

Western bumble bee: declines in the continental United States and range-wide information gaps

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Abstract. In recent decades, many bumble bee species have declined due to changes in habitat, climate, and pressures from pathogens, pesticides, and introduced species. The western bumble bee (*Bombus occidentalis*), once common throughout western North America, is a species of concern and will be considered for listing by the U.S. Fish and Wildlife Service (USFWS) under the Endangered Species Act (ESA). We attempt to improve alignment of data collection and research with USFWS needs to consider redundancy, resiliency, and representation in the upcoming species status assessment. We reviewed existing data and literature on *B. occidentalis*, highlighting information gaps and priority topics for research. Priorities include increased knowledge of trends, basic information on several life-history stages, and improved understanding of the relative and interacting effects of stressors on population trends, especially the effects of pathogens, pesticides, climate change, and habitat loss. An understanding of how and where geographic range extent has changed for the two subspecies of *B. occidentalis* is also needed. We outline data that could be easily collected in other research projects that would increase their utility for understanding range-wide trends of bumble bees. We modeled the overall trend in occupancy from 1998 to 2018 of *Bombus occidentalis* within the continental United States using existing data. The probability of local occupancy declined by 93% over 21 yr from 0.81 (95% CRI = 0.43, 0.98) in 1998 to 0.06 (95% CRI = 0.02, 0.16) in 2018. The decline in occupancy varied spatially by landcover and other environmental factors. Detection rates vary in both space and time, but peak detection across the continental United States occurs in mid-July. We found considerable spatial gaps in recent sampling, with limited sampling in many regions, including most of

Alaska, northwestern Canada, and the southwestern United States. We therefore propose a sampling design to address these gaps to best inform the ESA species status assessment through improved assessment of how the spatial distribution of stressors influences occupancy changes. Finally, we request involvement via data sharing, participation in occupancy sampling with repeated visits to distributed survey sites, and complementary research to address priorities outlined in this paper.

Key words: *Bombus*; bumble bee; conservation; Endangered Species Act; hierarchical model; *occidentalis*; occupancy; pollinator; sampling design; SARA; species of concern; western.

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INTRODUCTION

Many bumble bee species have recently declined in North America (Goulson et al. 2008, Cameron et al. 2011, Colla et al. 2012, Arbetman et al. 2017). In Canada and in the contiguous United States, this is particularly true for species within the subgenus *Bombus sensu stricto*. Four of the five North American species in this subgenus have been or are planned for consideration for listing under the U.S. Endangered Species Act (ESA) by the U.S. Fish and Wildlife Service (USFWS). Three of the four species in Canada have been assessed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and are listed or recommended for listing under the federal Species At Risk Act (SARA; Appendix S1).

The distribution and abundance of the western bumble bee (*Bombus occidentalis*, hereafter WBB) rapidly declined in recent decades (Cameron et al. 2011, COSEWIC 2014). WBB was assessed as Vulnerable by the International Union for the Conservation of Nature (IUCN; Hatfield et al. 2015). In Canada, two subspecies were assessed and recommended for listing under SARA: the northern subspecies (*B. o. mckayi*) as Special Concern and the southern subspecies (*B. o. occidentalis*) as Threatened. In the United States, a species status assessment, a best-available-science summary that serves as the foundation for ESA listing decisions in the United States, is planned for WBB late in 2020, targeting a listing decision for 2023.

Previously widespread across western North America (Koch and Strange 2009, Sheffield et al. 2016), *B. occidentalis* was also reared and

distributed for greenhouse pollination services in the 1990s until difficulties sustaining these colonies in the early 2000s made this financially impractical (Flanders et al. 2003). While a wealth of research has identified the fungal gut parasite *Nosema bombi* (Microsporidia) as a likely contributor to declines (Colla et al. 2006, Cordes et al. 2012), native bees experience a long list of stressors that can act synergistically to constrain populations (Goulson et al. 2015, Cameron and Sadd 2019), and causal links between the fungal parasite and bumble bee declines are not definitive (Cameron et al. 2016).

Species status assessments, SSAs, evaluate status through components of viability referred to as representation, resiliency, and redundancy (Smith et al. 2018; Appendix S1). These depend directly on an understanding of the spatial distribution of a species, how numbers and distributions are changing temporally, and the factors influencing those changes. The approaches to evaluating these components of species status can vary widely, depending on the amount and quality of available information, life-history characteristics, and the resources available for research and evaluation. They can include investigations into the taxonomic structure; status and trend of habitat, extents, and shifts in range or distribution; and estimates of demographic factors such as the number of populations, relative abundance, diversity, and connectivity, as well as evaluations of stressors potentially impacting populations of a species (Smith et al. 2018).

Currently, while the administrative process for ESA listing consideration is well developed, no process exists that ensures coordination of

research crucial to a new comprehensive SSA, even though conducting research takes substantial time and resources. Here, we construct a process for aligning research with USFWS needs. Specifically, we first review the existing literature for WBB based on needs for the listing consideration under the ESA. Next, we use an existing presence-based dataset compiled by a large community of bumble bee researchers to describe the current data available to answer status questions. We then address one of the research needs about the status of WBB. Specifically, using an occupancy framework with a subset of appropriate data, we evaluate changes in the probability of occupancy of WBB where sufficient data exist and focus on variables predicting detection, identifying optimal sampling dates. Finally, by developing a sampling design to address spatial information gaps identified as needed in the data review to assist status consideration, we create a framework for a wide range of biologists and citizen scientists to contribute to knowledge about the status of this historically widespread species. We request action from researchers and stakeholders to provide existing data and sample these gaps in the summers of 2020–2021 to contribute to an updated, more comprehensive model that can better evaluate drivers of spatial patterns of population occupancy change.

