JCLUC056-11_lucorum
POLLE2926-19	654_POLLE2926-19_lucorum
POLLE866-19	651_POLLE866-19_lucorum
SSGBA5273-14	588_SSGBA5273-14_terricola
UAMIC75113	658_UAMIC75113_mckayi Alaska

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Table A3. Collection and institutional information associated with the bumble bee specimens (3 of 4).

<b>ExtractionID/ BOLD ID</b>	<b>Species Name</b>	<b>Genus</b>	<b>Subgenus</b>	<b>Species</b>	<b>Author (Species)</b>	<b>Subspecies</b>	<b>Author (Subspecies)</b>
632__mckayi_Alaska	Bombus occidentalis mckayi	Bombus		occidentalis	Greene, 1858	mckayi	Ashmead 1902
657__mckayi_Alaska	Bombus occidentalis mckayi	Bombus		occidentalis	Greene, 1858	mckayi	Ashmead 1902
657__mckayi_Alaska	Bombus occidentalis mckayi	Bombus		occidentalis	Greene, 1858	mckayi	Ashmead 1902
ACUFI1823-15	Bombus lucorum	Bombus		lucorum	Linnaeus, 1761		
ACUFI1824-15	Bombus lucorum	Bombus		lucorum	Linnaeus, 1761		
ACUFI1825-15	Bombus lucorum	Bombus		lucorum	Linnaeus, 1761		
ACUFI1833-15	Bombus lucorum	Bombus		lucorum	Linnaeus, 1761		
ACUFI1837-15	Bombus lucorum	Bombus		lucorum	Linnaeus, 1761		
BBBO066-10	Bombus hypocrita	Bombus		hypocrita	Pérez, 1905		
BBBO252-10	Bombus hypocrita	Bombus		hypocrita	Pérez, 1905		
BBBO336-10	Bombus hypocrita	Bombus		hypocrita	Pérez, 1905		
BBBO372-10	Bombus hypocrita	Bombus		hypocrita	Pérez, 1905		
BBBO394-11	Bombus jacobsoni	Bombus		jacobsoni	Skorikov, 1912		
BBBO396-11	Bombus jacobsoni	Bombus		jacobsoni	Skorikov, 1912		
BBBO397-11	Bombus jacobsoni	Bombus		jacobsoni	Skorikov, 1912		
BBHEC139-09	Bombus terricola	Bombus		terricola	Kirby, 1837		
BBHEC143-09	Bombus terricola	Bombus		terricola	Kirby, 1837		
BBWP556-10	Bombus hypocrita	Bombus		hypocrita	Pérez, 1905		
BBWP557-10	Bombus hypocrita	Bombus		hypocrita	Pérez, 1905		
BEECD384-09	Bombus terricola	Bombus		terricola	Kirby, 1837		
BEECD387-09	Bombus terricola	Bombus		terricola	Kirby, 1837		
BEECD396-09	Bombus terricola	Bombus		terricola	Kirby, 1837		
BEECD397-09	Bombus terricola	Bombus		terricola	Kirby, 1837		

BEECD399-09	Bombus terricola	Bombus	terricola	Kirby, 1837		
BEECD400-09	Bombus terricola	Bombus	terricola	Kirby, 1837		
BEECD413-09	Bombus terricola	Bombus	terricola	Kirby, 1837		
BEECD439-09	Bombus terricola	Bombus	terricola	Kirby, 1837		
BEECD45609	Bombus occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BEECD73209	Bombus occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BEECD82410	Bombus occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BEECD871-10	Bombus terricola	Bombus	terricola	Kirby, 1837		
BEECE69510	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902
BEECE70910	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902
BEECE72910	Bombus occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BEECE823-10	Bombus terricola	Bombus	terricola	Kirby, 1837		
BEECF00310	Bombus occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BEECF063-10	Bombus terricola	Bombus	terricola	Kirby, 1837		
BEECF57411	Bombus occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BEECF79712	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902
BEECF81012	Bombus occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BEECF81112	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902

BEECF95513	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902
BLX1666	Bombus occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BLX1667	Bombus occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BLX1668	Bombus occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1859
BLX1669	Bombus occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1860
BLX1670	Bombus occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BLX1671	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1859	mckayi	Ashmead 1902
BLX1672	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1860	mckayi	Ashmead 1903
BLX1673	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1860	mckayi	Ashmead 1903
BLX1674	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1861	mckayi	Ashmead 1904
BLX1675	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1862	mckayi	Ashmead 1905
BLX1676	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1863	mckayi	Ashmead 1906
BLX1677	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1864	mckayi	Ashmead 1907
BLX1678	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1865	mckayi	Ashmead 1908
BLX1679	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1866	mckayi	Ashmead 1909

BLX1687	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1857	occidentalis	Greene, 1857
BLX1689	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BLX1715	Bombus occidentalis occidentalis mckayi	Bombus	occidentalis	Greene, 1866	mckayi	Ashmead 1909
BLX1716	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1856	occidentalis	Greene, 1856
BLX1717	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1857	occidentalis	Greene, 1857
BLX1718	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BLX1719	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BLX1720	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1859	occidentalis	Greene, 1859
BLX1721	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1860	occidentalis	Greene, 1860
BLX1722	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1861	occidentalis	Greene, 1861
BLX1723	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1862	occidentalis	Greene, 1862
BLX1724	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BLX1725	Bombus occidentalis occidentalis mckayi	Bombus	occidentalis	Greene, 1866	mckayi	Ashmead 1909



BLX1726	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1856	occidentalis	Greene, 1856
BLX1727	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1857	occidentalis	Greene, 1857
BLX1728	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BLX1729	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BLX1730	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1859	occidentalis	Greene, 1859
BLX1731	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1860	occidentalis	Greene, 1860
BLX1732	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1861	occidentalis	Greene, 1861
BLX1735	Bombus occidentalis mckayi occidentalis	Bombus	occidentalis	Greene, 1866	mckayi	Ashmead 1909
BLX1733	Bombus occidentalis occidentalis	Bombus	occidentalis	Greene, 1863	occidentalis	Greene, 1863
BLX1736	Bombus occidentalis mckayi occidentalis	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902
BLX1737	Bombus occidentalis mckayi occidentalis	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902
BLX1738	Bombus occidentalis mckayi occidentalis	Bombus	occidentalis	Greene, 1859	mckayi	Ashmead 1903
BLX1739	Bombus occidentalis mckayi occidentalis	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902
BLX1740	Bombus occidentalis mckayi occidentalis	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902

BLX1742	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902
BLX1743	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1859	mckayi	Ashmead 1903
BLX1744	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1860	mckayi	Ashmead 1904
BLX1975	Bombus occidentalis	Bombus	occidentalis	Greene, 1863	occidentalis	Greene, 1863
BLX1976	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902
BLX1977	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1859	mckayi	Ashmead 1903
BLX1978	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1860	mckayi	Ashmead 1904
BLX1979	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1861	mckayi	Ashmead 1905
BLX1980	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902
BLX1982	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902
BLX1983	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1859	mckayi	Ashmead 1903
BLX1985	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902
BLX1986	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1859	mckayi	Ashmead 1903
BLX1987	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902
BLX1988	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1859	mckayi	Ashmead 1903
BLX1992	Bombus occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BLX2016	Bombus occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858

BLX2159	Bombus occidentalis occidentalis Bombus	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BLX2160	occidentalis Bombus occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BLX2162	occidentalis Bombus occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BLX2163	occidentalis Bombus	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
BOWGF78609	occidentalis mckayi	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902
BWTWO706-09	Bombus terricola	Bombus	terricola	Kirby, 1837		
CNFNR1970-14	Bombus terricola	Bombus	terricola	Kirby, 1837		
CNFNR3985-14	Bombus terricola	Bombus	terricola	Kirby, 1837		
CNLMM030-14	Bombus terricola	Bombus	terricola	Kirby, 1837		
CNPEN061-14	Bombus terricola	Bombus	terricola	Kirby, 1837		
CNRME5015-12	Bombus terricola	Bombus	terricola	Kirby, 1837		
CNWLD88012	Bombus occidentalis occidentalis Bombus	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
CNWLN102713	occidentalis	Bombus	occidentalis	Greene, 1858	occidentalis	Greene, 1858
GBAH17804-19	Bombus hypocrita	Bombus	hypocrita	Pérez, 1905		
GBAH17805-19	Bombus hypocrita	Bombus	hypocrita	Pérez, 1905		
GBAH17806-19	Bombus hypocrita	Bombus	hypocrita	Pérez, 1905		
GBHAP1392-15	Bombus lucorum	Bombus	lucorum	Linnaeus, 1761		
GBHAP1394-15	Bombus lucorum	Bombus	lucorum	Linnaeus, 1761		
GBHAP1396-15	Bombus lucorum	Bombus	lucorum	Linnaeus, 1761		
GBHAP1397-15	Bombus lucorum	Bombus	lucorum	Linnaeus, 1761		
GBHAP1400-15	Bombus lucorum	Bombus	lucorum	Linnaeus, 1761		
GBHAP1401-15	Bombus lucorum	Bombus	lucorum	Linnaeus, 1761		
GBHAP1402-15	Bombus lucorum	Bombus	lucorum	Linnaeus, 1761		

GBHAP1403-15	Bombus lucorum	Bombus	lucorum	Linnaeus, 1761		
GBHAP1404-15	Bombus lucorum	Bombus	lucorum	Linnaeus, 1761		
GBHAP1406-15	Bombus lucorum	Bombus	lucorum	Linnaeus, 1761		
GBMIN70597-17	Bombus hypocrita	Bombus	hypocrita	Pérez, 1905		
GBMIN70599-17	Bombus hypocrita	Bombus	hypocrita	Pérez, 1905		
GBMIN70606-17	Bombus hypocrita	Bombus	hypocrita	Pérez, 1905		
GBMIN70611-17	Bombus hypocrita	Bombus	hypocrita	Pérez, 1905		
GBMIN70637-17	Bombus hypocrita	Bombus	hypocrita	Pérez, 1905		
GBMIN70640-17	Bombus hypocrita	Bombus	hypocrita	Pérez, 1905		
GMGMA546-14	Bombus lucorum	Bombus	lucorum	Linnaeus, 1761		
GMGMM191-14	Bombus lucorum	Bombus	lucorum	Linnaeus, 1761		
GMGMN003-14	Bombus lucorum	Bombus	lucorum	Linnaeus, 1761		
HC154	Bombus terricola	Bombus	terricola	Kirby, 1837		
HPPPK1128-13	Bombus terricola	Bombus	terricola	Kirby, 1837		
HPPPL584-13	Bombus terricola	Bombus	terricola	Kirby, 1837		
INRMA323017	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902
INRMA3232-17	occidentalis	Bombus	occidentalis	Greene, 1858		
INRMA3235-17	Bombus terricola	Bombus	terricola	Kirby, 1837		
JCLUC051-11	Bombus lucorum	Bombus	lucorum	Linnaeus, 1761		
JCLUC056-11	Bombus lucorum	Bombus	lucorum	Linnaeus, 1761		
POLLE2926-19	Bombus lucorum	Bombus	lucorum	Linnaeus, 1761		
POLLE866-19	Bombus lucorum	Bombus	lucorum	Linnaeus, 1761		
SSGBA5273-14	Bombus terricola	Bombus	terricola	Kirby, 1837		
UAMIC75113	Bombus occidentalis mckayi	Bombus	occidentalis	Greene, 1858	mckayi	Ashmead 1902

**Table A4.** Collection and institutional information associated with the bumble bee specimens (4 of 4).

<b>ExtractionID/ BOLD ID</b>	<b>Collection Year</b>	<b>Country</b>	<b>Full Locality</b>	<b>Latitude (DD)</b>	<b>Longitude (DD)</b>
632__mckayi_Alaska	2001	Canada	Nova Scotia		
657__mckayi_Alaska	2005	Canada	Alberta		
657__mckayi_Alaska	2002	Canada	Nova Scotia		
ACUFI1823-15	2009	Finland	Karelia ladogensis	61.475	29.578
ACUFI1824-15	2004	Finland	Nylandia	60.152	24.214
ACUFI1825-15	2001	Finland	Tavastia australis	61.448	23.555
ACUFI1833-15	2009	Finland	Nylandia	60.456	26.245
ACUFI1837-15	1998	Finland	Regio aboensis	60.243	21.305
BBBO066-10	1990	Russia	Ulaanbaatar		
BBBO252-10	2006	Japan	Hokkaido		
BBBO336-10	1989	Japan			
BBBO372-10	2009	Japan			
BBBO394-11	2008	China			
BBBO396-11	2007	China			
BBBO397-11	2007	China			
BBHEC139-09	2009	Canada	Newfoundland and Labrador	48.492	-54.022
BBHEC143-09	2009	Canada	New Brunswick	45.657	-65.015
BBWP556-10	2001	Russia		47.2553	142.806
BBWP557-10	2003	Russia	Sakhalinskaya Oblast		
BEECD384-09	2005	Canada	Northwest Territories	62.433	-114.35
BEECD387-09	2005	Canada	Northwest Territories	61.583	-117.149
BEECD396-09	2006	Canada	British Columbia	55.175	-126.361

BEECD397-09	2008	Canada	British Columbia	52.113	-123.424
BEECD399-09	2008	Canada	British Columbia	52.113	-123.424
BEECD400-09	2006	Canada	British Columbia	55.175	-126.361
			Northwest		
BEECD413-09	2003	Canada	Territories	62.466	-114.35
BEECD439-09	2008	Canada	Ontario	43.5	80.2
BEECD45609	2007	Canada	Alberta	49.638	-110.254
BEECD73209	2000	United States of America	Idaho	44.959	-113.645
BEECD82410	2007	United States of America	Colorado	40.366	-105.56
BEECD871-10	2008	United States of America	Massachusetts	42.703	-73.047
BEECE69510	2009	United States of America	Alaska	61.567	-149.233
BEECE70910	2009	United States of America	Alaska	64.85	-147.85
BEECE72910	2009	United States of America	Alaska	64.747	-148.086
BEECE823-10	2009	Canada	Manitoba	49.86	-99.961
BEECF00310	2010	Canada	Alberta	51.117	-114.233
BEECF063-10	2009	Canada	Ontario	45.037	-75.456
BEECF57411	2007	United States of America	Colorado	37.662	-106.647
			Northwest		
BEECF79712	2011	Canada	Territories	62.656	-129.135
BEECF81012	2010	Canada	British Columbia	49.263	-115.285
BEECF81112	2011	Canada	Yukon Territory	0.662	-135.078
BEECF95513	2012	Canada	British Columbia	58.84	-129.995
BLX1666	2008	United States of America	Colorado	38.8908	-106.9951
BLX1667	2007	United States of America	Utah	41.94909	-113.34954
BLX1668	2009	United States of America	Oregon	42.1836	-120.349
BLX1669	2009	United States of America	Oregon	42.38925	-122.21477
BLX1670	2000	Canada	Alberta	49.06384	-113.781881
BLX1671	2016	Canada	Yukon Territory	61.00834	-138.54204
BLX1672	2017	Canada	Yukon Territory	61.1512	-135.36674
BLX1673	2017	Canada	Yukon Territory	63.55753	-137.41338
BLX1674	2010	Canada	Yukon Territory	60.06329	-128.7177
BLX1675	2017	Canada	Yukon Territory	62.21093	-133.38381
BLX1676	2017	Canada	Yukon Territory	62.3777	-131.4895
BLX1677	2016	Canada	Yukon Territory	63.95761	-138.70944

BLX1678	2017	Canada	Yukon Territory	64.087559	-139.562
BLX1679	2016	Canada	Yukon Territory	64.51164	-138.23709
BLX1687	2015	Canada	Alberta	50.7729	-114.1633
BLX1689	2010	Canada	British Columbia	51.22444444	-116.6147222
BLX1715	2010	Canada	Yukon	62.82653	-136.58156
BLX1716	2009	United States of America	Colorado	38.83969	-105.98926
BLX1717	2007	United States of America	California	40.01786	-121.03238
BLX1718	2007	United States of America	Nevada	40.66422	-115.44721
BLX1719	2009	United States of America	Colorado	39.94036	-105.5595
BLX1720	2009	United States of America	Wyoming	41.34644	-106.18425
BLX1721	2008	United States of America	Utah	41.89436	-111.64246
BLX1722	2009	United States of America	Oregon	42.08349	-122.73063
BLX1723	2009	United States of America	Wyoming	42.73656	-108.83656
BLX1724	2009	United States of America	Oregon	42.90313	-122.30127
BLX1725	2014	Canada	Yukon Territory	64.6837	-140.97516
BLX1726	2008	United States of America	Idaho	44.98977	-116.18861
BLX1727	2008	United States of America	Oregon	45.15691	-118.06286
BLX1728	2009	United States of America	Montana	46.85804	-110.67823
BLX1729	2009	United States of America	Montana	48.02376	-115.01229
BLX1730	2016	United States of America	Washington	48.330922	-117.292598
BLX1731	2016	United States of America	Washington	48.60482	-118.29182
BLX1732	2016	United States of America	Washington	48.94057	-117.86782
BLX1735	2017	Canada	British Columbia	55.8664	-128.9806
BLX1733	2017	Canada	British Columbia	57.53334	-130.17909
BLX1736	2017	Canada	British Columbia	57.53334	-130.17909
BLX1737	2017	Canada	Yukon Territory	60.09119	-130.63946
BLX1738	2014	Canada	Yukon Territory	60.1704	-134.7175
BLX1739	2017	Canada	Yukon Territory	60.2106	-132.8161
BLX1740	2017	Canada	Yukon Territory	60.76551	-137.74744
BLX1742	2012	Canada	Yukon Territory	61.63383	-137.51277
BLX1743	2017	Canada	Yukon Territory	61.855049	-140.14555
BLX1744	2014	Canada	Yukon Territory	62.78479	-140.35216
BLX1975	2008	United States of America	Montana	44.7438	-111.259
BLX1976	2010	United States of America	Alaska	65.57734	-148.94633

BLX1977	2001	United States of America	Alaska	65.68369	-157.475274
BLX1978	2002	United States of America	Alaska	61.13777778	-152.0613889
BLX1979	2009	United States of America	Alaska	52.02084	-175.12766
BLX1980	1965	United States of America	Alaska	60.7928	-161.76731
BLX1982	2010	United States of America	Alaska	65.20435	-147.22871
BLX1983	1982	United States of America	Alaska	64.704	-148.3015
BLX1985	2010	United States of America	Alaska	64.91582	-154.83472
BLX1986	2009	United States of America	Alaska	63.9311	-145.3875
BLX1987	2009	United States of America	Alaska	67.4081	-150.1097
BLX1988	2012	United States of America	Alaska	63.73234	-148.91779
BLX1992	1962	United States of America	Washington	48.11806	-123.43056
BLX2016	1977	United States of America	California	36.79083	-121.79194
BLX2159	1971	Canada	British Columbia	49.1167	-125.8833
BLX2160	1965	United States of America	Idaho	46.7981	-116.8688
BLX2162	1970	Canada	Kaslo	49.9166	-1169166
BLX2163	1960	Canada	British Columbia	57.4666	-128.8
BOWGF78609	2009	Canada	Yukon Territory	60.605	-134.8686
			Newfoundland and Labrador	46.4417	-53.3139
BWTWO706-09	2007	Canada	Quebec	48.857	-64.376
CNFNR1970-14	2013	Canada	Quebec	48.857	-64.376
CNFNR3985-14	2013	Canada	Quebec	46.6507	-72.9698
CNLMM030-14	2013	Canada	Prince Edward Island	46.4123	-63.085
CNPEN061-14	2013	Canada	Manitoba	50.676	-99.898
CNRME5015-12	2012	Canada	Alberta	49.106	-113.819
CNWLD88012	2012	Canada	Alberta	49.083	-113.876
CNWLN102713	2012	Canada			
GBAH17804-19	2012	South Korea			
GBAH17805-19	2012	South Korea			
GBAH17806-19	2012	South Korea			
GBHAP1392-15	2012	Austria	Carinthia	46.4664	14.3775
GBHAP1394-15	2013	Austria	Salzburg	47.5413	13.197
			Lower Austria,		
GBHAP1396-15	2013	Austria	Raxalpe	47.693	15.704
GBHAP1397-15	2012	Austria	Carinthia	47.0644	12.8271



GBHAP1400-15	2013	Austria	Lower Austria, Raxalpe	47.802	15.016
GBHAP1401-15	2013	Austria	Vienna	48.2729	16.2291
GBHAP1402-15	2013	Austria	Carinthia	46.4664	14.3775
GBHAP1403-15	2013	Austria	Lower Austria, Raxalpe	47.702	15.714
GBHAP1404-15	2013	Austria	Salzburg	47.5237	13.2175
GBHAP1406-15	2013	Austria	Lower Austria, Raxalpe	47.679	15.72
GBMIN70597-17	2012	South Korea			
GBMIN70599-17	2012	South Korea			
GBMIN70606-17	2012	South Korea			
GBMIN70611-17	2012	South Korea	GW, Jeongsun		
GBMIN70637-17	2012	South Korea	GW, Jeongsun		
GBMIN70640-17	2012	South Korea	GW, Jeongsun		
GMGMA546-14	2013	Germany	Rhineland- Palatinate	50.552	7.17
GMGMM191-14	2014	Germany	Rhineland- Palatinate	50.552	7.17
GMGMN003-14	2014	Germany	Rhineland- Palatinate	50.552	7.17
HC154	2011				
HPPPK1128-13	2013	Canada	Nova Scotia	44.623	-63.569
HPPPL584-13	2013	Canada	Nova Scotia	44.623	-63.569
INRMA323017	2011	Canada	British Columbia	57.7735	-129.827
INRMA3232-17	2011	Canada	British Columbia	57.7735	-129.827
INRMA3235-17	2013	Canada	British Columbia	52.2932	-122.156
JCLUC051-11	2006	Ireland	Wicklow	52.969	-6.266
JCLUC056-11	1998	Denmark	Jutland	56.36	8.615
POLLE2926-19	2018	France	Centre-Val de Loire	47.8978	1.90048
POLLE866-19	2018	France	Centre-Val de Loire	47.8868	2.02398
SSGBA5273-14	2013	Canada	Newfoundland and Labrador	49.626	-57.922
UAMIC75113	2010	United States of America	Alaska	64.747	-148.086

**Table A5.** UCE summary statistics (1 of 2).

<b>Locus</b>	<b>Length</b>	<b>Informative Sites</b>	<b>Characters</b>	<b>Differences</b>	<b>GC content (%)</b>
uce-3	1376	2	1376	3	49.67
uce-4	1814	3	1814	6	53.98
uce-5	1310	4	1310	9	45.49
uce-6	1129	2	1127	3	33.05
uce-7	1853	0	1853	2	31.23
uce-8	1410	0	1410	2	38.8
uce-9	1976	4	1976	7	31.92
uce-10	1268	3	1208	4	37.85
uce-11	1623	2	1603	2	51.36
uce-12	1363	2	1363	2	52.13
uce-13	1519	0	1519	0	27.29
uce-18	955	1	945	3	46.57
uce-19	1506	3	1506	4	42.05
uce-20	951	1	951	2	46.31
uce-22	1262	5	1262	5	38.98
uce-23	1352	3	1352	5	46.67
uce-24	1214	4	1195	6	39.09
uce-27	1135	2	1118	2	33.49
uce-29	1404	3	1387	4	41.23
uce-30	1402	7	1395	8	40.27
uce-31	1298	9	1292	10	35.65
uce-32	1557	5	1557	5	36.34
uce-33	1164	4	1145	6	40.79
uce-34	2126	7	2126	8	44.56
uce-35	1033	3	1033	5	28.48
uce-36	1439	6	1439	6	47.83
uce-37	1128	3	1128	3	49.2
uce-38	1481	0	1481	0	32.37
uce-39	1947	7	1947	8	44.56
uce-40	2280	4	2280	5	44.95
uce-42	1355	2	1355	3	49.57
uce-43	1290	1	1284	3	48.01
uce-44	1408	7	1408	8	42.27
uce-46	1513	5	1513	6	33.03
uce-47	1537	7	1537	9	42.75
uce-48	1711	3	1711	3	40.65
uce-49	1399	3	1399	3	42.97
uce-50	1269	0	1269	0	38.53
uce-51	1901	2	1901	4	47.6
uce-54	1961	2	1961	3	46.14
uce-55	1535	7	1535	7	47.78
uce-57	1380	3	1380	3	53.5

uce-58	1368	2	1334	2	36.96
uce-59	1245	3	1245	6	37.8
uce-60	1379	2	1369	2	28.37
uce-64	1381	4	1381	4	42.12
uce-65	2042	7	2042	10	45.01
uce-66	1131	2	1131	4	56.28
uce-67	1261	6	1261	9	49.21
uce-68	1788	8	1788	8	45.25
uce-69	1672	4	1672	5	49.81
uce-71	2603	7	2603	9	51.29
uce-73	1606	3	1606	3	51.91
uce-74	1232	3	1232	4	47.51
uce-77	1190	7	1190	8	46.53
uce-82	1401	2	1401	2	49.08
uce-86	2552	5	2552	6	43.9
uce-87	1486	4	1486	4	47.17
uce-88	1409	4	1409	4	35.84
uce-93	1223	0	1223	4	43.86
uce-94	1398	6	1398	6	47.86
uce-95	1490	0	1483	1	34.41
uce-96	1256	4	1256	5	40.3
uce-97	1344	0	1335	0	40.47
uce-98	1606	3	1606	3	40.44
uce-99	1217	6	1217	8	43.49
uce-100	1424	9	1417	10	33.5
uce-103	1225	0	1225	0	31.43
uce-104	1381	1	1365	1	23.13
uce-106	1403	1	1402	1	34.79
uce-107	1329	2	1329	3	50.7
uce-109	582	0	582	0	49.55
uce-113	1686	4	1686	4	37.49
uce-114	1288	0	1288	0	31.3
uce-115	1341	4	1341	6	40.99
uce-116	2041	4	2041	5	41.37
uce-120	1322	1	1322	2	31.13
uce-121	1616	4	1616	5	38.07
uce-122	991	0	991	0	55.73
uce-127	1350	4	1350	4	45.57
uce-129	1439	0	1439	1	42.04
uce-130	1141	2	1137	4	44.34
uce-131	959	0	959	1	43.44
uce-132	1309	6	1309	6	35.74
uce-134	1444	1	1444	1	28.5
uce-135	1714	1	1714	1	55.27
uce-136	1646	4	1646	4	52.44
uce-137	1511	1	1502	1	31.37
uce-139	2059	5	2053	5	52.17
uce-140	1142	5	1142	7	51.07
uce-144	1020	1	1020	2	53.68

uce-145	1613	3	1602	3	28.92
uce-146	1854	6	1854	9	55.36
uce-147	1487	2	1487	3	47.23
uce-149	1436	7	1416	8	43.61
uce-150	1432	1	1432	3	34.75
uce-152	1024	3	1024	3	42.22
uce-153	1534	1	1534	1	43.55
uce-154	1889	4	1889	6	45.04
uce-155	2065	3	2065	5	52.18
uce-157	1494	4	1494	4	41.53
uce-158	1488	1	1488	1	51.35
uce-159	1213	5	1213	6	48.09
uce-160	1281	3	1281	4	46
uce-168	1412	2	1406	3	32.31
uce-169	1369	1	1369	5	49.52
uce-170	1874	0	1874	2	50.88
uce-171	1534	3	1534	4	39.75
uce-172	1202	1	1185	2	36.09
uce-173	1708	4	1708	4	41.8
uce-175	1412	5	1412	7	45.94
uce-176	1604	0	1604	0	31.22
uce-177	1653	2	1643	4	36.35
uce-181	1250	2	1249	3	40.28
uce-185	1786	3	1786	5	48.17
uce-186	1954	2	1954	2	40.39
uce-187	863	1	844	2	45.67
uce-188	1465	0	1465	0	37.98
uce-191	2121	2	2121	3	46.65
uce-192	1584	1	1579	1	42.55
uce-193	1643	0	1643	1	35.59
uce-194	1316	0	1316	0	45.87
uce-196	1631	4	1628	6	42.92
uce-197	1373	0	1368	1	30.14
uce-200	1777	3	1753	3	42.78
uce-201	1571	2	1571	2	46.88
uce-204	1830	2	1830	2	40.99
uce-205	1448	0	1448	1	39.43
uce-208	1546	1	1546	2	36.99
uce-211	1306	0	1296	1	36.33
uce-212	1345	2	1345	3	39.76
uce-213	1387	0	1368	0	40.36
uce-216	1388	8	1388	8	38.86
uce-217	1506	3	1506	6	39.42
uce-220	1530	3	1530	3	30.43
uce-228	1506	3	1506	3	52.5
uce-231	1186	1	1186	2	58.43
uce-232	771	0	771	0	61.85
uce-233	1489	1	1489	2	55.7
uce-234	1419	3	1419	4	57.71
uce-235	1712	4	1696	8	59.31
uce-236	1889	2	1889	3	55.18

uce-237	1321	1	1321	2	56.54
uce-238	1224	2	1224	2	59.84
uce-239	1710	0	1710	1	56.85
uce-240	1474	0	1474	1	52.8
uce-241	1597	0	1597	1	52.7
uce-242	1337	3	1320	5	55.24
uce-243	1518	3	1518	4	55.73
uce-244	1137	3	1137	4	42.66
uce-249	1158	2	1158	2	41.48
uce-252	1109	1	1107	1	32.23
uce-255	1174	6	1174	7	44.24
uce-256	1018	0	1018	1	44.5
uce-257	1506	2	1500	2	33.95
uce-258	1229	2	1229	2	45.26
uce-259	1513	0	1513	1	48.55
uce-260	1355	1	1355	1	48.99
uce-263	1462	3	1462	4	48.06
uce-265	1286	2	1282	4	45.59
uce-270	1543	5	1543	6	52.81
uce-271	1478	1	1478	1	47.82
uce-272	1569	3	1569	3	39.21
uce-274	1126	3	1106	4	35.21
uce-275	1400	3	1400	3	34.08
uce-276	1729	0	1729	0	42.05
uce-277	1118	6	1118	10	30.62
uce-278	1348	0	1348	0	38.04
uce-279	950	4	950	5	30.05
uce-280	1320	1	1320	2	42.22
uce-288	1276	0	1266	1	41.35
uce-291	1861	2	1861	2	54.88
uce-295	1176	3	1172	4	42.06
uce-297	1424	3	1424	4	44.67
uce-299	1425	2	1425	4	50.15
uce-301	1263	3	1263	5	44.59
uce-303	1254	1	1254	2	40.93
uce-304	998	2	998	3	50.14
uce-306	1230	2	1230	2	44.57
uce-310	2220	4	2220	4	41.06
uce-313	1432	4	1432	5	43.28
uce-316	1579	1	1558	2	40.03
uce-317	1808	0	1808	2	48.22
uce-319	1106	3	1106	3	41.27
uce-320	941	2	941	2	48.3
uce-325	1352	5	1351	5	39.24
uce-326	1200	5	1194	7	40.88
uce-327	737	3	737	4	42.01
uce-329	1657	3	1657	4	38.19
uce-330	1780	1	1780	2	43.75
uce-331	1397	4	1397	5	51.14
uce-332	1532	3	1532	4	40.54
uce-333	1592	1	1592	3	47.37

uce-334	1146	2	1146	2	47.45
uce-335	1177	0	1171	1	40.81
uce-336	1827	6	1810	6	44.34
uce-337	1645	7	1645	7	37.82
uce-340	1701	2	1701	2	34.11
uce-345	1479	3	1479	5	35.77
uce-346	1597	6	1597	7	41.61
uce-347	1342	6	1307	6	47.28
uce-349	1412	5	1412	5	40.11
uce-350	1324	2	1324	3	32.19
uce-351	1180	3	1180	3	35
uce-353	1136	4	1136	7	32.48
uce-354	1182	0	1170	0	29.94
uce-356	1395	1	1395	2	31.29
uce-359	636	0	636	0	50.54
uce-360	1437	5	1437	5	33.36
uce-361	1388	1	1354	2	27.94
uce-362	901	0	901	0	60.23
uce-363	1533	2	1533	2	39.16
uce-364	1076	7	1076	8	49.8
uce-365	1386	1	1386	3	44.03
uce-366	1421	2	1421	4	37.31
uce-367	1297	2	1297	2	31.63
uce-370	1433	1	1424	2	35.8
uce-373	1571	0	1571	1	35.26
uce-375	1282	2	1282	3	38.29
uce-378	777	1	777	1	25.34
uce-381	1393	3	1377	3	31.14
uce-382	1467	0	1467	0	30.28
uce-383	1398	3	1398	4	45.39
uce-388	2049	11	2044	14	38.97
uce-389	1549	2	1549	3	49.5
uce-390	1642	3	1642	4	52.01
uce-392	1372	1	1372	1	44
uce-394	1220	6	1220	7	48.13
uce-395	664	0	664	0	50.56
uce-396	1422	0	1422	1	48.76
uce-397	1101	5	1092	6	41.41
uce-399	1149	2	1149	2	47.52
uce-400	1550	2	1550	4	34.85
uce-401	1393	1	1356	2	41.1
uce-402	1970	1	1965	2	53.72
uce-404	2020	4	2011	5	54.56
uce-406	1558	5	1558	6	48.33
uce-408	1273	4	1273	4	48.36
uce-411	1234	0	1226	2	45.74
uce-412	1102	2	1102	2	47.27
uce-413	1371	3	1371	4	41.57
uce-415	1456	0	1456	1	52.99
uce-416	2119	5	2119	7	53.48
uce-423	1764	3	1764	7	52.74

uce-424	1974	4	1974	5	53.77
uce-427	1587	1	1587	2	48.29
uce-430	1329	3	1326	3	37.17
uce-433	1260	2	1252	2	38.92
uce-434	1351	4	1351	4	35.17
uce-435	1598	3	1598	3	41.55
uce-436	1657	1	1657	1	35.61
uce-437	1219	2	1214	2	46.15
uce-438	1678	5	1678	8	33.75
uce-441	1634	3	1634	5	35.87
uce-442	1611	0	1611	1	29.21
uce-446	1576	0	1547	3	43.63
uce-448	1011	2	1011	3	50.25
uce-449	1592	1	1592	1	28.46
uce-450	1380	0	1376	0	25.04
uce-453	1848	0	1839	0	51.02
uce-454	1681	5	1681	7	40.51
uce-455	1505	3	1505	5	42.06
uce-458	1180	1	1180	1	46.72
uce-459	1116	2	1116	2	52.59
uce-460	1149	2	1145	3	37.99
uce-463	1618	1	1618	3	45.75
uce-468	1203	2	1190	2	50.74
uce-472	1466	1	1466	1	53.18
uce-473	1543	2	1543	5	46.29
uce-475	1440	2	1436	2	49.02
uce-476	821	0	821	1	52.2
uce-478	1393	1	1379	2	53.74
uce-479	1524	1	1524	1	41.6
uce-481	1757	4	1757	4	44.35
uce-483	1728	1	1715	1	43.82
uce-484	1532	2	1532	4	44.43
uce-485	1397	2	1397	2	48.27
uce-487	2037	0	2026	0	47.72
uce-488	1551	2	1532	3	46.59
uce-491	1241	5	1241	8	41.05
uce-492	1241	8	1241	9	43.51
uce-495	1098	4	1098	5	41.2
uce-497	1353	3	1353	3	46.89
uce-498	1465	2	1465	4	40.48
uce-500	1466	2	1466	3	46.01
uce-501	2462	4	2462	4	45.22
uce-505	1469	3	1469	3	41.85
uce-506	1519	6	1519	7	38.81
uce-507	1510	6	1510	8	41.87
uce-508	1354	4	1351	5	49.3
uce-509	704	1	704	1	46.97
uce-510	1416	7	1416	9	40.5
uce-511	1416	4	1416	6	40.06
uce-513	1408	1	1408	2	48.14
uce-514	1472	2	1472	4	36.09

