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APPLYING RESOURCE SELECTION PROBABILITY FUNCTION (RSPF) TO UNDERSTAND FLORAL RESOURCE USE BY A COMMON BUMBLE BEE, *BOMBUS VANCOUVERENSIS*

By

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ABSTRACT

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Applying resource selection probability function (RSPF) to understand floral resource use by a common bumble bee, *Bombus vancouverensis*

Chairperson: Diana Six

Bumble bees (Hymenoptera: *Bombus*) are important pollinators in temperate ecosystems worldwide with seasonal caste variations involving queens, workers, and drones. Like all organisms, they must meet their nutrient requirements for successful growth and development by using several floral resources over time. When resource use is in greater proportion to its abundance on a landscape, that use is considered selective. To examine resource use within the context of abundance, a resource selection probability function (RSPF) was applied to examine floral resource use through a flowering season by a common bumble bee, *Bombus vancouverensis*. The RSPF framework was used to examine 1) resources used to meet nutritional requirements, 2) resources used by each caste, and 3) resources used during periods of high diversity. From June 3-August 10, 2022, floral resource abundance and phenology, and resource use by *B. vancouverensis* was collected at two sites in Western Montana, USA. Seven generalized linear models (GLM) were fit to examine early season (ES) and late season (LS) foraging. *B. vancouverensis* demonstrated selective use of two species during ES, and four species during LS. Selective use of these species may be the due to the superior or complementary nutrient profiles compared to other available resources. The use of RSPF in this study provides insights into resource use by *B. vancouverensis* and can be applied to other native pollinators and bumble bee ecology more generally. As land use alters floral resource availability and diversity and climate change and invasives alter plant community composition, understanding resource use may be crucial to bumble bee conservation.

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Chapter 1

1 INTRODUCTION

1.1 BACKGROUND

Bumble bees (Hymenoptera: *Bombus*) are social insects that are common in temperate regions worldwide and play a key role in many ecosystems (Goulson, 2009; Williams et al., 2014). Declines in bumble bee populations globally have been attributed to many factors including loss of foraging habitat or declines in plant diversity resulting in nutritional stress (Cameron et al., 2010; Goulson et al., 2015; Williams & Osborne, 2009; Woodard & Jha, 2017). Bumble bees rely primarily on pollen to meet their nutritional requirements (Vaudo et al., 2016). However, there are few data on the nutrient composition of pollen, especially in wild plants. Likewise, there is little information on whether bumble bees selectively forage to meet their nutritional demands. Detailed knowledge of bumble bee foraging strategies may give insight into bumble bee nutritional ecology and inform their conservation at a time when many populations are declining at alarming rates (Filipiak, 2019; Jochner et al., 2013; Moerman et al., 2017; Somme et al., 2015; Vaudo et al., 2016; Woodard et al., 2020).

Our current understanding of bumble bee nutritional requirements comes from studies focused on a small number of species and primarily on organic compounds. More complete information on foraging behavior and pollen quality can provide broad insight into how bumble bees meet nutrient requirements. For example, *Bombus impatiens* workers foraged on synthesized pollen with higher protein:lipid ratios (Vaudo et al., 2016) or compensated for lower quality pollen by consuming a larger amount (Tasei &

Aupinel, 2008). In solutions containing varying concentrations of carbohydrates, essential amino acids, and proteins, workers of *B. terrestris* showed a preference for carbohydrates when essential amino acids were abundant and proteins when carbohydrates were abundant (Stabler et al., 2015). Optimal nutrient intake supported increased immune functioning (Ruedenauer et al., 2015; Vaudo et al., 2015), higher rates of development and larger larvae (Moerman, Vanderplanck, et al., 2016; Vanderplanck et al., 2014; Vaudo et al., 2015), and greater adult survival (Somme et al., 2015; Watrous et al., 2019; Woodard et al., 2020). The results of these studies suggest it is advantageous to the individual and the hive to select and adjust pollen collections from different plants over time to meet their nutritional needs.

Research on preferences for various nutrients is often done in controlled laboratory settings with species acclimated to cultivation and trained to forage on synthesized solutions. These experiments can reveal much about individual needs within controlled conditions but may not predict bee behavior in natural systems. Furthermore, many experiments use manipulated hive structures with microcolonies of isolated workers or queens. The use of artificial systems limits the influence of colony-level nutrient requirements that can be directly influenced by the needs of growing larvae, timing of caste emergence, and seasonal shifts in floral availability. Research using wild populations can provide insights into how bumble bees manage spatial and temporal shifts in availability of various floral resources of differing nutrient quality.

As with most consumers, bumble bee foraging should be driven by their nutrient requirements (Filipiak, 2019). The bees must have access to either a single source of high-quality pollen, or a diverse supply of nutritionally variable but complementary pollen sources to meet their needs (Vaudo et al., 2015). Foraging on a diverse assortment of floral resources can have numerous benefits. Polyfloral diets allow bees to balance amino and fatty acid intake (Harmon-Threatt & Kremen, 2015; Vaudo et al., 2015), decrease the build-up of defensive secondary compounds produced by some plants (e.g., *Lupinus*, *Asteroideae*) (Muller & Kuhlman, 2008; Vaudo et al., 2015), and increase resistance to pathogens (Alaux et al., 2010; Pasquale et al., 2013). On the other hand, limited access to adequate resources decreases survival rates (Vaudo et al., 2015, 2016).