METHODS

Literature review

Because many life-history traits and stressors are common across bumble bee species, we build on the recent SSAs for rusty patched (*Bombus affinis*), yellowbanded (*Bombus terricola*), and Franklin bumble bees (*Bombus franklini*; Appendix S1). We reviewed the literature using Google Scholar and Web of Science (searched from 14 October 2018 to 16 November 2018), with terms to target WBB (western bumble bee, *Bombus occidentalis*, and *B. occidentalis*). We focused on (1) topics in prior bumble bee SSAs related to life-history traits, population status and trends, and stressors (Appendix S5: Table S1); (2) the historical range-wide abundance, distribution, and threats applicable to WBB; and (3) existing protocols for field data collection. We confined our review to WBB but emphasize that research of stressors on other bumble bees or native bees can often

appropriately be extended to WBB. After compiling the list of topics, we asked bumble bee experts to identify topics that were missing but important to WBB. We categorized the published research found in the literature review in each topic. Bumble bee expert co-authors reviewed the compilation for completeness. Then, 10 bumble bee experts individually ranked how well each topic was understood (1–5) and, within each category, prioritized the topics in order of the need for information. We then discussed the rankings to reach the framing of the priorities reported here. We repeated our literature search in November of 2019 to add newly published papers.

Bumble bee data assessment

To assess WBB data, we used the Bumble Bees of North America (BBNA) database, first assembled in 2014 (Williams et al. 2014) and maintained by Dr. Leif Richardson (<https://www.leifrichardson.org/bbna.html>). The database incorporates specimen- and photo-vouchered bumble bee records spanning more than a century and coming from >100 research, academic, private, and community science collections. The BBNA database (as of 03 May 2019) included over 305,091 records on 49 bumble bee species in Canada and the United States.

We assessed sampling gaps by identifying the distribution of sampling across landcover types, the amount of sampling by jurisdiction (e.g., U.S. state and Canadian province), and by identifying areas more than 200 km from any recent sampling. At that distance, we saw a reduced correlation in the observed presence across sites. To focus on sampling likely to include full bumble bee communities, we excluded known opportunistic citizen science efforts (e.g., iNaturalist.org, bumblebeewatch.org). Targeting the SSA slated to begin in 2020, we classified a sample as recent if it occurred in 2011 or later, which will be 10 yr prior to the SSA (following USFWS 2016). We evaluated historical vs. recent sampling locations. We also evaluated the availability of repeat samples appropriate for an occupancy analysis.

Modeling western bumble bee occupancy

Hierarchical occupancy models separate estimates of the true presence of a species from the

effects of the observation process, most notably species detectability (Royle and Dorazio 2008). We evaluated whether data were sufficient to fit occupancy models, which consider the true presence vs. true absence of an area, as a state that equals one if an area is occupied or zero if not. The occupancy probability can be viewed as the population average of the state variable (Royle and Dorazio 2008). Detection of animals can be influenced by many things, including, for bumble bee species, the number of individuals in an area, as well as their availability to be detected (e.g., present above ground when sampling is occurring). As such, we can use these models to learn how to improve sampling by understanding detection while simultaneously assessing occupancy status of WBB.

Because the availability of explanatory covariate data varies across the United States and Canada, we divided the geographic range of WBB into four regions for analysis (contiguous United States, northern Canada, southern Canada [based on subspecies], and Alaska) and modeled these regions separately. However, regions where the northern subspecies occurs had few sampling and presence records (Appendix S3: Fig. S1) and only basic models for northern/southern Canada and Alaska regions converged in initial analyses. Thus, we report modeling only for the contiguous United States, that is, the southern part of the range for the subspecies *B. o. occidentalis*.

We used a Bayesian hierarchical single-species occupancy model to estimate the occupancy status for *B. o. occidentalis* from 1998 to 2018 across 14 western states in the continental United States (Fig. 1a). We included only unique locations where two or more sampling occasions occurred within a single calendar year. Our analysis encompassed 1551 sites and 4817 sampling occasions (mean = 3.11, SD = 2.98). We reduced count-based survey data to binary presence-absence. Our analysis does not model colonization, and extinction rates of sites because few sites were resampled across multiple years.

We modeled site-specific occupancy as a function of year, elevation, landcover, linear and quadratic terms for latitude and longitude, plus a measure of spatial autocorrelation, measured as the proportion of occupied sites in the surrounding area, to account for the clumped nature of recent sampling and the likelihood

that adjacent sites may be more likely to be occupied.

We modeled detection as a function of landcover, site-specific bloom date, linear and quadratic forms of days since bloom initiation for each survey, and an interaction between site-specific bloom date and days since bloom initiation for each survey. We used the annual site-specific bloom date for each survey location from a model indexing the start of spring based on flowering events across the continental United States (USA National Phenology Network 2018). Sites can have earlier bloom dates due to latitude, elevation, snow, or other regional effects, and early bloom dates typically correlate with longer growing seasons and thus are an index of expected increased colony sizes at lower latitudes and elevations (J. Strange, *unpublished data*) that should increase detectability. Furthermore, because colony size increases and then declines seasonally, for each survey the days after bloom initiation captures another component of detectability (Koch et al. 2012). See Appendix S2 for more details on model formulation and methods.