uce-515	844	3	844	5	40.63
uce-516	1404	1	1404	1	46.2
uce-517	1544	7	1544	9	35.99
uce-518	1553	2	1553	2	38.51
uce-519	1114	2	1114	2	41.97
uce-520	1336	7	1318	9	37.57
uce-521	1140	3	1140	3	38.98
uce-525	1429	2	1429	2	44.26
uce-527	1428	4	1428	5	43.51
uce-528	1420	3	1420	8	35.21
uce-529	1447	5	1447	5	45.46
uce-530	1513	2	1513	5	40.37
uce-531	3066	3	3066	3	52.76
uce-534	1219	2	1215	2	40.93
uce-535	1359	1	1359	5	44.56
uce-537	1253	3	1253	4	36.91
uce-538	1512	4	1512	4	43.37
uce-540	510	0	510	1	43.2
uce-541	1364	1	1364	1	43.46
uce-542	1618	5	1618	7	44.27
uce-543	1379	2	1379	4	43.08
uce-544	1396	1	1379	3	42.44
uce-546	755	1	755	3	48.25
uce-547	1261	7	1259	9	42.42
uce-550	1602	0	1602	0	52.27
uce-551	1084	6	1084	7	39.6
uce-552	1038	4	1022	4	34.76
uce-553	1619	1	1619	2	57.81
uce-554	1394	2	1394	3	42.97
uce-555	1460	2	1460	3	46.05
uce-557	1383	6	1375	7	38.85
uce-558	1392	3	1392	3	44.26
uce-559	1287	1	1283	3	48.15
uce-560	1390	5	1381	5	43.32
uce-562	1528	7	1528	12	43.39
uce-563	1389	5	1389	6	38.78
uce-565	1164	7	1161	8	47.67
uce-566	1557	4	1557	5	38.35
uce-568	1696	6	1696	7	43.78
uce-573	1391	1	1361	4	40.13
uce-575	1355	1	1355	4	48.66
uce-577	1267	5	1267	5	41.63
uce-580	1358	0	1345	0	25.08
uce-581	1371	3	1369	4	35.64
uce-583	1304	7	1276	8	36.08
uce-584	2298	1	2298	1	45.59
uce-588	1710	4	1710	4	41.01
uce-589	1793	5	1768	7	35.07
uce-590	1181	1	1181	1	53.5
uce-594	1811	5	1811	6	36.18
uce-595	1305	4	1298	4	39.82



uce-598	1589	1	1589	1	36.28
uce-600	1184	0	1175	0	33.56
uce-604	1352	1	1352	1	37.43
uce-605	1129	1	1129	1	43.56
uce-607	472	1	445	1	34.5
uce-608	1234	2	1229	4	37.55
uce-609	1538	1	1538	1	41.3
uce-610	1161	3	1161	3	41.62
uce-612	1201	5	1201	7	45.48
uce-613	1569	3	1569	3	44.21
uce-614	1065	2	1053	3	42.14
uce-615	1571	1	1571	1	42.1
uce-616	1549	1	1549	2	43.55
uce-617	2095	3	2095	3	44.74
uce-618	1535	2	1535	3	26.27
uce-620	1213	4	1193	4	32.71
uce-621	1429	3	1420	4	30.33
uce-624	1512	0	1512	0	48.74
uce-625	1128	0	1116	1	34.18
uce-626	1085	1	1061	1	36.48
uce-627	1328	2	1328	3	33.74
uce-631	1180	3	1180	4	36.79
uce-632	1329	1	1316	1	31.86
uce-633	1423	1	1423	2	48.37
uce-634	1389	1	1389	1	44.71
uce-635	2054	4	2054	5	38.63
uce-638	796	0	796	0	26.68
uce-639	3278	9	3278	9	40.43
uce-640	1277	1	1277	2	54.86
uce-641	1257	7	1250	9	48.01
uce-642	911	3	911	4	54.27
uce-643	1540	0	1540	3	46.21
uce-645	1512	0	1512	0	32.16
uce-646	1622	0	1622	0	32.05
uce-647	1107	0	1091	0	31.73
uce-649	1480	4	1480	4	43.07
uce-650	1237	1	1237	1	61.26
uce-653	1023	0	1023	0	28.26
uce-654	1577	2	1557	2	46.57
uce-655	1340	3	1340	5	37.53
uce-656	1585	4	1585	4	48.24
uce-657	1395	1	1395	1	51.49
uce-658	1235	0	1230	1	51.51
uce-659	1236	0	1232	0	45.77
uce-660	1464	0	1438	0	43.6
uce-662	1601	3	1600	3	44.02
uce-666	2083	1	2083	1	50.87
uce-669	1311	4	1297	5	39.22
uce-672	2115	2	2115	5	45.54
uce-673	1257	5	1257	6	46.21
uce-676	1384	6	1350	6	43.84

uce-677	1562	3	1562	4	49.72
uce-680	2142	2	2142	5	57.65
uce-681	2072	1	2072	1	55.64
uce-682	1626	2	1626	3	47.14
uce-683	1443	7	1427	8	39.01
uce-684	1934	0	1934	2	35.16
uce-686	1647	1	1647	1	35.22
uce-688	1133	5	1116	5	40.47
uce-689	1453	0	1453	0	49.82
uce-690	1658	3	1658	3	44.11
uce-691	1492	0	1492	3	43.3
uce-693	1425	4	1425	5	38.99
uce-694	1476	4	1471	4	40.1
uce-695	1485	3	1485	3	39.07
uce-697	1568	3	1568	4	44.7
uce-698	1774	1	1774	2	47.28
uce-699	1678	5	1666	6	39.7
uce-700	1169	0	1169	0	49.1
uce-701	1263	3	1249	3	39.96
uce-702	1554	1	1554	1	49.41
uce-706	1680	4	1680	6	45.73
uce-707	1514	5	1494	5	43.62
uce-710	1592	5	1587	6	41.35
uce-711	1394	4	1394	5	41.36
uce-713	1539	1	1539	1	56.99
uce-714	1777	1	1722	2	41.45
uce-719	985	1	952	2	39.52
uce-721	1141	1	1141	1	47.86
uce-723	2039	3	2039	3	51.04
uce-728	1177	1	1177	1	36.06
uce-733	877	3	877	3	46.98
uce-734	1528	4	1526	5	40.64
uce-735	1619	2	1606	2	44.93
uce-739	1328	3	1328	5	59.99
uce-741	1493	5	1493	6	44.22
uce-742	1098	2	1098	5	50.93
uce-746	1187	7	1187	7	46.63
uce-747	2626	2	2626	2	54.6
uce-749	2373	5	2373	6	53.89
uce-750	1643	3	1643	5	45.9
uce-752	1016	3	1010	3	47.48
uce-753	2504	4	2500	5	49.58
uce-758	1752	3	1752	6	48.25
uce-764	1412	0	1412	0	33.03
uce-767	1516	3	1516	4	32.11
uce-768	1551	0	1551	0	29.67
uce-769	1658	10	1658	10	32.68
uce-773	2501	4	2495	5	47.91
uce-774	1182	0	1182	0	44.75
uce-775	889	0	884	2	39.96
uce-776	1386	3	1386	4	36.16

uce-777	1440	0	1440	1	49.45
uce-780	1453	0	1453	0	46.15
uce-783	2079	5	2079	7	49.75
uce-784	1392	2	1392	5	47.26
uce-785	1567	1	1567	1	48.32
uce-786	978	2	965	3	43.93
uce-787	1681	8	1676	8	40.58
uce-789	1335	1	1335	1	41.53
uce-791	1159	0	1120	0	30.89
uce-793	1001	1	1001	1	48.49
uce-796	674	1	674	1	31.66
uce-799	1608	2	1608	3	50.2
uce-800	2234	3	2234	3	50.35
uce-803	1736	2	1736	2	47.03
uce-805	1423	7	1423	7	39.21
uce-806	1424	1	1424	1	43.61
uce-809	1568	0	1568	1	42.97
uce-812	1356	5	1356	5	48.54
uce-815	1377	2	1377	2	52.01
uce-816	1335	4	1335	6	39.73
uce-817	1338	4	1333	5	39.55
uce-819	1527	6	1517	6	34.17
uce-820	1547	1	1545	1	37.24
uce-821	1277	4	1277	6	37.23
uce-822	1305	7	1291	11	39.81
uce-823	1402	1	1402	1	33.57
uce-829	1002	1	995	2	31.8
uce-830	1901	1	1901	3	50.87
uce-832	1273	0	1273	2	52.54
uce-833	1461	2	1461	2	54.31
uce-834	1827	8	1827	8	52.72
uce-835	1013	2	1013	2	54.76
uce-836	1195	5	1195	6	41.87
uce-837	938	3	938	6	51.3
uce-839	1254	6	1254	7	51.81
uce-842	1284	5	1284	6	36.41
uce-843	1407	1	1403	1	31.47
uce-844	1498	2	1498	4	55.07
uce-845	1301	4	1300	5	50.47
uce-847	1742	0	1742	0	50.14
uce-848	1366	0	1366	0	34.29
uce-850	1097	1	1097	1	38.41
uce-851	1637	6	1637	8	37.21
uce-852	1388	0	1366	0	31.21
uce-855	1397	4	1397	4	48.66
uce-857	1688	2	1688	2	50.09
uce-858	2238	9	2238	10	44.18
uce-860	1631	5	1631	8	46.41
uce-861	1533	2	1533	4	50.17
uce-862	1014	4	1008	5	54.48
uce-864	1848	5	1848	5	41.58

uce-867	934	1	929	1	48.93
uce-868	926	2	926	3	47.53
uce-869	1119	1	1106	2	51.2
uce-870	931	2	931	4	46.06
uce-871	1573	3	1572	3	51.1
uce-872	1340	6	1340	6	50.4
uce-873	1419	2	1419	2	50.68
uce-875	1317	2	1317	3	49.21
uce-876	1593	3	1593	3	49.64
uce-879	1436	3	1436	5	49.94
uce-880	1481	2	1481	2	31.36
uce-881	1603	2	1603	2	30.24
uce-882	1190	0	1190	0	39.87
uce-884	1507	5	1507	7	42.5
uce-885	1544	7	1544	9	48.3
uce-888	1795	1	1789	1	33.69
uce-896	1679	1	1679	1	37.02
uce-900	1982	1	1982	2	32.54
uce-901	1706	0	1706	0	53.07
uce-902	1401	2	1401	2	50.44
uce-903	1308	3	1308	4	45.21
uce-904	1478	2	1478	3	51.73
uce-905	1409	2	1409	3	40.63
uce-907	1470	1	1470	2	50.72
uce-908	1336	4	1326	4	41.77
uce-909	1489	8	1481	9	37.53
uce-910	1643	0	1640	0	39.99
uce-912	1541	3	1541	4	44.66
uce-913	1468	3	1468	4	53.01
uce-914	1753	8	1742	10	49.35
uce-915	1129	3	1129	4	48.23
uce-916	1291	0	1291	2	48.23
uce-917	1536	2	1536	3	53.1
uce-918	1397	2	1397	3	34.7
uce-921	1168	7	1168	8	40.33
uce-922	1320	2	1320	2	48.08
uce-923	1459	0	1450	0	27.15
uce-925	1578	4	1578	5	47.66
uce-927	1071	1	1071	1	45.49
uce-928	769	0	769	0	56.4
uce-929	1414	0	1414	1	46.16
uce-930	1765	3	1765	5	41.13
uce-931	1490	3	1490	4	41.3
uce-932	1036	3	1036	5	51.54
uce-935	1511	3	1511	4	46.84
uce-936	1721	4	1721	5	41.29
uce-938	1504	0	1504	0	29.63
uce-939	1213	0	1195	0	27.68
uce-941	1846	1	1846	1	46.87
uce-945	1468	1	1468	2	39.2
uce-946	1401	2	1394	3	41.44

uce-947	1671	5	1671	5	41.01
uce-948	1240	4	1237	7	31.69
uce-949	1517	6	1517	6	43.59
uce-950	1184	1	1184	1	47.29
uce-952	1530	3	1530	5	51.92
uce-953	1233	3	1222	3	42.36
uce-955	1465	5	1465	5	44.74
uce-956	1702	10	1702	14	49.76
uce-957	1377	3	1377	4	39.94
uce-958	1260	2	1215	2	43.64
uce-959	1820	3	1820	4	45.22
uce-960	1015	3	1015	3	42.65
uce-962	1560	5	1560	6	33.38
uce-963	1266	1	1266	1	53.62
uce-965	1731	1	1731	1	45.82
uce-966	1065	2	1065	4	46.77
uce-974	1370	1	1370	3	43.18
uce-975	1282	0	1282	1	38.05
uce-976	1198	2	1198	2	39.86
uce-977	1391	0	1391	0	45.47
uce-978	1684	8	1684	9	48.65
uce-979	1364	3	1364	3	48.38
uce-980	832	0	830	0	24.14
uce-983	1458	3	1458	3	46.99
uce-984	1526	5	1526	6	40.64
uce-985	1529	2	1529	2	37.8
uce-988	1281	3	1265	3	55.34
uce-989	1281	2	1281	3	55.45
uce-990	1344	2	1344	3	48.5
uce-991	1140	5	1138	5	49.49
uce-997	1320	4	1318	4	44.14
uce-999	1408	5	1408	7	50.32
uce-1004	1300	2	1300	4	53.6
uce-1006	1184	2	1184	2	44.04
uce-1008	1538	5	1521	5	38.01
uce-1009	1535	3	1535	3	49
uce-1011	1523	3	1523	3	41.86
uce-1012	1473	2	1473	3	49.01
uce-1013	2235	3	2235	4	55.1
uce-1014	1532	1	1532	3	50.78
uce-1015	1261	0	1261	1	50.02
uce-1016	1992	7	1984	8	50.4
uce-1019	1938	2	1938	4	46.05
uce-1020	2044	1	2044	3	48.2
uce-1023	1482	2	1476	4	47.73
uce-1024	1937	0	1937	2	50.84
uce-1026	1566	3	1566	3	56.8
uce-1027	1247	2	1247	4	47.18
uce-1028	1380	4	1380	4	47.64
uce-1029	1365	2	1362	6	49.02
uce-1031	2047	7	2047	8	45.85

uce-1033	1304	4	1298	6	34.35
uce-1034	2636	10	2636	14	49.31
uce-1035	1301	4	1294	4	51.01
uce-1037	1527	1	1527	1	50.41
uce-1038	1298	3	1298	3	48.74
uce-1046	2051	6	2041	6	42.04
uce-1047	1533	2	1533	2	42.2
uce-1049	1596	0	1596	0	33.48
uce-1050	1224	1	1223	1	43.71
uce-1052	1292	2	1292	4	55.02
uce-1055	2451	1	2433	2	36.45
uce-1058	1366	2	1353	3	40.87
uce-1061	2045	2	2027	3	52.2
uce-1062	1625	3	1625	7	38.37
uce-1063	1561	7	1561	7	42.16
uce-1064	1214	3	1214	3	52.52
uce-1066	1198	1	1198	2	29.64
uce-1067	1294	6	1293	8	45.83
uce-1070	1270	3	1270	4	40.62
uce-1071	1391	2	1391	2	49.12
uce-1075	1440	3	1428	4	39.19
uce-1076	1576	2	1576	3	48.38
uce-1078	1315	5	1315	5	43.69
uce-1079	1537	0	1535	1	51.26
uce-1080	1451	4	1451	4	53.19
uce-1081	1345	5	1345	5	47.14
uce-1082	1250	4	1250	5	52.48
uce-1083	1654	2	1652	2	41.48
uce-1085	1755	6	1745	7	36.34
uce-1090	1515	0	1515	0	28.91
uce-1091	1570	2	1570	3	29.51
uce-1092	1259	2	1253	3	40.83
uce-1093	1566	1	1566	3	44.08
uce-1094	1507	4	1507	4	50.64
uce-1095	1406	2	1406	3	53.01
uce-1096	1229	5	1229	7	42.37
uce-1097	1804	1	1728	1	42.29
uce-1098	1300	2	1287	2	32.45
uce-1099	1348	1	1348	1	40.71
uce-1102	1614	1	1614	1	36.66
uce-1104	1582	6	1582	7	44.29
uce-1105	1085	6	1085	7	45.53
uce-1107	1819	6	1819	7	46.13
uce-1109	1153	0	1143	0	27.81
uce-1110	1860	1	1860	1	39.81
uce-1111	2000	2	2000	5	57.56
uce-1112	2260	0	2260	0	35.44
uce-1114	1263	1	1249	1	47
uce-1119	2114	4	2114	7	42.31
uce-1122	1425	1	1411	2	50.93
uce-1124	1016	1	1016	2	51.85

uce-1125	1238	6	1238	6	47.09
uce-1126	1180	1	1180	1	43.38
uce-1127	1461	3	1452	3	47.84
uce-1128	1522	3	1522	4	51.86
uce-1131	1556	4	1551	5	43.44
uce-1133	1433	3	1433	4	50.79
uce-1134	1633	1	1633	2	42.09
uce-1135	2502	1	2502	1	41
uce-1138	1320	0	1320	0	47.23
uce-1139	1563	6	1563	10	44.75
uce-1140	1203	2	1175	3	26.94
uce-1143	1270	4	1270	6	37.08
uce-1144	1189	1	1189	3	36.34
uce-1149	1980	0	1980	2	44.58
uce-1150	1396	3	1396	5	34.62
uce-1155	1383	3	1376	5	38.55
uce-1156	1828	9	1828	10	38.08
uce-1159	1644	1	1644	1	46.37
uce-1163	1517	1	1517	2	50.41
uce-1166	1637	1	1637	2	46.37
uce-1167	2230	3	2230	5	51.82
uce-1168	2416	4	2416	6	45.09
uce-1169	1196	5	1196	7	38.72
uce-1170	1104	3	1104	3	47.67
uce-1171	1661	3	1661	4	47.92
uce-1172	1419	2	1419	4	51.14
uce-1173	1571	6	1571	8	46.89
uce-1174	1696	5	1690	6	45.6
uce-1175	1477	5	1477	5	55.75
uce-1176	1215	3	1215	5	53.06
uce-1177	1513	3	1513	4	51.34
uce-1178	1256	4	1256	6	44
uce-1181	1106	2	1080	3	42.08
uce-1182	1785	2	1785	3	48.65
uce-1188	1112	2	1112	3	43.2
uce-1189	1310	5	1282	6	39.42
uce-1190	1258	1	1251	2	28.22
uce-1191	1245	2	1243	4	37.73
uce-1193	1912	12	1897	13	47.59
uce-1194	960	0	960	0	29.83
uce-1195	1445	1	1445	1	30.98
uce-1196	1297	1	1297	1	27.37
uce-1202	1498	1	1498	2	48.38
uce-1203	1766	1	1766	1	42.23
uce-1204	1449	2	1449	3	48.41
uce-1205	1815	3	1815	4	33.62
uce-1206	1871	3	1871	3	51.98
uce-1207	1491	3	1491	4	46.39
uce-1208	1108	2	1101	3	44.57
uce-1209	1141	1	1141	1	50.53
uce-1211	1909	4	1909	5	35.59

uce-1213	1507	1	1507	2	32.08
uce-1214	1987	4	1987	4	31.09
uce-1216	1405	2	1405	2	54.57
uce-1217	1639	0	1639	1	52.53
uce-1219	1437	5	1437	6	53.95
uce-1220	970	0	970	1	56.87
uce-1223	1263	1	1262	2	41.8
uce-1225	1543	3	1543	4	36.61
uce-1232	1267	2	1267	2	55.52
uce-1233	812	0	809	0	26.9
uce-1234	1028	0	1014	1	50.88
uce-1235	1567	0	1567	2	32.01
uce-1236	1181	0	1176	0	30.97
uce-1237	1012	0	1004	0	34.65
uce-1238	1741	3	1741	3	36.05
uce-1239	1538	1	1536	2	40.81
uce-1240	2139	3	2139	4	53.93
uce-1241	1239	1	1239	2	49.01
uce-1242	1320	4	1320	4	47.48
uce-1243	1415	0	1415	0	30.3
uce-1244	1284	4	1284	4	56.19
uce-1245	944	1	944	3	57.07
uce-1252	1899	1	1899	2	46.02
uce-1253	1534	2	1532	2	42.79
uce-1257	1594	1	1594	1	38.81
uce-1258	1522	2	1522	3	39.76
uce-1259	1684	2	1684	4	45.2
uce-1260	1710	4	1710	5	45.89
uce-1263	1361	4	1361	4	53.65
uce-1267	1316	1	1303	2	42.74
uce-1268	1733	3	1733	5	48.44
uce-1269	1059	1	1059	1	49.6
uce-1274	1416	5	1416	5	43.87
uce-1278	826	2	826	2	51.34
uce-1279	1496	0	1496	4	42.93
uce-1281	1464	1	1464	1	41.72
uce-1282	1871	0	1843	0	48.46
uce-1283	1195	3	1183	4	46.64
uce-1284	1443	3	1443	4	42.27
uce-1285	1450	2	1450	3	39.47
uce-1286	1584	5	1584	6	39.68
uce-1287	1414	3	1414	5	41.75
uce-1288	1368	3	1368	5	40.48
uce-1289	1697	0	1697	2	50.56
uce-1291	846	0	846	1	57.94
uce-1292	1697	13	1697	15	36.33
uce-1296	1503	6	1503	8	36.9
uce-1297	1655	0	1653	0	47.88
uce-1301	2126	2	2126	3	49.12
uce-1303	1862	3	1862	4	41.73
uce-1304	1610	1	1582	2	50.52



uce-1305	1503	8	1503	9	40.98
uce-1306	1468	4	1468	5	53.26
uce-1308	1594	5	1593	5	44.09
uce-1314	1259	4	1242	6	45.69
uce-1315	1320	4	1320	5	46.94
uce-1317	2065	1	2065	3	50.51
uce-1323	1310	3	1310	3	51.41
uce-1324	1400	2	1400	5	48.16
uce-1325	1678	4	1678	5	58.4
uce-1328	2027	2	2027	3	42.14
uce-1330	1500	2	1500	2	48.95
uce-1331	1898	2	1898	4	44.8
uce-1335	1305	0	1305	0	27.37
uce-1337	1732	4	1732	5	53.01
uce-1339	1419	2	1419	2	52.36
uce-1340	1422	1	1422	2	56.12
uce-1342	1549	2	1549	2	43.03
uce-1343	2024	6	2024	7	44.49
uce-1345	1495	2	1485	3	45.99
uce-1348	1488	2	1456	3	44.44
uce-1349	1352	9	1352	11	41.89
uce-1352	1195	3	1174	4	49.86
uce-1353	1332	6	1315	6	42.66
uce-1357	1279	2	1278	5	43.39
uce-1358	1258	4	1258	5	49.5
uce-1359	1199	0	1199	2	43.3
uce-1362	1351	4	1351	4	38.45
uce-1365	1166	3	1134	3	30.66
uce-1366	1582	1	1582	2	34.85
uce-1368	1427	2	1427	2	34.28
uce-1372	1109	3	1103	3	39.04
uce-1374	1324	0	1324	0	47.28
uce-1377	1635	2	1611	4	49.11
uce-1378	1599	0	1599	1	41.84
uce-1379	1367	2	1367	3	38.54
uce-1380	1470	1	1470	1	31.85
uce-1381	1828	8	1828	11	37.15
uce-1383	1520	11	1520	15	34.76
uce-1384	1285	0	1279	0	28.94
uce-1386	2241	2	2241	4	57.01
uce-1391	1789	2	1789	5	49.22
uce-1392	1461	0	1461	0	54.57
uce-1393	1591	1	1591	2	40.69
uce-1394	1267	5	1244	7	41.86
uce-1395	1271	4	1259	8	41.18
uce-1400	1306	3	1306	6	46.99
uce-1403	1436	2	1436	3	49.98
uce-1405	1472	0	1472	1	27.23
uce-1414	1361	4	1355	6	43.63
uce-1415	1208	2	1204	6	37.72
uce-1416	1754	4	1742	5	40.61

uce-1417	1849	7	1849	9	44.78
uce-1418	1452	5	1440	8	46.35
uce-1419	1441	9	1436	9	44.37
uce-1420	1455	1	1455	2	51.16
uce-1421	1378	7	1378	8	44.5
uce-1422	1180	1	1180	1	49.76
uce-1423	1282	5	1282	5	43.65
uce-1424	1250	1	1244	1	46.26
uce-1425	1460	5	1450	6	45.24
uce-1426	1512	4	1512	6	39.08
uce-1428	1341	4	1341	5	45.79
uce-1429	1047	1	1047	2	48.52
uce-1430	1610	5	1610	5	46.79
uce-1432	1566	1	1558	1	32.36
uce-1434	1087	2	1078	4	46.47
uce-1438	1435	0	1435	0	36.43
uce-1440	2101	1	2100	1	33.72
uce-1441	1386	12	1386	13	39.25
uce-1442	879	1	874	2	40.99
uce-1443	1511	12	1511	14	39.4
uce-1445	1971	1	1971	2	33.34
uce-1446	1462	0	1462	0	38.59
uce-1447	1173	0	1173	0	35.73
uce-1451	1458	0	1458	1	36.16
uce-1452	2093	4	2092	7	43.51
uce-1457	1269	7	1269	7	36.02
uce-1459	1744	3	1744	4	44.36
uce-1460	1169	4	1169	5	41.46
uce-1462	1574	1	1569	2	50.93
uce-1463	1740	6	1740	6	37.85
uce-1464	1003	1	985	2	48.16
uce-1466	1433	6	1433	6	45.16
uce-1476	1727	6	1710	7	37.65
uce-1477	1278	4	1278	4	28.88
uce-1478	1351	3	1351	3	46.19
uce-1481	2184	3	2184	4	36.65
uce-1482	3187	1	3187	2	45.87
uce-1483	1365	1	1365	1	39.17
uce-1484	1054	1	1049	1	31.57
uce-1486	1299	5	1299	5	49.71
uce-1487	1470	2	1470	4	44.23
uce-1490	1486	1	1486	3	46.54
uce-1491	913	5	913	6	45.38
uce-1495	1465	1	1465	3	47.86
uce-1496	1216	2	1216	3	52.24
uce-1497	1555	1	1555	1	30.77
uce-1499	1479	7	1479	7	40.31
uce-1500	1331	2	1331	3	46.14
uce-1501	1082	0	1078	0	32.62
uce-1502	1018	3	1018	3	40.94
uce-1503	1452	2	1452	2	52.77

uce-1507	1132	0	1132	0	27.14
uce-1510	1482	0	1475	0	32.2
uce-10001	1149	1	1149	1	43.37
uce-10002	1430	2	1430	4	44.35
uce-10006	1590	1	1590	1	30.72
uce-10007	1371	1	1371	1	45.16
uce-10008	1480	5	1480	5	37.31
uce-10009	1687	0	1687	1	39.59
uce-10012	1106	4	1084	5	27.72
uce-10013	1606	0	1606	1	39.69
uce-10014	1307	2	1307	2	36.5
uce-10015	781	0	744	0	34.64
uce-10017	1100	0	1100	0	37.44
uce-10019	1154	3	1154	6	42.02
uce-10020	1242	1	1242	2	29.91
uce-10025	1193	3	1193	5	41.96
uce-10026	1528	10	1528	10	38.54
uce-10029	1728	6	1728	8	36.61
uce-10032	1303	2	1303	3	40.08
uce-10033	1791	14	1783	20	42.77
uce-10037	1365	1	1365	2	31.94
uce-10041	1468	0	1468	0	31.12
uce-10045	1086	0	1076	1	24.44
uce-10048	1412	0	1412	3	36.59
uce-10049	1251	1	1218	1	27.26
uce-10053	1517	4	1517	6	31.44
uce-10054	2054	3	2052	3	31.08
uce-10059	2436	5	2436	6	46.86
uce-10061	1367	3	1367	3	47.21
uce-10063	1422	2	1422	4	31.32
uce-10066	1175	2	1175	3	28.38
uce-10067	1512	0	1512	2	31.23
uce-10068	1806	3	1806	4	42.56
uce-10069	1465	4	1465	4	38
uce-10071	1409	2	1409	4	45.06
uce-10072	1037	0	1037	1	54.16
uce-10073	1462	3	1462	6	43.72
uce-10074	1371	3	1342	3	33.82
uce-10075	1323	4	1323	6	41.42
uce-10078	1090	2	1090	3	38.25
uce-10079	1138	3	1134	3	38.25
uce-10084	1759	2	1759	2	31.16
uce-10086	1178	0	1171	2	36.18
uce-10087	1647	4	1647	4	33.82
uce-10089	1986	2	1986	3	43.76
uce-10093	1616	4	1616	6	45.24
uce-10096	1296	1	1296	1	40.46
uce-10099	1383	3	1383	5	44.31
uce-10100	1242	0	1224	0	33.29
uce-10101	1184	3	1184	4	48.82
uce-10104	1479	1	1479	1	32.03

uce-10105	1576	3	1576	3	39.23
uce-10108	359	0	345	1	42.99
uce-10118	1086	1	1086	1	36.38
uce-10126	1632	2	1632	2	43.05
uce-10127	1559	4	1546	8	34.83
uce-10134	1966	3	1966	4	43.27
uce-10136	1270	0	1270	1	44.23
uce-10137	1155	0	1151	0	26.7
uce-10138	1443	0	1443	0	31.88
uce-10139	1214	0	1214	0	35.29
uce-10142	1761	0	1751	0	32.97
uce-10144	1305	2	1305	3	28.53
uce-10145	1432	2	1431	2	37.53
uce-10148	903	1	903	2	35.62
uce-10151	1556	5	1556	5	32.39
uce-10154	1547	2	1547	2	37.71
uce-10155	1862	1	1862	3	41.45
uce-10156	1655	4	1655	4	37.3
uce-10159	941	3	941	5	43.94
uce-10161	833	1	833	1	39.86
uce-10163	567	0	562	0	42.83
uce-10164	1051	3	1030	4	32.97
uce-10168	1389	2	1387	3	34.69
uce-10171	1238	1	1231	1	31.64
uce-10175	1311	0	1310	0	28.03
uce-10177	1207	0	1205	0	35.37
uce-10178	1351	1	1351	4	38.45
uce-10179	1048	1	1042	1	39.48
uce-10182	1236	0	1236	0	27.27
uce-10184	1406	0	1406	2	42.8
uce-10185	1267	5	1262	8	36.21
uce-10186	1309	3	1309	3	28.53
uce-10187	1175	1	1150	1	33.65
uce-10188	594	3	594	4	43.12
uce-10189	1365	4	1341	4	33.36
uce-10191	1461	2	1461	3	35.34
uce-10192	670	1	670	1	31.9
uce-10193	900	1	893	1	31.92
uce-10194	1134	0	1134	0	39.32
uce-10199	1262	2	1262	4	35.36
uce-10201	1504	2	1504	5	42.41
uce-10202	1494	4	1494	7	40.31
uce-10204	1816	11	1816	12	37.64
uce-10208	1359	3	1359	3	39.47
uce-10210	1565	1	1565	1	29.76
uce-10211	982	1	982	1	34.42
uce-10212	623	1	623	1	37.23
uce-10215	1194	2	1190	5	37.04
uce-10216	1326	3	1326	6	38.93
uce-10218	1357	4	1357	5	47.81
uce-10221	1505	5	1505	5	43.55

uce-10222	1034	4	1032	4	40.04
uce-10223	1314	2	1314	3	44.89
uce-10224	1080	6	1048	7	36.05
uce-10225	754	5	754	6	40.45
uce-10226	1518	8	1518	8	34.79
uce-10227	552	0	552	1	49.3
uce-10229	1930	6	1930	9	39.62
uce-10230	752	1	752	2	32.54
uce-10231	1434	2	1434	2	33.87
uce-10232	887	2	887	3	51.89
uce-10233	1025	7	1025	10	49.33
uce-10235	1252	0	1249	2	37.95
uce-10236	1208	2	1208	2	38.48
uce-10237	1452	4	1452	4	47.01
uce-10240	1041	2	1041	2	40.9
uce-10242	1373	4	1373	5	27.23
uce-10244	622	1	622	1	41.8
uce-10245	1340	0	1340	1	29.66
uce-10249	1069	3	1069	3	48.34
uce-10254	1766	5	1766	6	42.94
uce-10258	973	2	973	4	42.64
uce-10260	1122	0	1122	0	33.38
uce-10266	1376	10	1376	11	35.33
uce-10269	1309	5	1309	5	32.94
uce-10270	1540	4	1527	6	36.22
uce-10271	832	2	832	2	56.13
uce-10273	1354	2	1354	3	37.42
uce-10274	1156	6	1152	7	34.18
uce-10276	968	1	954	1	32.46
uce-10278	1539	0	1539	2	30.66
uce-10279	1747	0	1747	0	36.68
uce-10281	1769	1	1769	1	38.9
uce-10282	1377	1	1377	3	33.72
uce-10283	1511	3	1511	4	28.44
uce-10284	1195	0	1194	0	30.38
uce-10286	1868	0	1868	2	35.32
uce-10287	792	0	792	0	42.52
uce-10288	906	1	906	1	42.27
uce-10289	1050	1	1047	3	35.21
uce-10291	1412	3	1411	3	35.74
uce-10293	1428	3	1428	3	34.2
uce-10298	969	1	969	2	43.13
uce-10304	1520	1	1520	1	30.05
uce-10311	1073	3	1073	3	29.13
uce-10312	1389	1	1389	1	26.47
uce-10313	1453	0	1453	1	29.19
uce-10315	1512	0	1494	0	41.09
uce-10316	1049	2	1049	2	41.62
uce-10317	839	2	839	2	45.29
uce-10325	1485	0	1485	0	31.34
uce-10326	2383	2	2383	2	41.3