Nutritional demands must be met through available flowering resources, whose pollen has variable elemental composition among plant taxa (Filipiak et al., 2017; Filipiak & Filipiak, 2020). Thus, reduced floral diversity due to land use change and climate change may contribute to bumble bee population declines if nutritional demands can no longer be met (Carvell et al., 2006; Goulson et al., 2015; Naug, 2009; Potts et al., 2010; Vaudo et al., 2015). For example, mass-flowering monoculture crops result in decreased diversity and abundance of flowering species which can lead to lower pollinator density and abundance (Carvell et al., 2006; Filipiak, 2018; Holzschuh et al., 2016; Potts et al., 2010). Monoculture crops that are rich in pollen and nectar can provide an abundant source of floral resources, however, since they are only present for short periods, they may not provide nutrients for a long enough period as well as not providing the full spectrum of required nutrients (Filipiak, 2018; Goulson et al., 2015; Vaudo et al., 2015). Indeed, recent evidence suggests monofloral diets result in lower colony success due to nutritional stress (Moerman et al., 2017a). In contrast, a diversity of floral resources with staggered and prolonged flowering across the landscape positively influences pollinator density and fitness (Filipiak et al., 2017) as a diversity of flower species allows self-selection of pollen and sustained nutrient intake for the duration of the bees’ life cycles (Harmon-Threatt & Kremen, 2015; Vaudo et al., 2015).

1.2 BUMBLE BEES

Bumble bees are social insects with seasonal caste variations involving post-hibernation adult queens (gynes) at the beginning of the foraging season, workers mid- and late-season, and drones (males) and new queens at the end of the foraging season. Each caste performs different activities and is unique physiologically and so we can expect different nutrient requirements for each. Furthermore, larvae have nutritional needs that likely vary from adults.

In early spring, queen bees emerge from hibernation with their nutrient stores greatly depleted (Alford, 1969a; Woodard et al., 2020). Their demand for nutrient rich pollen and nectar is high during this period, especially as they construct nests and feed the larvae that will develop into the first cohort of workers (Woodard et al., 2020). The queen is the primary forager during this time, seeking energy rich stores for their own metabolic processes and protein rich pollen for larval development (Alford, 1969b; Woodard et al., 2020). Poor food resources can cause a delay in brood development which can lead to a cascade of problems by increasing the period of time the queen is the sole forager and caretaker of her brood. This can result in fewer and smaller initial workers to undertake nest care and foraging (Goulson et al., 2002; Watrous et al., 2019). The speed at which larvae develop as well as the resulting size of the workers have implications for resource collection, and thus production and quality of additional workers, drones, and queens (Sarro et al., 2021; Watrous et al., 2019).

At the start of summer, workers have matured and take over foraging for themselves as well as the queen and developing brood (Goulson, 2009; Ruedenauer et al., 2015). Resource collection is a key determinant of short-term nest survival as most nests store less than 25 mL of nectar and 5 g of pollen (Heinrich, 1979; Pelletier & McNeil, 2003). Therefore, spatial, and temporal availability of resources dictate much of the nest’s population dynamics including larval development and production of reproductives in the fall.

Bumble bees must acquire all required elements from pollen during the larval stage in order to develop into adults (Filipiak, 2018). This requires constant access to floral resources throughout the growth stage, and as central place foragers, this access must be within range of the nest. Variability in pollen nutritive quality between species requires foraging for flowers that may provide the best or only source of limiting elements. Nutritionally diverse pollens influence larval growth, with larvae raised on di- or tri-floral diets having better development and lower mortality (Vaudo et al., 2016), increased weight and number of larvae (Moerman et al., 2017a), and larger body sizes, than those fed with mono-floral diets (Génissel et al., 2002; Moerman, Vanderplanck, et al., 2016; Tasei & Aupinel, 2008). Adequate nutrition is important as the summer progresses so that more workers can be produced. Studies show access to nutrient-rich pollens resulted in increased egg laying and survival of immatures, which creates a positive feedback loop where more workers are produced and able to collect more resources (Carvell et al., 2006; Pelletier & McNeil, 2003; Sarro et al., 2021). Foraging by workers under natural conditions has high energetic costs, and these costs increase if workers must forage long distances to access higher quality pollen. In areas with sparse floral resources, evidence suggests workers will forage farther from the nest to gain access to high quality patches which increases their energetic demands (Woodard & Jha, 2017). Metabolic activity is fueled through the consumption of carbohydrates in nectar (Ruedenauer et al., 2015), but non-carbohydrate nutrient requirements of workers are closely matched to the needs of the developing larvae rather than strictly to their own needs (Vaudo et al., 2016). Experiments in which some bumble bee workers were kept separate from the growing brood, workers with and without brood exposure exhibited consistent protein to lipid ratio preferences indicating they do not alter foraging behavior in response to brood presence (Vaudo et al., 2016).