Sample design: identification of priority sites for future data collection

We used two similar approaches to prioritize sites and maximize information gain from future data collection on WBB. For Alaska and Canada, we considered the more challenging logistics in much of those regions (see Appendix S4 for details and design). Across the western continental United States, we used a spatially explicit weighting approach to randomly select areas of high priority within the historical range of *B. o. occidentalis* (described in Appendix S4). We identified 1000 sampling locations (10 × 10 km grid cells) in areas currently under-sampled, considering landcover, distance from recent sampling, and land ownership. As several bumble bee sampling efforts center around states, we allocated target grid cells across states proportionally to their *B. o. occidentalis* range overlap and by landcover class. We prioritized spatial gaps in previous sampling efforts based on distances between recently sampled and unsampled grid cells by scaling the raw distances to weights between 0 and 1. As distance increased, grid cells received higher weight, with those farther than

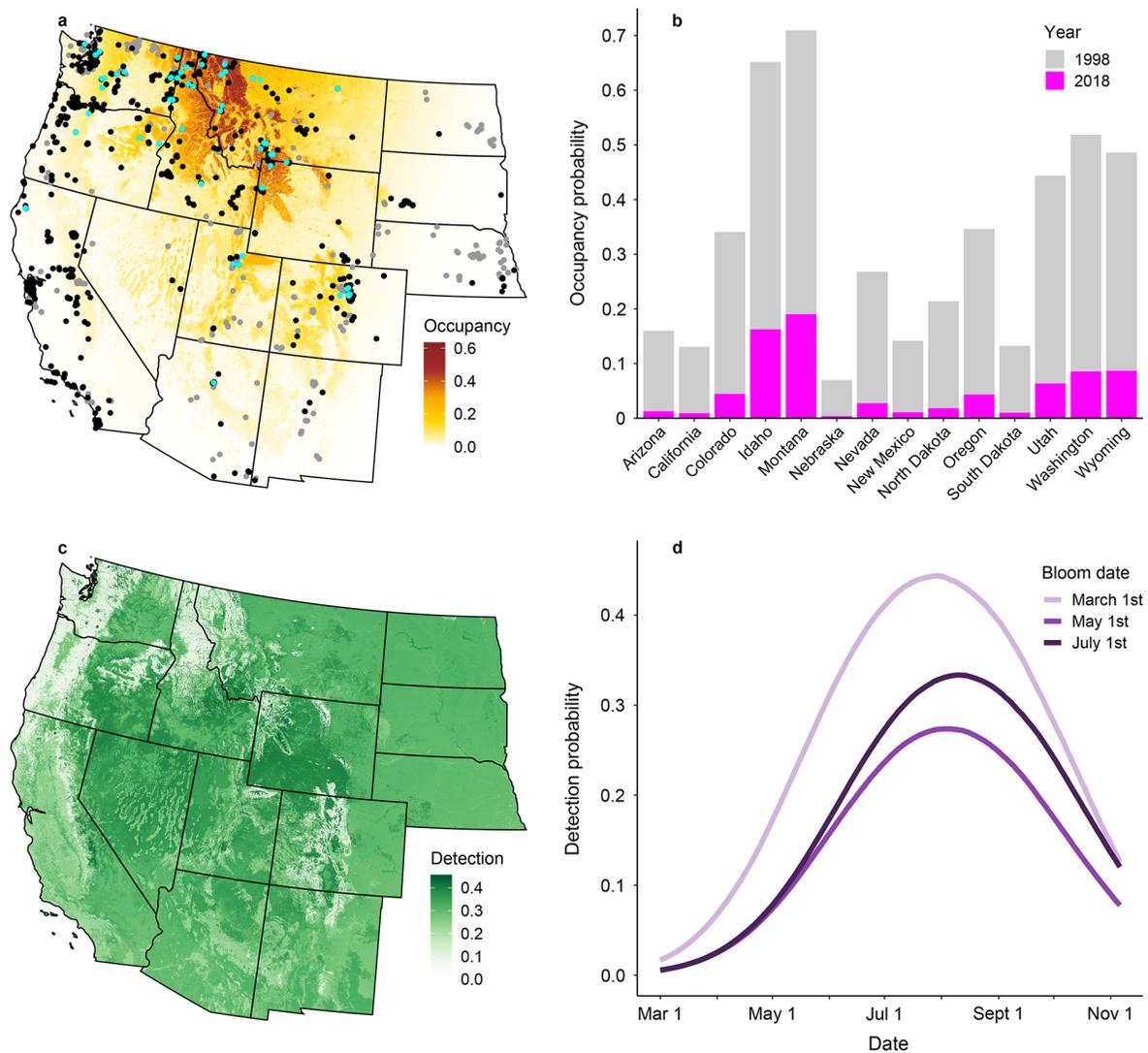


Fig. 1. Maps showing the predicted occupancy (a) and detection rates (c) for *B. o. occidentalis* across the western United States. (a) Points represent locations for surveys used in the occupancy model for *B. o. occidentalis*. Historical surveys occurring prior to 2011 are shown in gray; recent surveys (2011–2018) are shown in black (*B. o. occidentalis* not detected) and in cyan (*B. o. occidentalis* detected). (b) Change in mean occupancy for *B. o. occidentalis* 1998–2018 across 14 U.S. states. Each state's value is the mean occupancy from the predicted 1-km resolution raster model output (see 1a) for the year, which incorporates the effects of elevation, latitude, longitude, and landcover. (c) Detection rates for date of local bloom initiation. (d) Mean predicted detection probability for *B. o. occidentalis* plotted as a function of calendar date. Each line represents a different initial bloom date from March to July (light to dark). Mean detection is calculated across landcover categories.