uce-10327	2121	2	2121	4	41.93
uce-10329	1408	4	1408	4	37.79
uce-10330	1491	0	1491	0	36.47
uce-10331	1378	0	1371	0	37.38
uce-10332	1207	4	1204	6	39.88
uce-10334	426	0	426	0	49.61
uce-10339	2007	3	2007	4	53.66
uce-10340	1369	0	1369	1	37.04
uce-10342	1263	3	1263	3	33.35
uce-10344	1167	0	1167	0	40.62
uce-10345	1132	0	1132	0	33.3
uce-10349	1656	2	1656	2	33.78
uce-10351	1009	1	1009	1	45.42
uce-10352	1618	1	1618	1	34.89
uce-10353	1517	0	1517	1	36.04
uce-10355	1291	1	1291	1	43.34
uce-10356	1479	2	1479	2	30.92
uce-10357	1541	0	1541	0	34.18
uce-10360	1423	3	1414	4	35.43
uce-10361	1338	0	1324	0	37.93
uce-10362	1063	2	1063	3	37.47
uce-10363	1482	2	1473	2	32.91
uce-10366	1221	1	1221	1	29.29
uce-10367	1277	3	1273	4	41.28
uce-10368	695	5	689	5	52.3
uce-10372	1016	0	1011	1	29.94
uce-10375	2121	2	2118	2	35.6
uce-10378	1254	1	1254	1	30.85
uce-10383	1281	1	1275	1	27.91
uce-10384	1145	1	1123	1	49.34
uce-10386	1277	2	1277	2	34.28
uce-10388	1281	2	1267	2	28.87
uce-10389	1295	1	1295	2	29.95
uce-10391	863	4	863	4	47.88
uce-10392	1712	1	1702	3	36.84
uce-10393	1083	1	1071	1	36.41
uce-10394	1145	0	1138	1	33.67
uce-10401	1058	1	1058	1	48.22
uce-10405	1447	0	1447	3	35.89
uce-10406	1254	0	1254	1	34.11
uce-10407	1342	1	1333	1	31.51
uce-10408	1594	0	1594	1	32.5
uce-10411	1409	2	1409	3	27.1
uce-10412	1234	1	1234	1	45.08
uce-10413	1199	3	1199	3	40.12
uce-10414	1321	2	1321	4	35.59
uce-10416	913	5	913	7	40.72
uce-10417	1402	6	1402	6	41.6
uce-10423	1409	0	1395	1	37.85
uce-10424	1424	2	1424	2	31.35
uce-10425	1259	0	1259	0	31.53

uce-10427	1248	5	1248	5	34.81
uce-10429	1744	3	1744	5	35.32
uce-10430	1492	1	1492	1	31.58
uce-10432	1440	3	1431	4	33.64
uce-10433	1344	6	1344	8	36.57
uce-10434	1711	1	1711	2	34.6
uce-10440	1407	4	1407	5	32.67
uce-10442	1012	0	1009	0	29.61
uce-10443	989	0	988	0	43.65
uce-10447	1317	1	1317	1	32.67
uce-10450	1460	0	1460	0	39.69
uce-10451	1252	2	1252	2	35.52
uce-10452	1457	3	1457	3	28.84
uce-10454	1375	1	1375	2	47.54
uce-10457	1259	0	1258	0	50.53
uce-10458	1814	0	1814	1	35.13
uce-10459	1485	0	1485	0	31.58
uce-10464	1505	1	1491	2	26.75
uce-10466	752	0	752	0	28.36
uce-10467	2102	3	2096	5	31.25
uce-10468	962	0	962	0	27.57
uce-10469	1449	0	1449	0	32.74
uce-10470	1269	0	1269	1	33.74
uce-10472	1152	1	1128	1	29.87
uce-10474	1133	1	1133	2	41.35
uce-10475	766	0	766	2	62.73
uce-10477	1002	1	1002	2	33.88
uce-10478	1366	0	1366	0	34.65
uce-10479	1272	1	1257	1	28.12
uce-10480	1193	1	1193	1	32.53
uce-10482	1497	1	1487	3	28.23
uce-10486	1230	0	1217	1	33.33
uce-10490	1268	3	1268	4	33.13
uce-10492	1265	1	1259	2	42.11
uce-10497	1089	0	1089	0	28.53
uce-10499	753	2	753	2	53.57
uce-10500	1061	0	1061	1	48.39
uce-10501	852	2	852	2	42.37
uce-10502	1517	5	1517	6	37.22
uce-10504	1023	1	1023	1	41.53
uce-10505	577	0	577	0	37.69
uce-10506	1709	0	1709	2	36.34
uce-10512	961	3	961	3	46.57
uce-10513	1092	2	1092	3	53.09
uce-10514	822	6	822	6	43.08
uce-10515	1249	0	1249	1	32.53
uce-10518	1507	1	1507	1	34.89
uce-10519	1490	1	1490	1	30.52
uce-10523	1250	3	1240	8	30.46
uce-10525	959	1	959	1	30.45
uce-10526	1262	0	1262	0	31.85

uce-10527	676	0	676	0	36.69
uce-10528	1851	2	1851	4	43.84
uce-10529	1693	6	1693	8	45.25
uce-10534	1152	0	1152	1	35.34
uce-10535	1514	2	1514	2	36.81
uce-10537	1151	5	1151	6	37
uce-10538	758	0	758	1	39.62
uce-10540	567	0	567	0	52.35
uce-10545	1128	1	1128	1	47.31
uce-10546	871	1	871	2	41.87
uce-10548	1296	2	1296	2	29.74
uce-10549	819	1	819	1	37.62
uce-10550	1543	0	1543	1	32.97
uce-10551	711	0	711	0	29.58
uce-10552	1396	0	1396	0	33.01
uce-10553	1062	1	1062	2	39.19
uce-10554	1333	0	1319	0	34.77
uce-10555	1414	3	1414	4	30.94
uce-10558	1175	0	1167	0	35.04
uce-10559	1369	1	1369	2	40.54
uce-10566	1125	0	1125	2	35.13
uce-10568	1036	1	1036	2	47.66
uce-10569	850	7	850	8	36.48
uce-10575	1285	0	1285	2	42.94
uce-10576	987	2	987	3	52.68
uce-10577	977	5	973	5	31.59
uce-10579	1539	1	1509	1	35.8
uce-10583	1269	0	1269	1	33.88
uce-10586	1511	0	1511	0	28.31
uce-10588	1277	4	1277	5	48.22
uce-10592	1005	7	1004	7	41.86
uce-10593	1331	4	1302	5	43.86
uce-10595	1280	5	1280	7	34.99
uce-10596	1115	3	1115	5	38.97
uce-10599	1345	1	1345	2	49.9
uce-10600	1100	4	1073	4	44.75
uce-10603	529	0	529	0	62.6
uce-10604	1481	2	1481	2	49.41
uce-10607	1207	4	1207	4	46.97
uce-10608	1617	2	1617	2	39.76
uce-10609	1054	3	1054	4	48.11
uce-10615	1358	0	1358	0	33.42
uce-10616	1434	3	1423	4	29.55
uce-10619	1265	0	1265	0	39.09
uce-10622	1527	0	1527	0	36.34
uce-10627	477	0	477	0	49.9
uce-10633	3657	3	3657	5	54.5
uce-10634	1332	5	1332	6	40.75
uce-10636	1384	0	1384	2	30.04
uce-10637	1214	1	1198	2	32.61
uce-10640	1096	2	1096	2	42.75



uce-10642	1335	4	1327	4	39.46
uce-10644	680	2	680	2	38.54
uce-10648	1184	2	1180	3	28.92
uce-10651	1282	1	1282	1	38.57
uce-10653	1347	1	1347	2	28.77
uce-10660	2235	0	2235	2	34.94
uce-10663	1514	2	1514	2	45.45
uce-10665	1476	1	1476	1	41.65
uce-10666	1338	2	1338	3	33.43
uce-10667	1346	2	1346	3	50.37
uce-10670	1282	3	1280	4	26.34
uce-10673	974	2	974	2	54.7
uce-10676	795	1	795	1	32.28
uce-10677	1685	3	1685	5	38.75
uce-10685	1226	2	1209	2	29.57
uce-10696	966	0	966	0	42.53
uce-10697	1275	2	1260	3	45.78
uce-10699	921	2	921	3	53.54
uce-10701	1076	2	1071	2	39.86
uce-10702	1456	0	1456	0	33.95
uce-10703	1275	4	1275	5	34.3
uce-10704	1541	2	1541	4	51
uce-10706	1440	0	1440	0	33.92
uce-10707	461	0	461	0	34.09
uce-10708	1334	3	1334	3	33.6
uce-10709	887	0	882	1	31.5
uce-10713	1072	1	1072	1	42.62
uce-10714	1391	2	1391	2	32.67
uce-10716	851	0	851	0	39.52
uce-10719	1508	8	1508	9	48.91
uce-10722	1290	2	1290	3	39.71
uce-10725	1439	2	1439	5	39.64
uce-10727	1677	0	1659	3	45.85
uce-10730	1221	4	1221	4	40.34
uce-10733	1201	1	1201	1	32.05
uce-10734	1540	2	1540	2	38.66
uce-10735	1276	0	1276	0	33.47
uce-10738	1691	0	1681	0	31.96
uce-10741	1304	3	1304	6	32.34
uce-10742	1939	3	1939	4	53.4
uce-10743	1144	0	1144	0	45.15
uce-10751	1098	5	1097	5	30.85
uce-10752	1162	0	1142	0	29.31
uce-10753	1273	1	1257	1	24.35
uce-10756	1513	0	1513	0	27.99
uce-10758	1155	1	1152	1	26.78
uce-10762	1146	1	1137	2	32.46
uce-10765	857	1	848	1	47.17
uce-10767	1400	3	1400	4	32.79
uce-10768	1028	0	1028	0	37.78
uce-10770	1197	1	1197	2	35.27

uce-10771	580	0	580	0	33.65
uce-10772	831	0	818	0	35.87
uce-10775	1545	1	1545	4	26.95
uce-10776	1153	2	1140	2	26.95
uce-10778	1088	3	1088	5	46.67
uce-10780	731	0	731	0	41.56
uce-10782	1841	0	1841	0	32.11
uce-10783	1005	3	1005	3	39.63
uce-10784	1431	3	1421	3	44.43
uce-10785	752	0	752	1	41.25
uce-10786	1208	1	1208	3	34.45
uce-10789	1494	1	1494	1	44.47
uce-10790	990	1	986	1	35.27
uce-10791	1126	3	1126	4	36.96
uce-10794	1404	0	1401	1	34.02
uce-10795	1316	1	1316	1	45.71
uce-10796	1479	5	1465	7	32.92
uce-10797	977	0	952	1	28.16
uce-10798	1525	1	1525	1	35.85
uce-10799	720	0	720	1	29.25
uce-10801	1358	0	1358	0	31.12
uce-10802	1391	4	1391	4	32.55
uce-10803	1371	2	1345	2	36.4
uce-10807	1855	4	1842	5	35.72
uce-10808	1409	1	1409	1	36.27
uce-10811	1126	3	1124	4	32.71
uce-10819	1147	2	1147	3	31.98
uce-10820	1685	0	1685	1	31.49
uce-10821	1412	4	1412	5	28.08
uce-10822	1475	2	1475	3	28.85
uce-10828	1141	0	1141	1	36.19
uce-10829	1300	2	1300	4	43.95
uce-10831	1496	2	1496	3	34.29
uce-10833	1442	0	1442	1	29.08
uce-10835	823	3	802	3	34.07
uce-10836	1314	7	1314	9	32.42
uce-10839	1080	0	1080	0	47.08
uce-10840	1329	0	1329	0	30.1
uce-10842	932	0	932	1	61.59
uce-10843	1275	3	1275	3	53.89
uce-10847	1356	4	1351	4	63.59
uce-10848	1540	5	1540	8	56.81
uce-10849	1339	2	1339	2	55.75
uce-10852	1192	2	1192	2	35.97
uce-10854	626	1	626	1	61.94
uce-10856	1051	4	1051	6	47.78
uce-10860	981	1	981	2	31.64
uce-10861	1628	1	1628	3	31.16
uce-10864	931	2	931	4	47.68
uce-10872	834	8	834	9	42.24
uce-10879	1163	1	1154	2	26.67

uce-10880	1099	8	1092	9	33.61
uce-10881	1422	1	1422	1	40.7
uce-10882	1451	6	1451	7	37.51
uce-10883	1312	1	1296	2	36.34
uce-10885	1979	2	1979	4	33.06
uce-10888	1460	2	1460	2	32.31
uce-10890	1010	1	1010	2	40.52
uce-10891	1785	4	1785	4	41.9
uce-10892	1544	1	1544	4	33.91
uce-10893	1308	2	1308	3	35.83
uce-10896	1188	2	1184	3	55.66
uce-10898	1689	0	1689	1	46.26
uce-10900	1145	2	1145	2	32.75
uce-10901	1491	2	1466	3	32.3
uce-10904	1531	2	1531	2	29.89
uce-10905	1215	2	1204	2	24.97
uce-10908	1038	0	1038	0	34.57
uce-10910	1039	1	1034	1	31.71
uce-10913	1376	0	1376	1	31.65
uce-10914	2224	0	2224	1	33.18
uce-10921	2308	2	2302	2	28.49
uce-10922	572	0	572	1	45.72
uce-10923	1142	0	1142	1	34.28
uce-10926	1344	0	1329	0	31.96
uce-10929	1559	0	1559	0	33.63
uce-10930	1602	0	1602	3	30.98
uce-10932	1543	0	1543	0	37.06
uce-10936	1162	1	1162	1	38.8
uce-10942	1247	0	1247	0	33.89
uce-10946	1394	9	1394	10	40.07
uce-10947	604	0	604	0	47.25
uce-10949	920	1	920	3	46.34
uce-10952	841	1	841	2	56.98
uce-10955	1539	1	1539	1	41.85
uce-10956	1221	4	1221	4	40.57
uce-10957	1675	1	1675	1	39.58
uce-10963	470	0	470	0	50.69
uce-10965	1215	0	1215	2	32.4
uce-10966	1316	0	1302	1	31.12
uce-10967	1353	2	1353	2	30.23
uce-10970	1065	0	1063	0	34.51
uce-10974	1074	1	1073	2	32.57
uce-10977	1323	5	1304	5	31.17
uce-10978	1245	2	1245	2	40.54
uce-10979	695	0	695	1	46.99
uce-10985	591	2	591	2	37.36
uce-10988	1605	4	1605	4	40.79
uce-10989	1411	3	1411	3	35.76
uce-10991	2103	2	2103	2	30.34
uce-10993	1181	2	1181	4	32.6
uce-10997	1309	0	1309	1	35.72

uce-11000	723	2	712	2	38.04
uce-11001	1127	6	1121	6	34.85
uce-11002	1186	5	1186	7	39.38
uce-11009	1551	2	1540	2	39.74
uce-11010	661	0	661	1	31.23
uce-11014	1387	1	1387	1	32.95
uce-11016	1342	1	1342	1	32.13
uce-11022	1345	1	1345	2	29.02
uce-11023	1113	7	1090	7	31.71
uce-11024	1526	0	1526	0	34.18
uce-11026	1424	1	1424	2	31.25
uce-11027	1389	0	1389	1	27.41
uce-11038	1097	0	1097	1	29.78
uce-11040	1186	3	1180	3	31.67
uce-11041	1743	5	1743	5	56.45
uce-11042	1363	3	1363	4	36.08
uce-11044	1087	3	1087	4	49.03
uce-11045	1524	2	1524	8	35.35
uce-11046	1639	4	1639	6	38.06
uce-11048	1210	5	1210	5	49.29
uce-11053	1566	1	1566	1	52.76
uce-11055	1401	4	1401	4	46.07
uce-11056	1603	2	1603	3	37.54
uce-11057	1429	2	1429	2	37.48
uce-11060	1387	5	1387	7	37.19
uce-11061	1797	4	1797	6	35.76
uce-11063	1235	3	1235	5	35.93
uce-11066	1203	4	1203	6	43.28
uce-11068	1006	4	1006	4	39.75
uce-11069	1187	2	1187	2	49.88
uce-11070	1368	4	1368	5	44.62
uce-11072	1248	7	1237	10	41.28
uce-11073	1403	2	1389	4	40.02
uce-11074	1548	2	1548	2	35.42
uce-11075	1587	2	1587	2	29.06
uce-11076	1137	3	1123	4	42.42
uce-11077	802	2	802	2	44.03
uce-11078	1036	0	1036	0	31.69
uce-11079	910	1	910	1	28.96
uce-11081	1427	3	1427	3	31.24
uce-11083	1229	0	1229	0	28.24
uce-11084	1026	3	1026	4	44.65
uce-11085	1512	0	1512	0	28.96
uce-11087	1216	1	1216	1	33.53
uce-11090	1660	4	1660	4	38.14
uce-11091	1496	5	1496	5	47.21
uce-11094	1063	0	1057	0	44.85
uce-11095	941	1	941	2	37.2
uce-11098	1299	5	1299	5	41
uce-11099	1012	2	1012	2	48.41
uce-11101	1926	1	1884	1	51.26

uce-11103	1303	3	1303	3	51.17
uce-11104	1418	1	1418	1	46.57
uce-11110	631	1	620	1	38.28
uce-11112	1297	3	1279	4	44.07
uce-11115	1452	1	1452	2	30.52
uce-11116	1137	2	1137	4	39.52
uce-11117	930	2	930	2	34.63
uce-11118	2192	4	2192	5	34.48
uce-11119	1539	2	1539	3	31.97
uce-11121	1404	4	1404	4	43.45
uce-11123	1044	3	1044	3	43.97
uce-11124	1274	0	1274	0	40.44
uce-11125	790	0	790	0	47.25
uce-11128	530	0	530	0	33.42
uce-11129	1684	3	1684	5	43.61
uce-11130	1372	0	1372	0	33.01
uce-11138	1492	1	1492	2	34.42
uce-11140	1255	0	1255	1	37.49
uce-11144	1184	0	1184	1	45.65
uce-11145	1576	2	1576	2	36.09
uce-11146	1278	0	1278	1	39.35
uce-11149	469	0	469	0	31.59
uce-11150	1451	1	1451	2	31.4
uce-11151	1202	0	1202	2	29.27
uce-11155	1405	0	1405	0	27.22
uce-11158	1266	0	1266	1	42.37
uce-11161	1017	3	1017	3	45.38
uce-11163	1423	0	1423	0	34.02
uce-11165	1026	0	1006	0	34.94
uce-11166	878	0	878	0	39.78
uce-11170	1310	4	1310	4	43.8
uce-11172	1488	0	1472	2	55.47
uce-11175	542	0	542	0	34.16
uce-11177	1872	0	1872	1	46.91
uce-11179	1116	4	1116	4	39.19
uce-11183	1693	2	1693	2	36.56
uce-11186	1103	9	1103	10	38.35
uce-11188	1367	4	1367	4	42.79
uce-11189	1118	6	1101	6	38.15
uce-11191	908	3	908	3	55.02
uce-11193	1008	9	1008	9	44.06
uce-11194	1095	2	1080	3	28.61
uce-11195	1323	0	1311	0	27.32
uce-11196	1402	3	1392	3	38.74
uce-11197	969	1	969	2	30.99
uce-11198	1380	2	1380	2	30.49
uce-11200	1578	4	1578	4	54.41
uce-11202	1431	2	1431	4	50.34
uce-11203	580	0	580	0	54.52
uce-11216	1268	0	1255	0	33.47
uce-11217	1381	5	1381	5	36.8

uce-11218	1370	6	1358	8	28.98
uce-11219	1581	2	1581	2	47.91
uce-11220	922	0	922	1	31.26
uce-11221	1340	3	1340	4	30.73
uce-11224	1487	6	1487	6	33.4
uce-11225	898	1	898	4	39.15
uce-11226	1281	2	1281	2	27.29
uce-11231	1014	1	1014	1	42.98
uce-11235	951	2	951	2	44.08
uce-11238	1887	1	1887	1	38.21
uce-11239	1152	3	1137	7	27.9
uce-11243	1284	1	1264	1	29.24
uce-11244	1171	9	1171	9	38.44
uce-11245	981	0	981	1	28.73
uce-11246	665	3	629	3	41.41
uce-11249	821	0	821	0	33.14
uce-11252	1517	0	1517	1	29.45
uce-11254	879	0	879	0	32.45
uce-11257	974	0	974	0	32.11
uce-11261	991	0	986	0	28.35
uce-11262	976	2	964	2	29.07
uce-11263	1301	0	1296	0	25.99
uce-11264	1434	0	1434	0	30.76
uce-11268	2024	3	2024	4	40.36
uce-11275	1348	1	1348	1	36.01
uce-11276	1374	0	1374	0	33.77
uce-11277	1281	0	1279	0	32.61
uce-11278	997	2	997	2	36.56
uce-11282	1246	0	1246	2	37.9
uce-11283	1472	2	1472	3	34.75
uce-11284	1022	0	1022	2	35.18
uce-11285	1315	0	1315	0	32.72
uce-11286	1007	3	1002	3	38.88
uce-11288	1545	1	1545	1	26.96
uce-11289	1001	0	1000	0	24.64
uce-11291	1700	1	1700	2	35.24
uce-11292	647	2	647	2	41.46
uce-11293	555	0	555	0	34.51
uce-11296	1303	2	1303	3	37.94
uce-11298	1292	1	1291	2	29.59
uce-11299	1234	0	1234	1	31.31
uce-11303	1486	4	1486	5	35.91
uce-11304	941	3	941	3	39.82
uce-11310	684	0	684	0	47.33
uce-11311	1166	1	1166	3	46.76
uce-11312	1442	3	1442	6	38.05
uce-11313	1973	2	1973	3	37.73
uce-11316	1313	0	1313	0	30.95
uce-11317	1458	1	1437	1	34.52
uce-11319	1512	5	1512	5	49.99
uce-11320	1396	6	1396	7	51.9

uce-11323	2206	2	2206	5	46.86
uce-11325	1782	5	1782	6	46.7
uce-11326	1089	8	1089	9	50.7
uce-11327	1312	2	1312	2	33.13
uce-11329	1289	0	1289	1	36.35
uce-11332	1183	0	1183	0	29.94
uce-11337	1129	1	1129	1	35.93
uce-11338	1551	0	1551	0	29.34
uce-11339	1305	0	1305	0	29.63
uce-11341	1075	2	1075	2	33.22
uce-11343	1188	1	1188	2	34.99
uce-11344	1123	0	1118	0	44.26
uce-11345	1390	0	1390	1	29.28
uce-11346	1097	3	1097	3	43.44
uce-11347	1270	1	1262	2	29.56
uce-11349	1607	1	1607	1	32.69
uce-11353	1391	2	1385	2	28.25
uce-11354	529	0	529	0	39.82
uce-11357	626	1	622	2	55.67
uce-11358	1956	2	1951	3	53.02
uce-11359	1487	4	1487	5	37.19
uce-11361	802	1	802	2	47.52
uce-11368	1309	5	1309	6	37.09
uce-11371	699	3	699	3	52.35
uce-11373	1289	3	1289	3	50.91
uce-11376	1323	0	1320	0	27.64
uce-11377	1190	2	1189	2	30.21
uce-11380	1722	2	1722	3	34.39
uce-11381	1212	1	1212	1	29.98
uce-11382	1344	0	1342	0	30.29
uce-11383	1237	1	1237	1	34.38
uce-11386	898	0	898	1	44.53
uce-11388	867	0	867	1	32.12
uce-11390	1040	1	1040	2	28.2
uce-11391	1182	0	1173	0	28.68
uce-11393	1518	0	1518	0	30.24
uce-11394	1379	1	1371	1	26.2
uce-11397	1528	1	1527	1	37.45
uce-11399	1927	3	1927	3	45.98
uce-11407	1585	1	1580	1	41.23
uce-11408	1537	3	1537	7	35.99
uce-11410	1625	2	1625	2	57.29
uce-11411	539	0	539	0	52.14
uce-11412	1098	0	1098	1	53.91
uce-11413	913	0	913	1	57.14
uce-11415	1380	1	1377	2	51.62
uce-11418	1432	7	1432	7	31.55
uce-11420	1238	2	1238	3	26.74
uce-11421	1201	1	1194	1	30.09
uce-11422	1176	0	1176	2	29.85
uce-11423	1463	1	1463	1	32.03

uce-11425	764	1	764	1	32.53
uce-11427	918	1	914	2	29.29
uce-11428	1670	1	1670	1	35
uce-11432	1098	0	1098	1	28.38
uce-11434	890	0	890	0	38.93
uce-11435	762	1	762	1	40.15
uce-11436	1427	1	1427	1	29.95
uce-11437	1407	0	1402	1	28.04
uce-11439	1317	0	1317	0	33.14
uce-11441	1283	5	1262	6	40.76
uce-11442	1527	0	1527	1	48.29
uce-11446	1384	2	1384	2	33.56
uce-11448	2137	4	2137	7	46.17
uce-11454	1484	2	1484	2	42.27
uce-11455	1663	7	1663	7	48.24
uce-11456	1017	0	1017	0	46.43
uce-11458	1516	2	1496	2	34.04
uce-11460	2474	2	2474	4	36.63
uce-11461	974	0	974	0	31.69
uce-11462	1258	0	1258	0	32.63
uce-11464	1439	0	1439	0	29.51
uce-11465	523	0	523	0	30.67
uce-11468	1449	0	1449	1	34
uce-11469	1517	1	1517	2	34.25
uce-11470	1412	0	1412	2	52.61
uce-11471	1389	2	1379	2	30.49
uce-11473	841	4	841	5	47.79
uce-11474	1740	5	1740	6	37.1
uce-11475	553	0	553	1	46.62
uce-11476	898	5	898	6	56.51
uce-11477	1348	0	1348	0	38.13
uce-11482	1480	0	1480	0	29.83
uce-11488	1922	6	1922	7	50.56
uce-11489	2122	4	2122	7	39.36
uce-11490	1240	1	1240	2	50.37
uce-11493	1158	1	1158	2	42.13
uce-11494	1492	0	1485	0	29.58
uce-11498	1217	1	1206	2	25.99
uce-11503	591	0	591	0	32.25
uce-11504	1273	0	1273	0	30.15
uce-11507	1526	3	1526	4	45.03
uce-11517	438	2	438	2	47.09
uce-11518	1062	1	1062	1	46.71
uce-11520	1160	0	1160	0	46.85
uce-11522	1077	1	1077	1	44.36
uce-11523	1274	0	1274	0	36.01
uce-11525	1513	7	1513	7	38.41
uce-11526	1400	3	1400	4	48.48
uce-11529	947	1	947	3	38.6
uce-11531	1057	2	1057	2	51.05
uce-11532	1133	6	1133	6	38.76



uce-11533	1064	2	1064	3	36.3
uce-11534	1089	3	1089	4	40.83
uce-11535	1182	3	1182	8	38.44
uce-11537	651	2	651	3	56.86
uce-11538	1418	3	1418	4	30.34
uce-11539	1491	0	1491	0	33.04
uce-11540	1383	5	1383	6	35.21
uce-11543	1381	1	1381	1	33.7
uce-11547	1256	3	1256	4	42.17
uce-11548	1635	1	1635	1	46.37
uce-11564	1278	3	1259	4	39.43
uce-11565	1104	1	1102	2	34.9
uce-11566	1176	0	1176	0	40.67
uce-11567	994	2	994	2	31.05
uce-11569	981	2	974	3	37.06
uce-11570	1138	0	1138	0	37.35
uce-11573	920	1	920	1	35.11
uce-11575	893	1	893	1	38.25
uce-11577	1408	1	1408	1	29.34
uce-11580	871	0	871	0	51.17
uce-11581	1549	2	1549	3	35.24
uce-11583	1203	9	1203	10	43.07
uce-11584	872	4	872	4	42.56
uce-11585	1267	8	1267	9	40.06
uce-11593	1395	0	1395	0	31.69
uce-11594	1160	1	1160	2	27.71
uce-11596	908	0	908	0	53.23
uce-11600	1350	0	1350	0	32.94
uce-11601	1531	3	1531	4	33.05
uce-11604	1324	0	1324	0	28.32
uce-11605	1260	0	1251	0	28.97
uce-11609	1151	2	1151	3	32.09
uce-11613	1344	4	1344	4	31.41
uce-11617	1076	4	1067	4	33.19
uce-11618	906	0	906	1	55.34
uce-11623	1058	0	1052	2	56.28
uce-11629	1429	4	1429	4	46.25
uce-11631	1687	7	1687	8	44.59
uce-11633	1291	2	1291	4	47.73
uce-11634	1293	5	1291	8	44.09
uce-11641	1294	1	1294	1	45.26
uce-11644	1205	0	1205	1	28.57
uce-11645	1111	0	1111	0	31.13
uce-11647	1521	1	1521	1	34.11
uce-11648	1502	1	1502	1	32.39
uce-11654	1295	3	1295	3	46.02
uce-11656	1255	3	1255	5	44.29
uce-11658	1354	1	1354	1	46.3
uce-11664	1463	1	1463	1	37.48
uce-11666	1423	6	1423	9	43.13
uce-11667	1458	0	1458	0	29.89

uce-11670	1442	1	1431	1	36.28
uce-11671	1082	1	1082	1	35.85
uce-11672	1500	5	1500	10	37.95
uce-11673	991	0	991	0	55.36
uce-11674	857	2	857	6	54.34
uce-11675	1443	5	1443	8	37.51
uce-11679	1598	0	1589	0	37.85
uce-11682	1642	0	1642	0	33.93
uce-11683	1473	0	1473	1	36.58
uce-11684	1316	1	1298	1	31.62
uce-11685	1467	0	1467	0	24.11
uce-11687	1510	3	1510	5	38.12
uce-11688	851	0	849	1	56.47
uce-11691	1732	6	1732	9	41.42
uce-11693	1562	2	1562	3	38.76
uce-11695	1614	12	1613	16	45.82
uce-11698	990	1	974	1	32.08
uce-11702	740	1	740	1	48.46
uce-11704	418	1	418	1	59.67
uce-11705	1438	0	1438	0	35.03
uce-11706	1215	5	1215	6	30.61
uce-11713	1314	0	1286	0	32.83
uce-11714	1355	2	1355	2	28.36
uce-11715	1130	6	1130	7	40.99
uce-11716	1442	3	1418	4	38.73
uce-11717	1352	2	1352	2	31.74
uce-11718	478	0	478	0	31.21
uce-11719	1082	2	1082	3	34.49
uce-11721	791	0	791	0	30.93
uce-11722	1349	4	1349	4	36.52
uce-11725	1340	1	1340	2	31.68
uce-11728	1088	0	1084	0	29.24
uce-11729	788	0	788	0	36.19
uce-11730	1487	3	1487	4	40.58
uce-11731	1279	2	1278	2	35.93
uce-11732	1646	3	1646	3	40.32
uce-11733	1639	0	1639	1	38.24
uce-11736	1494	0	1494	0	34.92
uce-11737	1377	4	1377	4	34.71
uce-11740	1326	3	1326	4	38.55
uce-11741	1421	4	1421	5	38.46
uce-11742	1555	2	1555	2	38.21
uce-11744	1632	2	1627	5	40.21
uce-11745	1539	3	1539	5	42.6
uce-11746	1321	2	1321	2	48.6
uce-11747	1313	3	1313	7	42.2
uce-11749	1427	1	1427	1	37.13
uce-11750	1294	1	1294	1	38.67
uce-11754	1367	8	1365	9	35.55
uce-11759	1529	5	1529	8	35.04
uce-11763	1370	3	1370	3	36.43

uce-11765	1310	3	1298	4	35.28
uce-11766	1544	12	1543	12	34.22
uce-11767	1040	0	1040	0	34.21
uce-11771	1386	3	1386	5	35.69
uce-11772	889	2	838	5	35.86
uce-11773	1573	1	1573	2	34.65
uce-11775	1335	4	1305	7	40.83
uce-11776	1271	7	1261	7	38.78
uce-11778	429	2	429	2	45.31
uce-11780	1585	1	1583	1	41.41
uce-11784	1420	4	1420	5	36.19
uce-11785	1174	0	1174	0	51.58
uce-11787	1476	1	1476	4	27.79
uce-11789	958	0	950	0	30.34
uce-11791	1654	1	1649	1	33.77
uce-11792	1439	2	1439	2	39.22
uce-11796	1426	0	1426	0	33.84
uce-11799	1675	2	1675	2	31.98
uce-11800	1345	4	1329	4	34.34
uce-11802	1333	0	1333	0	30.53
uce-11808	1053	4	1053	5	44.22
uce-11809	1276	6	1276	7	42.7
uce-11812	1431	0	1431	0	39.21
uce-11819	1028	1	1028	3	39.07
uce-11820	1267	0	1266	0	29.3
uce-11823	1826	1	1826	4	41.65
uce-11824	1029	0	1029	0	29.77
uce-11826	901	1	870	2	28.62
uce-11828	1196	1	1193	2	31.54
uce-11831	942	0	941	0	28.18
uce-11832	1057	1	1057	1	44.27
uce-11833	1076	0	1076	0	27.8
uce-11837	1173	1	1173	1	29.41
uce-11839	1100	6	1100	7	37.69
uce-11840	741	1	741	2	53.89
uce-11841	1133	4	1133	5	40.31
uce-11843	999	5	988	5	44.94
uce-11844	1539	0	1539	0	39.31
uce-11847	1085	4	1085	5	45.52
uce-11850	1277	0	1277	1	31.3
uce-11851	1387	2	1387	2	37.52
uce-11852	1383	0	1383	0	30.3
uce-11853	1181	2	1167	2	37.26
uce-11858	1662	0	1662	0	34.21
uce-11860	1092	1	1092	1	44.95
uce-11863	1778	2	1772	4	51.81
uce-11865	1229	1	1229	2	44.18
uce-11868	854	0	854	0	47.29
uce-11876	917	2	917	2	45.22
uce-11879	1106	1	1106	1	43.42
uce-11880	1001	4	1001	5	42.06

uce-11881	1114	1	1114	1	41.86
uce-11882	1223	0	1206	1	37.57
uce-11884	776	2	766	2	42.49
uce-11889	831	0	831	0	30.92
uce-11897	1391	0	1391	1	32.83
uce-11899	781	0	781	1	40.64
uce-11900	1357	2	1357	3	30.84
uce-11901	1165	4	1165	5	44.52
uce-11902	1465	0	1465	1	33.54
uce-11903	704	0	704	0	28.19
uce-11905	1516	1	1516	2	31.57
uce-11906	1031	1	1031	2	27.66
uce-11909	1425	5	1425	5	38.46
uce-11910	1131	0	1131	0	44.49
uce-11912	980	0	978	0	24.75
uce-11914	1381	2	1381	2	30.77
uce-11922	1844	1	1844	1	38.57
uce-11923	1165	2	1165	4	46.95
uce-11925	1293	2	1293	3	49.6
uce-11926	1574	0	1574	1	47.41
uce-11927	1327	3	1327	3	53.23
uce-11930	889	1	889	2	36.5
uce-11931	1045	1	1045	2	32.08
uce-11932	1438	5	1438	7	42.51
uce-11936	1411	2	1403	2	37.57
uce-11939	1531	10	1525	11	35.84
uce-11940	1271	5	1271	6	36.83
uce-11941	1612	1	1612	1	32.11
uce-11944	1277	5	1272	5	33.83
uce-11946	973	2	973	2	49.39
uce-11947	1361	0	1361	0	23.53
uce-11948	1298	1	1298	1	25.15
uce-11949	1012	4	1005	4	28.05
uce-11952	1238	0	1238	0	30.29
uce-11956	1439	1	1439	1	33.79
uce-11963	1534	2	1534	2	30.93
uce-11965	883	0	883	0	32.5
uce-11969	1541	0	1538	0	33.67
uce-11971	1504	0	1504	1	32.43
uce-11972	1440	6	1426	6	34.83
uce-11978	1186	0	1186	0	42.7
uce-11981	1186	1	1186	1	25.79
uce-11982	1624	0	1624	0	33.9
uce-11983	988	1	988	1	32.78
uce-11984	517	0	517	1	43.22
uce-11986	786	0	786	1	41.83
uce-11987	1083	2	1078	3	51.11
uce-11989	1809	0	1809	0	36.41
uce-11995	1771	1	1771	2	31.66
uce-11997	869	0	854	0	32.91
uce-11998	1229	0	1229	1	44.41