To optimize nutrients for themselves and for the larvae and queen that they support, workers must make foraging decisions based on quality and accessibility. There is an added challenge in that floral resources shift over time. This means that workers must actively adapt their foraging strategies to match the availability of high-quality resources (Woodard & Jha, 2017). This underscores the difference between floral diversity and floral quality. With access to high-quality sources of pollen and nectar workers can minimize the cost of foraging and still match the demand of the nest (Filipiak, 2018). Low quality, but abundant floral resources can negatively impact fitness by imposing nutritional stress. Even though there may be plenty of resources available, those resources may not meet the specific demands of the individual or the nest (Filipiak, 2019). In fact, during times of resource shortages, larvae are often ejected from the nest to reserve resources for the queen and fully grown workers (Plowright et al., 1999) with obvious negative implications for fitness over time. Early floral resources have direct impacts on nest size in later months. Therefore, as resources decline in the late summer and early fall, more workers determine the success of the nest as they shift to rearing queens and drones.

Drones eclose in late summer or early fall. Their nutritional requirements as adults are likely driven by development of mature male gonads which occurs 6-20 days after eclosion (Cameron, 1985) but little else is known about their nutritional needs. Since they do not forage for the nest, all drone foraging should be driven by their own individual nutritional requirements, which are energetically intensive. Drones typically fly in circuits until they find a new queen to mate with (Goulson, 2009), an activity that along with foraging for food, has a high metabolic cost, and therefore requires high consumption of carbohydrates (Stone, 1995). The physiological differences between drones and queens suggest differences in elemental composition as nutrients are allocated to different sexual organs and activities (Filipiak, 2018). After drones mate with a newly emerged queen or queens, they die, while mated queens prepare for hibernation.

Availability of floral resources dictates the proportion of reproductives, with high resource availability resulting in the production of more queens and resource shortages resulting in more drones (Pelletier & McNeil, 2003). New adult queens spend their first few days post-eclosion in the nest before they forage on their own. Consequently, their nutrient requirements must be met through workers, requiring a significant shift in their foraging strategy (Woodard et al., 2020). Early foraging focuses on the collection of high protein diets that support larvae, whereas growing queens need pollen with high lipid and glycogen contents (Woodard et al., 2020). Evidence suggests that pollen and nectar limitations at this time have strong effects on survival of pre-diapause queens (Woodard et al., 2020). The consumption and storage of adequate amounts of lipids and glycogens in their bodies before they leave the nest has a strong effect on fitness (Alford, 1969b; Woodard et al., 2020). Further, of the queens that survive, there may be holdover effects of poor nutrition prior to hibernation that increase mortality and lower fecundity (Woodard et al., 2020). Without consistent access to nutrient-rich pollen and nectar both pre and post diapause, queen bees may be less likely to establish new broods (Woodard et al., 2020). Consistent access to late season, high-quality pollens is therefore likely key to their survival and subsequent fitness.

The seasonality of caste emergence highlights the necessity of specific nutrients being available at specific times and within the confines of foraging distance (Vaudo et al., 2015). This makes pollen availability and quality crucial in supporting the life cycle of bumble bees. To better understand the nutritional ecology of bumble bees, including the nutritional needs of each caste, I will use a resource selection probability function (RSPF) to determine if foraging is selective and whether selectivity shifts by caste by focusing on a common species in Montana, *B. vancouverensis*.

1.3 STUDY SYSTEM AND HYPOTHESES

One of the more common bumble bee species in western Montana and one that is easy to identify by sight is *Bombus vancouverensis* (formerly *B. bifarius*). *B. vancouverensis*, is found throughout the Rocky Mountains in a range of habitats including open prairies, mountain meadows, and urban areas, which allows it access to a wide variety of flowering species. Known floral associations include species in *Vaccinium*, *Centaurea*, *Lupinus*, and *Penstemon* (Williams et al., 2014). In another study in western Montana, *B. vancouverensis* represented 20% of all bees (n=512) out of 18 species captured (Lichtenberg, unpublished data). It was primarily observed foraging on huckleberry (*Vaccinium membranaceum*), and glacier lily (*Erythronium grandiflorum*) in the early spring, Alberta beardtongue (*Penstemon albertinus*), owl clover (*Orthocarpus tenuifolius*) and lupine (*Lupinus* spp.) in the early and mid-summer, and snowberry (*Symphoricarpos occidentalis*), spotted knapweed (*Centaurea stoebe*) and clover (*Trifolium pratense*) in the late summer.

My study focused on *B. vancouverensis* to test the following hypotheses:

Hypothesis 1: Bombus vancouverensis forages selectively because they are collecting pollen to meet their nutritional requirements.

Hypothesis 2: The degree of foraging selectivity by B. vancouverensis is determined by resource diversity because high diversity of resources provides opportunity to access the highest quality resources.

Hypothesis 3: Shifts in B. vancouverensis foraging patterns through the season is due to the production of different castes (possibly due to each caste's different nutrient requirements).

Using a resource selection probability function (RSPF), I will examine the probability of each floral species' use based on its abundance and compare it to the probability of use if all species have equal abundances. If hypothesis 1 is supported, some floral species will have a probability of use that is higher than the random probability of use given its abundance. The same data will be used to examine resource use throughout the foraging season (Hypothesis 3). Using Shannon's Diversity Index calculated at a daily timestep, I will determine which resources are used selectively and determine if selective use occurs during times of high resource diversity (high Shannon's Diversity Index) (Hypothesis 2).