200 km assigned the maximum weight of 1. Because of the challenges of gaining permission to access private lands, we assigned cells with majority private lands a 0, thus selecting only cells most readily accessible to the broadest

group of data collection partners. For example, Idaho encompasses 6.7% of the historical range in the United States and thus received 67 of the 1000 cells across the western United States. As 30% of *B. o. occidentalis* range in Idaho is

shrubland, we selected 20 cells (30% of 67) of those that are primarily non-private shrubland, with probability based on their distance weights.

RESULTS

Research priorities

Out of 156 papers reviewed, 115 studied WBB. Twenty-seven articles focused on WBB specifically whereas the remaining papers studied WBB and other *Bombus* species more generally or other ecological processes (e.g., nectar robbing) in which WBB played a role. Bumble bee experts identified eight additional papers. We evaluated eight survey protocols found in our search. Across nearly all topics, the average assessment of our understanding of topics was between somewhat understood and poorly understood. The co-authors varied in their knowledge about subtopics, and we thus identified the top research priorities without ranking them within a category.

For the status category, while at least some research on WBB (*B. o. occidentalis* + *B. o. mckayi*) exists on several topics addressed in prior bumble bee species status assessments (e.g., COSEWIC 2014, USFWS 2016), we found that important questions remain around trends in the number of populations, abundance at local scales, range, and occupancy. Generally speaking, our review suggested substantial gaps in knowledge regarding what drives observed population changes and the extent to which those changes translate into large-scale patterns across varied landscapes (Appendix S5). We also found no research addressing the species' distribution relative to catastrophic threats to populations, a topic assessed in most SSAs.

In the life-history category, we found no research for several stages, namely, brood initiation, late summer needs, home range size, or dispersal needs or patterns (Appendix S5). We know very little about the overwintering stage of the life cycle and the specific needs during that time. Previous commercial rearing and limited rearing in research laboratories have resulted in slightly more knowledge about WBB than many other bumble bee species and other native bees. However, inference from laboratory studies does not necessarily extend to wild bee populations, so we urge caution in applying this information

appropriately. We also found no research on the minimum viable population size.

To understand what is driving apparent WBB population declines, we must understand stressors to those populations. Research shows that pathogens, pesticides, habitat loss and degradation, climate change, livestock grazing, competition from non-native bees, and synergistic effects of these stressors can affect WBB or closely related bees (Appendix S5). However, the effect size of these stressors relative to each other is poorly quantified. We identified pathogens, pesticides, climate change, and habitat loss to be priority research needs, because we believe them to be of greatest concern for this species (Appendix S5). Pathogens and their interaction with other stressors are of particular interest because the timing of declines coincides with the outbreak of *N. bombi* in rearing facilities (Flanders et al. 2003) and high prevalence in declining wild populations (Cordes et al. 2012, Koch and Strange 2012, Cameron et al. 2016). Furthermore, relative to other non-declining wild bumble bees, WBB has significantly higher *N. bombi* prevalence in both the contiguous United States and Alaska (Cameron et al. 2011, Koch and Strange 2012). However, diverse pathogens and parasites are associated with bumble bees, including WBB, and warrant continued investigation (Cordes et al. 2012, Mullins et al. 2019). We also identified drought and fire suppression as specific mechanisms likely contributing to habitat loss and degradation for WBB through their effects on the availability of flowering plants and the connectivity of habitat, and suggest that they be specifically addressed in status assessments (Loffland et al. 2017).

The large scale of the species' distribution suggests that addressing any of these stressors will be costly and impact large numbers of people. A better understanding of the relative contribution of each stressor to overall population changes will help prioritize conservation action and focus limited efforts on the issues of greatest need. This, combined with a good understanding of the mechanistic underpinning of each stressor, will help inform the development of optimal ways to minimize, mitigate, or address these stressors (Appendix S5).

Across the topics considered, the knowledge is limited and raises many new questions. For

example, recent research on the taxonomy and systematics of WBB concludes that the WBB species group comprises 2 monophyletic lineages: *B. o. occidentalis* and *B. o. mckayi* (Sheffield et al. 2016). However, future research should determine whether the 2 lineages are subspecies, or should be elevated to species. Increased sample sizes have led to re-classification of other bumble bee subspecies to species (Williams et al. 2019, Ghisbain et al. 2020), and each WBB subspecies has a distinct cytochrome oxidase I genotype in the Barcode of Life Data System (Ratnasingham and Hebert 2007). Assessment of the genetic distinctness of these two subspecies, and whether they represent separate species would clearly have an impact on how the USFWS addresses potential listing under the Endangered Species Act. Furthermore, increased precision of the distribution of the two species, including the location of the boundary between them, which is currently coarsely defined, could be useful (Williams et al. 2014, Sheffield et al. 2016).

While existing sample designs, which include the spatial distribution of samples, vary widely depending on project objectives, the underlying protocols for surveying bumble bees are well developed. Most projects either hand-net bumble bees in a specified unit of area for timed intervals or deploy a number of blue vane traps for a timed interval (Appendix S5). However, not all projects consistently record the size of area surveyed or temporal duration of survey and some target a specific number of bees vs. a timed interval (e.g., 100 bees; Strange and Tripodi 2019).