uce-12002	1499	1	1499	2	29.83
uce-12003	1227	2	1227	3	32.34
uce-12005	1255	1	1240	1	30.56
uce-12010	1086	1	1086	1	28.1
uce-12013	1197	2	1197	3	35.56
uce-12016	1203	5	1173	5	36.76
uce-12017	2649	1	2649	2	39.1
uce-12018	1568	2	1568	2	30.65
uce-12020	898	1	888	1	28.59
uce-12021	1435	1	1431	1	31.91
uce-12022	1463	1	1463	1	30.18
uce-12023	1331	3	1331	4	28.49
uce-12024	909	0	909	0	40.33
uce-12025	1380	1	1380	2	39.65
uce-12027	1288	0	1288	1	31.51
uce-12029	932	2	929	2	36.07
uce-12030	1258	2	1258	2	36.29
uce-12032	1327	0	1327	1	32.05
uce-12033	1508	7	1508	8	26.48
uce-12036	2588	0	2588	0	30.45
uce-12037	1358	0	1358	0	32.92
uce-12042	1352	1	1352	1	29.07
uce-12045	1217	1	1217	1	40.62
uce-12046	1394	1	1394	1	34.47
uce-12050	1331	4	1326	4	40.54
uce-12052	1039	0	1030	0	26.7
uce-12054	924	1	918	1	31.36
uce-12055	1907	3	1907	4	38.54
uce-12059	1477	2	1477	2	33.39
uce-12060	1390	1	1390	2	34.76
uce-12061	1006	0	1006	1	30.68
uce-12062	1310	2	1310	2	36.93
uce-12063	1285	6	1285	6	45.01
uce-12065	1698	1	1698	2	31.75
uce-12066	1206	0	1170	0	30.29
uce-12067	1546	1	1546	2	35.09
uce-12068	790	1	790	1	38.07
uce-12074	1367	0	1367	5	29.99
uce-12076	1510	3	1510	3	35.01
uce-12077	1554	0	1549	0	32
uce-12078	1555	1	1552	1	34.64
uce-12079	1406	0	1398	1	33.97
uce-12080	922	2	911	2	43.17
uce-12081	1394	0	1394	0	36.44
uce-12085	1393	0	1393	1	38.9
uce-12088	1446	2	1446	4	33.39
uce-12090	1479	0	1478	1	36.29
uce-12091	1132	2	1132	2	33
uce-12095	924	0	924	0	43.75
uce-12098	1555	1	1555	1	32.19
uce-12100	869	0	869	0	29.66

uce-12101	1219	2	1219	2	31.69
uce-12103	937	1	937	1	36.72
uce-12104	1315	1	1315	1	40.02
uce-12105	1281	0	1233	1	32.22
uce-12108	1301	0	1294	0	30.05
uce-12110	1703	3	1703	3	36.52
uce-12111	1382	1	1382	2	33.94
uce-12117	1341	6	1341	6	35.63
uce-12123	1429	1	1421	2	40.4
uce-12124	1055	1	1055	1	27.53
uce-12125	951	4	951	4	35.79
uce-12126	1338	0	1338	1	34.38
uce-12127	1556	2	1556	3	40.56
uce-12129	1153	2	1153	4	40.03
uce-12130	1372	0	1339	0	33.4
uce-12133	1263	5	1263	6	37.98
uce-12135	1076	1	1072	2	34.04
uce-12136	1110	4	1103	4	35.56
uce-12137	1499	0	1497	1	29.87
uce-12139	1168	1	1168	1	28.47
uce-12141	1319	0	1319	1	38.64
uce-12142	1126	1	1126	3	44
uce-12143	1313	4	1310	8	48.23
uce-12144	1548	7	1548	9	41
uce-12145	1069	4	1064	5	44.5
uce-12147	1400	1	1400	1	32.91
uce-12150	1604	0	1598	1	35.53
uce-12154	1239	1	1239	1	49.44
uce-12159	1119	1	1119	2	28.85
uce-12167	1406	6	1406	6	34.86
uce-12169	1238	0	1238	0	31.89
uce-12171	1039	2	1039	3	32.61
uce-12172	1692	5	1692	6	35.49
uce-12176	1346	3	1334	5	39.16
uce-12178	1088	0	1088	1	43.45
uce-12179	1219	8	1219	10	48.57
uce-12180	1206	1	1197	1	38.74
uce-12182	1615	0	1615	0	35.39
uce-12185	1243	2	1243	2	33.54
uce-12186	1059	0	1058	1	29.98
uce-12187	759	2	759	2	53
uce-12189	1850	4	1838	5	30.89
uce-12190	936	0	905	2	36.06
uce-12192	1188	1	1188	2	31
uce-12193	1607	6	1607	7	37.05
uce-12195	1165	1	1165	1	31.76
uce-12196	1431	1	1431	1	34.56
uce-12198	999	2	999	2	42.65
uce-12200	1406	1	1389	1	32.59
uce-12201	1215	0	1215	1	46.62
uce-12204	1268	0	1268	0	31.53

uce-12208	932	2	932	3	57.73
uce-12212	1453	0	1453	0	36.04
uce-12215	1623	4	1623	5	37.44
uce-12216	1510	3	1510	3	36.97
uce-12217	1209	1	1209	1	44.23
uce-12218	1521	1	1521	3	32.66
uce-12219	1502	0	1502	3	38.76
uce-12220	1425	1	1425	1	30.16
uce-12224	802	1	802	1	60.08
uce-12225	1339	1	1339	1	28.28
uce-12228	1593	3	1593	4	46.51
uce-12229	1487	1	1487	1	45.83
uce-12231	745	2	745	3	43.18
uce-12233	820	0	820	1	42.04
uce-12237	1339	1	1339	1	29.27
uce-12238	888	5	888	8	43.83
uce-12239	1105	0	1105	0	30.07
uce-12244	1798	4	1798	5	33.55
uce-12245	1468	0	1468	1	27.39
uce-12246	1437	1	1437	2	33.4
uce-12248	1390	2	1390	3	38.11
uce-12249	1116	0	1116	0	43.07
uce-12252	1137	1	1134	1	32.6
uce-12254	615	0	602	0	34.12
uce-12257	1301	1	1301	2	34.9
uce-12258	1375	2	1375	2	31.01
uce-12261	1841	0	1841	0	39.22
uce-12262	862	0	862	0	40.53
uce-12263	1164	2	1145	2	31.87
uce-12266	1367	1	1365	1	43.74
uce-12269	880	0	880	0	30.34
uce-12273	1235	0	1231	0	39.97
uce-12275	1209	2	1209	2	38.24
uce-12277	1089	3	1052	4	40.15
uce-12282	1347	1	1347	1	46.08
uce-12283	1318	2	1318	3	57.04
uce-12285	517	1	514	2	41.21
uce-12287	1024	0	1010	1	33.85
uce-12290	1515	1	1515	1	30.51
uce-12292	1267	2	1248	2	28.47
uce-12294	1173	1	1173	2	36.5
uce-12295	1396	1	1396	2	36
uce-12296	1171	3	1171	3	52.33
uce-12297	1282	2	1282	5	48.07
uce-12299	1328	2	1328	2	34.53
uce-12300	1841	0	1841	0	35.8
uce-12301	1495	0	1495	0	29.76
uce-12302	1291	1	1291	1	23.07
uce-12304	1036	1	1036	1	35.43
uce-12305	1547	2	1547	4	31.34
uce-12309	1502	3	1502	4	33.88

uce-12315	1376	0	1376	0	35.32
uce-12317	1009	0	1009	0	30
uce-12319	1161	1	1161	1	31.46
uce-12324	1059	1	1059	3	38.01
uce-12325	1941	1	1941	1	34.78
uce-12328	1213	1	1213	1	36.01
uce-12330	1019	1	1019	1	36.44
uce-12332	969	0	969	0	27.04
uce-12341	754	2	754	3	41.62
uce-12342	1520	3	1520	5	36
uce-12343	1539	3	1525	6	36.24
uce-12349	1452	0	1452	0	37.87
uce-12350	1607	8	1607	8	31.58
uce-12353	1290	0	1290	0	32.37
uce-12354	1283	0	1283	0	30.84
uce-12357	1497	1	1497	2	33.21
uce-12358	1502	0	1502	0	34.84
uce-12360	1539	2	1539	4	30.74
uce-12361	1179	1	1179	1	35.49
uce-12364	1220	0	1219	2	37.23
uce-12366	1564	0	1564	1	33.56
uce-12367	889	2	889	2	54.16
uce-12369	1618	1	1618	3	41.44
uce-12370	913	0	913	0	45.55
uce-12371	1232	3	1232	3	37.49
uce-12373	1455	3	1455	3	38.69
uce-12374	1520	7	1520	7	42.5
uce-12375	1644	3	1644	5	39.59
uce-12376	1435	4	1435	4	31.36
uce-12377	930	7	919	7	35.79
uce-12382	1434	0	1429	0	29.95
uce-12385	1487	0	1487	0	36.57
uce-12386	743	0	734	1	33.76
uce-12388	1675	0	1675	1	31.03
uce-12392	1609	5	1609	6	37.91
uce-12393	1116	3	1116	3	45.61
uce-12394	1253	4	1253	7	49.14
uce-12399	1149	3	1149	4	40.27
uce-12403	440	0	433	0	31.79
uce-12405	844	1	844	2	46.76
uce-12406	1303	3	1303	6	37.15
uce-12407	1483	6	1483	6	39.12
uce-12408	1634	3	1629	5	38.05
uce-12409	1512	7	1512	7	33.06
uce-12411	1238	3	1234	3	37.44
uce-12412	1530	3	1530	6	34.1
uce-12413	1110	0	1110	0	26.26
uce-12418	1481	3	1481	3	53.41
uce-12420	1806	2	1785	5	52.18
uce-12422	1583	1	1583	1	33.18
uce-12427	1097	2	1097	2	24.72



uce-12428	1443	0	1443	1	31.22
uce-12430	1470	0	1470	0	31.81
uce-12435	1493	2	1493	3	39.3
uce-12439	1481	4	1478	5	32.21
uce-12440	1447	7	1447	8	31.73
uce-12442	1603	1	1603	3	34.11
uce-12444	1047	0	1047	0	30.14
uce-12445	1165	1	1149	1	22.07
uce-12447	1554	0	1554	1	27.19
uce-12449	850	0	850	0	35.14
uce-12450	587	0	587	0	46.96
uce-12454	1522	3	1522	4	38.61
uce-12456	988	8	980	10	37.39
uce-12457	1417	0	1406	0	23.59
uce-12458	1550	4	1550	7	38.42
uce-12460	1302	5	1302	5	47.51
uce-12462	1414	2	1414	2	30.95
uce-12464	958	0	958	0	24.78
uce-12468	1398	0	1371	0	35.33
uce-12474	1398	6	1398	7	37.12
uce-12475	503	2	503	3	42.48
uce-12477	1162	1	1162	1	27.44
uce-12478	898	3	879	4	26.81
uce-12479	1505	0	1493	0	30.61
uce-12480	731	0	731	0	37.56
uce-12481	925	0	925	0	31.9
uce-12482	1709	1	1709	1	43.6
uce-12491	1592	0	1592	0	34.01
uce-12492	1416	0	1416	1	30.68
uce-12493	1560	2	1560	2	33.48
uce-12495	1569	1	1569	1	39.43
uce-12499	1512	1	1512	1	35.08
uce-12502	1501	0	1501	0	29.65
uce-12503	1002	0	1002	1	31.6
uce-12507	1188	1	1188	2	30.22
uce-12508	1297	1	1297	2	32.27
uce-12510	2190	3	2190	4	34.59
uce-12512	1013	0	1013	0	30.7
uce-12513	1408	1	1408	1	28.68
uce-12514	1601	5	1601	5	36.41
uce-12515	1416	3	1407	3	33.98
uce-12516	1616	2	1616	2	33.48
uce-12517	1130	1	1125	3	43.67
uce-12520	1138	0	1138	0	45.56
uce-12526	1083	2	1071	4	31.32
uce-12529	1633	2	1633	2	29.21
uce-12531	777	0	777	2	33.53
uce-12532	1643	4	1643	4	39.29
uce-12533	859	6	859	6	42.77
uce-12534	1050	8	1050	9	44.56
uce-12535	1470	3	1470	5	36.9

uce-12536	653	6	653	6	43.05
uce-12537	1512	3	1511	4	38.62
uce-12540	1551	7	1551	8	39.44
uce-12541	1076	0	1069	0	38.66
uce-12542	1029	1	1029	2	29.38
uce-12545	1035	1	1035	1	36.76
uce-12553	936	2	922	3	48.62
uce-12554	1282	9	1282	11	36.44
uce-12557	1574	3	1574	4	35.92
uce-12558	1235	3	1235	4	35.22
uce-12561	1093	1	1093	1	41.97
uce-12562	1468	2	1454	2	46.22
uce-12563	537	0	536	0	46.63
uce-12564	1362	6	1362	8	32.43
uce-12565	1236	5	1236	7	42.91
uce-12566	1886	1	1886	1	32.83
uce-12567	1361	0	1361	0	30.03
uce-12571	1383	0	1383	0	28.06
uce-12578	1520	1	1520	2	37.27
uce-12579	1982	0	1982	0	38.39
uce-12580	1517	1	1517	2	33.26
uce-12581	1486	1	1486	2	32.26
uce-12582	1201	0	1201	1	32.65
uce-12583	926	1	926	1	33.23
uce-12584	542	1	542	2	39.59
uce-12586	761	0	749	0	28.01
uce-12588	634	1	634	1	52.23
uce-12589	1239	5	1239	9	48.26
uce-12590	1531	0	1531	2	30.76
uce-12591	780	1	780	1	36.37
uce-12593	1501	1	1490	2	37.26
uce-12594	1571	1	1571	1	32.9
uce-12597	1064	1	1064	2	46.03
uce-12603	1765	2	1765	2	49.4
uce-12605	1285	2	1285	2	45.7
uce-12608	1285	1	1285	2	41.51
uce-12609	967	4	967	4	35.8
uce-12614	1473	6	1473	7	41.08
uce-12615	1223	0	1223	1	33.64
uce-12616	1145	0	1145	0	35.49
uce-12621	1189	1	1189	3	45.82
uce-12623	1018	5	1016	6	39.65
uce-12624	1154	2	1154	3	37.51
uce-12630	1355	3	1355	3	43.65
uce-12633	1844	2	1844	5	46.45
uce-12635	1629	3	1617	4	35.82
uce-12636	1815	0	1815	3	51.7
uce-12637	1043	5	1043	5	52.41
uce-12641	1023	3	1023	5	47.49
uce-12648	1558	0	1547	1	33.1
uce-12650	1494	1	1494	1	27.17

uce-12651	1171	2	1157	3	27.95
uce-12654	921	0	898	1	46.13
uce-12656	1738	1	1738	1	33.89
uce-12657	971	2	971	2	37.65
uce-12661	1054	2	1054	8	38.31
uce-12664	951	1	951	1	51.02
uce-12669	1576	5	1576	5	45.27
uce-12670	923	1	923	1	49.3
uce-12671	1747	7	1747	9	42.33
uce-12672	1596	1	1575	2	34.19
uce-12675	1011	0	1011	1	51.8
uce-12677	1369	0	1369	2	57.46
uce-12679	1558	5	1558	5	47.2
uce-12680	1254	3	1254	4	52.34
uce-12681	1433	1	1433	1	48.29
uce-12682	1759	1	1759	2	54.78
uce-12685	1472	2	1472	2	52.93
uce-12686	649	0	649	0	55.97
uce-12691	1459	0	1459	0	37.09
uce-12693	1322	0	1311	3	29.98
uce-12697	887	0	887	0	29.69
uce-12698	1343	0	1343	1	35.02
uce-12699	923	1	908	1	53.14
uce-12700	1794	3	1794	5	41.57
uce-12701	700	2	700	3	46.47
uce-12706	721	1	721	1	44.27
uce-12707	1330	5	1328	5	43.97
uce-12708	2014	1	2014	2	40.32
uce-12709	2123	2	2123	3	38.6
uce-12713	972	0	943	0	38.18
uce-12714	1398	0	1398	0	28.98
uce-12715	1328	0	1327	0	28.18
uce-12717	1324	2	1280	3	30.77
uce-12718	1379	2	1379	2	33.52
uce-12719	1531	3	1531	4	30.2
uce-12728	1509	0	1509	0	29.36
uce-12731	1351	1	1348	2	32.2
uce-12733	1338	5	1334	9	42.18
uce-12735	1303	1	1296	2	31.55
uce-12736	1309	2	1309	2	39.23
uce-12742	1302	0	1299	0	29.55
uce-12746	1655	8	1655	9	35.89
uce-12747	1703	1	1703	1	45.56
uce-12748	1147	3	1147	4	32.11
uce-12749	1335	0	1335	0	33.08
uce-12754	1100	2	1100	3	47.6
uce-12755	1552	1	1552	5	44.85
uce-12756	1371	4	1371	5	50.4
uce-12757	966	1	966	1	51.66
uce-12758	1075	1	1075	2	44.59
uce-12760	1173	9	1173	9	43.61

uce-12761	758	1	758	1	34.57
uce-12762	1732	0	1732	1	34.48
uce-12765	1494	1	1494	3	50.33
uce-12766	1666	2	1634	3	44.7
uce-12769	1325	4	1299	5	36.58
uce-12770	1438	3	1438	3	49.68
uce-12777	1466	0	1456	0	37.88
uce-12779	872	2	872	4	41.17
uce-12780	1263	3	1263	3	39.99
uce-12781	1279	3	1279	3	42.55
uce-12782	894	3	878	4	34.68
uce-12783	1117	4	1117	4	32.27
uce-12784	782	1	782	3	43.57
uce-12786	461	0	461	0	42.32
uce-12789	920	1	920	2	41.98
uce-12791	1455	4	1455	5	38.73
uce-12794	1453	1	1441	1	43.23
uce-12796	1456	4	1428	4	34.03
uce-12803	1273	1	1273	1	31.89
uce-12804	421	0	410	0	27.81
uce-12805	1347	1	1347	2	33.42
uce-12806	1229	0	1229	0	42.95
uce-12807	1338	0	1317	1	30.78
uce-12808	1080	1	1080	1	39.73
uce-12809	1528	1	1511	1	35.37
uce-12812	1473	3	1473	4	49.61
uce-12819	1414	3	1414	4	33.44
uce-12820	696	1	696	1	32.66
uce-12823	1093	0	1093	0	37.63
uce-12824	1371	0	1371	0	37.96
uce-12826	1523	2	1523	4	29.74
uce-12831	768	2	768	2	54.81
uce-12836	965	2	960	2	33.87
uce-12839	1422	1	1418	2	33.83
uce-12840	1326	1	1326	1	34.91
uce-12845	1157	5	1157	5	46.07
uce-12846	1590	2	1590	2	35.17
uce-12849	1191	2	1191	2	29.49
uce-12852	1386	3	1386	3	29.94
uce-12853	1186	0	1186	0	30.3
uce-12854	1431	4	1431	4	30.64
uce-12857	1428	1	1428	2	43.3
uce-12858	1542	0	1542	0	48.78
uce-12866	1214	0	1214	0	29.52
uce-12867	1470	1	1470	1	39.32
uce-12868	1147	0	1147	0	33.77
uce-12869	1191	0	1178	0	30.37
uce-12874	1395	5	1395	7	41.21
uce-12875	1501	3	1501	3	29.41
uce-12880	1271	0	1256	0	27.62
uce-12883	620	0	609	0	36.81

uce-12886	1208	2	1195	3	33.39
uce-12889	1286	1	1286	1	30.9
uce-12890	1350	0	1350	0	34.72
uce-12894	1298	1	1298	1	34.1
uce-12895	1232	1	1227	1	34.13
uce-12900	1563	4	1563	4	38.96
uce-12901	1315	1	1315	1	33.32
uce-12902	695	0	693	0	29.59
uce-12903	1053	2	1053	2	28.41
uce-12904	1050	0	1050	0	31.72
uce-12906	1387	2	1387	2	33.56
uce-12908	1366	1	1366	2	50.62
uce-12909	1002	1	1002	2	48.08
uce-12910	1584	1	1584	2	39.11
uce-12912	1402	0	1402	0	36.9
uce-12913	1413	0	1413	0	35.64
uce-12914	909	0	909	0	42.36
uce-12916	1196	0	1196	1	37.53
uce-12917	1354	3	1353	4	32.45
uce-12920	966	0	966	0	30.86
uce-12921	1537	1	1525	1	44.87
uce-12923	1401	0	1401	1	33.85
uce-12926	1464	3	1449	7	37.98
uce-12935	1774	5	1774	8	38.7
uce-12938	1477	4	1477	4	39
uce-12943	1386	1	1386	2	45.18
uce-12947	1219	4	1219	7	40.4
uce-12956	1174	0	1170	1	47.78
uce-12958	1360	5	1360	5	47.59
uce-12960	1298	3	1282	3	38.43
uce-12962	1362	9	1361	10	35.39
uce-12966	2460	2	2460	7	48.54
uce-12970	1352	0	1339	1	40.1
uce-12973	1275	1	1275	1	40.83
uce-12974	1273	1	1273	1	32.12
uce-12975	1094	0	1094	0	28.58
uce-12979	810	0	801	0	32.95
uce-12981	1668	0	1668	0	34.24
uce-12983	1326	0	1326	0	32.01
uce-12985	1465	0	1465	0	30.69
uce-12986	1570	1	1570	2	35.61
uce-12987	1215	2	1215	2	54.87
uce-12989	1704	3	1704	4	42.41
uce-12992	1360	1	1360	2	50.04
uce-12996	1341	6	1341	7	44.55
uce-12998	498	2	498	2	33.98
uce-13000	601	1	601	1	48.37
uce-13001	827	0	827	0	53.65
uce-13002	1157	1	1157	1	52.89
uce-13004	1284	6	1279	9	34.49
uce-13007	601	0	601	0	55.44

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**Table A6.** UCE summary statistics (1 of 2).

<b>Locus</b>	<b>Gaps</b>	<b>A Count</b>	<b>C Count</b>	<b>G Count</b>	<b>T Count</b>
uce-3	10353	14841	18432	14014	18040
uce-4	10856	16374	23831	21224	22043
uce-5	11094	18577	12758	15569	15362
uce-6	7786	18990	8606	9718	18124
uce-7	25509	29918	9848	14589	23904
uce-8	9767	19812	12440	14404	22537
uce-9	21362	31155	15796	12703	29640
uce-10	12109	18716	11273	11019	17891
uce-11	13739	20525	19386	20240	16998
uce-12	10784	14747	16306	17865	16626
uce-13	11080	26661	9715	10472	27136
uce-18	7848	11069	8559	11803	12291
uce-19	12312	21780	14531	15122	19085
uce-20	6635	12582	9817	11331	11940
uce-22	9511	16635	10319	11062	16835
uce-23	11707	14136	14309	13039	17113
uce-24	10735	17753	10289	12092	17115
uce-27	14959	16027	7797	8481	16296
uce-29	16064	19951	12617	13176	16816
uce-30	12626	21477	11296	15237	17876
uce-31	13971	19431	10744	10186	18356
uce-32	14367	24544	12537	13924	21820
uce-33	5929	15576	12121	12047	19511
uce-34	19714	28394	22042	22221	26685
uce-35	7364	17358	7616	6174	17270
uce-36	13775	16834	16487	15471	18017
uce-37	7979	13448	13982	13171	14588
uce-38	9883	25124	11094	12553	24282
uce-39	22616	25294	22369	16134	22619
uce-40	27216	27872	21773	23382	27437
uce-42	9977	17063	17819	14847	16174
uce-43	13737	16849	11690	15777	12897
uce-44	12128	21851	12658	15544	16667
uce-46	15920	24160	10512	12212	21924
uce-47	15528	18467	17077	13079	21921
uce-48	15864	23151	14794	17707	24300
uce-49	10965	18986	15359	13595	19439
uce-50	8371	16943	10899	10811	17695
uce-51	16675	29410	17641	25091	17639
uce-54	17242	19970	24119	18597	29888
uce-55	11433	16963	18386	16493	21150
uce-57	9283	16443	15960	20417	15177

uce-58	11607	19682	11283	12238	20430
uce-59	10338	19951	9416	13030	16985
uce-60	7646	18883	7031	7231	17127
uce-64	7246	15357	11046	10333	14020
uce-65	29536	24252	17634	18704	20142
uce-66	11534	9950	14340	12904	11215
uce-67	8292	16280	13428	14138	12173
uce-68	15328	25893	15710	22663	20534
uce-69	14234	18938	18143	18909	18392
uce-71	29015	27422	30931	28955	29445
uce-73	14625	17059	22033	17058	19161
uce-74	8990	15068	13410	15095	16429
uce-77	10919	16253	12494	13431	13543
uce-82	14885	15387	17717	12799	16267
uce-86	25668	33529	24906	26562	32247
uce-87	10629	20673	12308	20529	16105
uce-88	10834	21222	12794	11600	22454
uce-93	12015	17578	10975	13255	13442
uce-94	9645	16392	18362	14489	19400
uce-95	10311	25153	11498	13669	22809
uce-96	9453	17700	13160	11373	18650
uce-97	9773	20359	13331	13171	18630
uce-98	11756	22831	16998	14618	23733
uce-99	9979	14527	11826	13472	18348
uce-100	11405	21094	12118	10777	24350
uce-103	8952	22401	8831	9914	18502
uce-104	9440	26366	8147	7554	25829
uce-106	10265	22370	10756	13006	22171
uce-107	10018	16113	14943	17713	15637
uce-109	5647	6156	5852	5480	5383
uce-113	10859	26914	14920	16404	25319
uce-114	5526	21074	7634	10796	19370
uce-115	10515	19414	13781	12688	18698
uce-116	24713	27656	19940	17123	24864
uce-120	9714	22367	10604	9415	21932
uce-121	11060	25601	15394	14230	22595
uce-122	7337	8679	14837	12000	12643
uce-127	10193	17618	14634	15175	17980
uce-129	10005	23471	16495	13178	17435
uce-130	7088	14922	13490	11699	16697
uce-131	8167	11622	10286	9495	14134
uce-132	14393	20681	11112	9945	17173
uce-134	9548	25203	9340	10982	25791
uce-135	10274	16688	23758	21723	20113
uce-136	13485	15766	23771	17494	21660
uce-137	15594	23494	11406	10244	23878
uce-139	20447	23084	23787	25700	22286
uce-140	10495	11709	14135	12584	13887
uce-144	10007	9716	12056	11043	10218

uce-145	13193	23193	11638	9734	29344
uce-146	13483	18920	25800	23187	20580
uce-147	10097	23070	12761	21095	14762
uce-149	13856	21387	14053	14977	16143
uce-150	9703	23033	12624	11871	22961
uce-152	9754	15002	9808	9854	11902
uce-153	9271	18808	17599	13099	20991
uce-154	17167	22364	21499	18414	26340
uce-155	18070	31282	18935	30896	14392
uce-157	15342	20012	14087	14286	19937
uce-158	9754	19674	18641	18372	15399
uce-159	10189	15045	13491	14275	14928
uce-160	10596	15345	14397	13725	17673
uce-168	10735	22800	11402	10680	23455
uce-169	12555	15387	15887	15858	16977
uce-170	17611	25458	17764	25717	16520
uce-171	13184	22523	15345	12949	20369
uce-172	5695	21778	10460	11777	17602
uce-173	12986	25594	16716	17839	22513
uce-175	12104	15483	17378	13390	20717
uce-176	9606	25017	13609	10938	29050
uce-177	10586	23070	14072	15129	28058
uce-181	11211	16673	11715	11965	18436
uce-185	16498	20323	22040	18187	22968
uce-186	13032	32915	17484	21451	24542
uce-187	6521	13764	7887	10812	8481
uce-188	10445	19628	13309	13881	24777
uce-191	17127	25590	24666	22758	28635
uce-192	11321	19140	18868	14055	25320
uce-193	8320	23623	12544	12563	21814
uce-194	9896	16021	15489	12566	17092
uce-196	10854	19278	18235	14908	24799
uce-197	9541	22082	9304	10992	24969
uce-200	15780	22444	17539	16759	23436
uce-201	10077	14444	18742	11888	20257
uce-204	18880	22236	20229	14035	27100
uce-205	13890	21944	13028	13468	18758
uce-208	8528	24709	13709	15162	24468
uce-211	12306	14793	10104	10573	21442
uce-212	12531	16862	12457	12508	20962
uce-213	15017	16553	12082	12085	19161
uce-216	14120	18033	13584	11133	20858
uce-217	12677	23442	13359	14891	19967
uce-220	9775	28821	10218	12883	23983
uce-228	15303	16156	16704	18747	15920
uce-231	6968	7980	16068	12431	12295
uce-232	4783	7047	6667	10879	3777
uce-233	12749	14913	14227	19309	11763
uce-234	9443	16295	19952	19637	12718
uce-235	28050	13381	19907	19302	13520
uce-236	14007	20830	22215	26340	18614



uce-237	8729	12477	15684	16726	12434
uce-238	8447	9419	15557	16008	11769
uce-239	14329	17029	23935	22357	18110
uce-240	11914	15508	19064	18227	17831
uce-241	12775	18372	19489	20913	17883
uce-242	10609	13210	17194	16827	14358
uce-243	9922	18846	19624	21374	13724
uce-244	9721	16959	10249	12280	13326
uce-249	8399	16712	11276	12141	16320
uce-252	7871	17498	7297	8395	15498
uce-255	8431	15144	12129	12709	16157
uce-256	7085	13472	11866	10348	14237
uce-257	9703	23484	14084	11254	25811
uce-258	9586	16786	13499	13313	15640
uce-259	14254	16655	18014	16198	19607
uce-260	10448	16100	16478	15576	17278
uce-263	8843	21796	16827	18271	16135
uce-265	10167	16861	14659	13535	16794
uce-270	10472	18250	23524	16576	17586
uce-271	7738	13775	17194	12327	18432
uce-272	14133	23923	13200	15711	20897
uce-274	9033	17428	10227	8794	17574
uce-275	10296	24297	10749	12459	20599
uce-276	11416	26963	16755	19155	22535
uce-277	9404	18501	7728	7538	16083
uce-278	10365	18816	11091	10603	16525
uce-279	5348	17497	7127	6681	14647
uce-280	10276	16443	11646	15226	20329
uce-288	7861	14615	13832	12462	22686
uce-291	11077	20742	25507	24587	20442
uce-295	9619	17062	10993	12164	14842
uce-297	11370	19403	15489	15056	18426
uce-299	12207	13699	18042	15143	19284
uce-301	10569	15902	14023	12803	17431
uce-303	10480	16771	10514	13942	18517
uce-304	10056	11625	12701	9777	10731
uce-306	9148	15831	13824	12799	17278
uce-310	30548	27690	19703	18802	27577
uce-313	10408	22914	13920	16282	16668
uce-316	12751	21491	14078	12421	18209
uce-317	20514	17354	19130	15439	19771
uce-319	10053	14644	10388	11026	15825
uce-320	8633	10293	10153	10673	12003
uce-325	11853	19566	14401	10656	19236
uce-326	9370	17718	11779	11374	15759
uce-327	4747	8592	7324	6471	10453
uce-329	10276	26059	13710	17804	24943
uce-330	14943	21990	14520	17102	18665
uce-331	13405	17303	15950	17204	14370
uce-332	12776	21072	15476	14126	22342
uce-333	12186	20577	18531	17171	19095

uce-334	9093	15153	11831	14305	13794
uce-335	8092	15942	11828	11287	17586
uce-336	15418	23332	18871	18849	24015
uce-337	13403	23793	14219	14928	24132
uce-340	9850	24172	14429	12383	27618
uce-345	12470	19309	12450	12186	24930
uce-346	16795	20023	16754	12806	21457
uce-347	16669	15420	14130	13523	15410
uce-349	11993	20272	12853	14055	19899
uce-350	8133	21390	10175	10650	22472
uce-351	9475	17407	9394	10419	19385
uce-353	9194	19814	8826	8851	16931
uce-354	10489	19416	8417	8262	19608
uce-356	7364	23506	10228	11041	23191
uce-359	6402	6563	6940	7181	7258
uce-360	9537	21010	11814	11848	26263
uce-361	8249	23833	7870	8438	18234
uce-362	9546	8884	12352	11202	6670
uce-363	15350	20988	13883	13726	21901
uce-364	10201	13209	10501	14426	11919
uce-365	10538	18815	15403	14134	18726
uce-366	10907	21209	13635	11985	21840
uce-367	9005	20881	10718	9408	22620
uce-370	8580	24456	10677	14465	20637
uce-373	10381	25893	13004	13246	22310
uce-375	10491	19759	11617	11363	17280
uce-378	6563	14046	5009	4354	13540
uce-381	9575	24797	9542	11767	22327
uce-382	10220	28475	10747	10593	20650
uce-383	9300	19974	14997	16315	17702
uce-388	29761	20425	17690	14630	30189
uce-389	14424	19236	14052	20980	16503
uce-390	14405	18037	22611	16865	18392
uce-392	12536	18321	14048	13636	16919
uce-394	10118	14313	14270	13740	15879
uce-395	6759	7264	7296	7416	7121
uce-396	11962	16795	15213	16399	16419
uce-397	13637	13013	9984	8989	13831
uce-399	7719	13706	14483	12427	16009
uce-400	12657	25506	12289	13010	21788
uce-401	11460	20294	12334	15016	18904
uce-402	16185	18522	24093	25415	24135
uce-404	19979	21189	26388	24426	21138
uce-406	11732	21721	16475	20024	17296
uce-408	9980	15490	14054	14981	15510
uce-411	13411	11635	12303	13171	18584
uce-412	7174	14149	13305	12477	14607
uce-413	9330	20978	13770	14268	18430
uce-415	10326	16664	18123	19610	16813
uce-416	18421	22625	19959	25717	17109
uce-423	17497	19790	19956	22917	18624