Studies have shown the importance of multifloral diets in larval development (Vaudo et al., 2016), queen diapause (Woodard et al., 2020), and colony success (Abbas et al., 2014; Pelletier & McNeil, 2003). In my preliminary research, *B. vancouverensis* was observed foraging on up to three different species of concurrently flowering species although many more species were in flower, suggesting they may be foraging selectively. Selective foraging implies that, despite the presence of several flower species, there is a process of selection among them that may be associated with nutrient quality (Ruedenauer et al., 2015).

Additionally, the nutritional requirements of bumble bees are likely to be caste-specific and vary over the foraging season as demands shift to accommodate the needs of workers, drones, and queens as well as those of the developing brood (Vaudo et al., 2015, 2016; Watrous et al., 2019; Woodard et al., 2020). In early spring, queens forage to provide for themselves, larvae, and nest-bound queens. When the initial brood emerges as adult workers, they begin foraging for themselves, larvae, and the now nest-bound queens. In the late summer, the workers must feed larvae that develop into drones and new queens. Finally, newly eclosed queens must forage to prepare for overwintering. Sexual dimorphism is also expected to play a large role in driving nutritional needs, with body size, gonad production, and other physiological characteristics likely to create substantial differences in elemental requirements over time (Filipiak, 2018; Goos et al., 2017). If pollen from different species of plants differs in quality, these differences may impose different limitations on each caste and sex due to caste- or sex-specific physiological differences (Filipiak, 2018) and result in caste-dependent selective foraging. Hypothesis 3 examines these shifts as each caste is produced.

By investigating whether foraging is selective and its variability by caste, we can begin to understand how bees may meet nutritional challenges in their habitat and how anthropogenic shifts in plant diversity and composition may influence their populations and persistence on the landscape.

Chapter 2

2 APPLYING RESOURCE SELECTION PROBABILITY FUNCTION (RSPF) TO UNDERSTAND FLORAL RESOURCE USE BY A COMMON BUMBLE BEE

Bumble bees (Hymenoptera: *Bombus*) are important pollinators in temperate ecosystems worldwide with seasonal caste variations involving queens, workers, and drones. Bumble bees, like all organisms, must meet their nutrient requirements for successful growth and development. Bumble bees use a number of floral resources over time. When resource use is in greater proportion to its abundance on a landscape, that use is considered selective. To examine resource use within the context of abundance, a resource selection probability function (RSPF) was applied to examine floral resource use through a flowering season by a common bumble bee, *Bombus vancouverensis*. The RSPF framework was used to examine 1) resources used to meet nutritional requirements, 2) resources used by each caste, and 3) resources used during periods of high diversity. From June 3-August 10, 2022, floral resource abundance and phenology, and resource use by *B. vancouverensis* was collected at two sites in Western Montana, USA. Seven generalized linear models (GLM) were fit to examine early season (ES) and late season (LS) foraging. *B. vancouverensis* demonstrated selective use of two species during ES, and four species during LS. Selective use of these species may be the due to the superior or complementary nutrient profiles compared to other available resources. The use of RSPF in this study provides insights into resource use by *B. vancouverensis* and can be applied to other native pollinators and bumble bee ecology more generally. As land use alters floral resource availability and diversity and climate change and invasives alter plant community composition, understanding resource use may be crucial to bumble bee conservation.

2.1 INTRODUCTION

Bumble bees (Hymenoptera: *Bombus*) are social insects with seasonal castes of adult queens (gynes), workers, and drones (males) that forage for floral resources in diverse and dynamic environments. Due to the spatiotemporal variability in the availability of flowers, plant species use by bumble bees is determined by active decision-making based on a variety of visual and chemical cues. While bumble bees are considered generalist pollinators, some species exhibit a narrow dietary breadth (Goulson et al., 2005; Goulson & Darvill, 2004) and preferences for some flowering species over others have been documented (Brian, 1957; Wood et al., 2019). Resource selection probability functions (RSPF) use the availability of a resource and its use by an organism to determine if that use is selective. When organisms exhibit resource use disproportionate to availability, use is considered selective (Manly et al., 2007). In the context of pollinators, preference for particular flowers has clear implications for conservation, particularly when some bumble bee population declines are due to a reduction in plant biodiversity due to changes in land-use, spread of invasive species, and climate change (Goulson et al., 2008, 2015; Williams & Osborne, 2009). Understanding possible preferences is a valuable tool in conservation because it can help us predict how changes to floral resource availability affects population viability and species persistence. The RSPF framework can be applied to a variety of pollinator species and ecosystems. Using floral availability as starting point, the framework can be applied to all pollinators within a given area, giving insight to potential competition for resources or highly used resources and pollinator specific preferences and use patterns. Applied broadly, the same framework can be used during multi-year studies, potentially elucidating how changes in temperature impact resource use, how floral availability may affect species long-term, and determine if there is continuity of preference year after year.

Part of understanding resource use in bumble bees involves understanding their needs over the annual life cycle of a nest. The cycle begins with queens that have hibernated over winter emerging in late spring at the beginning of the flowering season. At this time, the queens must feed themselves adequately to produce the first cohort of workers. Spring bloom periods are typically short and can be erratic with cool temperatures, low levels of sunlight and variable weather (Kudo & Ida, 2013). Overwintered queens and early workers must overcome resource limitations during this time to establish nests that can survive until more consistent temperatures and flowering occurs later in the season (Woodard et al., 2020).