Overview of existing sampling

As population declines of WBB in North America were observed, culminating in the current effort by agencies in the United States and Canada to consider the species for protection, land managers, and others began efforts to collect pertinent occurrence information. Data collection did not always occur with coordinated protocols or sample design across agencies or jurisdictions, limiting how the entirety of data can be used at a range-wide scale. Past sampling includes some targeted to specific research questions, agency-specific needs, community science efforts, and baseline data collection or monitoring efforts at up to a tri-state scale (Pacific Northwest Bumble Bee Atlas, www.pnwbumblebee

tlas.org). As a result, data collection varied spatially, with concentrations near larger urban centers and the locations of a few long-term studies (Fig. 1a; Appendix S3: Fig. S1). Many U.S. states and Canadian provinces within the range of the WBB (i.e., ND, NV, NE, NM, AZ, AK, BC, NT, SA) also had limited sampling recently (2011–present), especially in remote and inaccessible regions (i.e., AK, NV, NT, Table 1; Appendix S3: Fig. S1). Repeat sampling of sites that enables modeling detectability is moderately rare (Fig. 1a), and a well-developed framework for recording sampling effort (e.g., area and time of surveys, number of observers or traps) is needed and would improve the options for range-wide population analyses.

B. o. occidentalis occupancy modeling results

In the western continental United States, the predicted mean occupancy of *B. o. occidentalis* declined by 0.75 over 21 yr from 0.81 (95% CRI = 0.43, 0.98) in 1998 to 0.06 (95% CRI = 0.02, 0.16) in 2018, a 93% reduction. This prediction for mean occupancy is across landcover categories at mean elevation, latitude, and longitude. The effect of landcover on occupancy was variable (Fig. 2a), with open- and closed-canopy forests tending to have highest occupancy compared to other landcover types such as shrubland and grassland, which had the lowest occupancy (Fig. 2a; Appendix S2: Table S1). For example, mean occupancy in closed-canopy forests (0.34, 95% CRI = 0.11, 0.70) was nearly six times higher than in shrubland (0.06, 95% CRI = 0.02, 0.20). State-level changes in occupancy, that incorporate the specific landcover and physical features within each state, also suggest larger declines in some states than others, even though interactions of landcover and other covariates were not explicitly modeled (Fig. 1b).

Detection rates varied substantially across space and time (Fig. 1c, d). Mean detection probability across all observations was 0.26 (95% CRI = 0.13, 0.45). The landcover type influenced detection rates at sites (Fig. 2b). Dense vegetation classes such as closed-canopy forest had lower detectability relative to open environments such as sparsely vegetated areas, grasslands, and shrublands (Fig. 2b; Appendix S2: Table S1). For example, probability of detection was four times larger in shrubland (0.36, 95% CRI = 0.13, 0.68)

Table 1. Breakdown of the percent and number of 10 × 10 km grid cells within the historical range of *Bombus occidentalis* which have been sampled recently (2011–2018) or across the period examined (1965–2018). Also shown are the percent and number of grid cells 200 km or greater away from the nearest recently sampled grid cell.

Province/State	Sampled 2011–2018		Sampled 1965–2018		Unsampled†		Total grid cells
	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	
Canada							
Yukon	3.0	146	7.8	378	0.5	24	4841
Alberta	2.6	125	9.0	437	0.2	9	4872
Saskatchewan	1.2	41	5.2	177	2.7	91	3397
British Columbia	1.1	106	6.5	597	6.3	582	9249
Northwest Territories	0.6	20	1.7	55	23.3	771	3299
United States							
Washington	5.9	103	31.8	554	0.0	0	1742
Montana	5.0	190	18.8	714	0.0	0	3802
California	3.0	116	41.0	1587	0.6	25	3870
Idaho	2.8	60	24.1	520	0.0	0	2161
Oregon	2.6	66	25.7	645	0.0	0	2512
South Dakota	2.1	26	12.1	150	5.7	71	1241
Colorado	1.5	41	24.2	654	0.0	0	2702
Wyoming	0.9	23	10.6	271	0.0	0	2545
Utah	0.6	14	22.6	497	0.0	0	2199
Alaska	0.5	69	3.4	437	26.5	3426	12905
Arizona	0.5	10	9.1	191	7.9	167	2103
New Mexico	0.3	6	9.1	189	5.7	117	2035
Nebraska	0.2	5	3.4	98	0.6	17	2865
Nevada	0.2	2	13.6	175	27.4	354	1290
North Dakota	0.1	1	3.5	31	0.3	3	878

† Unsampled refers to ≥200 km from nearest recent sample.

than in closed-canopy forest (0.09, 95% CRI = 0.04, 0.17). Perhaps most noteworthy, we successfully modeled seasonal life-history changes, reflecting the spatial patterns of known changes in availability and abundance that affect detection, through modeling the interaction between the bloom date and days post-bloom (Fig. 1d; Appendix S2: Table S1).

DISCUSSION

We document a continued and large decline (93%) in the probability of occupancy of *B. o. occidentalis* across the western United States in the last 21 yr, underscoring that this subspecies warrants conservation efforts. An accurate assessment of species viability requires placing trend estimates for individual populations, as well as evaluations of the associated drivers, in a broader analytical framework that allows us to characterize the patterns and drivers of range-

wide population change for both *B. o. occidentalis* and *B. o. mckayi*. Specifically, viability assessment will require a better understanding of the relative contribution of stressors in driving regional population trends, and the effective application of conservation action to mitigate impacts will require a mechanistic understanding of how the most important stressors are operating. While substantial opportunistic and some regional sampling exists, range-wide data are unevenly distributed, with severely low levels in Alaska, Nevada, North Dakota, and northwest Canada and very low levels in Nebraska, New Mexico, Arizona, and Utah (Table 1; Fig. 1a; Appendix S3: Fig. S1). A more even distribution of sampling will permit an improved assessment of the spatial drivers of changes in occupancy in the western continental United States. Opportunistic sampling or single-visit study designs provide presence at one point in time which is useful for validation and answering some