uce-424	17038	22800	25210	25068	20428
uce-427	11165	19535	20566	16959	20647
uce-430	11468	17765	10942	12456	21793
uce-433	10493	16837	11905	11471	19854
uce-434	8097	23859	12397	11366	19937
uce-435	10082	21511	19095	12572	23032
uce-436	9580	22579	18851	10779	31003
uce-437	9410	17179	13376	13783	14516
uce-438	12033	22252	15376	12275	32032
uce-441	16393	23734	12143	14210	23390
uce-442	11070	28955	12434	10682	27075
uce-446	15573	19769	15796	14540	19426
uce-448	7826	12521	12423	12095	11751
uce-449	11476	26426	10489	11617	29144
uce-450	9232	25511	8625	8068	24464
uce-453	10486	17741	28488	18016	26909
uce-454	15235	22266	15674	15606	23674
uce-455	12589	20514	14826	14064	19277
uce-458	11082	14791	12250	12341	13256
uce-459	8097	12775	13808	14211	12489
uce-460	6649	18629	11170	10748	17148
uce-463	17750	19007	18529	14063	19641
uce-468	13862	12526	14183	12968	13829
uce-472	8947	18259	18896	19224	15304
uce-473	13795	20947	17387	16224	18055
uce-475	11380	14779	16772	17177	20532
uce-476	6521	8349	11068	8672	9724
uce-478	11726	15756	18272	17347	14907
uce-479	12399	22822	13114	15960	18001
uce-481	10101	22327	19267	19107	25833
uce-483	16265	23029	17165	18110	22199
uce-484	13430	21927	13716	18436	18283
uce-485	9857	14094	11076	13161	11883
uce-487	20237	25596	20275	24499	23465
uce-488	15393	19410	16669	16627	18757
uce-491	12971	17239	10152	13052	16082
uce-492	9960	15930	12354	13552	17700
uce-495	8341	15869	10691	10751	14738
uce-497	12455	18157	12468	17221	15467
uce-498	11325	20294	14629	13993	21799
uce-500	11990	19450	14035	17543	17612
uce-501	32561	27136	22815	24808	30552
uce-505	10675	21123	14549	15413	20504
uce-506	16379	19906	12938	13718	22123
uce-507	15654	19156	15165	12419	19146
uce-508	10342	15985	18008	14277	17212
uce-509	7550	6547	6891	6096	8116
uce-510	15869	17501	12279	13408	20239
uce-511	12894	19367	13026	13577	20432
uce-513	9716	16266	16204	16398	18856
uce-514	10846	22142	12393	13444	23607

uce-515	9962	9902	6677	8477	12246
uce-516	13464	17843	13292	16814	17211
uce-517	12745	22699	14657	11878	24485
uce-518	14190	21481	13942	14087	23268
uce-519	7025	15341	11688	11080	16136
uce-520	11881	16702	10447	10687	18419
uce-521	10363	15837	9923	10924	16793
uce-525	10617	20257	15804	14918	18428
uce-527	10197	21038	13409	15703	16765
uce-528	10929	21866	11094	12560	21651
uce-529	14603	15711	14818	14726	19727
uce-530	11536	22551	15663	13887	21091
uce-531	43894	31052	34394	33039	29317
uce-534	10192	16930	12498	11271	17373
uce-535	7926	16469	12928	14426	17560
uce-537	9169	18014	12134	9919	19679
uce-538	11292	21127	16507	14662	19572
uce-540	5385	5527	4547	3481	5030
uce-541	9534	18141	15102	13953	19654
uce-542	14321	22320	17161	16612	20194
uce-543	10616	19132	14436	14261	18779
uce-544	14195	19283	13266	13888	17544
uce-546	9631	8089	8592	7162	8806
uce-547	11643	15812	14611	9873	17416
uce-550	13426	15855	22717	17160	20554
uce-551	9656	14797	10368	9846	16037
uce-552	7216	17242	8219	9479	15972
uce-553	14811	18722	17836	26012	13283
uce-554	10095	17967	15811	12796	20001
uce-555	10613	17228	16989	15777	21153
uce-557	15049	22262	11317	12926	15894
uce-558	10640	21597	15726	14064	15925
uce-559	11618	16110	13677	15429	15238
uce-560	11828	19904	14365	14231	17512
uce-562	12257	19382	16614	15199	22116
uce-563	10930	19141	13331	12594	21788
uce-565	9859	12737	13709	10998	14389
uce-566	12622	24156	13446	15153	21815
uce-568	14929	23750	14497	19806	20298
uce-573	10114	20427	13946	13255	20154
uce-575	9225	17712	18740	13032	15816
uce-577	8931	18126	11623	14196	18076
uce-580	9354	28350	8164	8224	20598
uce-581	12202	20726	10783	12232	20833
uce-583	15432	17236	10490	10292	19574
uce-584	22650	22852	27398	19893	33597
uce-588	16652	23810	17052	15389	22857
uce-589	15143	23953	17678	12222	31412
uce-590	8764	13789	14804	15892	12887
uce-594	14997	24165	15013	12978	25208
uce-595	10983	15527	10418	10674	16343

uce-598	11450	27590	11701	16427	21816
uce-600	8605	19619	8984	10381	18715
uce-604	9332	19819	12815	12030	21716
uce-605	7888	13692	13409	10202	16904
uce-607	5701	6046	3388	3438	6915
uce-608	11608	19176	9246	12343	16731
uce-609	10509	17183	18300	12930	27206
uce-610	8322	16464	11974	11137	15958
uce-612	9728	14809	13678	12484	16557
uce-613	10743	20005	17868	15535	22144
uce-614	10019	15018	10299	10164	13075
uce-615	14511	22429	17662	13269	20105
uce-616	9113	20106	13798	14614	16721
uce-617	17632	23525	20714	17326	23458
uce-618	9428	26305	12238	7864	30125
uce-620	12679	21553	8481	8799	13990
uce-621	8984	26475	9634	11482	22020
uce-624	16424	15585	19158	14105	19400
uce-625	9192	19474	9423	9028	16051
uce-626	9166	15454	9253	9567	17320
uce-627	10093	21946	11218	10470	20641
uce-631	7994	17420	8659	12712	19295
uce-632	8377	20625	10241	10377	23475
uce-633	9815	16790	17703	16094	19286
uce-634	10121	19556	15136	14496	17086
uce-635	16206	30679	19058	19114	29967
uce-638	5829	12379	4433	5906	16029
uce-639	48172	31332	28849	25897	49318
uce-640	10662	11542	17067	16314	15927
uce-641	12325	17816	14013	13864	12374
uce-642	9209	9854	11361	11328	9264
uce-643	16367	19923	14175	18114	17661
uce-645	10239	23859	11083	12370	25609
uce-646	10208	25946	14011	11825	28842
uce-647	9497	17120	7770	8889	18716
uce-649	10963	20970	15622	15355	19970
uce-650	13639	11646	15702	18376	9909
uce-653	5946	19131	7172	7336	17703
uce-654	11812	17873	17431	16723	21319
uce-655	13310	18903	11549	11617	19661
uce-656	11726	15840	19956	14910	21573
uce-657	10043	15159	17009	18045	17864
uce-658	13811	12846	14752	13758	13993
uce-659	7029	12110	12621	14142	19606
uce-660	13640	18767	15967	13832	19778
uce-662	12715	19080	18705	15167	23989
uce-666	14172	21436	32909	19224	28907
uce-669	11815	17605	13185	10972	19839
uce-672	17872	24362	24018	21781	30407
uce-673	8063	11823	9783	10889	12236
uce-676	13139	15803	15628	12587	20347

uce-677	10747	18736	18544	19603	19842
uce-680	9549	32503	23528	38880	13350
uce-681	19082	19197	26631	26162	22888
uce-682	10124	22576	18945	19208	20203
uce-683	13774	21762	12670	13477	19125
uce-684	16613	20197	17009	11831	32984
uce-686	9317	24015	15986	12634	28633
uce-688	7769	17536	8525	14006	15612
uce-689	12029	16451	17486	17057	18345
uce-690	13238	21865	17080	18038	22627
uce-691	11755	24642	14683	16406	16066
uce-693	12909	19993	12950	13132	20816
uce-694	9425	19248	14834	12758	21963
uce-695	11071	23660	13801	14365	20263
uce-697	12181	19177	17163	16646	22641
uce-698	12662	21044	21580	19406	24652
uce-699	13714	24769	15274	16586	23625
uce-700	6572	16939	13039	15879	13035
uce-701	12589	16854	10218	12512	17292
uce-702	10520	19256	19275	18525	19448
uce-706	15800	22282	15901	19894	20203
uce-707	12640	20400	15475	15996	20273
uce-710	14150	21529	14366	16647	22460
uce-711	12554	21385	13916	13177	17032
uce-713	11112	18711	19048	23732	13581
uce-714	15519	23939	17731	16345	24201
uce-719	9656	15289	8548	9433	12234
uce-721	8583	13277	14004	12471	15561
uce-723	18243	24356	23842	25122	22621
uce-728	6878	17216	9776	11513	20529
uce-733	8951	10302	8602	9442	10061
uce-734	11968	22867	13001	16911	20821
uce-735	17208	21482	14299	17976	18080
uce-739	9591	12262	19030	19829	13656
uce-741	11165	18260	17629	14408	22146
uce-742	6423	12447	11949	11624	10261
uce-746	9643	15886	12385	13563	13808
uce-747	30189	26684	31547	30827	25183
uce-749	27314	24960	29560	27336	23718
uce-750	14155	18699	20773	14959	23422
uce-752	9233	12932	10809	11341	11565
uce-753	32126	24389	30061	22295	28849
uce-758	14859	22111	19897	20273	20972
uce-764	8931	23722	12838	10330	23251
uce-767	8722	26692	12376	12085	25021
uce-768	8766	27779	10011	13162	27138
uce-769	11415	25797	12996	11992	25674
uce-773	31270	28152	25444	26672	28518
uce-774	7549	15676	14713	11530	16724
uce-775	8773	11871	8808	7225	12218
uce-776	10248	20024	11943	12414	22987

uce-777	10425	13897	12897	13282	12859
uce-780	9822	20720	15483	17539	17804
uce-783	21774	22089	23316	22738	24428
uce-784	9138	19124	15705	16816	17169
uce-785	13881	19653	19079	16614	18525
uce-786	10021	12191	9149	10080	12349
uce-787	15533	22156	16505	15396	24546
uce-789	9557	17786	12799	14282	20336
uce-791	9573	19878	8071	9020	18362
uce-793	7800	13155	11145	11770	11185
uce-796	7578	8795	4465	4446	10438
uce-799	13440	21197	17581	20875	16955
uce-800	17008	17705	25750	15182	22651
uce-803	16207	21965	18651	19447	20946
uce-805	14098	21658	12417	13301	18214
uce-806	14291	18491	14648	13894	18420
uce-809	10837	23870	16652	15750	19131
uce-812	12957	17565	14364	16204	14846
uce-815	12925	16947	15678	17704	13858
uce-816	10818	19409	12800	12605	19128
uce-817	11140	21642	12313	12913	16920
uce-819	14044	23296	12260	12159	23753
uce-820	12786	25587	14729	12769	20761
uce-821	10400	20418	11052	11697	17945
uce-822	15156	16941	12000	11062	17921
uce-823	10893	24380	10710	11992	20537
uce-829	7767	16319	8039	7016	15969
uce-830	20546	21996	22771	20934	20209
uce-832	9799	13324	18697	13608	15860
uce-833	13624	16609	17920	19114	14549
uce-834	15522	20265	20580	25176	20769
uce-835	11724	9077	13198	11446	11283
uce-836	11295	15680	12460	10328	15962
uce-837	7072	11403	11147	11690	10278
uce-839	12371	14431	15833	14143	13446
uce-842	11666	18723	10017	11450	18764
uce-843	10668	26007	10505	10932	20680
uce-844	8143	16295	20870	20842	17738
uce-845	7889	11541	18147	13988	19990
uce-847	14728	24105	17809	22843	16325
uce-848	6915	21955	11464	12394	23768
uce-850	9216	17975	10066	9990	14185
uce-851	12955	22561	15117	14172	26867
uce-852	8298	23798	9838	11829	23965
uce-855	9731	17261	17170	15480	17193
uce-857	12330	20267	21425	19748	20758
uce-858	26470	22641	21490	17238	26299
uce-860	10081	20936	20137	16063	20857
uce-861	10891	19004	18650	18954	18349
uce-862	10028	11202	13368	11554	9618
uce-864	11947	16161	15052	13787	24365

uce-867	6776	12194	9316	12502	10582
uce-868	7017	10716	9902	10970	12325
uce-869	8826	13569	11805	15761	12703
uce-870	7921	11940	11633	8731	11911
uce-871	14039	20233	16901	20936	15979
uce-872	14940	10841	17800	12492	18967
uce-873	10158	16134	21370	13753	18049
uce-875	9739	16117	14916	15935	15728
uce-876	11766	21517	17493	20160	16679
uce-879	15964	13428	17538	14649	18837
uce-880	10845	24863	11586	11021	24621
uce-881	11596	29558	11365	12277	24972
uce-882	9495	16760	11247	11539	17599
uce-884	12515	19653	17893	12012	20812
uce-885	14220	15981	18797	16094	21372
uce-888	11437	26052	19329	10687	33015
uce-896	13206	27181	13780	16137	23720
uce-900	17506	31730	10416	17425	25987
uce-901	15469	15478	25275	17216	22098
uce-902	8294	13773	16504	13937	16141
uce-903	11008	16834	12778	15361	17267
uce-904	9704	19888	20087	17710	15379
uce-905	9950	21564	13228	14787	19375
uce-907	10257	15540	18941	16118	18524
uce-908	11242	18166	15009	11547	18852
uce-909	12231	21259	14136	12569	23189
uce-910	11812	28864	15139	16930	19263
uce-912	9235	17766	19933	13796	24025
uce-913	13539	18389	14518	19547	11811
uce-914	13946	21140	21597	19964	21521
uce-915	9487	13463	13432	12483	14359
uce-916	8400	15602	14961	15234	16808
uce-917	9790	19065	18097	21561	15967
uce-918	9487	21561	11825	12029	23330
uce-921	11283	15398	10448	10439	15504
uce-922	10910	21364	13163	16500	10663
uce-923	8196	27457	8982	10974	26095
uce-925	11993	18084	21465	14936	21890
uce-927	8031	13910	11910	11721	14404
uce-928	6521	5876	9506	10671	9721
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uce-930	20049	23033	16777	15630	23351
uce-931	13218	21870	14208	14795	19349
uce-932	8348	11539	13136	10859	11026
uce-935	7721	16955	18082	17225	23122
uce-936	10744	21326	19522	15835	28949
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uce-939	8042	22595	9326	7253	20712
uce-941	21651	18444	16565	14816	17132
uce-945	11742	21795	13277	14344	21050
uce-946	13441	18784	13894	13045	19292



uce-947	13124	26980	14878	18113	20481
uce-948	11480	19248	9334	9031	20347
uce-949	10496	21002	16097	15698	20142
uce-950	12459	14229	10867	12919	12278
uce-952	13035	19079	16376	20546	15114
uce-953	11635	15824	11247	9939	13005
uce-955	11834	19568	15798	15610	19230
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uce-958	12788	18191	12889	12325	14367
uce-959	19243	23734	17414	19974	21555
uce-960	11201	13509	9576	9888	12666
uce-962	11933	24120	10357	14818	26132
uce-963	10417	13400	14765	17664	14650
uce-965	15585	17939	16625	15099	19571
uce-966	9822	12698	10694	11610	12686
uce-974	12600	17464	13126	13376	17414
uce-975	9106	20627	12576	11276	18207
uce-976	10462	16134	9298	10888	14316
uce-977	8967	19423	15042	16297	18167
uce-978	16044	21453	17758	20317	18732
uce-979	10098	18122	15185	16881	16098
uce-980	6235	15533	5662	3881	14449
uce-983	8919	20910	19694	14479	17646
uce-984	12224	21395	16697	13064	22076
uce-985	11276	24275	12839	15261	21973
uce-988	9892	12491	17090	16427	14555
uce-989	8147	10706	13169	14277	11346
uce-990	8353	12333	11855	12774	13821
uce-991	12913	14119	11655	13549	11604
uce-997	10985	17242	14415	13367	17911
uce-999	9766	17427	16421	18344	16890
uce-1004	8648	16498	15767	18619	13268
uce-1006	11062	15542	11770	12035	14711
uce-1008	17680	19727	12839	12594	21750
uce-1009	15254	17634	17039	16852	17646
uce-1011	11027	22009	15394	15692	21166
uce-1012	11358	18501	16400	18458	17771
uce-1013	17645	22746	27587	31654	25528
uce-1014	15143	17148	19909	15969	17623
uce-1015	9926	12830	13021	16074	16243
uce-1016	25954	19598	21518	21621	22861
uce-1019	18010	19832	23187	18501	28998
uce-1020	14915	21701	27584	20402	29862
uce-1023	8875	18837	17485	17890	19905
uce-1024	23568	22412	19796	23370	19326
uce-1026	9988	18941	21196	22941	14630
uce-1027	8051	14850	15428	13132	17124
uce-1028	8891	18230	16056	16527	17576
uce-1029	12567	16647	16113	15197	15916
uce-1031	28845	22668	18936	20395	23788

uce-1033	10597	19713	10721	10722	21271
uce-1034	44753	26382	23206	26215	24424
uce-1035	10915	14778	16599	14335	14928
uce-1037	9930	17902	19307	18792	19581
uce-1038	9384	16814	15758	15098	15634
uce-1046	24191	28435	19434	18680	24116
uce-1047	14525	19841	15046	15049	21387
uce-1049	12193	25351	14301	11542	25989
uce-1050	9127	16797	12857	13116	16647
uce-1052	9105	13537	17092	17705	14913
uce-1055	33985	31950	15138	19820	29010
uce-1058	16285	18142	10749	13858	17462
uce-1061	20579	24833	24747	24290	20071
uce-1062	15398	25088	14187	14819	21508
uce-1063	10716	18681	18746	13591	25682
uce-1064	9522	15852	15506	15201	11903
uce-1066	6990	17783	8165	7518	19444
uce-1067	11131	16594	12987	14528	15930
uce-1070	10836	16959	11859	12111	18085
uce-1071	8073	15415	19155	15141	20112
uce-1075	10928	20504	13481	13277	21010
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uce-1078	9410	16430	12985	15075	19740
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uce-1080	8056	20511	15931	23007	13751
uce-1081	11516	17159	13245	16832	16568
uce-1082	12701	14477	18035	12033	12754
uce-1083	14181	24381	18208	14328	21526
uce-1085	16934	25467	15790	13770	26319
uce-1090	11034	27662	10706	10630	24808
uce-1091	8271	25974	10360	12680	29065
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uce-1093	11038	20858	16780	15629	20259
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uce-1095	11535	16169	17679	17947	15406
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uce-1099	11080	19513	12125	14094	18676
uce-1102	14844	23831	10522	14805	19926
uce-1104	12734	19303	17431	16169	22955
uce-1105	7717	15275	10880	12779	13024
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uce-1125	9149	14773	14227	14114	17065
uce-1126	9750	15094	13171	11267	16798
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uce-1128	10823	15870	22214	16378	19947
uce-1131	13948	21710	17525	14266	19687
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uce-1134	14723	22202	15041	17254	22228
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uce-1170	8043	14162	12349	12235	12827
uce-1171	13255	19902	18981	16853	19042
uce-1172	9998	18936	14950	20578	15002
uce-1173	16824	19349	15505	17860	18438
uce-1174	13745	19860	19112	17927	24332
uce-1175	9402	14764	21999	18871	17676
uce-1176	11248	12833	14304	15828	13827
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uce-1178	11677	16576	13130	12127	15570
uce-1181	11110	11294	13771	7153	17502
uce-1182	12280	20151	23123	19533	24873
uce-1188	11056	13307	12055	10068	15786
uce-1189	15116	18789	9965	12478	15702
uce-1190	10055	23426	7728	8958	19023
uce-1191	8667	16712	11037	10587	18982
uce-1193	20003	20893	19326	22108	24742
uce-1194	7161	15694	6871	7028	17006
uce-1195	8637	26145	11031	10917	22745
uce-1196	6863	25037	9175	8825	22732
uce-1202	12819	19113	16971	17413	17572
uce-1203	20718	21305	17486	15528	23859
uce-1204	12490	17368	13096	20140	18050
uce-1205	14103	21813	16146	12063	33885
uce-1206	18372	20376	21115	23802	21111
uce-1207	8827	19967	17118	17524	20060
uce-1208	8542	14373	12666	11181	15286
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uce-1211	17449	26595	16288	15551	31021

uce-1213	8587	26308	11788	12528	25181
uce-1214	17576	33047	13019	16115	31515
uce-1216	9409	15864	19102	18699	15606
uce-1217	14781	14768	22777	17672	21786
uce-1219	8918	14388	20177	18428	18561
uce-1220	8005	9694	13335	12452	9864
uce-1223	11130	14884	12970	11939	19805
uce-1225	12872	20834	15297	11622	25783
uce-1232	8578	12299	18866	15761	15448
uce-1233	4606	14624	4290	6704	15248
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uce-1236	7227	22455	8756	9121	17396
uce-1237	5763	15380	6989	10302	17226
uce-1238	16430	27164	13401	15824	24677
uce-1239	15259	18094	14726	14196	23853
uce-1240	14324	24080	31396	25479	24505
uce-1241	8616	16950	14299	15483	14036
uce-1242	8317	14556	17273	13251	19203
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uce-1252	14217	19104	23777	18624	30622
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uce-1257	15261	24895	13263	14837	19414
uce-1258	11039	20191	12982	12279	18087
uce-1259	13127	17862	14765	15839	19239
uce-1260	15422	19694	20891	15195	22848
uce-1263	8840	16155	16468	19678	15075
uce-1267	14022	16514	13099	12404	17657
uce-1268	11780	21743	20830	20475	22220
uce-1269	8722	12220	11056	14035	13271
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uce-1278	9330	10239	9497	9038	7326
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uce-1281	15800	21006	12171	15442	17565
uce-1282	24308	16678	22543	16452	24795
uce-1283	8526	15675	13669	13564	15486
uce-1284	9636	21391	13235	16846	19700
uce-1285	8493	18467	14936	13763	25541
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uce-1288	9558	19936	13264	13881	19969
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uce-1291	7238	8765	11627	11627	8119
uce-1292	14500	24166	15443	13816	27107
uce-1296	13145	21280	13057	12594	22589
uce-1297	15348	22567	18517	18509	17739
uce-1301	12311	19631	30447	20938	33603
uce-1303	11410	25028	17018	20957	27997
uce-1304	10687	17662	21306	15587	18478

uce-1305	13697	20931	14476	14401	20663
uce-1306	9488	17163	18594	19357	16138
uce-1308	12867	21047	14216	17359	18993
uce-1314	10199	14977	14176	12804	17089
uce-1315	11098	16447	13981	15509	16885
uce-1317	14518	23246	22007	23857	21687
uce-1323	10472	15230	12538	15077	10873
uce-1324	14623	13944	16204	14511	19118
uce-1325	11369	23923	21804	26435	10437
uce-1328	29303	24926	17929	17555	23799
uce-1330	12224	21251	19139	15993	15393
uce-1331	22205	28275	19223	17593	17094
uce-1335	13299	19973	8828	7537	23443
uce-1337	17912	20339	17502	23500	16007
uce-1339	9678	17787	17708	18835	15456
uce-1340	9694	12716	23191	15258	17351
uce-1342	11760	18687	15355	14914	21381
uce-1343	17847	21727	15324	17258	18924
uce-1345	9495	19988	15718	18416	20103
uce-1348	9591	17068	18688	14081	23900
uce-1349	12560	17775	12491	13965	18921
uce-1352	9346	11600	14035	11693	14271
uce-1353	11154	14753	12191	12028	17806
uce-1357	11195	17917	11886	14332	16294
uce-1358	8825	17106	13240	17262	14015
uce-1359	10640	18185	12402	12062	13855
uce-1362	13870	18908	12408	11347	19123
uce-1365	8433	16630	9128	7950	21989
uce-1366	9984	27290	13770	13627	23921
uce-1368	10348	24951	11607	12242	20764
uce-1372	12582	17609	11136	8195	12582
uce-1374	16301	14708	13514	13835	15786
uce-1377	11319	17390	21043	18365	23443
uce-1378	9748	20502	18112	13267	23118
uce-1379	10304	21361	11651	13883	19353
uce-1380	10886	25150	11501	11252	23531
uce-1381	19496	26361	16655	14129	25727
uce-1383	14211	22708	13503	11143	23555
uce-1384	7463	23337	9129	9538	22493
uce-1386	16253	25197	23496	37506	20803
uce-1391	16954	24363	19623	20462	16993
uce-1392	14743	19332	18662	17938	11141
uce-1393	10887	26632	14339	17486	19752
uce-1394	10896	19463	11431	13708	15454
uce-1395	10612	15998	10543	12303	16636
uce-1400	10072	16859	12701	16317	15881
uce-1403	9390	19996	17934	17566	15530
uce-1405	13607	23929	10504	8234	26158
uce-1414	9037	18528	14886	12048	16273
uce-1415	8259	18699	9199	10922	14529
uce-1416	19577	23670	14108	16404	20957

uce-1417	14006	27732	18928	21168	21710
uce-1418	10533	17526	15638	17169	20446
uce-1419	14966	20188	14236	14928	16378
uce-1420	14699	16048	16781	17385	16567
uce-1421	12972	19746	14685	13882	15883
uce-1422	9093	13912	16033	12321	14721
uce-1423	12136	18356	11657	13826	14535
uce-1424	10807	16306	13445	13940	15502
uce-1425	10735	19009	16302	15832	19882
uce-1426	10494	20959	13787	15204	24228
uce-1428	11710	15198	14860	13549	18438
uce-1429	9096	11905	12021	12014	13596
uce-1430	11056	19988	15936	18063	18677
uce-1432	9119	26766	9723	15196	25326
uce-1434	9764	13552	10993	12254	13222
uce-1438	8737	19146	12876	13215	26386
uce-1440	24729	31581	13027	17603	28615
uce-1441	10074	19702	15280	11232	21328
uce-1442	8716	11756	8744	7861	12147
uce-1443	13750	21026	14029	13895	21916
uce-1445	16362	27387	17302	14043	35282
uce-1446	14311	16526	14198	11871	24966
uce-1447	7942	16925	8637	11993	20191
uce-1451	7974	23562	13160	13477	23475
uce-1452	18112	32492	18250	24862	23492
uce-1457	11105	17809	11669	9926	20555
uce-1459	11840	18653	21740	15561	28126
uce-1460	8069	15384	14150	9645	18216
uce-1462	11149	18130	20865	18348	19652
uce-1463	13821	27887	15474	16178	24080
uce-1464	10126	11662	9984	12189	12207
uce-1466	12664	18512	15231	15288	18553
uce-1476	11205	27555	14968	16578	24679
uce-1477	6665	23866	8338	10404	22295
uce-1478	10195	18539	13529	16707	16686
uce-1481	22993	26134	17513	16481	32631
uce-1482	37028	30674	36123	28751	45896
uce-1483	9520	19141	12912	12768	20734
uce-1484	9559	17442	8046	7569	16408
uce-1486	12229	15175	14551	15533	15256
uce-1487	8359	20597	13468	18597	19829
uce-1490	10289	18804	15087	16779	17799
uce-1491	9274	10573	8402	8520	9794
uce-1495	11062	18544	15312	18657	18465
uce-1496	10942	9941	17404	12455	17354
uce-1497	10793	23449	11261	11732	28290
uce-1499	12485	21502	13771	14581	20485
uce-1500	10296	16218	15157	12643	16229
uce-1501	10113	16678	9343	6772	16604
uce-1502	7416	13780	10822	9064	14908
uce-1503	10437	15555	16376	21023	17921

uce-1507	7999	20021	8573	6461	20338
uce-1510	10777	25866	11330	11448	22089
uce-10001	11658	16180	9726	12624	13007
uce-10002	11979	13950	15506	14695	23950
uce-10006	11644	29153	10833	12944	24466
uce-10007	11524	17756	14653	14815	18028
uce-10008	10560	22899	13232	13747	22442
uce-10009	12773	28048	17376	14966	21309
uce-10012	11031	19051	6668	6829	16145
uce-10013	10224	28556	14114	17524	19518
uce-10014	11876	16179	11808	9143	20265
uce-10015	6638	11513	6376	5391	10694
uce-10017	8227	15456	9736	8601	15180
uce-10019	7455	14991	14126	8924	16820
uce-10020	8429	22748	8162	10118	20095
uce-10025	11048	14284	11255	11639	17389
uce-10026	16377	21497	12443	13631	20092
uce-10029	14527	26001	14800	15311	26129
uce-10032	10171	17787	13557	11089	19061
uce-10033	19368	28008	15215	18632	17282
uce-10037	9335	22635	13034	8398	23038
uce-10041	10317	25322	10928	10990	23183
uce-10045	10184	19325	6797	5047	17291
uce-10048	9148	22631	10857	14731	21705
uce-10049	10163	23401	7935	8050	19256
uce-10053	11621	25230	11637	11419	25045
uce-10054	24833	32857	14107	13923	29304
uce-10059	20076	26465	35812	18703	35360
uce-10061	11277	15875	15177	14993	17863
uce-10063	8455	25930	10263	12028	22956
uce-10066	8770	21330	9716	6470	19514
uce-10067	10569	26933	11595	11549	24026
uce-10068	14240	25079	20211	16771	24835
uce-10069	10306	23420	12076	14629	20144
uce-10071	11229	17158	15325	15167	20025
uce-10072	8589	10550	13079	13719	12135
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uce-10074	10819	21100	9389	12451	21646
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uce-10078	9532	17957	9956	9745	13850
uce-10079	11786	17071	10260	9610	15001
uce-10084	13160	32961	10726	15317	24581
uce-10086	10190	16229	8910	10846	18615
uce-10087	13421	24565	15234	11421	27591
uce-10089	22334	30291	17054	21844	19693
uce-10093	17621	20993	14779	18193	18910
uce-10096	11002	19235	11063	13847	17429
uce-10099	10841	16607	17031	12480	20489
uce-10100	8351	19081	8964	10996	20918
uce-10101	7927	11865	14881	13042	17405
uce-10104	11945	25042	10970	11735	23132

uce-10105	9583	25292	14214	16651	22516
uce-10108	2779	3702	2712	2730	3514
uce-10118	7579	16439	10961	8014	16737
uce-10126	12716	21782	15765	18102	23027
uce-10127	12133	22749	14414	11768	26240
uce-10134	22273	26548	15919	22079	23277
uce-10136	13079	16260	13482	11067	14692
uce-10137	5064	21930	7162	7215	17534
uce-10138	11513	23905	11010	11082	23298
uce-10139	7018	18497	8642	9017	13884
uce-10142	13564	29613	13187	14858	27394
uce-10144	8141	23418	8133	10019	22064
uce-10145	8482	23072	10270	15568	19936
uce-10148	12667	7665	6904	4668	13246
uce-10151	10617	25537	12908	11376	25142
uce-10154	11574	24605	11682	16625	22146
uce-10155	14210	14448	20779	14235	35014
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uce-10159	7544	11914	8635	10793	12869
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uce-10163	6417	5127	4761	4390	7088
uce-10164	14478	14022	7417	6870	15018
uce-10168	10173	21581	11269	12184	22577
uce-10171	11369	19763	8647	9299	19012
uce-10175	8916	22943	8095	9615	22536
uce-10177	7483	18144	10207	11055	20703
uce-10178	11312	18706	11162	13059	20066
uce-10179	7828	14075	9295	10373	16069
uce-10182	8917	21555	9151	7294	22299
uce-10184	10357	20514	13825	15443	18597
uce-10185	11631	19058	10401	11077	18785
uce-10186	10368	24110	6802	11154	20870
uce-10187	14042	17030	7023	10393	17312
uce-10188	5403	7872	4345	6645	6623
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uce-10191	12199	22246	10720	13884	22767
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uce-10193	6869	14114	8017	5590	14910
uce-10194	9034	16956	10593	10823	16098
uce-10199	8436	18890	12125	9433	20526
uce-10201	10449	22145	15689	14961	19476
uce-10202	14603	20094	13375	13859	20239
uce-10204	15108	26360	16864	15729	27635
uce-10208	8310	17971	14007	11679	21419
uce-10210	11396	25021	12918	9306	27434
uce-10211	8738	14226	8859	7061	16108
uce-10212	5368	6169	4981	3225	7669
uce-10215	11172	17677	9415	11216	17384
uce-10216	11675	19486	11366	12999	18730
uce-10218	10896	16528	15883	15238	17447
uce-10221	13289	20606	15935	14979	19471



uce-10222	8399	13933	9313	10507	15752
uce-10223	9083	19709	14772	14181	15839
uce-10224	8474	15792	9971	8777	17466
uce-10225	5385	9859	6698	6680	9832
uce-10226	12654	21829	13131	11516	24360
uce-10227	5876	5422	4747	5146	4753
uce-10229	22379	25011	18288	15671	26731
uce-10230	8172	9038	4723	5587	12336
uce-10231	13585	23320	10992	11606	20801
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uce-10233	8968	12425	10868	12519	11595
uce-10235	11887	17840	11125	10497	17511
uce-10236	8162	17001	10771	11656	18850
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uce-10240	8624	14702	9373	10515	14041
uce-10242	7928	24142	7993	10784	26041
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uce-10254	18470	22183	15632	18900	23711
uce-10258	10195	13093	8801	9254	11199
uce-10260	12132	16035	9128	7798	17739
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uce-10269	12342	18434	11557	8522	22449
uce-10270	15438	25015	12802	12840	20145
uce-10271	7356	7891	10036	11987	9322
uce-10273	16526	17585	10327	11862	19524
uce-10274	9141	19582	9081	9528	16248
uce-10276	9203	13487	7394	6587	15601
uce-10278	10997	26590	10003	13046	25548
uce-10279	16209	27055	12650	16648	23523
uce-10281	13695	29424	13951	17880	20576
uce-10282	10306	22202	10245	12285	22074
uce-10283	10688	25971	11057	9968	26932
uce-10284	7115	20008	9949	7856	20797
uce-10286	11170	33022	14080	18266	26202
uce-10287	7810	11123	7230	8306	9883
uce-10288	9267	11094	9011	8133	12325
uce-10289	10800	15682	7669	9230	15419
uce-10291	8866	22280	10420	14669	22837
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uce-10298	7431	13671	9408	10372	12413
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uce-10332	8901	16220	13240	10165	19066
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uce-10344	11766	15097	11737	10031	16721
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uce-10353	13748	22345	12982	12680	23197
uce-10355	10157	14441	15445	11484	20769
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uce-10361	9539	20279	13556	11243	20311
uce-10362	8749	15147	10183	8045	15278
uce-10363	10807	25343	10696	13060	23086
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uce-10372	8257	16508	6421	7835	16859
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uce-10383	10573	21031	9546	7523	23063
uce-10384	8807	11854	13220	13509	15585
uce-10386	10529	19281	12545	8363	20794
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uce-10393	8814	16460	9739	8740	15812
uce-10394	6406	20736	10437	8609	16787
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uce-10427	9686	19847	9079	11440	18588
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uce-10432	11635	23838	11548	11180	20999
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uce-10440	6578	22207	6996	11079	15048
uce-10442	6690	14479	6033	5470	12868
uce-10443	8268	10206	8340	10501	14113
uce-10447	10112	20566	10771	10019	22284
uce-10450	10777	22901	12005	16168	19909
uce-10451	8916	21038	9618	12119	18421
uce-10452	8189	25009	8240	12929	27225
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uce-10472	7163	20717	10914	6217	19501
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uce-10475	7060	5430	12489	9511	7640
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uce-10497	6546	14975	5234	5947	13036
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uce-10501	9780	10140	8996	6713	11231
uce-10502	11358	21788	14126	12703	23460
uce-10504	10980	13804	9385	8999	12074
uce-10505	6068	5058	4027	3254	6981
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uce-10575	10381	14765	12898	12994	19637
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uce-10577	9830	14264	6607	7262	15772
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uce-10604	9622	17191	16287	15545	15405
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uce-10663	10785	20168	16281	17348	20202
uce-10665	12502	20368	13379	15841	20566
uce-10666	8702	21845	12414	9727	22240
uce-10667	9990	16397	17722	15212	16055
uce-10670	9690	21624	9191	7166	24121
uce-10673	10138	12943	12548	11211	6730
uce-10676	6983	10767	6423	4410	11962
uce-10677	23355	20045	14425	13091	23444
uce-10685	9475	19990	9989	7509	21693
uce-10696	8872	13333	8671	10150	12104
uce-10697	12428	19544	14887	12113	12428
uce-10699	6533	10704	11674	11950	9794
uce-10701	5940	15959	11401	10252	16704
uce-10702	10250	23335	11732	12467	23752
uce-10703	9707	19671	9163	11563	20021
uce-10704	13854	18774	17184	18192	15210
uce-10706	10694	22471	11350	12373	23752
uce-10707	4557	4584	2730	2317	5174
uce-10708	12716	15499	10207	8381	21231
uce-10709	7958	15029	5179	7961	13545
uce-10713	11779	13436	9708	10401	13636
uce-10714	11753	21896	9711	11900	22636
uce-10716	6684	12282	7989	7866	11984
uce-10719	14499	19635	15285	18930	16099
uce-10722	15477	18128	11488	11050	16097
uce-10725	10322	21248	13175	14675	21164
uce-10727	11981	23788	17338	15617	15126
uce-10730	9798	17983	12068	11561	16966
uce-10733	7765	19467	9394	9670	20960
uce-10734	15065	23475	12359	15154	20187
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uce-10738	12516	31662	11023	15244	24251
uce-10741	9378	21470	9450	11133	21593
uce-10742	29940	12026	24252	17743	24623
uce-10743	11536	17027	10883	12833	11785
uce-10751	10530	17924	8025	7694	17315
uce-10752	10548	19250	6769	8872	18471
uce-10753	9558	20707	7003	7406	24068
uce-10756	8645	27808	8707	12585	26983
uce-10758	9398	19446	7828	6974	21034
uce-10762	7920	17886	9477	8410	19337
uce-10765	6849	10673	10358	8646	10609
uce-10767	8395	21151	10189	12763	25902
uce-10768	8819	13662	10071	7956	16032
uce-10770	6786	13849	8057	8546	16627