Bumble bees must acquire all required nutrients from pollen during the larval stage in order to develop into adults (Filipiak, 2018). A nest initiating queen must have constant access to floral resources as she forages to support the first cohort of brood development and then via workers later in the season. As workers take over foraging, they must actively adapt their strategies to match the shifting availability of resources to meet their own needs, those of the growing brood, and the now nest-bound queen (Goulson, 2002; Ruedenauer et al., 2015; Woodard & Jha, 2017). As the summer continues, and more floral resources become available, a positive feedback loop supports an increase in the number of workers which in turn allows greater foraging and may increase the production of workers during the foraging season and more reproductives (males and queens) late in the season (Pelletier & McNeil, 2003). The colony cycle draws to a close in late summer and early fall as the nest produces drones as well as new queens that mate, feed, and then enter hibernation. During this time, the new queens must have access to high quality resources as limitations at this time can have strong effects on survival and fitness (Woodard et al., 2020). Without consistent access to nutrient-rich pollen and nectar pre- and post-diapause, new queens may be less likely to successfully establish new broods (Woodard et al., 2020).

The seasonality of caste production and the likelihood that castes have dissimilar nutritional needs related to their different activities suggests that differential foraging may occur to meet these demands (Vaudo et al., 2015). As central place foragers, the availability of floral resources must be within a feasible foraging distance from the nest. Estimates of this distance vary from 100-2,750 m, depending on bee body size, with larger bees having greater foraging distances (Darvill et al., 2004; Kleijn & Raemakers, 2008). Since foraging is energetically expensive, with an increased distance to high quality forage comes an increased energetic cost, potentially impacting the colony’s growth and overall fitness (Pelletier & McNeil, 2003; Sutcliffe & Plowright, 2011).

Ephemerality of floral resources in multiple dimensions, both temporally and spatially, forces foraging to be highly dynamic. Therefore, continuity of floral resources over time likely plays an important role in colony success. Nests typically contain less than 25 mL of nectar and 5 g of pollen on average, which only provides enough sustenance for a few days in a mature colony (Heinrich, 1979; Pelletier & McNeil, 2003). Thus, there should be a tight linkage between availability and use within the nest.

Consistent access to nutrients increases egg production while decreasing development time, positively affecting overall fitness (Hemberger et al., 2022; Pelletier & McNeil, 2003; Pendrel & Plowright, 1981). While the need for resources is constant, times of increased demand can affect population dynamics. Early season resources influence the success of a nest, including queen fecundity, number of workers produced, and resistance to parasitism (Goulson, 2002; Pelletier & McNeil, 2003; Watrous et al., 2019; Woodard et al., 2020). Late season floral resources affect the ratio of reproductives, with more queens produced relative to males when resources are abundant (Hemberger et al., 2022; Pelletier & McNeil, 2003). However, high resource availability does not necessarily equate to high resource quality. Not all floral resources are equal. Even if one floral resource is abundant, if it does not meet the nutritional demands of individual or the nest, fitness may still be compromised (Filipiak, 2019).

Bumble bee foraging should involve a process of selection driven by their nutritional requirements (M. Filipiak, 2019). They must have access to either a single source of high quality pollen, or a diverse supply of nutritionally variable but complementary pollen sources to meet their needs (Vaudo et al., 2015). Foraging on a diverse assortment of floral resources is likely to be beneficial in many ways. Polyfloral diets allow bumble bees to balance amino and fatty acid intake (Harmon-Threatt & Kremen, 2015; Vaudo et al., 2015), decrease the build-up of defensive secondary compounds produced by some plants (Muller & Kuhlman, 2008; Vaudo et al., 2015), and increase pathogen resistance (Alaux et al., 2010; Pasquale et al., 2013). On the other hand, limited access to adequate nutrition decreases survival rates (Vaudo et al., 2015, 2016). For example, monofloral diets, can reduce colony success due to direct nutrient limitation (M. Filipiak et al., 2017; Moerman et al., 2017b). Selective foraging for pollen that provides a complete diet would be expected to optimize fitness. In fact, evidence suggests bumble bees preferentially forage on species with higher protein and amino acid contents (Moerman et al., 2017b) and that contain specific protein:lipid ratios (Vaudo et al., 2016).

While nectar is used for an energy source, pollen is high in proteins required for adult maintenance and the production of larvae (Moerman, Roger, et al., 2016). Accordingly, bumble bees exert greater selectivity for pollen quality than for nectar quality (Kleijn & Raemakers, 2008). In one study, individual bees carried pollen from an average of 1.44 plant taxa per foraging trip despite the presence of up to 30 plant taxa within their foraging range (Kleijn & Raemakers, 2008). Another study found less than 5% of pollen loads contained four or more species of plants, while 57% of pollen loads were from one taxon (Heinrich, 1976). This implies that while a variety of flowering species may be available near a nest site, only a handful may be used. Brian (1951) noted that out of 27 species of flowers available, only pollen from five species were collected by the observed species.