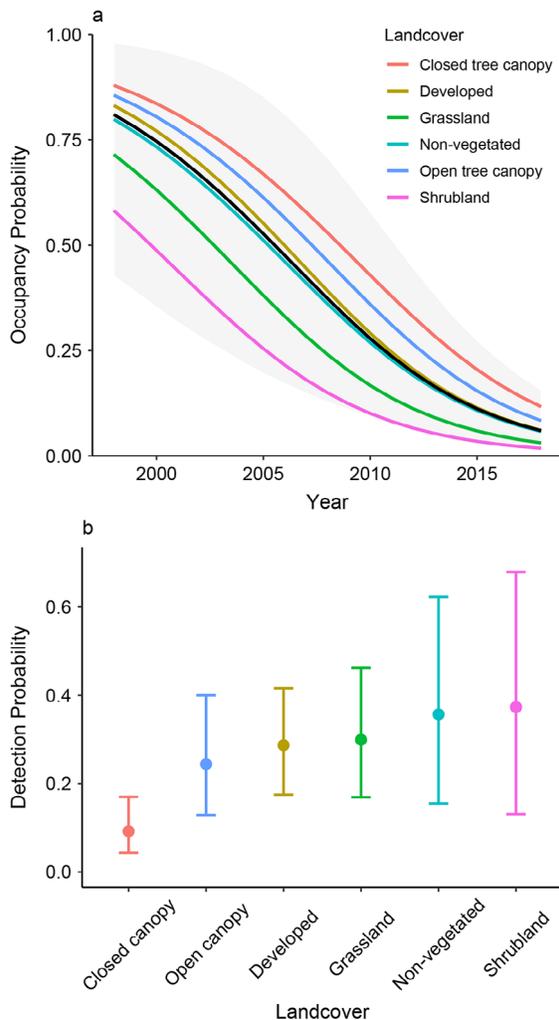


Fig. 2. (a) Occupancy probability for *Bombus occidentalis* plotted over time as a function of six landcover categories. The black line and shaded region represent the mean occupancy probability and 95% credible interval region across all landcover categories. Additional colored lines represent changes in mean occupancy by landcover. (b) Detection probability for *B. occidentalis* across six landcover categories. These predictions are made holding all other explanatory values at their mean. Error bars represent the 95% credible intervals.

questions. However, these data alone are not suitable for use in modeling current WBB occupancy status or causes of change in occupancy because modeling detectability requires repeat visits.

Our results highlight a strong influence of the timing of surveys on detection rates and suggest guidelines for optimum detection of *B. occidentalis* (Fig. 1d). A major goal of sampling any wildlife population is to maximize the efficiency of sampling, thereby reducing cost and increasing information gain (Reynolds et al. 2011). Our analyses show detection rates vary spatially by landcover and seasonally (Fig. 1c; Appendix S2: Table S1) and are directly tied to availability and bee abundance.

Overall, peak detection rate occurs mid-July across the contiguous United States, but maximum detection rates occur where spring begins sooner and seasons are longer overall (e.g., lower elevations and latitudes, Fig. 1c), likely because colonies have enough floral resources to reach larger sizes. In contrast, where blooms begin later, the highest detection rate (and likely peak colony size) will be only a short time after bloom onset (Fig. 1d). Characterizing these patterns can allow biologists to maximize their detection probability of *B.o. occidentalis* in the field, considering logistical constraints such as an inability to reach high elevation sites in spring. Furthermore, researchers should plan for more repeated visits to sites when sampling occurs in areas with denser vegetation (e.g., closed-canopy forests). Also, if managers need confidence in the presence or absence of WBB, the model can be used to identify the timing and number of sampling bouts to approach a cumulative detection probability near 1 (Fig. 1d). For example, the number of visits (n) required to determine with high confidence the absence of WBB from a site can be calculated using this formula adapted from Wintle et al. (2005):

$$n = \frac{\log\left(\frac{\psi}{1-\psi}\right) - \log\left(\frac{\psi'}{1-\psi'}\right)}{\log(1-p)}$$

Here, p is the expected detection probability of the species at the site, ψ represents the prior belief of the occupancy status of the species at the site, and ψ' is the desired confidence of the accuracy of the estimate. Therefore, if detection probability in mid-July is 0.25 and prior estimates or other knowledge of occupancy at the site is 0.50, 10 visits would be required to reach 95% confidence of absence. The number of required visits will change as a function of all

three variables listed. As prior belief of occupancy or detection increases, the number of required visits declines. For example, under the same conditions above but with a detection rate of 0.50, the number of required visits to reach 95% confidence decreases to four. Collectively our results underscore substantial previous research supporting the importance of conducting sampling in a manner that supports modeling of detection probabilities, that is, repeat sampling of sites within a season and collection of auxiliary information like effort (MacKenzie et al. 2002, Royle and Dorazio 2008, Guillera-Aroita et al. 2014).

IMPLICATIONS AND A CALL TO COLLABORATION

We developed two questions key for development of a WBB status assessment. First, what are the occupancy and trends in occupancy for *B. o. occidentalis* and *B. o. mckayi* and how have those trends been influenced by stressors? Second, how and where has geographic range extent changed for the respective subspecies? To assess the viability of the species as a whole, local and regional trend estimates and the associated drivers of the trend are needed.

Here, we propose a sampling design, using standard protocols, to answer these questions explicitly by filling in spatial gaps in sampling with repeated surveys of sites within a year. This will enable us to estimate spatially explicit population trends based on interactions of covariates like elevation and stressors that can be mapped, such as patterns in pesticide use, precipitation, and temperature. While fine-scale areas without historical sampling cannot be directly assessed, enough historical data exist that under this design, new analyses should be able to evaluate the two questions above, to learn for example, whether *B. o. occidentalis* is declining in arid regions while increasing in wet, high elevation areas. Additional sampling and the auxiliary covariate data are needed to successfully model these kinds of interaction effects and better document occupancy and other status indicators in much of Alaska and Canada.