uce-10771	4888	6764	3363	3384	6541
uce-10772	9005	11871	8317	4551	11130
uce-10775	13779	25241	8637	10137	25636
uce-10776	10515	19084	5791	8468	19557
uce-10778	8689	13996	11098	12774	13283
uce-10780	6897	9407	5612	7016	8349
uce-10782	15610	24423	16039	12053	34971
uce-10783	10629	15058	8800	9293	12500
uce-10784	11646	19165	15779	14648	18898
uce-10785	6782	10640	8040	6535	10115
uce-10786	10855	18601	11117	8450	18625
uce-10789	12115	17625	16624	11871	17959
uce-10790	6670	13280	8469	7337	15724
uce-10791	8008	15701	10604	9327	18290
uce-10794	8838	21591	11129	12610	24456
uce-10795	14515	15343	14120	12934	16784
uce-10796	10762	25066	11781	11942	23273
uce-10797	10632	12467	5332	5979	16394
uce-10798	12447	19499	14660	10948	26321
uce-10799	8013	11164	3923	5105	10675
uce-10801	9702	18991	10656	8301	22966
uce-10802	9725	21860	10168	10663	21307
uce-10803	18480	17809	10137	11082	19268
uce-10807	13058	27361	17259	15181	31021
uce-10808	10958	20817	13590	11056	22483
uce-10811	7426	17905	8035	9425	18013
uce-10819	8152	18919	7707	10228	19226
uce-10820	13352	25215	14010	11500	30283
uce-10821	9989	22730	9871	9129	25941
uce-10822	15987	21442	9241	9974	25956
uce-10828	5799	19697	8567	12046	16646
uce-10829	10586	16985	12141	15201	17887
uce-10831	9523	25781	10683	14263	22030
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uce-10835	8817	12332	6661	6037	12241
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uce-10839	9954	14868	10420	12861	11297
uce-10840	9894	21937	10592	8431	22241
uce-10842	6606	10128	14529	12975	7022
uce-10843	10385	13758	18215	14669	14373
uce-10847	11353	9519	20628	18714	13010
uce-10848	9129	15257	22271	20663	17380
uce-10849	9710	15024	17378	17518	12676
uce-10852	8456	18336	9037	11930	18993
uce-10854	8101	3249	6462	7131	5105
uce-10856	10659	13122	12761	10269	12045
uce-10860	6367	16097	9213	5842	16436
uce-10861	16847	24809	12757	10403	26352
uce-10864	7650	12292	9680	11088	10495
uce-10872	4090	9223	6958	6814	9611
uce-10879	8648	21463	9232	5833	19952

uce-10880	11331	16098	7760	9118	17237
uce-10881	10536	18295	14945	13175	22681
uce-10882	12698	21721	11938	13777	21122
uce-10883	13024	20876	10153	11335	16772
uce-10885	13992	31708	12885	15857	26487
uce-10888	10778	24141	9782	13154	23905
uce-10890	9131	14619	8961	10258	13591
uce-10891	18250	25769	17775	16458	21708
uce-10892	11746	23568	11118	13697	24791
uce-10893	12422	19051	12381	9413	19981
uce-10896	8499	13766	14852	17447	11964
uce-10898	14039	17644	20085	16396	24731
uce-10900	8660	19172	8912	9253	18123
uce-10901	11342	22823	12375	10928	26028
uce-10904	13573	24914	10508	11061	25680
uce-10905	11672	21423	7078	6998	20869
uce-10908	6691	17405	8304	9480	16248
uce-10910	6004	18754	7776	8772	16878
uce-10913	9572	25374	9363	11996	20751
uce-10914	17923	40657	13829	19330	26133
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uce-10926	10567	21195	11735	8514	21909
uce-10929	9610	28179	11326	14800	23389
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uce-10932	10789	24227	12182	15839	23371
uce-10936	7468	19005	10014	12339	16246
uce-10942	7710	21280	11057	9999	19786
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uce-10949	8896	9749	11875	7450	12630
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uce-10955	11257	25459	15433	15279	17217
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uce-10989	10033	23689	12185	11979	19719
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uce-11000	8830	5973	5951	5268	12297
uce-11001	13795	15485	8487	8305	15913
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uce-11016	9413	20627	11176	9514	23080
uce-11022	10258	21723	11031	7851	24457
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uce-11038	12273	18806	4976	8355	12634
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uce-11042	12694	20649	11727	11233	20025
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uce-11069	9998	13119	14405	13763	15187
uce-11070	9133	22409	14301	15808	14957
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uce-11268	23474	31794	13683	20953	19392
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uce-11277	9657	21494	7729	10845	16887
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uce-11293	5236	6556	3932	3646	7825
uce-11296	9108	20480	13006	11223	19151
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uce-11299	8876	19405	7250	11608	21965
uce-11303	7947	22753	13107	13389	24534
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uce-11469	11704	25250	11212	13872	22914
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uce-11498	6574	23060	7463	8543	22512
uce-11503	4345	6958	3266	3338	6915
uce-11504	9034	20781	8800	9967	22706
uce-11507	10931	19056	19614	13946	21909
uce-11517	4387	4279	3568	3029	3133
uce-11518	9277	12618	9980	11979	12432
uce-11520	7880	15553	12576	13622	14169
uce-11522	10060	13687	11291	10523	13674
uce-11523	11539	18405	11666	8955	18231
uce-11525	12588	21867	13782	13930	22561
uce-11526	10901	14796	15642	13686	16375
uce-11529	8773	13017	8548	8172	13575
uce-11531	10879	11484	9746	14916	12167
uce-11532	12011	14959	10814	9124	16540

uce-11533	10026	15065	9176	8814	16503
uce-11534	9247	16063	10697	9981	13907
uce-11535	8930	16471	10099	11915	18777
uce-11537	7209	6105	7605	6803	4828
uce-11538	9988	22549	9995	11067	25809
uce-11539	10207	24544	11627	12586	24532
uce-11540	10712	24002	11019	12479	19236
uce-11543	8373	22473	13580	9198	22331
uce-11547	10614	16622	12159	13025	17916
uce-11548	14098	19343	20358	14800	21326
uce-11564	9019	16557	12725	11433	20556
uce-11565	8526	19632	9473	9128	15065
uce-11566	9472	16603	11964	10967	16850
uce-11567	7857	16455	7390	7454	16508
uce-11569	6765	14391	8742	8745	15312
uce-11570	9159	16876	11455	8924	17314
uce-11573	5150	11638	6558	6493	12481
uce-11575	7564	10151	7548	4931	9991
uce-11577	9416	23978	10239	10135	25080
uce-11580	7892	9075	10587	9442	10038
uce-11581	8818	26919	11746	15173	22539
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uce-11585	12839	16865	11191	12091	17966
uce-11593	9014	22135	13480	7981	24115
uce-11594	7647	21448	8208	7674	19983
uce-11596	8130	8255	11483	10288	10876
uce-11600	9984	19347	10554	9725	21940
uce-11601	10320	26078	10616	14310	24412
uce-11604	7272	21935	11033	7908	25996
uce-11605	6121	25331	9509	9162	20437
uce-11609	7213	17854	10645	7726	21018
uce-11613	8205	22596	9550	11090	22479
uce-11617	9583	16991	9200	7619	16863
uce-11618	7191	9516	10159	13438	9526
uce-11623	10392	10202	12945	14550	11159
uce-11629	12862	18258	14804	16260	17840
uce-11631	12735	25446	16793	19652	19846
uce-11633	9579	14172	15484	14449	18612
uce-11634	12745	15338	13942	12362	18021
uce-11641	9942	16982	15545	12164	16537
uce-11644	9875	21778	7222	9238	19367
uce-11645	9506	18171	7706	8705	18128
uce-11647	12893	26265	10236	14422	21360
uce-11648	9575	26789	11153	12987	23608
uce-11654	10777	20149	14477	13937	13180
uce-11656	9284	18269	13153	13864	15710
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uce-11666	11711	15403	16937	12383	23254
uce-11667	9740	25670	9958	11533	24747

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uce-11671	11046	14472	8862	8123	15925
uce-11672	11281	25253	13090	14504	19872
uce-11673	8102	11188	12365	13322	9528
uce-11674	8239	9176	9991	11147	8582
uce-11675	13238	20770	11537	13807	21456
uce-11679	10003	28770	15075	14409	19633
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uce-11685	10695	27713	8684	8547	26513
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uce-11688	8182	7090	10149	11180	9353
uce-11691	16856	25261	17295	15900	21680
uce-11693	9946	21765	13873	14966	23798
uce-11695	18715	18877	16617	16220	19955
uce-11698	9192	15473	7285	7550	15940
uce-11702	9963	5162	7397	6421	9537
uce-11704	4316	2712	4022	4626	3134
uce-11705	8281	21292	11952	11338	21913
uce-11706	7273	18330	8291	8450	19621
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uce-11718	4547	4436	2990	1856	6247
uce-11719	10623	18241	6554	9188	11658
uce-11721	8680	12287	5944	4827	11767
uce-11722	10321	22851	11566	12253	18553
uce-11725	9108	22566	8996	11893	22477
uce-11728	9094	18404	7031	8126	18273
uce-11729	6151	9629	4827	5780	9073
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uce-11731	8756	19616	10009	11203	18203
uce-11732	12989	24325	15232	16697	22933
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uce-11736	10888	23658	13522	11890	23706
uce-11737	13029	19102	10028	12214	22739
uce-11740	10625	20569	11828	12704	18530
uce-11741	9648	22353	13704	13193	20678
uce-11742	13442	23754	14320	13819	21745
uce-11744	17630	21013	15528	14134	23087
uce-11745	13216	21903	13578	17507	19980
uce-11746	10441	17885	15415	15464	14771
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uce-11749	9967	21323	10618	14296	20854
uce-11750	9137	19887	11488	12501	18157
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uce-11759	8989	24993	11993	12182	19822
uce-11763	12730	21509	9257	12560	16554

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uce-11766	16549	21898	12511	11415	24091
uce-11767	8614	15820	9505	7116	16145
uce-11771	13110	16690	10530	9032	18552
uce-11772	9906	13397	7440	6224	11039
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uce-11775	12654	18069	12742	12613	18682
uce-11776	15271	17122	11188	9999	16325
uce-11778	4047	4077	2837	3687	3799
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uce-11785	14328	13476	12021	14497	11422
uce-11787	11638	24304	9490	10245	26979
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uce-11791	12084	29323	10604	16035	22924
uce-11792	12796	19519	14528	12057	21684
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uce-11799	12057	24404	14453	11688	31198
uce-11800	13861	21895	8749	12358	18457
uce-11802	8552	23702	9272	10909	22213
uce-11808	9590	12306	10260	10642	14064
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uce-11812	11580	21149	12843	14040	20524
uce-11819	8342	12544	10696	8134	16824
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uce-11823	21747	24462	14624	18911	22512
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uce-11850	8352	21253	9778	9589	21263
uce-11851	11210	18599	15117	9298	22061
uce-11852	8912	24380	9496	11273	23387
uce-11853	12378	14029	10615	7215	15994
uce-11858	12610	28064	12595	14933	24870
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uce-11863	8822	19177	15995	19967	14271
uce-11865	10788	16652	13364	12277	15743
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uce-11876	11418	10096	6986	9830	10271
uce-11879	15779	7468	9535	5704	12390
uce-11880	6151	13238	10565	10002	15099

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uce-11882	10850	20024	10963	10692	15959
uce-11884	8198	10486	6857	7466	8897
uce-11889	9644	11788	6722	4427	13124
uce-11897	9323	25342	11696	10818	20717
uce-11899	7074	11129	6580	6731	8317
uce-11900	10417	24083	10655	9570	21267
uce-11901	10697	16616	13014	10748	13000
uce-11902	12809	21229	12978	10242	24782
uce-11903	7684	10020	4824	3925	12267
uce-11905	10215	26142	9186	13912	23925
uce-11906	6232	18210	8258	5705	18300
uce-11909	13355	20495	12400	13153	20397
uce-11910	9760	15991	11345	11988	13121
uce-11912	6482	17823	7333	4402	17860
uce-11914	11626	23017	9154	11062	22477
uce-11922	17052	27701	18590	14665	25256
uce-11923	12246	12874	13275	11605	15240
uce-11925	10548	14478	16450	14231	16701
uce-11926	13395	21472	16260	19182	17835
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uce-11930	7272	12082	7329	7864	14348
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uce-11932	13238	20080	12610	15992	18608
uce-11936	12468	20656	10956	12986	19128
uce-11939	10532	25504	13503	12900	21766
uce-11940	11480	18648	11545	10439	19064
uce-11941	10404	29415	11481	14164	24808
uce-11944	12874	17365	11085	8755	21433
uce-11946	8084	11110	11509	10929	11883
uce-11947	8760	28765	8260	7612	22819
uce-11948	8109	24953	8842	7402	23382
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uce-11963	9879	25911	11198	12315	26601
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uce-11971	9702	25791	10654	13023	23550
uce-11972	12191	23153	11000	12838	21458
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uce-12002	7671	29375	9012	13743	24143
uce-12003	10562	17981	9315	9491	21363
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uce-12010	9897	12487	7119	3834	15533
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uce-12016	11175	17719	10601	10054	17819
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uce-12052	7161	16861	5586	7758	19779
uce-12054	6926	15753	7852	5912	14377
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uce-12076	10049	25214	13651	12433	23213
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uce-12133	10360	20720	11197	11249	15939
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uce-12147	10617	22156	14363	7946	23318
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uce-12182	9039	29953	11144	17093	21596
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uce-12186	6018	12347	9037	5349	21258
uce-12187	6181	9606	9666	8782	6751
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uce-12212	11760	21305	12845	12239	23219
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uce-12254	7340	7469	4368	3620	7953
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uce-12258	9779	23817	8382	12460	22562
uce-12261	13586	28777	17771	17331	25631
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uce-12282	8013	19322	14998	15449	16303
uce-12283	13109	12637	15460	16909	11739
uce-12285	7365	4941	3538	3867	5622
uce-12287	6946	16270	7033	7949	13002
uce-12290	9345	24968	9271	13765	27491
uce-12292	5832	19248	6072	8137	16459
uce-12294	9624	17626	9205	10832	17228
uce-12295	7306	23930	11095	13913	20536
uce-12296	9123	14121	13312	16230	12790
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uce-12301	10337	23110	10033	11805	28435
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uce-12325	12318	26752	13975	13468	24714
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uce-12349	11271	20101	12619	13903	23418
uce-12350	13411	25284	10664	11999	23813
uce-12353	9138	19298	11575	8854	23375
uce-12354	10451	22535	8979	9561	19039
uce-12357	12638	25451	10198	13448	22097
uce-12358	8958	23678	14463	11724	25289
uce-12360	12442	22823	11631	11036	28252
uce-12361	10830	15232	11674	7915	20373
uce-12364	12076	14881	9690	9887	18126
uce-12366	11588	26423	13270	12234	24069
uce-12367	7451	9472	11094	11833	9934
uce-12369	10895	20295	16021	16340	25439
uce-12370	7659	12202	8841	10542	10971
uce-12371	8619	19498	10070	12103	17470
uce-12373	8681	17780	10916	13312	20606
uce-12374	8592	21514	12214	17078	18122
uce-12375	13327	21927	12924	17598	24644
uce-12376	8995	25788	10109	12273	23195
uce-12377	9427	13771	7520	7746	13616
uce-12382	7128	24872	8226	12830	24380
uce-12385	10731	21092	15667	10861	24921
uce-12386	7218	9506	6101	4255	10813
uce-12388	13258	28767	10603	13873	25624
uce-12392	11736	23211	14258	15451	25448
uce-12393	11619	12205	12106	11099	15467
uce-12394	10869	14752	13594	15546	15407
uce-12399	9630	16297	12225	9347	15696
uce-12403	4963	6098	3026	2530	5823
uce-12405	6762	11369	7890	9470	8397
uce-12406	10436	14786	9898	9460	17964
uce-12407	12023	23661	13253	14533	19578
uce-12408	15909	22902	14314	14448	23931
uce-12409	14162	23393	12924	10386	23807
uce-12411	7183	17526	10172	10315	16704
uce-12412	9476	21979	12532	10326	22187
uce-12413	12384	18545	6958	5821	17342
uce-12418	11478	17573	17706	20461	15718
uce-12420	25488	20106	20010	19466	16066
uce-12422	9903	29921	13873	12252	22699
uce-12427	7535	20978	6259	6792	18771

uce-12428	9675	25910	8119	13635	22026
uce-12430	13378	24500	10440	11492	22510
uce-12435	7906	22437	14034	15714	23517
uce-12439	9179	24037	11570	10756	22951
uce-12440	10721	22360	8568	11902	21693
uce-12442	14027	28572	10761	15076	21332
uce-12444	10559	17022	8357	5815	15832
uce-12445	9701	22444	6781	5477	20837
uce-12447	11142	24950	10590	10042	30300
uce-12449	8037	11184	6840	6168	12821
uce-12450	5104	4449	5058	4674	6543
uce-12454	10412	22555	14445	13856	22442
uce-12456	7094	16752	8173	9494	12827
uce-12457	9778	25499	6423	9321	25497
uce-12458	12948	21269	16128	12249	24206
uce-12460	10502	15390	14778	14872	17370
uce-12462	7009	19227	8908	8180	18892
uce-12464	10076	15263	4523	5561	15351
uce-12468	12996	18996	11458	11610	23228
uce-12474	10599	20970	11782	12822	20717
uce-12475	5409	5215	4460	3713	5850
uce-12477	3785	20305	9451	7369	24162
uce-12478	6660	18007	5734	5961	13926
uce-12479	10463	26458	10595	12003	24761
uce-12480	7575	9338	5249	6459	10122
uce-12481	9950	12290	7368	4507	13060
uce-12482	14425	24175	15430	20011	21663
uce-12491	10003	21280	10049	13081	23595
uce-12492	9027	25730	10352	11206	22981
uce-12493	13438	23890	13346	11400	25286
uce-12495	11322	23937	14600	15584	22421
uce-12499	10281	25230	11495	14602	23064
uce-12502	10880	25780	8868	12828	25700
uce-12503	10108	14406	6796	6790	15006
uce-12507	8771	18797	8694	8760	21506
uce-12508	9795	24055	11908	8368	18506
uce-12510	13520	45439	15201	22545	25935
uce-12512	9433	16129	5551	7726	13837
uce-12513	8638	23041	10947	8782	26032
uce-12514	14377	21554	12331	14492	25301
uce-12515	9963	24887	10608	12471	19951
uce-12516	10215	27178	14086	12794	26223
uce-12517	7838	15524	13220	10992	15706
uce-12520	8010	14390	12663	12724	15941
uce-12526	8158	19166	8776	7664	16884
uce-12529	10987	26941	10948	12552	30020
uce-12531	5575	12256	5461	6739	11927
uce-12532	13063	20185	16298	13432	25744
uce-12533	8867	10681	7633	8047	10299
uce-12534	10394	13485	9316	11787	12768
uce-12535	11716	24729	12873	13180	19822

uce-12536	5478	8302	6513	5467	7543
uce-12537	10629	22805	12961	14469	20784
uce-12540	11294	22293	12952	16850	23467
uce-12541	9287	17653	8821	10468	12951
uce-12542	8353	14383	8346	6128	20414
uce-12545	5986	17346	7855	9728	12905
uce-12553	9682	11424	10282	10041	10051
uce-12554	13767	18914	10515	10632	17964
uce-12557	13250	20806	13968	12931	27189
uce-12558	9507	19626	10397	10178	18217
uce-12561	7612	13963	12701	9333	16506
uce-12562	13613	19571	14563	17143	17318
uce-12563	5183	6162	4958	5145	5402
uce-12564	10301	18243	9083	10986	23573
uce-12565	9161	16247	11914	13328	17330
uce-12566	18527	24377	14901	13069	32856
uce-12567	10567	22908	10013	9703	23025
uce-12571	7709	25467	10542	9027	24703
uce-12578	8544	20545	12689	12451	21771
uce-12579	16428	31312	13535	18203	19622
uce-12580	11932	27664	13673	10611	21072
uce-12581	10452	21380	7942	11216	18852
uce-12582	11100	16093	9326	7834	19300
uce-12583	7558	13385	7954	6767	16192
uce-12584	5167	5739	3990	3620	5874
uce-12586	7964	12603	4376	4905	11246
uce-12588	6526	5021	6865	5620	6400
uce-12589	10268	16132	12663	15268	13814
uce-12590	10343	27257	11305	11415	23885
uce-12591	6444	9366	5163	6111	10356
uce-12593	7159	25200	16269	12380	23048
uce-12594	9636	27606	11102	14671	24961
uce-12597	8704	15293	11550	11868	12169
uce-12603	12193	22513	20505	22295	21334
uce-12605	8777	15670	13818	15054	18641
uce-12608	10067	20102	12317	13374	16100
uce-12609	7352	15351	8479	7929	14074
uce-12614	9818	22425	14442	15408	20395
uce-12615	11156	19741	9180	10106	18305
uce-12616	8668	18432	8268	10598	15864
uce-12621	12781	15902	12036	12619	13246
uce-12623	9908	13047	9222	9051	14762
uce-12624	10025	16951	10109	9937	16448
uce-12630	9879	16960	14641	13580	19465
uce-12633	13585	26527	18899	21903	20506
uce-12635	15309	27184	13054	14137	21540
uce-12636	25240	18703	19753	19744	18200
uce-12637	10320	10455	11405	13249	11936
uce-12641	8382	13328	12026	10716	11813
uce-12648	11412	25678	11352	13237	24011
uce-12650	9957	25953	7500	11712	25554

uce-12651	9419	19070	9575	6121	21391
uce-12654	6833	13212	10524	10118	10889
uce-12656	12580	31002	11009	16534	22727
uce-12657	10139	15222	6541	9749	11754
uce-12661	8492	17498	9120	10241	13673
uce-12664	7167	11778	11945	11083	10332
uce-12669	13880	17897	16399	16558	21946
uce-12670	6438	10058	10791	11060	12418
uce-12671	16775	20605	17106	17202	26144
uce-12672	13376	21610	14983	11001	28406
uce-12675	12038	10086	11855	10713	10913
uce-12677	10328	12966	17645	19684	14672
uce-12679	16143	17018	18008	14815	19706
uce-12680	7746	16425	15200	17499	13354
uce-12681	11875	16005	16510	16507	19351
uce-12682	17193	15869	15836	20037	13738
uce-12685	10463	15866	19772	17541	17318
uce-12686	7443	5412	6993	7731	6169
uce-12691	8405	22187	11295	15889	23928
uce-12693	9852	23248	8402	10440	20768
uce-12697	8387	13090	5250	6217	14067
uce-12698	8718	21234	9539	13745	21972
uce-12699	7593	7408	12577	10365	12822
uce-12700	17281	19152	19567	15016	29448
uce-12701	7507	5772	6093	6359	8569
uce-12706	7468	8774	6418	7193	8360
uce-12707	13190	16520	13652	13296	17822
uce-12708	10614	18938	24990	16201	42041
uce-12709	17205	25766	20677	17751	35366
uce-12713	6280	14863	9487	8897	14905
uce-12714	8806	23821	8710	11022	24531
uce-12715	6027	24627	10476	8408	23502
uce-12717	13762	19815	9366	9215	21986
uce-12718	8811	23648	12701	10230	21834
uce-12719	8990	25621	9505	13211	26878
uce-12728	11533	26313	10254	11171	25233
uce-12731	7674	20461	10485	11403	25633
uce-12733	12515	18767	13976	12350	17320
uce-12735	8743	22355	9377	10887	21606
uce-12736	8964	18291	12327	12914	20808
uce-12742	9452	21426	9735	9020	23279
uce-12746	16731	23924	15332	11927	24766
uce-12747	12845	23366	15423	20625	19703
uce-12748	9244	18654	9987	7670	18677
uce-12749	9375	21204	11287	10345	22549
uce-12754	9376	12838	13271	11590	14525
uce-12755	12376	24918	15401	18030	16187
uce-12756	13778	15626	13768	17290	14943
uce-12757	7748	11236	10860	12583	10703
uce-12758	7519	14774	12313	10699	13820
uce-12760	11441	15310	12369	11290	15278

uce-12761	7241	8152	5539	3750	9428
uce-12762	11140	27242	16280	13322	29008
uce-12765	11652	17080	18723	17524	18685
uce-12766	14296	24300	14867	19705	18462
uce-12769	11581	18417	11382	11041	20454
uce-12770	11067	14169	18644	15861	20787
uce-12777	13416	22232	14022	11997	20429
uce-12779	7267	11239	9098	7657	12699
uce-12780	10636	15047	11628	11395	19496
uce-12781	10771	17486	10376	15518	17473
uce-12782	8543	12186	6903	6875	13769
uce-12783	7626	18791	8180	9183	17655
uce-12784	8315	9059	7299	7816	10521
uce-12786	5585	4283	4130	3262	5790
uce-12789	7476	12749	9296	8808	12271
uce-12791	9946	22465	12049	15092	20473
uce-12794	9632	14752	14159	11200	18548
uce-12796	13115	21363	11018	11771	22813
uce-12803	9275	20772	8155	11618	21468
uce-12804	3079	5214	2436	1976	6240
uce-12805	7943	21077	11802	10305	22958
uce-12806	12488	16164	12828	10839	15276
uce-12807	9932	24065	8494	11514	20923
uce-12808	7134	14558	12030	8736	16942
uce-12809	12747	21911	13010	12747	25153
uce-12812	13912	16072	16499	17524	18481
uce-12819	10726	20852	8916	13028	22834
uce-12820	6238	9327	5483	4299	10845
uce-12823	6320	12697	12342	7492	20171
uce-12824	9849	20785	13879	11008	19884
uce-12826	8139	24362	11852	8824	24496
uce-12831	9090	5446	6531	8692	7105
uce-12836	7766	14514	7089	8256	15450
uce-12839	8888	24447	13483	10449	22365
uce-12840	8402	22914	11617	10908	19089
uce-12845	9872	14965	13955	11347	14653
uce-12846	11451	26007	13271	14019	24292
uce-12849	5786	19750	10432	7177	22360
uce-12852	8589	25594	10554	10115	22764
uce-12853	10473	20707	8909	8040	18287
uce-12854	9294	24804	10713	10991	24334
uce-12857	9795	21134	11344	18423	17844
uce-12858	10839	16178	19527	17306	22502
uce-12866	6598	21716	10333	7788	21549
uce-12867	11359	19320	14512	12232	21957
uce-12868	11877	17522	6710	10583	16393
uce-12869	8767	22865	8448	9147	17469
uce-12874	16056	18248	13947	11632	18237
uce-12875	8685	24650	11004	10721	27495
uce-12880	7424	22626	11041	6216	22598
uce-12883	5829	9550	5846	4331	7924



uce-12886	7557	19102	10323	9739	20927
uce-12889	9393	20187	10710	8246	22194
uce-12890	9292	20363	9589	13435	22921
uce-12894	7922	18981	8118	10868	17713
uce-12895	13189	16086	7591	8511	14991
uce-12900	9903	18044	16721	12915	28382
uce-12901	10515	21385	11373	9662	20705
uce-12902	3520	13180	3988	6281	11256
uce-12903	8940	15716	6159	6558	16330
uce-12904	6904	17433	9321	7140	18002
uce-12906	8923	21767	12295	10778	23909
uce-12908	12587	14396	15016	16644	16487
uce-12909	7633	12240	10965	11861	12411
uce-12910	12469	21501	15683	14133	24918
uce-12912	11131	20180	12974	11888	22339
uce-12913	16007	19390	12163	10332	21236
uce-12914	7037	11115	8948	9250	13645
uce-12916	8330	20653	11428	10580	15985
uce-12917	9682	22785	9546	11920	21891
uce-12920	6030	15927	7809	7022	17308
uce-12921	14116	18430	17772	14512	21242
uce-12923	11514	21758	12662	9996	22526
uce-12926	11705	22819	13367	13325	20768
uce-12935	15694	25881	16742	15633	25394
uce-12938	11285	21844	14739	13120	21724
uce-12943	8554	19172	12858	17095	17165
uce-12947	8982	18469	12067	11882	16864
uce-12956	7656	15059	13662	11289	12208
uce-12958	9558	17287	15320	16374	17621
uce-12960	11436	17468	12975	10067	19444
uce-12962	8838	22169	12637	11227	21401
uce-12966	26802	30394	21666	26219	20379
uce-12970	8157	19866	12265	14826	20598
uce-12973	9445	19484	10678	14096	16422
uce-12974	8106	21683	9012	11284	21203
uce-12975	7631	18038	8122	5641	16362
uce-12979	5889	11625	6005	5933	12668
uce-12981	12324	26586	10570	14909	22347
uce-12983	8784	22407	10428	10532	22105
uce-12985	9623	25758	9666	12558	24435
uce-12986	9652	24180	11971	15903	26214
uce-12987	14728	10608	13193	14724	12357
uce-12989	15805	22657	15884	17886	23192
uce-12992	8944	17002	16789	16843	16582
uce-12996	11011	18181	13198	15354	17352
uce-12998	4352	6012	2585	3382	5581
uce-13000	6498	6575	5978	6287	6515
uce-13001	7358	8112	9871	10139	9178
uce-13002	9357	12514	15370	13337	13057
uce-13004	11047	20689	9792	11197	19179
uce-13007	4694	4909	6463	6929	5853

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**Table A7.** SODA species assignments based on the maximum likelihood UCE phylogeny.

Specimen	Subspecies	Species Assignment
<i>Bombus occidentalis</i> BLX1983	mckayi	0
<i>Bombus occidentalis</i> BLX1987	mckayi	0
<i>Bombus occidentalis</i> BLX1677	mckayi	1
<i>Bombus occidentalis</i> BLX1977	mckayi	1
<i>Bombus occidentalis</i> BLX1679	mckayi	2
<i>Bombus occidentalis</i> BLX1715	mckayi	2
<i>Bombus occidentalis</i> BLX1736	mckayi	3
<i>Bombus occidentalis</i> BLX1740	mckayi	3
<i>Bombus occidentalis</i> BLX1739	mckayi	4
<i>Bombus occidentalis</i> BLX1988	mckayi	4
<i>Bombus occidentalis</i> BLX1743	mckayi	5
<i>Bombus occidentalis</i> BLX1979	mckayi	5
<i>Bombus occidentalis</i> BLX1674	mckayi	6
<i>Bombus occidentalis</i> BLX1980	mckayi	6
<i>Bombus occidentalis</i> BLX1742	mckayi	7
<i>Bombus occidentalis</i> BLX1978	mckayi	7
<i>Bombus occidentalis</i> BLX1671	mckayi	8
<i>Bombus occidentalis</i> BLX1744	mckayi	8
<i>Bombus occidentalis</i> BLX1735	mckayi	9
<i>Bombus occidentalis</i> BLX1738	mckayi	9
<i>Bombus occidentalis</i> BLX1986	mckayi	9
<i>Bombus occidentalis</i> BLX1668	occidentalis	10
<i>Bombus occidentalis</i> BLX1716	occidentalis	10
<i>Bombus occidentalis</i> BLX1724	occidentalis	10
<i>Bombus occidentalis</i> BLX1731	occidentalis	11
<i>Bombus occidentalis</i> BLX1733	occidentalis	11
<i>Bombus occidentalis</i> BLX1669	occidentalis	12
<i>Bombus occidentalis</i> BLX1722	occidentalis	12
<i>Bombus occidentalis</i> BLX1687	occidentalis	13
<i>Bombus occidentalis</i> BLX1717	occidentalis	13
<i>Bombus occidentalis</i> BLX1719	occidentalis	14
<i>Bombus occidentalis</i> BLX1729	occidentalis	14
<i>Bombus occidentalis</i> BLX1718	occidentalis	15
<i>Bombus occidentalis</i> BLX1726	occidentalis	15
<i>Bombus occidentalis</i> BLX1721	occidentalis	15
<i>Bombus occidentalis</i> BLX1732	occidentalis	15
<i>Bombus occidentalis</i> BLX1666	occidentalis	15
<i>Bombus occidentalis</i> BLX1975	occidentalis	15
<i>Bombus occidentalis</i> BLX1667	occidentalis	16
<i>Bombus occidentalis</i> BLX1720	occidentalis	16
<i>Bombus occidentalis</i> BLX1730	occidentalis	16
<i>Bombus occidentalis</i> BLX1723	occidentalis	16

<i>Bombus occidentalis</i> BLX1727	occidentalis	16
<i>Bombus occidentalis</i> BLX1728	occidentalis	16
<i>Bombus terricola</i> HC154		17
<i>Bombus occidentalis</i> BLX1675	mckayi	18
<i>Bombus occidentalis</i> BLX1678	mckayi	18
<i>Bombus occidentalis</i> BLX1672	mckayi	19
<i>Bombus occidentalis</i> BLX1673	mckayi	19
<i>Bombus occidentalis</i> BLX1737	mckayi	19
<i>Bombus occidentalis</i> BLX1725	mckayi	19
<i>Bombus occidentalis</i> BLX1985	mckayi	19
<i>Bombus occidentalis</i> BLX1676	mckayi	20
<i>Bombus occidentalis</i> BLX1741	mckayi	20
<i>Bombus occidentalis</i> BLX1976	mckayi	21
<i>Bombus occidentalis</i> BLX1982	mckayi	21

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**Table A8.** PTP, mPTP, ABGD and ASAP group assignments for maximum likelihood COI barcoding sequences four, five, six and seven species are identified. PTP and mPTP found solutions for five species. ABGD found solutions for four, five and seven species, with four as the most likely. ASAP found solutions for four, five, six, and seven species, with four identified as the most likely.