Several hypotheses have been put forth to explain selectivity by bumble bees. Preference for some plants over others has been suggested to be related to tongue length (Carvell et al., 2006; de Keyzer et al., 2016; Wood et al., 2019). Wood et al. (2019) found considerable variation in composition of pollen collected by several bumble bee species, with longer-tongued species collecting fewer pollen types on average. However, the relationship between tongue length and dietary breadth has been contested (de Keyzer et al., 2016; Williams & Osborne, 2009). For example, an increase in geographic range was found to increase dietary breadth, irrespective of tongue length (i.e. Sheffield et al., 2016; Williams et al., 2009; Williams & Osborne, 2009). Bumble bees with larger geographic ranges have access to a wider range of floral species, and this, rather than tongue length, may have a greater influence on their foraging patterns (de Keyzer et al., 2016; Kleijn & Raemakers, 2008; Wood et al., 2019). Studies on floral resource preferences can also be difficult to interpret because pollen and nectar collecting behaviors are seldom distinguished and variation in foraging over time is typically not linked to the shifting demands of the nest (de Keyzer et al., 2016; Kleijn & Raemakers, 2008).

To best understand resource use by bumble bees and how foraging is related to their nutritional ecology, I used an approach that investigates their preference for floral resources over time and in relation to seasonal production of their castes. Preference, or selectivity, can be estimated using ranked importance functions such as the Resource Selection Function (RSF), and Resource Selection Probability Function (RSPF) (Johnson et al., 2006; Manly et al., 2007). These functions rely on the assumption that use is selective if a resource is used disproportionate to its availability. The resource is ranked according to its probability of use when its availability is equal to that of another resource (Johnson, 1980). For pollinators, RSFs and RSPFs can be applied to examine the interactions between floral resource abundance and use. RSF and RSPF can be estimated using generalized linear modeling (GLM) or generalized additive modeling (GAM) but require the input of relevant landscape predictors (Henry et al., 2012). Depending on the response variable, landscape predictors can include ranked resources that can be based on quantity of actively flowering species, species richness, or diversity indices (Henry et al., 2012). The choice of predictors or covariates should be based on the ecology of the organism, or the question being asked (Boyce et al., 2002; Burnham & Anderson, 2001).

I applied a RSPF approach to understanding foraging preferences over time in a common western bumble bee, *Bombus vancouverensis*. I tested the hypothesis that floral resource use is non-random and that resource use shifts in a nonrandom manner over time because of shifts in floral resources of different quality and differential nutritional requirements of seasonally produced castes. In this paper, I report the results of the RSFP models in relation to observations on *B. vancouverensis* over a foraging season. Nutrient analyses and the relationships of nutrient quality with foraging patterns will be reported in a companion paper (Brassfield et al., in prep).

I hypothesized that (1) *B. vancouverensis* forages selectively because they are selecting pollen to meet their nutritional requirements, (2) The degree of foraging selectivity by *B. vancouverensis* is determined by resource diversity because high diversity of resources provides opportunity to access the highest quality resources and (3) shifts in *B. vancouverensis* foraging are due to the production of different castes (possibly due to each caste's different nutrient requirements).

2.2 METHODS

2.2.1 STUDY SITE

The study site consisted of montane meadows in a matrix of coniferous forest located on the west side of Flathead Lake (Polson, MT, USA) on the traditional lands of the Ksanka, Qlispe' and Selis people. In accordance with a request from the Selis Qlispe' Culture Committee, the specific location is not provided. The area contains a broad diversity of flowering plants, and supports at least six bumble bee species (Brassfield et al., unpublished data), including *B. mixtus*, *B. melanopygus*, *B. appositus*, *B. insularius*, *B. occidentalis*, and the focal species, *B. vancouverensis* nearctica (formerly *B. bifarius* see Heraghty et al., 2020). *B. vancouverensis* was chosen for study because of its ubiquity not only at the site, but also throughout the western USA. Additionally, it is one of the easiest to identify by sight, making it a good choice for observational studies.

2.1.2 ESTIMATES OF FLORAL RESOURCE AVAILABILITY

Two permanent 50 m radius plots were established, one in a forested area at an elevation of 1200 m, the second in an open meadow at an elevation of 1600 m, 1.8 km away. These were selected to encompass the full diversity at the site within the foraging distances of local bees. Using methods developed in Szigeti et al. (2016), each plot was visited weekly and scanned to estimate the relative proportions of all flowering plant species. Since many flowers occur in inflorescences, or only as a part of a large plant, percent coverage of each plant was not used, but rather the relative abundance of flowers by species relative to those of other flowering species flowering concurrently was used to provide a measure of availability. Species making up less than 5% of the total composition on a particular date were placed into the “other” category. For each date, all observations totaled 100%. These data allowed me to estimate of flower availability by plant species relative to others over the foraging season.

2.1.3 ESTIMATES OF FLORAL USE

Four smaller short-term 3x3 m plots were also established within each 50 m plot. These plots were re-evaluated weekly for floral resource coverage to ensure they contained 50% or more coverage of actively flowering species. If plots did not, a new plot was established with 50% or greater coverage of floral resources. Since floral resources shift over time, establishing these plots helped account for those shifts. These plots were used for observational surveys to estimate floral use by *B. vancouverensis*. In addition to estimating availability by percent cover, I also tracked flower phenology over time to estimate floral resource availability as well as timing of peak flowering for each species. To do this, all flowering plant species in the large plots were assigned a category using the following criteria: 0 – no buds, 1 – more buds than flowers, 2 – more flowers than buds (considered peak flowering), 3 – more seed pods than flowers, and 4 – no flowers/only seed pods.