The data collection framework we propose includes recording information on the presence and abundance of the species along with

auxiliary data that will expand the options for use of the data. Repeat sampling and recording data on factors affecting detection such as area and time of surveys, and the number of observers is key to modeling detection. By tracking sampling where no bumble bees of any species were detected, which was not possible for this analysis with the existing database, we can account for potential bias in overestimated detection and thus slightly underestimated occupancy rates. Recording habitat information (e.g., potential pesticide applications, nesting habitat information), pathogen sampling, and genetic sampling can provide useful information to connect stressors to declines. We further suggest that bumble bee researchers focused on other questions also collect the same suite of data, even at sites that may differ from those identified in our sampling design and particularly at long-term study areas because these data could serve important roles for understanding range-wide variability and monitoring (Andelt et al. 2009).

In the long term, development of a US-wide or tri-national (Canada, United States, Mexico) bumble bee sampling framework, analogous to the monarch butterfly monitoring network (Cariveau et al. 2019), which includes a nested spatial design could meet both local management needs and allow incorporation of those data in range-wide assessments (Irvine et al. 2018). Such a cohesive database that adds survey effort information (i.e., method of sampling, area sampled, time sampled) and other data discussed above could greatly improve the options for analyses in the future and would be straightforward based on protocol similarity. While long-term monitoring and coordination will have substantial costs, it would result in the best possible dataset for decision making.

In the short term, the spatially distributed sampling design we suggest here is a step toward providing data that will improve the assessment of redundancy, resiliency, and representation for bumble bees, by informing a landscape scale assessment of stressors that drive changes in occupancy, and contributing to development of a current baseline that could be used to refine trend calculations and

inform future analyses. We used only publicly available records and coauthor data collated in the BBNA, but we are certain that more information exists. For example, some agencies conduct pollinator surveys that are only accessible to their offices. If you have any additional sampling data that could inform future versions of this research, especially in high priority areas, please contact the USFWS at westernbb@fws.gov. At this time, we welcome and invite participation in planned western bumble bee occupancy surveys for 2020 and 2021. Please see www.usgs.gov/westernbb for details. More research focusing on the uncertainties around the stressors likely to have the largest effects (pathogens, pesticides, climate, and habitat loss), evaluating the success of various conservation efforts (e.g., Cole et al. 2019), and assessing the locations and appropriate taxa level of the two subspecies is urgently needed. In addition, community science data collection efforts such as Bumble bee watch and iNaturalist can be used in model validation and for learning locations of remnant populations.

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LITERATURE CITED

- Andelt, W. F., G. C. White, P. M. Schnurr, and K. W. Navo. 2009. Occupancy of random plots by white-tailed and gunnison's prairie dogs. *Journal of Wildlife Management* 73:35–44.
- Arbetman, M. P., G. Gleiser, C. L. Morales, P. Williams, and M. A. Aizen. 2017. Global decline of bumblebees is phylogenetically structured and inversely related to species range size and pathogen incidence. *Proceedings of the Royal Society B: Biological Sciences* 284:20170204.
- Cameron, S. A., H. C. Lim, J. D. Lozier, M. A. Duennes, and R. Thorp. 2016. Test of the invasive pathogen hypothesis of bumble bee decline in North America. *Proceedings of the National Academy of Sciences of the United States of America* 113:4386.
- Cameron, S. A., J. D. Lozier, J. P. Strange, J. B. Koch, N. Cordes, L. F. Solter, and T. L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences of the United States of America* 108:662–667.
- Cameron, S. A., and B. M. Sadd. 2019. Global trends in bumble bee health. *Annual Review of Entomology* 65:209–232.
- Cariveau, A. B., et al. 2019. The integrated monarch monitoring program: from design to implementation. *Frontiers in Ecology and Evolution* 7:167.
- Cole, J. S., R. B. Siegel, H. L. Loffland, M. W. Tingley, E. A. Elsey, and M. Johnson. 2019. Explaining the birds and the bees: deriving habitat restoration targets from multi-species occupancy models. *Ecosphere* 10:e02718.
- Colla, S. R., F. Gadallah, L. Richardson, D. Wagner, and L. Gall. 2012. Assessing declines of North American bumble bees (*Bombus* spp.) using museum specimens. *Biodiversity and Conservation* 21:3585–3595.
- Colla, S. R., M. C. Otterstatter, R. J. Gegear, and J. D. Thomson. 2006. Plight of the bumble bee: pathogen spillover from commercial to wild populations. *Biological Conservation* 129:461–467.
- Cordes, N., W. F. Huang, J. P. Strange, S. A. Cameron, T. L. Griswold, J. D. Lozier, and L. F. Solter. 2012. Interspecific geographic distribution and variation of the pathogens *Nosema bombi* and *Crithidia* species in United States bumble bee populations. *Journal of Invertebrate Pathology* 109:209–216.
- COSEWIC. 2014. COSEWIC assessment and status report on the Western Bumble Bee *Bombus occidentalis*, *occidentalis* subspecies (*Bombus occidentalis occidentalis*) and the *mckayi* subspecies (*Bombus occidentalis mckayi*) in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Canada. www.registrelep-sararegistry.gc.ca/default_e.cfm
- Flanders, R. V., W. F. Whelung, and C. Al. 2003. For nonnative crops, whence pollinators of the future? Pages 99–111 in K. Strickier and J. H. Cane, editors. *Laws and Regulations on the import, movement and release of bees in the United States*. Thomas Say Publications in Entomology, Lanham, Maryland, USA.
- Ghisbain, G., J. D. Lozier, S. R. Rahman, B. D. Ezray, L. Tian, J. M. Ulmer, S. D. Heraghty, J. P. Strange, P. Rasmont, and H. M. Hines. 2020. Substantial