Specimen	N = 4	N = 5	N = 6	N = 7
<i>B. hypocrita</i> BBBO066-10	3	3	3	3
<i>B. hypocrita</i> BBBO252-10	3	3	3	3
<i>B. hypocrita</i> BBBO336-10	3	3	3	3
<i>B. hypocrita</i> BBBO372-10	3	3	3	3
<i>B. hypocrita</i> BBWP556-10	3	3	3	3
<i>B. hypocrita</i> BBWP557-10	3	3	3	3
<i>B. hypocrita</i> GBAH17804-19	3	3	3	3
<i>B. hypocrita</i> GBAH17805-19	3	3	3	3
<i>B. hypocrita</i> GBAH17806-19	3	3	3	3
<i>B. hypocrita</i> GBMIN70597-17	3	3	3	3
<i>B. hypocrita</i> GBMIN70599-17	3	3	3	3
<i>B. hypocrita</i> GBMIN70606-17	3	3	3	3
<i>B. hypocrita</i> GBMIN70611-17	3	3	3	3
<i>B. hypocrita</i> GBMIN70637-17	3	3	3	3
<i>B. hypocrita</i> GBMIN70640-17	3	3	3	3
<i>B. jacobsoni</i> BBBO394-11	4	4	4	4
<i>B. jacobsoni</i> BBBO396-11	4	4	4	4
<i>B. jacobsoni</i> BBBO397-11	4	4	4	4
<i>B. lucorum</i> JCLUC056-11	2	2	2	2
<i>B. lucorum</i> JCLUC051-11	2	2	2	2
<i>B. lucorum</i> POLLE866-19	2	2	2	2
<i>B. lucorum</i> ACUFI1823-15	2	2	2	2
<i>B. lucorum</i> ACUFI1824-15	2	2	2	2
<i>B. lucorum</i> ACUFI1825-15	2	2	2	2
<i>B. lucorum</i> ACUFI1833-15	2	2	2	2
<i>B. lucorum</i> ACUFI1837-15	2	2	2	2
<i>B. lucorum</i> GBHAP1392-15	2	2	2	2
<i>B. lucorum</i> GBHAP1394-15	2	2	2	2
<i>B. lucorum</i> GBHAP1396-15	2	2	2	2
<i>B. lucorum</i> GBHAP1397-15	2	2	2	2
<i>B. lucorum</i> GBHAP1400-15	2	2	2	2
<i>B. lucorum</i> GBHAP1401-15	2	2	2	2
<i>B. lucorum</i> GBHAP1402-15	2	2	2	2
<i>B. lucorum</i> GBHAP1403-15	2	2	2	2
<i>B. lucorum</i> GBHAP1404-15	2	2	2	2
<i>B. lucorum</i> GBHAP1406-15	2	2	2	2
<i>B. lucorum</i> GMGMA546-14	2	2	2	2
<i>B. lucorum</i> GMGMM191-14	2	2	2	2
<i>B. lucorum</i> GMGMN003-14	2	2	2	2
<i>B. lucorum</i> POLLE2926-19	2	2	2	2
<i>B. mckayi</i> BLX1677	1	1	5	5
<i>B. mckayi</i> INRMA323017	1	1	5	5
<i>B. mckayi</i> BEECE70910	1	1	5	5
<i>B. mckayi</i> BEECE72910	1	1	5	5
<i>B. mckayi</i> BEECF81112	1	1	5	5
<i>B. mckayi</i> BEECF95513	1	1	5	5
<i>B. mckayi</i> BOWGF78609	1	1	5	5

<i>B. mckayi</i> BEECE69510	1	1	5	5
<i>B. mckayi</i> BEECF79712	1	1	5	5
<i>B. mckayi</i> BLX1675	1	1	5	5
<i>B. mckayi</i> BLX1736	1	1	5	5
<i>B. mckayi</i> BLX1737	1	1	5	5
<i>B. mckayi</i> BLX1739	1	1	5	5
<i>B. mckayi</i> BLX1740	1	1	5	5
<i>B. mckayi</i> BLX1742	1	1	5	5
<i>B. mckayi</i> BLX1976	1	1	5	5
<i>B. mckayi</i> BLX1980	1	1	5	5
<i>B. mckayi</i> BLX1982	1	1	5	5
<i>B. mckayi</i> BLX1985	1	1	5	5
<i>B. mckayi</i> BLX1987	1	1	5	5
<i>B. mckayi</i> UAMIC75113	1	1	5	5
<i>B. occidentalis</i> BLX1718	1	1	1	1
<i>B. occidentalis</i> BLX1719	1	1	1	1
<i>B. occidentalis</i> BLX2159	1	1	1	1
<i>B. occidentalis</i> BLX1670	1	1	1	1
<i>B. occidentalis</i> BLX1689	1	1	1	1
<i>B. occidentalis</i> BLX1724	1	1	1	1
<i>B. occidentalis</i> BLX1729	1	1	1	1
<i>B. occidentalis</i> BLX1992	1	1	1	1
<i>B. occidentalis</i> BEECD45609	1	1	1	1
<i>B. occidentalis</i> BEECD46209	1	1	1	1
<i>B. occidentalis</i> BEECD73209	1	1	1	1
<i>B. occidentalis</i> BEECD82310	1	1	1	1
<i>B. occidentalis</i> BEECD82410	1	1	1	1
<i>B. occidentalis</i> BEECF00210	1	1	1	1
<i>B. occidentalis</i> BEECF00310	1	1	1	1
<i>B. occidentalis</i> BEECF57411	1	1	1	1
<i>B. occidentalis</i> BEECF81012	1	1	1	1
<i>B. occidentalis</i> BLX1666	1	1	1	1
<i>B. occidentalis</i> BLX1728	1	1	1	1
<i>B. occidentalis</i> BLX2016	1	1	1	1
<i>B. occidentalis</i> BLX2160	1	1	1	7
<i>B. occidentalis</i> BLX2162	1	1	1	1
<i>B. occidentalis</i> BLX2163	1	1	1	1
<i>B. occidentalis</i> CNWLD88012	1	1	1	1
<i>B. occidentalis</i> CNWLN102713	1	1	1	1
<i>B. occidentalis</i> INRMA323217	1	1	1	1
<i>B. terricola</i> 639 NovaScotia	1	5	6	6
<i>B. terricola</i> 657 Alberta	1	5	6	6
<i>B. terricola</i> BBHEC139-09	1	5	6	6
<i>B. terricola</i> BBHEC143-09	1	5	6	6
<i>B. terricola</i> BEECD384-09	1	5	6	6
<i>B. terricola</i> BEECD387-09	1	5	6	6
<i>B. terricola</i> BEECD396-09	1	5	6	6
<i>B. terricola</i> BEECD397-09	1	5	6	6
<i>B. terricola</i> BEECD399-09	1	5	6	6
<i>B. terricola</i> BEECD400-09	1	5	6	6
<i>B. terricola</i> BEECD413-09	1	5	6	6
<i>B. terricola</i> BEECD439-09	1	5	6	6
<i>B. terricola</i> BEECD871-10	1	5	6	6
<i>B. terricola</i> BEECF063-10	1	5	6	6

<i>B. terricola</i> BWTWO706-09	1	5	6	6
<i>B. terricola</i> CNFNR1970-14	1	5	6	6
<i>B. terricola</i> CNFNR3985-14	1	5	6	6
<i>B. terricola</i> CNLMM030-14	1	5	6	6
<i>B. terricola</i> CNPEN061-14	1	5	6	6
<i>B. terricola</i> CNRME5015-12	1	5	6	6
<i>B. terricola</i> HC154	1	5	6	6
<i>B. terricola</i> HPPPK1128-13	1	5	6	6
<i>B. terricola</i> HPPPL584-13	1	5	6	6
<i>B. terricola</i> INRMA3235-17	1	5	6	6
<i>B. terricola</i> SSGBA5273-14	1	5	6	6

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**Table A9.** mPTP and GMYC species assignments based on the Bayesian COI barcoding phylogeny.

Specimen	mPTP	GMYC
639 <i>Bombus terricola</i> NovaScotia	7	31
657 <i>Bombus terricola</i> Alberta	7	14
<i>Bombus hypocrita</i> BBBO066-10	5	1
<i>Bombus hypocrita</i> BBBO252-10	4	3
<i>Bombus hypocrita</i> BBBO336-10	4	2
<i>Bombus hypocrita</i> BBBO372-10	4	3
<i>Bombus hypocrita</i> BBWP556-10	4	2
<i>Bombus hypocrita</i> BBWP557-10	4	2
<i>Bombus hypocrita</i> GBAH17804-19	5	1
<i>Bombus hypocrita</i> GBAH17805-19	5	1
<i>Bombus hypocrita</i> GBAH17806-19	5	1
<i>Bombus hypocrita</i> GBMIN70597-17	5	1
<i>Bombus hypocrita</i> GBMIN70599-17	5	1
<i>Bombus hypocrita</i> GBMIN70606-17	5	1
<i>Bombus hypocrita</i> GBMIN70611-17	5	1
<i>Bombus hypocrita</i> GBMIN70637-17	3	18
<i>Bombus hypocrita</i> GBMIN70640-17	5	1
<i>Bombus jacobsoni</i> BBBO394-11	2	4
<i>Bombus jacobsoni</i> BBBO396-11	2	4
<i>Bombus jacobsoni</i> BBBO397-11	2	4
<i>Bombus locorum</i> ACUFI1823-15	1	7
<i>Bombus locorum</i> ACUFI1824-15	1	7
<i>Bombus locorum</i> ACUFI1825-15	1	5
<i>Bombus locorum</i> ACUFI1833-15	1	6
<i>Bombus locorum</i> ACUFI1837-15	1	5
<i>Bombus locorum</i> GBHAP1392-15	1	6
<i>Bombus locorum</i> GBHAP1394-15	1	6
<i>Bombus locorum</i> GBHAP1396-15	1	7
<i>Bombus locorum</i> GBHAP1397-15	1	7
<i>Bombus locorum</i> GBHAP1400-15	1	7
<i>Bombus locorum</i> GBHAP1401-15	1	7
<i>Bombus locorum</i> GBHAP1402-15	1	7
<i>Bombus locorum</i> GBHAP1403-15	1	19
<i>Bombus locorum</i> GBHAP1404-15	1	7
<i>Bombus locorum</i> GBHAP1406-15	1	7
<i>Bombus locorum</i> GMGMA546-14	1	7
<i>Bombus locorum</i> GMGMM191-14	1	6
<i>Bombus locorum</i> GMGMN003-14	1	7
<i>Bombus locorum</i> JCLUC051-11	1	6

Bombus locorum JCLUC056-11	1	7
Bombus locorum POLLE2926-19	1	7
Bombus locorum POLLE866-19	1	7
Bombus mckayi BEECE69510	8	9
Bombus mckayi BEECE70910	8	9
Bombus mckayi BEECE72910	8	8
Bombus mckayi BEECF79712	10	10
Bombus mckayi BEECF81112	10	10
Bombus mckayi BEECF95513	10	10
Bombus mckayi BLX1675	10	10
Bombus mckayi BLX1677	8	8
Bombus mckayi BLX1736	8	8
Bombus mckayi BLX1737	10	10
Bombus mckayi BLX1739	8	8
Bombus mckayi BLX1740	10	10
Bombus mckayi BLX1742	10	22
Bombus mckayi BLX1976	10	10
Bombus mckayi BLX1980	9	21
Bombus mckayi BLX1982	9	20
Bombus mckayi BLX1985	8	8
Bombus mckayi BLX1987	8	8
Bombus mckayi BOWGF78609	8	8
Bombus mckayi INRMA323017	10	10
Bombus mckayi UAMIC75113	10	10
Bombus occidentalis BEECD45609	12	11
Bombus occidentalis BEECD46209	12	11
Bombus occidentalis BEECD73209	12	11
Bombus occidentalis BEECD82310	12	13
Bombus occidentalis BEECD82410	12	12
Bombus occidentalis BEECF00210	12	11
Bombus occidentalis BEECF00310	12	13
Bombus occidentalis BEECF57411	12	11
Bombus occidentalis BEECF81012	12	11
Bombus occidentalis BLX1666	12	13
Bombus occidentalis BLX1670	12	12
Bombus occidentalis BLX1689	12	12
Bombus occidentalis BLX1718	12	13
Bombus occidentalis BLX1719	12	13
Bombus occidentalis BLX1724	12	11
Bombus occidentalis BLX1728	12	12
Bombus occidentalis BLX1729	12	12
Bombus occidentalis BLX1992	12	24
Bombus occidentalis BLX2016	12	26
Bombus occidentalis BLX2159	12	25



Bombus occidentalis BLX2160	11	27
Bombus occidentalis BLX2162	11	28
Bombus occidentalis BLX2163	12	23
Bombus occidentalis CNWLN102713	12	11
Bombus occidentalis INRMA323217	12	12
Bombus terricola BBHEC139-09	7	11
Bombus terricola BBHEC143-09	7	16
Bombus terricola BEECD384-09	7	16
Bombus terricola BEECD387-09	7	16
Bombus terricola BEECD396-09	7	16
Bombus terricola BEECD397-09	7	14
Bombus terricola BEECD399-09	7	15
Bombus terricola BEECD400-09	7	15
Bombus terricola BEECD413-09	6	16
Bombus terricola BEECD439-09	7	29
Bombus terricola BEECD871-10	7	30
Bombus terricola BEECF063-10	7	14
Bombus terricola BWTWO706-09	7	17
Bombus terricola CNFN1970-14	7	16
Bombus terricola CNFN3985-14	7	17
Bombus terricola CNLMM030-14	7	17
Bombus terricola CNPEN061-14	7	16
Bombus terricola CNRME5015-12	7	16
Bombus terricola HC154	7	15
Bombus terricola HPPPK1128-13	7	15
Bombus terricola HPPPL584-13	7	16
Bombus terricola INRMA3235-17	7	14
Bombus terricola SSGBA5273-14	7	16
Bombus occidentalis CNWLD88012	12	16

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## APPENDIX B

## Chapter III supplemental tables and figures

**Table B1.** The geographical clusters included in the population genetics analyses. GeoCluster is the cluster number,  $N$  is the number of specimens included in the cluster,  $N$  no siblings is the number of individuals in the cluster after all but one sibling from each sibling set was removed, SibSets is the number of sibling sets within each geographic cluster, and Species is the species that the cluster represents.

GeoCluster	N	N no siblings	SibSets	Species
1	6	6	0	<i>B. occidentalis</i>
2	1	1	0	<i>B. occidentalis</i>
3	3	3	0	<i>B. occidentalis</i>
4	17	17	0	<i>B. occidentalis</i>
5	4	4	0	<i>B. occidentalis</i>
6	5	5	0	<i>B. occidentalis</i>
7	13	11	2	<i>B. occidentalis</i>
8	15	14	1	<i>B. occidentalis</i>
9	67	44	13	<i>B. occidentalis</i>
10	11	10	1	<i>B. occidentalis</i>
11	26	21	4	<i>B. occidentalis</i>
12	2	2	0	<i>B. occidentalis</i>
13	5	5	0	<i>B. occidentalis</i>
14	2	2	0	<i>B. occidentalis</i>
15	1	1	0	<i>B. occidentalis</i>
16	1	1	0	<i>B. occidentalis</i>
17	12	12	0	<i>B. occidentalis</i>
18	2	2	0	<i>B. occidentalis</i>
19	7	5	1	<i>B. occidentalis</i>
20	19	19	0	<i>B. occidentalis</i>
21	12	12	0	<i>B. occidentalis</i>
22	6	6	0	<i>B. occidentalis</i>

23	1	1	0	<i>B. occidentalis</i>
24	1	1	0	<i>B. occidentalis</i>
25	5	5	0	<i>B. occidentalis</i>
26	2	2	0	<i>B. occidentalis</i>
27	5	5	0	<i>B. occidentalis</i>
28	2	2	0	<i>B. occidentalis</i>
29	2	2	0	<i>B. occidentalis</i>
30	1	1	0	<i>B. occidentalis</i>
31	2	2	0	<i>B. occidentalis</i>
32	5	5	0	<i>B. occidentalis</i>
33	8	8	0	<i>B. occidentalis</i>
34	2	2	0	<i>B. occidentalis</i>
35	1	1	0	<i>B. occidentalis</i>
36	2	2	0	<i>B. occidentalis</i>
37	1	1	0	<i>B. occidentalis</i>
38	1	1	0	<i>B. occidentalis</i>
39	1	1	0	<i>B. occidentalis</i>
40	1	1	0	<i>B. occidentalis</i>
41	21	21	0	<i>B. occidentalis</i>
42	1	1	0	<i>B. occidentalis</i>
43	4	4	0	<i>B. occidentalis</i>
44	1	1	0	<i>B. occidentalis</i>
45	2	2	0	<i>B. occidentalis</i>
46	1	1	0	<i>B. occidentalis</i>
47	1	1	0	<i>B. occidentalis</i>
48	1	1	0	<i>B. occidentalis</i>
49	1	1	0	<i>B. occidentalis</i>
50	2	2	0	<i>B. occidentalis</i>
51	2	2	0	<i>B. occidentalis</i>
52	1	1	0	<i>B. occidentalis</i>
53	1	1	0	<i>B. occidentalis</i>

54	1	1	0	<i>B. occidentalis</i>
55	1	1	0	<i>B. occidentalis</i>
56	2	2	0	<i>B. occidentalis</i>
57	3	3	0	<i>B. occidentalis</i>
58	1	1	0	<i>B. occidentalis</i>
59	1	1	0	<i>B. occidentalis</i>
60	1	1	0	<i>B. occidentalis</i>
61	2	2	0	<i>B. occidentalis</i>
62	3	3	0	<i>B. occidentalis</i>
63	1	1	0	<i>B. occidentalis</i>
64	1	1	0	<i>B. occidentalis</i>
65	3	3	0	<i>B. occidentalis</i>
66	1	1	0	<i>B. occidentalis</i>
67	1	1	0	<i>B. occidentalis</i>
68	3	3	0	<i>B. occidentalis</i>
69	1	1	0	<i>B. occidentalis</i>
70	2	2	0	<i>B. occidentalis</i>
71	4	4	0	<i>B. occidentalis</i>
72	1	1	0	<i>B. occidentalis</i>
73	2	2	0	<i>B. occidentalis</i>
74	1	1	0	<i>B. occidentalis</i>
75	1	1	0	<i>B. occidentalis</i>
76	1	1	0	<i>B. occidentalis</i>
77	1	1	0	<i>B. occidentalis</i>
78	2	2	0	<i>B. occidentalis</i>
79	2	2	0	<i>B. occidentalis</i>
80	1	1	0	<i>B. occidentalis</i>
81	10	9	2	<i>B. occidentalis</i>
82	2	2	0	<i>B. occidentalis</i>
83	1	1	0	<i>B. occidentalis</i>
84	1	1	0	<i>B. occidentalis</i>

85	7	7	0	<i>B. occidentalis</i>
86	1	1	0	<i>B. occidentalis</i>
87	1	1	0	<i>B. occidentalis</i>
88	4	4	0	<i>B. occidentalis</i>
89	1	1	0	<i>B. occidentalis</i>
90	1	1	0	<i>B. occidentalis</i>
91	1	1	0	<i>B. mckayi</i>
92	2	2	0	<i>B. mckayi</i>
93	1	1	0	<i>B. mckayi</i>
94	4	4	0	<i>B. mckayi</i>
95	4	4	0	<i>B. mckayi</i>
96	33	33	0	<i>B. mckayi</i>
97	11	11	0	<i>B. mckayi</i>
98	31	31	0	<i>B. mckayi</i>
99	46	46	0	<i>B. mckayi</i>
100	5	4	1	<i>B. mckayi</i>
101	13	10	2	<i>B. mckayi</i>
102	4	4	0	<i>B. mckayi</i>
103	30	30	0	<i>B. mckayi</i>
104	7	7	0	<i>B. mckayi</i>
105	9	8	1	<i>B. mckayi</i>
106	12	12	0	<i>B. mckayi</i>
107	106	106	0	<i>B. mckayi</i>
108	1	1	0	<i>B. mckayi</i>
109	53	49	4	<i>B. mckayi</i>
110	3	3	0	<i>B. mckayi</i>
111	41	41	0	<i>B. mckayi</i>
112	1	1	0	<i>B. mckayi</i>
113	1	1	0	<i>B. mckayi</i>
114	2	2	0	<i>B. mckayi</i>
115	18	18	0	<i>B. mckayi</i>

116	15	15	0	<i>B. mckayi</i>
117	6	6	0	<i>B. mckayi</i>
118	1	1	0	<i>B. mckayi</i>
119	7	7	0	<i>B. mckayi</i>
120	1	1	0	<i>B. mckayi</i>
121	1	1	0	<i>B. mckayi</i>
122	1	1	0	<i>B. mckayi</i>
123	6	6	0	<i>B. mckayi</i>
124	4	4	0	<i>B. mckayi</i>
125	1	1	0	<i>B. mckayi</i>
126	9	9	0	<i>B. mckayi</i>
127	28	28	0	<i>B. mckayi</i>
128	2	2	0	<i>B. mckayi</i>
129	13	13	0	<i>B. mckayi</i>
130	9	9	0	<i>B. mckayi</i>
131	4	4	0	<i>B. mckayi</i>
132	2	2	0	<i>B. mckayi</i>
133	1	1	0	<i>B. mckayi</i>
134	1	1	0	<i>B. mckayi</i>
135	10	10	0	<i>B. mckayi</i>
136	2	2	0	<i>B. mckayi</i>
137	1	1	0	<i>B. mckayi</i>
138	1	1	0	<i>B. mckayi</i>
139	1	1	0	<i>B. mckayi</i>
140	1	1	0	<i>B. mckayi</i>
141	1	1	0	<i>B. mckayi</i>

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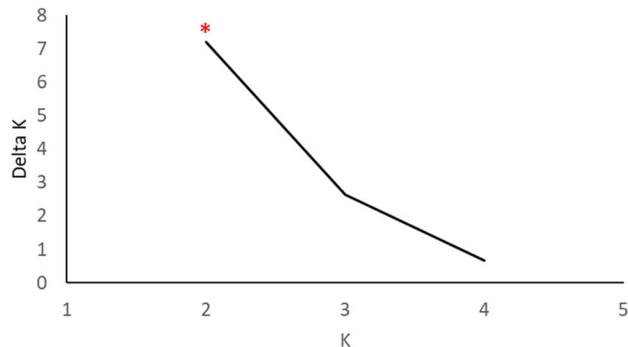
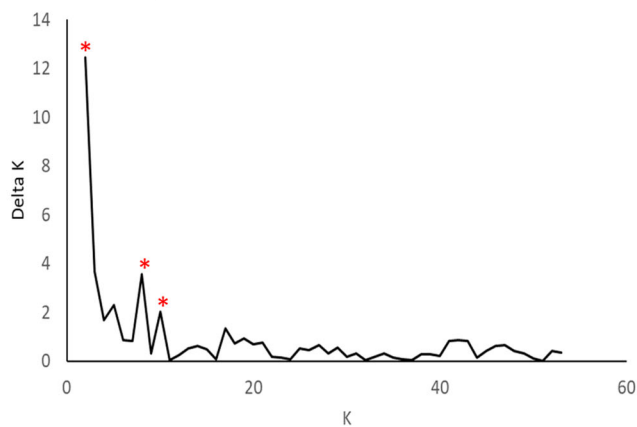
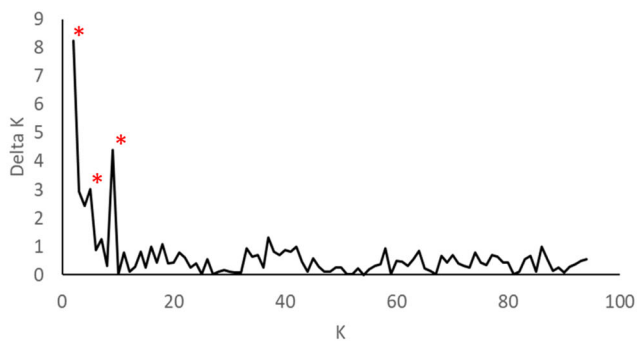
**Table B2.** Weighted ranks of Land cover values used to create habitat quality values.

Number of specimens	Land cover Class Description	Absolute Rank	Weighting factor	Weighted Rank
2156	Tree cover, needleleaved, evergreen, closed to open (>15%)	1	0.4546	980.0413
898	Herbaceous cover	2	0.1893	170.0198
586	Mosaic tree and shrub (>50%)/herbaceous cover (<50%)	3	0.1236	72.4006
337	Shrubland	4	0.0711	23.9445
158	Grassland	5	0.0333	5.2633
119	Urban Areas	6	0.0251	2.9857
98	Tree cover, needleleaved, evergreen, closed (>40%)	7	0.0207	2.0249
94	Tree cover, flooded, fresh or brakish water	8	0.0198	1.863
83	Bare areas	9	0.0175	1.4525
63	Water bodies	10	0.0133	0.8368
35	Mosaic natural vegetation (tree, shrub, herbaceous cover)(>50%)/cropland(<50%)	11	0.0074	0.2583
34	Tree cover, mixed leaf type(broadleaved and needleleaved)	12	0.0072	0.2437
29	Tree cover, broadleaved, deciduous, closed to open (>15%)	13	0.0061	0.1773
28	Cropland, rainfed	14	0.0059	0.1653
11	Shrub or herbaceous cover, flooded, fresh/saline brakish water	15	0.0023	0.0255
5	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	16	0.0011	0.0053
3	Tree cover, Broadleaved, deciduous, closed (>40%)	17	0.0006	0.0019
2	mosaic cropland (>50%)/natural vegetation (tree, shrub, herbaceous cover) (<50%)	18	0.0004	0.0008
2	Tree cover, needleleaved, deciduous, closed to open (>15%)	18	0.0004	0.0008
1	Tree cover, broadleaved, evergreen, closed to open (>15%)	19	0.0002	0.0002

1	Lichens and moss	19	0.0002	0.0002
0	Tree or shrub cover	20	0	0
0	Cropland, irrigated or post-flooding	20	0	0
0	Tree cover, broadleaved, deciduous, open (15-40%)	20	0	0
0	Tree cover, needleleaved, evergreen, open (15-40%)	20	0	0
0	Tree cover, needleleaved, deciduous, closed (>40%)	20	0	0
0	Tree cover, needleleaved, deciduous, open (15-40%)	20	0	0
0	Mosaic herbaceous cover (>50%)/tree and shrub (<50%)	20	0	0
0	Shrubland evergreen	20	0	0
0	Shrubland deciduous	20	0	0
0	Sparse tree (15%)	20	0	0
0	Sparse shrub	20	0	0
0	Sparse herbaceous cover (<15%)	20	0	0
0	Tree cover, flooded, saline water	20	0	0
0	Consolidated bare areas	20	0	0
0	Unconsolidated bare areas	20	0	0

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a. *Bombus mckayi* and *Bombus occidentalis*b. *Bombus mckayi*c. *Bombus occidentalis*

**Figure B1.** The Delta K values reported for each tested value of K for the three Structure analyses. Asterisks highlight values of K that had relatively high probabilities of representing the true structure within each analysis. The value of K with the highest support was accepted for these analyses, but the other highlighted values may represent within-species hierarchical structure.

## APPENDIX C

## Chapter IV supplemental tables and figures

**Table C1.** The questions and response options included in the questionnaire.

Question	Choices	Statistical Test
1. What organization are you associated with?	Short answer	None
2. In your opinion, how important is the conservation of native species?	1: Very important, 2: Somewhat important 3: Not very important 4: Not important 5: I do not know	None
3. Are some species more valuable than other species?	1: No 2: Yes	binomial test
4. Please rank the following characteristics in importance when deciding which species to conserve	Pick one : 1: The species is important to humans 2: The species plays an important role in its environment 3: The species is not similar to any other species	Cochran's $Q$ test
5. Please rank the following characteristics in importance when deciding which species to conserve	Pick one : 1: The species is important to humans 2: The species plays an important role in its environment 3: the species is not similar to any other species	Cochran's $Q$ test
6. Please rank the following characteristics in importance when deciding which species to conserve	Pick one : 1: The species is important to humans 2: The species plays an important role in its environment 3: the species is not similar to any other species	Cochran's $Q$ test
7. Do you have experience collecting data for a traditional conservation study to determine the conservation status of any species?	1: No 2: Yes	Binomial test
8. What type of experience do you have collecting data for traditional conservation studies to determine the conservation status of any species?	1: I do not currently collect this type of data, but I have done so in the past 2: I participate in volunteer opportunities to collect this type of data 3: I collect this type of data professionally	Spearman's $\rho$

9. How many traditional conservation studies have you participated in, professionally or voluntarily?	1: 1 to 5 2: 6 to 9 3: More than 10	Spearman's $p$
10. Do you have experience collecting data for a molecular conservation study to determine the conservation status of any species?	1: No 2: Yes	binomial test
11. What type of experience do you have collecting data for molecular conservation studies to determine the conservation status of any species?	1: I do not currently collect this type of data, but I have done so in the past 2: I participate in volunteer opportunities to collect this type of data 3: I collect this type of data professionally	Spearman's $p$
12. How many molecular conservation studies have you participated in, professionally or voluntarily?	1: 1 to 5 2: 6 to 9 3: More than 10	Spearman's $p$
13. How many meetings or public hearings have you attended that were about conservation actions on public lands?	1: More than 10 2: 6 to 9 3: 1 to 5 4: 0	Spearman's $p$
14. What level of training do you have in conservation science?	1: No formal training in conservation science 2: 2-year degree or on-the-job training 3: 4-year degree in conservation science or related biological science 4: Graduate degree in conservation science or related biological science	Pearson's $\chi^2$ Spearman's $p$
15. Which of the following groups best describes you?	1: Researcher who uses molecular techniques to conduct conservation studies 2: Researcher who uses traditional techniques to conduct conservation studies 3: Researcher who uses both traditional and molecular techniques to conduct conservation studies 4: Professional land manager who uses the results of conservation studies to make land management decisions when possible 5: Non-professional conservationist who contributes to conservation studies and decision-making when possible 6: Professional whose livelihood is affected by land management decisions that are made to promote conservation 7: None of the above	Pearson's $\chi^2$
16. If none of the above, please explain	Short answer	None

17. In the past year what is the primary way that you have learned about conservation studies?	1: By reading articles in scientific journals written by researchers who conducted the studies 2: By attending scientific presentations given by the researchers who conducted the studies 3: By reading popular science articles (for example magazines, newspapers, or online articles) written by professional journalists about the studies 4: By watching television programs or listening to radio broadcasts that were produced by professional broadcasters 5: other	Pearson's $\chi^2$
18. If other, please explain	Short answer	None
19. Do you think conservation decisions or actions should be made based on the results of (well- executed) traditional studies?	1: No 2: Sometimes 3: Yes	Spearman's $p$
20. Do you think conservation decisions or actions should be made based on the results of (well- executed) molecular studies?	1: No 2: Sometimes 3: Yes	Spearman's $p$
21. In a few sentences, please describe one conservation study in which you participated. What were the goals of the study? What was your role in the study? What were the results of the study?	Short answer	None

**Table C2.** The number of respondents from each organization that participated in the survey.

Organization	# of surveys
Acadiana Native Plant Project	3
Acushnet Conservation Commission	1
Affiliation not provided	17
Agricultural University of Tirana, Albania	1
Agriculture and Agri-Food Canada	1
Alaska Center for Conservation Science	1
Alaska Department of Fish and Game	1
Alaska Plant Materials Center	1
Allegheny Land Trust	1
Altar Valley Conservation Alliance	2
Arizona Game and Fish Department	1
Arizona Master Naturalist Association	1
Arizona Native Plant Society	62
Arizona Site Steward Program	1
Arizona State University	1
Arizona-Sonora Desert Museum	2
Arkansas Department of Transportation	1
Arkansas Master Naturalist	2
Arkansas Native Plant Society	30
Arkansas Natural Heritage Commission	2
Audubon Society	2
Australian Institute of Agricultural Science	1
Avalonia Land Conservancy, Inc.	3
Baton Rouge Audubon Society	1
bear river land conservancy	1
Bee Monitoring RCN	1
Biological Society of Western Pennsylvania	1
Boise Foothills Learning Center	1
Bolton Land Trust	1
Botanical Society of Western Pennsylvania	16
Bournemouth University	1
Boyd Woods Audubon Sanctuary (belongs to Litchfield Hills Audubon Society)	1

Brewster Conservation Trust	1
Briarwood Nature Preserve (Caroline Dorman Nature Preserve)	1
Brigham Young University	2
Bur Oak Land Trust	1
Bureau of Land Management	32
California Native Plant Society	1
Carolinian canada	1
Connecticut Botanical Society	2
Center for Coastal Management - UCC, Ghana	1
Center for Native Plants	1
Central Arizona Conservation Association	1
Central Arkansas Master Naturalists	1
Central Pine Barrens Commission	1
Centre for Ecological Research	1
Centro de Observacion Marino para el estudio de riesgos del ambiente costero (COSTAR)	1
Charleston Audubon and Natural History Society	1
Chicago Botanic Garden	2
Chinese Academy of Forestry	1
City of Albuquerque, New Mexico	1
City of Bloomington, Indiana, Parks and Recreation	1
City of Boise, Idaho	2
City of Flagstaff, Arizona, Open Space Program	1
City of New York, New York Parks & Recreation, Forestry Division	1
Clayton County Conservation Board (Iowa)	1
Cochise Native Plant Society	1
Coconino Natural Resource Conservation District	1
Coldwater Creek Biological Field Station	1
Colorado Native Plant Society	2
Colorado Natural Heritage Program	2
Colorado Plateau Native Plant Program	1
Connecticut Botanical Society	14
Connecticut Botanical Society	6
Connecticut Bureau of Natural Resources	1
Connecticut Department of Energy and Environmental Protection	18
Connecticut Department of Natural Resources	1
Connecticut Horticultural Society	1

Connecticut State Fisheries Division	1
Copenhagen University	2
Cornell Lab of Ornithology	1
Credit Valley Conservation Authority	1
Dead Sea and Arava Science Center	1
Delaware County Soil and Water Conservation District	1
Denver Botanic Gardens	3
Desert Botanical Garden	3
Dixie State University	1
DNR-WLD-SWR	1
Dubois County Soil & Water Conservation District (primary affiliation)	1
Ducks Unlimited	1
East Baton Rouge Master Gardeners of LA	2
Ecological Society of America	1
Edmonton Native Plant Society	1
Ernst Conservation Seeds, Inc.	1
Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas (CSIC)	1
Estonia Ministry of Environment	1
European Council for the Conservation of Fungi	1
European forest genetic resources programme (EUFORGEN)	1
Ezemvelo KZN Wildlife, KwaZulu-Natal, South Africa	1
Fairchild Tropical Botanic Garden	1
Fisheries and Oceans Canada	1
Fisheries Research Bureau of Iowa Department of Natural Resources	1
Florida Native Plant Society	5
Fly Fishers International	1
Folly Beach Turtle Watch Program	1
Fondazione Edmund Mach-G Genomic Biodiversity Knowledge for Resilient Ecosystems (BiKE)	1
For Lands Sake!	1
Fort Lewis College - Academic	1
Friends of Murrysville Parks	2
Friends of Sonoita Creek	1
Friends of the Environment	1
Friends of the Verde River	1
FrogWatch	1