To document which flower species were visited and in what frequencies over the foraging season, 15-minute observational surveys of *B. vancouverensis* visitations were completed ten times per week split evenly between the two sites, for a total of 150 observation minutes in the small plots. These surveys were completed between active hours (7am – 5pm) on days when conditions supported foraging, including low wind (less than 30 km/hr), sunny (or partly cloudy/brightly overcast), and temperatures above 12°C as detailed by Bishop & Armbruster (1999). All *B. vancouverensis* visitors were recorded by flower species.

2.1.4 RSPF FUNCTION MODELING

The conceptual framework behind RSPF relies on a logistic equation (Eq. 1) (Johnson et al., 2006).

$$w^{*}(x) = Cexp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \cdots \beta_k x_k) = Cexp(\beta' x)$$

Equation 1: Resource Selection Probability Function (RSPF) exponential form where a vector, $\boldsymbol{x}$, with covariates $\boldsymbol{\beta}_i$, to determine the probability, $\boldsymbol{w}^{*}(\boldsymbol{x})$.

Typically referred to as a used/unused design, the statistical underpinnings of RSPF have been discussed in detail in Johnson et al. (2006), Lele & Keim (2006), and Manly et al. (2007), with a general consensus reached on the use of regression modeling to estimate all parameters. RSPF assumes x is the vector of environmental covariates βi, used to determine the probability of resource use, are location or observation specific and represent resources used non-destructively by an organism. Each vector (x_i) is associated with a y_i variable where $y_i = 1$ if the resource is used, and $y_i = 0$ if the resource is unused. These conditions produce an estimate of absolute probabilities for each resource when not all covariates are categorical. When most or all covariates are categorical, probabilities are relative. Under these assumptions, I fit eight generalized linear models using the floral resource and use data. In this study, given the data were primarily categorical (floral species, flowering stage), the estimated probabilities are relative.

There were over 1000 observations of 67 floral resources by *B. vancouverensis* included from observations made weekly from June 3 to August 2022. To limit the processing of categorical variables and examine foraging effort in two separate periods, the data were split to examine early season flowering (ES; June 3-June 28, n=455), late season flowering (LS; July 5-August 10, n=338), and single observations of floral species removed. ES and LS were fit using the same covariates: flower species only (FL), relative abundance only (AB), flower:abundance (FL:AB) (interaction), flowering stage (FS), and the diversity model (DI). The FL, AB, FL:AB and FS models used the binomial use/non-use independent variable. FL models used flowering species as predictor dummy variable denoting presence or absence. The same binomial variable was used in the AB model with relative abundance as a numerical predictor variable. Finally, flower species was combined with relative abundance as an interaction predictor variable. The FS model used each phenological stage (1-4) as a categorical predictor variable. Finally, the DI model used the probability output from the FL:AB model to calculate the range of probability per day, averaged by week as the numerical predictor variable, and flower species abundance as the proportion of community composition to calculate Shannon’s Diversity Index on a daily timestep, also averaged by week as the independent variable.

All models were evaluated on Akaike Information Criterion (AIC) (Table 1). Model outputs were used to calculate probability of use according to the fit model. These were evaluated using analysis of variance (ANOVA) and Tukey’s honestly significant difference test (HSD) to determine if the resulting probabilities were different between groups to ensure the model was treating each floral species as a unique variable. Tukey’s HSD was used to determine the specific differences between species, so only species flowering concurrently were used in the final analysis. Probability of use by floral species was compared across models to determine if resource use was impacted by abundance. All analysis was done using RStudio (RStudio Team, 2020).

2.3 RESULTS

2.3.1 FLORAL RESOURCE OVERVIEW

Over the period of observation, 62 unique species were observed flowering with an average peak flowering time of 13 days. Members of the family Asteraceae were the most common at the site (27%), followed by Rosaceae (12%, Table 1). ES (weeks 1-2) exhibited the greatest species evenness, averaging 12 floral species with a majority comprising 5-10% of total floral resources available (Figure 1). LS (weeks 3-5) flowering had similar averages of flowering species available during weeks 3-4, but substantially less evenness especially during week 5, when the number of flowering species fell to an average of nine, with one species dominating at 60% (Figure 1). ES and LS contained similar unique species counts, with ES models processing 28 floral species, LS models processing 34 species. Nine species were found in both models (Table 1).

2.3.2 RSPF MODELS

To examine the effects of flowering species abundance on use by *B. vancouverensis*, six GLMs, three each for ES and LS, were fit using data on floral use and abundance. Table 2 presents each model input as well as the AIC. Model outputs were converted to probability of use (PU).

All ES models identified the same five plant species as having the highest PUs. Similarly, the three LS models identified five species with the highest PU for that period. Average PUs of the ten plant species for the ES and LS models are presented in Table 3. Figures 2 and 3 show the average PU for each species in the ES and LS models respectively. LS models had greater average PUs across species (*n* = 34) (Figure 3) but also exhibited the greatest variability in PUs (*M* = 0.139, *SD* = 0.267).

The AB model predicted an exponential relationship between floral abundance and PU but the combined full season model exhibits a greater variability in the PU, suggesting a potential change in the effects of abundance on foraging later in the season as species diversity and evenness decrease (Figure 4).