- genetic divergence and lack of recent gene flow support cryptic speciation in a colour polymorphic bumble bee (*Bombus bifarius*) species complex. *Systematic Entomology*. <https://doi.org/10.1111/syen.12419>
- Goulson, D., G. C. Lye, and B. Darvill. 2008. Decline and conservation of bumble bees. *Annual Review of Entomology* 53:191–208.
- Goulson, D., E. Nicholls, C. Botías, and E. L. Rotheray. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* 347:1255–1257.
- Guillera-Arroita, G., J. J. Lahoz-Monfort, D. I. MacKenzie, B. A. Wintle, and M. A. McCarthy. 2014. Ignoring imperfect detection in biological surveys is dangerous: a response to ‘fitting and interpreting occupancy models’. *PLOS ONE* 9: e99571.
- Hatfield, R., S. Jepsen, R. Thorp, L. Richardson, S. Colla, and S. Foltz Jordan. 2015. *Bombus occidentalis*. The IUCN Red List of Threatened Species 2015. <http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T44937492A46440201>
- Irvine, K. M., T. J. Rodhouse, W. J. Wright, and A. R. Olsen. 2018. Occupancy modeling species-environment relationships with non-ignorable survey designs. *Ecological Applications* 28:1616–1625.
- Koch, J. B., and J. P. Strange. 2009. Constructing a species database and historic range maps for North American Bumblebees (*Bombus sensu stricto* Latreille) to inform conservation decisions. *Uludag Bee Journal* 3:97–108.
- Koch, J. B., and J. P. Strange. 2012. The status of *Bombus occidentalis* and *B. moderatus* in Alaska with special focus on *Nosema bombi* incidence. *Northwest Science* 86:212–220.
- Koch, J., J. P. Strange, and P. Williams. 2012. Bumble bees of the western United States. Publication No. FS-972. USDA Forest Service Research Notes, San Francisco, California, USA.
- Loffland, H. L. J. S., M. W. Polasik, E. A. Tingley, C. Eley, G. Loffland, and R. B. S. Lebuhn. 2017. Bumble bee use of post-fire chaparral in the Central Sierra Nevada. *Journal of Wildlife Management*. <https://doi.org/10.1002/jwmg.21280>
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2245.
- Mullins, J. L., J. P. Strange, and A. D. Tripodi. 2019. Why Are Queens Broodless? Failed Nest Initiation Not Linked to Parasites, Mating Status, or Ovary Development in Two Bumble Bee Species of *Pyrobombus* (Hymenoptera: Apidae: *Bombus*). *Journal of Economic Entomology*. <https://doi.org/10.1093/jee/toz330>
- Ratnasingham, S., and P. D. N. Hebert. 2007. BOLD: the barcode of life data system (<http://www.barcodinglife.org>). *Molecular Ecology Notes* 7:355–364.
- Reynolds, J. H., W. L. Thompson, and B. Russell. 2011. Planning for success: identifying effective and efficient survey designs for monitoring. *Biological Conservation* 144:1278–1284.
- Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Academic Press, San Diego, California, USA.
- Sheffield, C. S., L. Richardson, S. Cannings, H. Ngo, J. Heron, and P. H. Williams. 2016. Biogeography and designatable units of *Bombus occidentalis* Greene and *B. terricola* Kirby (Hymenoptera: Apidae) with implications for conservation status assessments. *Journal of Insect Conservation* 20:189–199.
- Smith, D. R., N. L. Allan, C. P. McGowan, J. A. Szyman-ski, S. R. Oetker, and H. M. Bell. 2018. Development of a species status assessment process for decisions under the U.S. Endangered Species Act. *Journal of Fish and Wildlife Management* 9:302–320.
- Strange, J. P., and A. D. Tripodi. 2019. Characterizing bumble bee (*Bombus*) communities in the United States and assessing a conservation monitoring method. *Ecology and Evolution* 9:1061–1069.
- U.S. Fish and Wildlife Service. 2016. Rusty patched bumble bee (*Bombus affinis*) Species Status Assessment. Version 1.0 June 2016. <https://www.fws.gov/midwest/Endangered/insects/rpbb/pdf/SSAReportRPBBwAdd.pdf>
- USA National Phenology Network. 2018. Spring Indices, First Bloom - Spring Index 1998-2018. Region: North America. https://www.usanpn.org/data/spring_indices
- Williams, P. H., et al. 2019. The arctic and alpine bumblebees of the subgenus *Alpinobombus* revised from integrative assessment of species’ gene coalescents and morphology (Hymenoptera, Apidae, *Bombus*). *Zootaxa* 4625:1–68.
- Williams, P. H., R. W. Thorp, L. L. Richardson, and S. R. Colla. 2014. Bumble bees of North America: an identification guide. Volume 87. Princeton University Press, Princeton, New Jersey, USA.
- Wintle, B. A., R. P. Kavanagh, M. A. McCarthy, M. A. Burgman. 2005. Estimating and dealing with detectability in occupancy surveys for forest owls and arboreal marsupials. *Journal of Wildlife Management* 69:905–917.

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Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3141/full>