Fungal Diversity Survey(FunDis)	1
Garden Club of America	1
GB Pant National Institute of Himalayan Environment	2
Georgina Brock Garden Club (Ontario, Canada)	1
Glacier National Park	1
Golden Hills	1
Great Basin Institute	1
Hamden Land Conservation Trust	1
Harris County	1
Hawaii Cooperative Studies Unit, University of Hawaii at Hilo	1
Herpetological Association in Bosnia and Herzegovina	1
High Park Volunteer Stewards, Toronto Field Naturalists	1
Idaho Department of Fish and Game	1
Idaho Master Naturalists	3
Idaho Native Plant Society	14
Indiana Invasives Society	1
Indiana Native Plant Society	7
Indiana Phenology	1
Institute for Applied Ecology	1
Institute for Environment and Nature, Croatia	1
Institute of Botany, Czech Academy of Sciences and The Czech Union for Nature Conservation	1
Institute of Ecology and Biological Resources	1
Instituto Alexander von Humboldt	1
Instituto da Conservação da Natureza e das Florestas (ICNF)	1
Instituto Tecnológico de Sonora	1
Intermountain West Joint Venture	1
International Commission for Plant-Pollinator Relationships	1
International Union for Conservation of Nature	5
Iowa Department of Natural Resources	7
Iowa Native Plant Society	5
Iowa Natural Heritage Foundation	3
Iowa Prairie Network	2
Irvine Ranch Conservancy	2
iSea	1
Israel gene bank	1
Kansas Conservation Association	1



Kansas Native Plant Society	1
Kentucky Department of Fish and Wildlife Resources	17
King County Noxious Weed Control Program	1
Kinnikinnick Native Plant Society	1
Knoop Group, Little Rock Adopt-a-Park	1
Lady Bird Johnson Wildflower Center	1
Latah Soil and Water Conservation District	2
Lauritzen Gardens, Omaha, Nebraska	1
Loess Hills Preservation Society	1
Louisiana Master Naturalists of Greater Baton Rouge	14
Louisiana Native Plant Society	3
Louisiana State University	1
Malawi Plant Genetic Resources Centre	1
Marine Biodiversity Observation Network (MBON)	1
Marshall University	1
Massachusetts Native Plant Society	1
Mauritian Wildlife Foundation	1
Meise Botanic Garden	1
Metamorphic Ecological Research and Consulting, LLC	1
Miami University	1
Michigan Department of Natural Resources	10
Michigan State University	1
Minnesota Department of Natural Resources	2
Minnesota Native Plant Society	2
Mississippi Native Plant Society	3
Montana Natural Heritage Program	4
Montgomery Botanical Center	1
Morton Arboretum	1
MPG Ranch	1
Myrick Park Center	1
Mystic Aquarium	2
National Agricultural Research Center (NARC)	1
National Oceanic and Atmospheric Administration	3
National Park Service	19
National Parks and Wildlife Service, Ireland	1
National Parks Conservation Association	1
Native Fish Society	1

Native Hawaiian Plant Society	1
Native Plant Initiative of Greater New Orleans	1
Native Plant Society of New Mexico	2
Native Plant Society of northeastern Ohio	1
Native Plant Society of Oregon	3
Native Plant Society of Saskatchewan	1
Native Plant Trust	4
Natural Areas Association	1
Natural History Museum of Utah	1
Natural Land Institute	1
Natural Resources Conservation Service	9
Natural Resources Defense Council	1
Natural Resources Defense Fund	1
Nature Coast Native Plant Society	1
Nature Conservancy	6
Nature Conservancy of Canada	1
NatureScot (Scottish Natural Heritage)	1
NatureServe	1
Nebraska Game and Parks Commission	1
Nebraska Master Naturalist	2
Nebraska Public Power District	1
Nebraska Statewide Arboretum	1
New England Plant Conservation Program of the New England Wildlife Federation	1
New Jersey Audubon	1
New Jersey Department of Environmental Protection	1
New Jersey Department of Environmental Protection	1
New Mexico Energy, Minerals, and Natural Resources Department	1
New Orleans Native Plant Society	1
New York City Parks	1
Nez Perce Tribe Wildlife Program	1
No affiliation	31
Nord University	1
North American Butterfly Association	1
North American Native Plant Society (NANPS)	7
North Carolina State University	1
Northern Arizona University	1

Northwest Arkansas Master Naturalists	1
Northwest conservation district (Connecticut)	1
Northwest Iowa Group of Sierra Club	1
Office of National Marine Sanctuaries	1
Ohio Department of Natural Resources	2
Onondaga Environmental Institute	1
Oregon State University	1
Pennsylvania Department of Conservation and Natural Resources	3
Pennsylvania Fish & Boat Commission	1
Pennsylvania Game Commission	4
Pennsylvania Natural Heritage Program	2
Peters Creek Watershed Association	1
Pheasants Forever	1
Pine Hill Preserve	1
Pine Ridge Gardens	1
Pizzo & Associates, Ltd.	1
Plant Conservation Alliance	1
Poland Township Park District (Ohio)	1
Polk County (Iowa) Conservation	2
Pollinators Corridors	1
Portneuf Resource Council	1
Prairie Dawgs	1
Project Swallowtail	1
Raptor Conservation Nebraska	1
Regional Water Authority - New Haven, Connecticut	2
Reneco International Wildlife Consultants	1
Research Institute of Wildlife Ecology, University of Veterinary Medicine Vienna, Austria	1
Rhode Island Fish and Wildlife	1
Rhode Island Wild Plant Society	1
Rhodes University	1
Royal Belgian Institute of Natural Sciences	1
S.P.E.C.I.E.S.	1
SA Fen Corp	1
Sagebrush Ecosystem Alliance	1
Sagebrush Steppe Land Trust	1

San Francisco State University	1
Santa Barbara Botanic Garden	2
SE Climate Adaptation Science Center	1
SeaDance	1
Sierra Club	2
Simplot	1
Slovak Academy of Sciences	1
Society for Conservation Biology	1
Society for Ecological Restoration	1
Sonoran Seed Collaborative	1
South African National Biodiversity Institute	1
South Carolina Master Gardeners	1
South Carolina Native Plant Society	9
South Carolina Native Plant Society	2
South Dakota Department of Game, Fish and Parks	5
Southern Indiana Cooperative Invasives Management	1
Spanish Society for Plant Conservation Biology	1
State of Maine	1
State of Utah	1
Swedish Environmental Protection Agency	1
Technical University in Zvolen	1
Tennessee Native Plant Society	3
Tetra Tech	1
Texas Tech University	1
The Group on Earth Observations Biodiversity Observation Network (GEO BON)	2
The Last Green Valley	1
The Morton Arboretum	1
The Reveg Edge, professional restoring arid grasslands in the West	3
The Woods on Point Clair Natural Heritage Area	1
Three rivers Birding club 3RBC	1
Town of Winthrop (Massachusetts)	1
Trout Unlimited	1
Tucson Native Plant Society	1
U.S. Department of Agriculture	2
U.S. Department of Defense	1

U.S. Fish and Wildlife Service	18
U.S. Forest Service	23
U.S. Geological Survey	45
Ukrainian Mountain Forestry Research Institute	1
United Plant Savers	1
Universidade de Vigo	1
University of Arizona	2
University of Belgrade, Faculty of Biology	1
University of Birmingham	1
University of British Columbia	2
University of California Los Angeles	3
University of Colorado	1
University of Florida	2
University of Fribourg, Switzerland	1
University of Illinois Urbana-Champaign	1
University of Maryland	1
University of Minnesota Landscape Arboretum	1
University of New South Wales	1
University of Rochester	1
University of Sydney	1
University of Trieste	1
University of Venda	1
University of Wageningen	1
Urban Wildlife Identification Network	1
US Army Corps of Engineers	1
USDA National Laboratory for Genetic Resource Preservation	1
Utah Department of Agriculture and Food	1
Utah Division of Wildlife Resources	3
Utah Native Plant Society	6
Utah State University	11
Virginia Department of Conservation and Recreation	1
Virginia Department of Wildlife Resources	17
Virginia Division of Natural Heritage	1
Virginia Tech	1
Wayne Invasive Plant Education and Removal (WIPER), Indiana	1
West Virginia Natural Heritage Program	1

West Virginia University	1
Western Association of Fish and Wildlife Agencies (WAFWA)	1
Western Pennsylvania Botanical Society	2
Westfield Green Together	1
Westmoreland Land Trust	1
Wilderness Society	1
Wildlife Management Institute	1
WildOnesSEPA	1
Wissahickon Nature Club	1
Woodbury County Conservation Board	1
WSP USA	1
Wyoming Game and Fish Department	4
Wyoming Mining Natural Resource Foundation	1
Xerces Society	1
Yale University	1

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**Table C3.** Self-identified conservation roles of respondents that selected “other” on their questionnaire.

Role	Count
Science Administrator	22
Activist	1
Economist	1
Science Educator	10
Private Land-Owner who uses native plants	22
Financial donor to conservation organizations	5
Voter	2
Native plant producer	1
Conservation consultant	8
General interest	33
Policy-maker	1
Conservation Social Scientist	1
Conservation student	1
Wildlife Veterinarian	1

**Table C4.** The pairwise correlations associated with the Pearson's rank correlations reported in the main text. A) Role in conservation, B) training in conservation, C) type of experience, D) conservation topic of interest, E) type of experience, F) way of learning about conservation (respondents with graduate degrees included), G) way of learning about conservation (respondents with graduate degrees excluded), H) conservation decisions based on molecular studies, I) conservation decisions based on traditional studies.

A) Role in Conservation

Group 1	Group 2	$\chi^2$	df	Adjusted <i>p</i>
Land Manager	Molecular and Traditional Researcher	7.07	1	0.55
Land Manager	Molecular Researcher	65.15	1	< 0.0001
Land Manager	Non-professional Conservationist	1.18	1	0.66
Land Manager	Other	5.35	1	0.18
Land Manager	Traditional Researcher	5.45	1	< 0.0001
Land Manager	Professional Affected by Conservation Decisions	44.8	1	< 0.0001
Molecular and Traditional Researcher	Molecular Researcher	31.7	1	< 0.0001
Molecular and Traditional Researcher	Non-professional Conservationist	13.93	1	0.0017
Molecular and Traditional Researcher	Other	24.35	1	< 0.0001
Molecular and Traditional Researcher	Traditional Researcher	0.11	1	0.74
Molecular and Traditional Researcher	Professional Affected by Conservation Decisions	17.26	1	0.0003
Molecular Researcher	Non-professional Conservationist	81.73	1	< 0.0001
Molecular Researcher	Other	102.4	1	< 0.0001
Molecular Researcher	Traditional Researcher	35.22	1	< 0.0001
Molecular Researcher	Professional Affected by Conservation Decisions	2.46	1	0.47
Non-professional Conservationist	Other	1.51	1	0.66
Non-professional Conservationist	Traditional Researcher	11.64	1	0.005
Non-professional Conservationist	Professional Affected by Conservation Decisions	59.25	1	< 0.0001



Conservationist	Conservation Decisions			
Other	Traditional Researcher	21.38	1	< 0.0001
Other	Professional Affected by Conservation Decisions	77.75	1	< 0.0001
Traditional Researcher	Professional Affected by Conservation Decisions	20.00	1	< 0.0001

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### B) Training in Conservation

Group 1	Group 2	$\chi^2$	df	Adjusted <i>p</i>
Land Manager	Molecular and Traditional Researcher	143.77	1	< 0.0001
Land Manager	Molecular Researcher	8.84	1	0.003
Land Manager	Non-professional Conservationist	73.76	1	< 0.0001
Molecular and Traditional Researcher	Molecular Researcher	89.09	1	< 0.0001
Molecular and Traditional Researcher	Non-professional Conservationist	362.55	1	< 0.0001
Molecular Researcher	Non-professional Conservationist	129.38	1	< 0.0001

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### C) Taxonomic Groups of Interest

Group 1	Group 2	$\chi^2$	df	Adjusted <i>p</i>
Amphibians	Birds	25.25	1	< 0.0001
Amphibians	Fish	14.08	1	0.0042
Amphibians	Fungi	18.24	1	0.0005
Amphibians	Invertebrates	10.98	1	0.02
Amphibians	Lichens	0.44	1	1
Amphibians	Mammals	20.57	1	0.0017
Amphibians	Plants	4.63	1	0.44
Amphibians	Reptiles	156.82	1	< 0.0001
Amphibians	Unnamed Species	2.95	1	0.86
Amphibians	Landscape	0.02	1	1
Birds	Fish	1.86	1	1

Birds	Fungi	68.45	1	< 0.0001
Birds	Invertebrates	3.32	1	0.77
Birds	Lichens	19.6	1	0.0002
Birds	Mammals	71.2	1	< 0.0001
Birds	Plants	9	1	0.0049
Birds	Reptiles	71.79	1	< 0.0001
Birds	Unnamed Species	41.78	1	< 0.0001
Birds	Landscape	24.04	1	< 0.0001
Fish	Fungi	52.56	1	< 0.0001
Fish	Invertebrates	0.21	1	1
Fish	Lichens	9.78	1	0.033
Fish	Mammals	55.25	1	< 0.0001
Fish	Plants	2.75	1	0.87
Fish	Reptiles	93.22	1	< 0.0001
Fish	Unnamed Species	27.84	1	< 0.0001
Fish	Landscape	13.14	1	0.0067
Fungi	Invertebrates	47.61	1	< 0.0001
Fungi	Lichens	23.06	1	< 0.0001
Fungi	Mammals	0.2	1	1
Fungi	Plants	35.77	1	< 0.0001
Fungi	Reptiles	215.16	1	< 0.0001
Fungi	Unnamed Species	8	1	0.07
Fungi	Landscape	19.2	1	0.003
Invertebrates	Lichens	7.18	1	0.12
Invertebrates	Mammals	50.28	1	< 0.0001
Invertebrates	Plants	1.44	1	1
Invertebrates	Reptiles	100.8	1	< 0.0001
Invertebrates	Unnamed Species	23.68	1	< 0.0001
Invertebrates	Landscape	10.13	1	0.03
Lichens	Mammals	25.48	1	< 0.0001
Lichens	Plants	2.25	1	1
Lichens	Reptiles	146.07	1	< 0.0001

Lichens	Unnamed Species	5.57	1	0.27
Lichens	Landscape	0.28	1	1
Mammals	Plants	38.35	1	< 0.0001
Mammals	Reptiles	218.07	1	< 0.0001
Mammals	Unnamed Species	9.94	1	0.03
Mammals	Landscape	21.55	1	0.003
Plants	Reptiles	120.9	1	< 0.0001
Plants	Unnamed Species	14.25	1	0.004
Plants	Landscape	4.07	1	0.57
Reptiles	Unnamed Species	182.77	1	< 0.0001
Reptiles	Landscape	154.62	1	< 0.0001
Unnamed Species	Landscape	3.43	1	0.77

#### D) Conservation topic of interest

Group 1	Group 2	$\chi^2$	df	Adjusted <i>p</i>
Communities	Endemic	92.35	1	< 0.0001
Communities	Habitat Assessment	81.81	1	< 0.0001
Communities	Habitat Restoration	72.32	1	< 0.0001
Communities	Invasive	52.46	1	< 0.0001
Communities	Medicinal	95.16	1	< 0.0001
Communities	Native	2.75	1	1
Communities	Non-Native	92.35	1	< 0.0001
Communities	Pests	92.35	1	< 0.0001
Communities	Rare	81.23	1	< 0.0001
Communities	Water	67.93	1	< 0.0001
Endemic	Habitat Assessment	1.6	1	1
Endemic	Habitat Restoration	4.57	1	0.62
Endemic	Invasive	13.5	1	0.006
Endemic	Medicinal	0.2	1	1
Endemic	Native	117.28	1	< 0.0001
Endemic	Non-Native	< 0.0001	1	1

Endemic	Pests	< 0.0001	1	1
Endemic	Rare	267.13	1	< 0.0001
Endemic	Water	6.25	1	0.2
Habitat Assessment	Habitat Restoration	0.89	1	1
Habitat Assessment	Invasive	7	1	0.2
Habitat Assessment	Medicinal	2.78	1	1
Habitat Assessment	Native	106.47	1	< 0.0001
Habitat Assessment	Non-Native	1.6	1	1
Habitat Assessment	Pests	1.6	1	1
Habitat Assessment	Rare	255.69	1	< 0.0001
Habitat Assessment	Water	1.8	1	1
Habitat Restoration	Invasive	3.13	1	1
Habitat Restoration	Medicinal	6.23	1	0.29
Habitat Restoration	Native	96.53	1	< 0.0001
Habitat Restoration	Non-Native	4.57	1	0.62
Habitat Restoration	Pests	4.57	1	0.62
Habitat Restoration	Rare	244.69	1	< 0.0001
Habitat Restoration	Water	0.17	1	1
Invasive	Medicinal	15.7	1	0.002
Invasive	Native	75	1	< 0.0001
Invasive	Non-Native	13.5	1	0.006
Invasive	Pests	13.5	1	0.006
Invasive	Rare	218.94	1	< 0.0001
Invasive	Water	1.88	1	1
Medicinal	Native	120.13	1	< 0.0001
Medicinal	Non-Native	0.2	1	1
Medicinal	Pests	0.2	1	1
Medicinal	Rare	270.06	1	< 0.0001
Medicinal	Water	8.07	1	0.11
Native	Non-Native	117.28	1	< 0.0001
Native	Pests	117.28	1	< 0.0001
Native	Rare	55.97	1	< 0.0001

Native	Water	91.86	1	< 0.0001
Non-Native	Pests	< 0.0001	1	1
Non-Native	Rare	267.13	1	< 0.0001
Non-Native	Water	6.25	1	0.29
Pests	Rare	267.13	1	< 0.0001
Pests	Water	6.25	1	0.29
Rare	Water	239.34	1	< 0.0001

## E) Type of Experience

Group 1	Group 2	$\chi^2$	df	Adjusted <i>p</i>
Molecular	Molecular and Traditional	232.78	1	< 0.0001
Molecular	Traditional	260.10	1	< 0.0001
Molecular	None	218.20	1	< 0.0001
Molecular and Traditional	Traditional	1.23	1	0.54
Molecular and Traditional	None	0.38	1	0.54
Traditional	None	2.97		0.26

## F) Way of Learning about Conservation (Respondents with graduate degrees included)

Group 1	Group 2	$\chi^2$	df	Adjusted <i>p</i>
Scientific Papers	Scientific Presentations	75.41	1	< 0.0001
Scientific Papers	Popular Articles	94.10	1	< 0.0001
Scientific Papers	Television or Radio	292.17	1	< 0.0001
Scientific Papers	Other	229.46	1	< 0.0001
Scientific Papers	No Response	277.00	1	< 0.0001
Scientific Presentations	Popular Articles	1.17	1	0.56
Scientific Presentations	Television or Radio	93.92	1	< 0.0001
Scientific Presentations	Other	52.86	1	< 0.0001

Scientific Presentations	No Response	83.10	1	< 0.0001
Popular Articles	Television or Radio	76.27	1	< 0.0001
Popular Articles	Other	39.06	1	< 0.0001
Popular Articles	No Response	66.28	1	< 0.0001
Television or Radio	Other	7.69	1	0.022
Television or Radio	No Response	0.49	1	0.56
Other	No Response	4.36	1	0.11

G) Way of learning about Conservation (Respondents with graduate degrees excluded)

Group 1	Group 2	$\chi^2$	df	Adjusted <i>p</i>
Scientific Papers	Scientific Presentations	0.21	1	1
Scientific Papers	Popular Articles	1.08	1	1
Scientific Papers	Television or Radio	35.77	1	< 0.0001
Scientific Papers	Other	18.11	1	0.0001
Scientific Papers	No Response	24.03	1	< 0.0001
Scientific Presentations	Popular Articles	0.33	1	1
Scientific Presentations	Television or Radio	41.03	1	< 0.0001
Scientific Presentations	Other	22.09	1	< 0.0001
Scientific Presentations	No Response	28.51	1	< 0.0001
Popular Articles	Television or Radio	48.01	1	< 0.0001
Popular Articles	Other	27.55	1	< 0.0001
Popular Articles	No Response	34.57	1	0.38
Television or Radio	Other	2.45	1	1
Television or Radio	No Response	1.39	1	1
Other	No Response	0.47	1	1

## H) Conservation decisions based on molecular studies

Group 1	Group 2	$\chi^2$	df	Adjusted <i>p</i>
No	Sometimes	415.15	1	< 0.0001
No	Yes	369.38	1	< 0.0001
Sometimes	Yes	2.42	1	0.12

## I) Conservation decisions based on traditional studies

Group 1	Group 2	$\chi^2$	df	Adjusted <i>p</i>
No	Sometimes	356.38	1	< 0.0001
No	Yes	61.71	1	< 0.0001
Sometimes	Yes	193.84	1	< 0.0001

## CURRICULUM VITAE

## Ashley T. Rohde

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Education:

- Bachelor of Arts, Department of Biology, Kalamazoo College, Kalamazoo, MI  
Major: Biology Minor: Spanish Literature Graduation Date: June 2006
- Masters of Science, Department of Biological Sciences, Boise State University, Boise, ID  
Defense Date: March 2014 Graduation Date: May 2014
- Doctorate of Philosophy, Department of Wildland Resources, Utah State University,  
Logan, UT  
Defense Date: April 2022

PhD Dissertation Research:

**Conservation genetics of a declining bumble bee in western North America; the influence of geography, dispersal limitation, and anthropogenic activity**

Landscape genetics is an interdisciplinary field that combines aspects of population genetics, landscape ecology, and spatial statistics to measure genetic discontinuities and diversity patterns across landscapes and to correlate them with environmental features. Over the course of two independent studies, I used landscape genetic techniques to measure the gene flow and genetic structure across the species-wide distribution of a native bumble bee species of conservation concern in North America (*Bombus occidentalis*, the western bumble bee). In a third study, I surveyed over 1,000 conservationists from across the United States and Canada to determine how the results of molecular ecology studies (for any species) are understood and applied to conservation actions and policy decisions.

**Chapter 1: Genome-wide nuclear markers reveal patterns of genetic structure in putative subspecies of a bumble bee species of conservation concern (*Bombus occidentalis* Greene)**

*Bombus occidentalis* was once common in western North America, but comparisons of early museum records and studies from before 1997 against recent museum records and collections indicate that populations have declined dramatically along the west coast and in the Rocky Mountains and Intermountain West since the mid 1990's. To complicate the problem further, previous studies are conflicted about the species status of *Bombus occidentalis* Greene with up to five subspecies proposed, and two subspecies (*B. occidentalis occidentalis* and *B. occidentalis mckayi*) most commonly accepted. The two most commonly recognized subspecies are broken primarily into northern (*B. occidentalis mckayi*) and southern (*B. occidentalis occidentalis*) taxa, with a geographic overlap in the distributions in northern British Columbia, Canada. A recent phylogenomic study using COI-barcoding found support to elevate *B. occidentalis mckayi* to species status. Species definition for these taxa is



particularly important because it is currently under consideration for listing as endangered by the Endangered Species Act in the USA and has some protection under the Species At Risk Act in parts of Canada. Decisions regarding appropriate protections for *Bombus occidentalis* may be influenced by the inclusion or exclusion of *B. occidentalis mckayi* in those decisions, as evidence suggests decreases in population abundances and ranges are primarily occurring within the range of *B. occidentalis occidentalis*, while populations of *B. occidentalis mckayi* appear to be stable at this time. I genotyped 100 specimens of *B. occidentalis* from across the range of the species, including both putative subspecies, using ultra-conserved elements (UCEs). These nuclear markers are found throughout the genomes of most plants and animals, and provide a complementary dataset to the existing COI-barcode dataset, which is derived from a single, quickly evolving gene. Analysis of this dataset is ongoing, but preliminary results support two distinct clades that represent *B. occidentalis occidentalis* and *B. occidentalis mckayi*.

## **Chapter 2: The influence of geography, dispersal limitation, and anthropogenic change on the population genetic characteristics of a bumble bee of conservation concern (*Bombus occidentalis*) over 80 years in western North America**

Although a pattern of decrease in abundance for *B. occidentalis* has been clearly demonstrated in previous studies, the cause of the decline remains uncertain and new studies are required to determine if the decline is ongoing. I used observation records, museum specimens from 13 independent institutions, and spatial environmental data to measure changes in genetic structure, genetic diversity, and patterns of gene flow of *Bombus occidentalis* from 1960 to 2020. I genotyped over 2,000 specimens collected from across the entire range of *B. occidentalis*, from Alaska to New Mexico using microsatellite ISSR analysis. I compared measures of genetic inbreeding among populations throughout time to determine if populations are becoming more isolated. I used spatial models along with environmental predictor variables including weather, geography, and land use data to estimate landscape resistance among populations. Finally, I used structural equation models to compare genetic distances among populations to resistance distances and estimate the relative influence of the predictor variables on gene flow across the landscape. Analysis of this dataset is ongoing.

## **Chapter 3: Measuring attitudes among stakeholders toward molecular techniques in conservation studies**

Conservation science is an amalgamation of data-driven biological studies and social actions. In order to bridge the gap between data and action, practitioners must overcome two barriers: understanding of the results of studies and motivation to change the current conservation status of the target taxa. Molecular techniques are being used increasingly commonly and to great effect in conservation studies. However, these studies are not intuitively easy to understand for practitioners and stakeholders who are not specifically trained to interpret their results. A lack of detailed understanding of the results of genetic conservation studies may lead to a sense of helplessness that undermines motivation for action in some groups. I surveyed conservationists from government and non-government conservation organizations in the USA and Canada to determine how members learn about conservation issues, how well

they understand molecular methods used in conservation studies, and how scientists can better communicate the results of these studies. Analysis of this dataset is ongoing.

Other Ongoing Research:

**Analysis of population structure of several widespread bumble bee species across their ranges determines current conservation status and potential for future decline**

In collaboration with Dr. James Strange of the Ohio State University, I worked on a team that collected bumble bees from across the western United States and Canada in the summers of 2017 through 2019, visiting historical and previously unsampled sites. Dr. Strange and I will genotype these specimens, measure changes in population structure, and use community genetics methods to measure genetic interactions among species within communities.

**Development of a novel method to detect environmental DNA left on flowers by insect pollinators**

In collaboration with Dr. David Pilliod and Matthew Laramie at the USGS Forest and Rangeland Ecosystem Science Center, as well as a large network of collaborators from multiple federal agencies, I am working to develop methods for collecting insect pollinator DNA from previously visited flowers. We are currently conducting field and controlled garden studies to optimize collection methods and compare detection probabilities using qPCR methods (to detect single target species) and metabarcoding methods (broad taxonomic identification).

Master's Thesis Research:

**Influence of wildfire disturbance and post-fire seeding on vegetation and insects in sagebrush habitats.**

I conducted the first investigation of insect community response to post-fire seeding on public rangelands by comparing the composition of insect communities at burned-and-seeded and burned-and-unseeded sagebrush-steppe ecological sites in southwestern Idaho to unburned areas. I captured and identified 24,862 insects to the level of family (129 families) at three burned areas over two years. Insect communities in burned plots were not similar to those in unburned plots, regardless of treatment. Treated plots had insect communities with greater inter-annual variability in composition, suggesting they may be less stable than communities in unburned or burned-and-unseeded plots. This study was published in the journal *Insect Conservation and Diversity* (see publications below).

Work Experience:

Post-doctoral Researcher: April 2022 to present, 40 hours per week  
New Mexico State University

- Development and execution of original research related to the conservation status of pollinating insects

Student Trainee\*: June 2020 to December 2020, 40 hours per week  
United States Geological Survey

\*Continuation of my PhD dissertation work started in 2017 under the title of Research Assistant at Utah State University

Research Assistant: January 2017 to June 2020, 40 hours per week  
January 2021 to April 2022, 20 hours per week  
Utah State University and USDA-ARS Pollinating Insect Laboratory

- Use of microsatellite markers and UCEs to address hypotheses regarding the conservation status of *Bombus occidentalis*, a bumble bee of conservation concern in the USA and Canada
- Use of specialized softwares including Geneious (microsatellite marker scoring), ArcGIS (mapping), Survey123 (data collection) MaxEnt (Species distribution modeling), R (statistical analyses, particular packages of interest include ResistanceGA, Spagedi, and LAVANT), Phyluce (analysis of UCE datasets), and various softwares used to clean and analyze microsatellite genotype datasets (Colony, HP-Rare, BOTTLENECK, FSTAT, GENEPOP, MaxEnt)
- DNA extraction and benchtop laboratory genetic sample preparation including amplification using PCR
- Organization and preparation of collecting permits, field computers, forms, and gear in 2017 and 2018
- Field collection of bees and vegetation data, summer 2017 and 2018
- Organization of insect samples, including labeling, identification, and databasing into the USDA Pollinating Insect Collection Database
- Procurement of loaned bumble bee specimens from 13 institutions across the United States and Canada for use in genetic analyses
- Preparation and submission of manuscripts for publication in peer-reviewed scientific journals
- Preparation and submission of grant proposals
- Coordinator of the 2017 BOMBUSS conference, sponsored by USDA-ARS (BOMBUSS)

Science Reporter: August 2018 to August 2020, 10 hours per week  
Utah Public Radio

- Interviews of scientists and other subjects for science stories
- Production of two-minute science news segments for radio broadcast
- Production of six-minute feature science news segments for radio broadcast and for original series including Women 20/20, Diagnosed, and Driven to Succeed
- Winner of four first-place awards from 2019 to 2021 from the Society of Professional Journalists in various categories for science-based stories
- All stories can be accessed at [www.upr.org](http://www.upr.org)

Ecologist: May 2014 to December 2017, 40 hours per week

United States Geological Survey

- Design and implementation of protocols for field data collection
- Insect and vegetation sample management and identification
- Direction of biological technicians
- Data Analysis using programs such as R, SAS, PCOrd, and HyperNiche
- Assistance in writing proposals, reports, and peer reviewed papers

Ecological SCEP Student: August 2009 to May 2014, 30 hours per week from Sept. through May, 40 hours per week from May through August  
United States Geological Survey

- Identification of terrestrial and aquatic arthropods
- Technical writing including proposals and study plans
- Vegetation identification and arthropod trapping

Relevant Work Experience Prior To August 2009:

Quality Management Microbiologist: August 2008 to May 2009  
IEH Technologies

Biological Technician: May 2008 to August 2008 and May 2009 to August 2009  
United States Geological Survey

Chemistry Technician: August 2007 to February 2007  
Cephalon Pharmaceuticals, Quality Control Laboratory

Biological (June Sucker) Technician: June 2007 to July 2007  
Utah State Dept. of Natural Resources, Wildlife Resources

ESR Technician/Fuels Reduction Technician: June 2006 to May 2007  
Eastern Nevada Landscape Coalition

Publications:

**Rohde, A.T.**, and Pilliod, D.S. (2021). Spatiotemporal dynamics of insect pollinator communities in sagebrush steppe associated with weather and vegetation. *Global Ecology and Conservation* (accepted, in press).

Graves, T.A., Janousek, W.M., Gaulke, S.M., Nicholas, A.C., Keinath, D.A., Bell, C.M., Cannings, S., Hatfield, R.G., Heron, J.M., Koch, J.B., Loffland, H.L., Richardson, L.L., **Rohde A.T.**, Rykken, J., Strange, J.P., Tronstad, L.M., and Sheffield, C.S. (2020). Western bumble bee: declines in the continental United States and range-wide information gaps. *Ecosphere* 11(6):e03141.

**Rohde, A.T.**, D.S. Pilliod, and Novak, S.J. (2019). Insect communities in big sagebrush habitat are altered by wildfire and post-fire restoration seeding. *Insect Conservation and Diversity* 12:216-230.

Pilliod, D.S., **Rohde, A.T.**, Charnley, S., Davee, R.R., Dunham, J.B., Gosnell, H., Grant, G.E., Hausner, M.B., Huntington, J.L., Nash, C. (2017). Survey of beaver-related restoration practices in rangeland streams of the western USA. *Environmental Management* 61(1):58-68.

Pilliod, D.S., and **Rohde, A.T.** (2016). Insect community responses to climate and weather across elevation gradients in the Sagebrush Steppe, eastern Oregon: U.S. Geological Open-File Report 2016–1083, 50 p., <https://doi.org/10.3133/ofr20161183>.

**Rohde, A.T.** (2014). Influence of wildfire disturbance and post-fire seeding on vegetation and insects in sagebrush habitats (master's thesis). Retrieved from ScholarWorks (accession number 832). <https://scholarworks.boisestate.edu/td/832/>.

#### Grants and Awards:

2020; “Status and Conservation of the Western Bumble Bee, *Bombus occidentalis*” Funding source: U.S. Geological Survey/U.S. Fish and Wildlife Service Science Support Partnership Program

2018; Utah State University Ecology Center Graduate Student Research Award

2013; Northwest Climate Science Center Early Career Scientist Climate Boot Camp Nominee/Attendee

2012; Pilliod, D.P. and Rohde A.T. “Forecasting insect community responses to changes in climate in great basin sagebrush steppe.” Funding source: Oregon State Bureau of Land Management

2010; USGS STAR Award

#### Selected Recent Presentations:

**Rohde, A.T.**, Everett, J., Pilliod, D.S., and Strange, J.P. “Genetic measurements of the conservation status of a North American Bumble bee pollinator in decline, *Bombus occidentalis*” Oregon Chapter of the Wildlife Society, Eugene, Oregon, February 5-7, 2020.

**Rohde, A.T.**, Pilliod, D.S., and Evers, L. “Spatio-temporal dynamics of insect pollinator communities in sagebrush-steppe.” Joint meeting of the Entomological Society of America and the Entomological Society of Canada, Vancouver, BC, November 11-14, 2018.

**Rohde, A.T.**, Knoblett, J., and Strange, J. “Microsatellite marker development in *Osmia lignaria*, a common and ecologically important North American pollinator.” National meeting of the Entomological Society of America, November 5-8, 2017.

**Rohde, A.T.**, Pilliod, D.P., and Halford, A. “Diverse pollinator assemblages use planted forb “island” restoration treatments within burned areas in shrub-steppe habitats.” Pacific Branch Entomological Society of America. Portland, OR, April 2-5, 2017.

**Rohde, A.T.**, Pilliod, D.S., and Halford, A. “Effects of Shrubland Techniques on Insect Pollinators and Communities.” Natural Areas Association. Fort Collins, CO, October 10-12, 2017.

**Rohde, A.T.**, and Strange, J.P. “Microsatellite marker development in *Osmia lignaria*, a common and ecologically important North American bee pollinator.” Entomological Society of America. Fort Collins, CO, November 5-8, 2017.