Following the conceptual framework of the RSPF, the PU of a species must be higher than the PU based on its relative abundance. In the context of this study, selective use is indicated by a PU that is predicted to be higher by the FL model than by the AB model. Each floral species used in the FL model was compared to the predicted PU by the AB model (Figure 5). The FL model found no relationship between floral species abundance and its predicted PU. The ten floral resources with the highest PU from the ES and LS models (Table 4) were used to examine differences in mean PU predicted by the FL and AB models using Tukey's HSD test. Tukey's HSD test was used in pairwise comparisons between the PU as predicted by each model to determine the mean difference between values and, within this study, was used to determine the key differences between AB and FL models. The ten species had statistically significant PU differences between models ($p < 0.05$), which suggest that these species in particular were used more often than expected given their abundance (difference < 0). KN, LU, OS, CO, MU, BT, YBT and OC have mean differences that suggest selection for these floral species over others present (difference > 0) (Table 4, Figure 6). BT and YBT had an average abundance of 12% and 10%, respectively, but combined make up over 2/3 of floral use in the first half of week 3, shortly after the decline in LU flowering (Figure 13). Prior to that, LU was used in accordance with availability, with a maximum abundance of 60% during its flowering period. However, *B. vancouverensis* showed some preferential foraging for LU as it was selected over other species that were equally available (prior to its site dominance) and throughout phenological stages 1-3.

The third model applied to ES and LS was a combination model with an interaction between floral resource and abundance (FL:AB). PU was predicted by both the ES (Figure 7A) and LS (Figure 7B) model to increase as percent abundance increased. Both graphs were plotted using a threshold determined by the data distribution in each model to reduce noise (PU > 0.06 and >0.1, respectively). The interaction model demonstrated a relationship between PU and availability as it changes for each species, making it well-suited for temporal calculations. Examinations of species richness and flowering stage used PUs calculated from this model.

2.3.3 SPECIES RICHNESS AND SELECTIVE FORAGING

To examine the relationship between species richness and use, Shannon’s Diversity Index was calculated on a daily timestep and averaged by week (1-5, Figure 8A). The daily range of PU was used to determine when *B. vancouverensis* was potentially selectively foraging as indicated by a higher PU for particular flowering species (Figure 8B). To examine the relationship between species richness and selective foraging, a linear model was fit using the daily Shannon’s Diversity Index and range of PU for the FL:AB model. If *B. vancouverensis* selectively forages during times of high species richness, a positive linear relationship would be observed between range of PU and Shannon’s Diversity Index. However, the plotted results of the linear model, where the range of PU as predicted by the FL:AB model, exhibited no relationship with Shannon’s Diversity Index ($R^2 = 0.133$, F (1, 572), $p < 0.05$) (Figure 9).

2.3.4 FLOWERING STAGE AND PROBABILITY OF USE

Of the phenology stages recorded, three were chosen for use in analysis (stage 1=more buds than flowers, stage 2= more flowers than buds, stage 3=more seed than flowers). Average PU for each of these flowering phenology stages was calculated using the FL:AB model. The results of ANOVA followed by Tukey's HSD found a significantly higher difference between flower phenology stage 2 than stage 1 and 3 (F (5,787) = 6.038, $p < 0.001$) (Table 5). Means, range, outliers, and frequency of observations for PUs by stage and frequency of observations are shown in Figure 10.

The FL:AB model was used to examine the timing of flowering of each species by phenological class and observed PU. The average PU by day and by phenology stage is shown in Figure 11 for the ten species that showed the greatest PU. As each flowering species completed flowering, the PU decreased accordingly (Figure 11).

2.3.5 FLOWERING PHENOLOGY AND CASTE USE

Early season queens were observed until the beginning of June at which time workers began to emerge and dominate until the beginning of August where the first new queens and drones begin emerging (Figure 12). Over time, shifts in flower preference occurred, matching the observed PU and flowering (Figure 11).

Sum visitation was used to determine the percent use of each flowering species by week (Figure 13). Weeks 2-4 show the greatest variation in floral species composition, which is also demonstrated by Shannon's Diversity Index during those same weeks. Week 1 shows exclusive use of KK and LU which was used by queens and workers respectively (see Figure 12).

2.4 DISCUSSION

Organisms must acquire the necessary nutrients for survival and production of young from their environment. If resources vary in quality, this should lead to selective foraging to conserve energy and optimize fitness. Furthermore, as the number of available resources increases, organisms are faced with more complex decision-making regarding the use of those resources. For pollinators, many floral species may be available at a given point in time, but they are likely to vary in quality. Since bumble bees rely on pollen for food and are nutritionally constrained to foraging on available floral resources within the range of their nest, the use of certain pollen sources over others may be central to acquiring the nutrients they need for survival and reproduce.

This study used a resource selection probability function to determine the probability of flowering plant resource use by a bumble bee, *Bombus vancouverensis*, at a site in western Montana through a foraging season (June 3-August 10, 2022). While 67 flowering species were observed at the site, only 16 species were used by *B. vancouverensis*. The models identified ten of these species to have a higher probability of use and six species that were used in greater proportions than expected given their percent abundance, indicative of selective foraging. Selective foraging by *B. vancouverensis* supported my hypothesis that *B. vancouverensis* selectively forages for pollen from specific plants to meet their nutritional needs. While I did not analyze the nutrient content of the pollen, my results suggest these plants provide either superior nutrient profiles or serve as complementary sources. It may also be that these plants provide greater amounts of pollen reducing energy requirements for foraging. Future work can link selective foraging with elemental analyses and estimates of differential pollen production to determine the bases for selectivity.

Not only did species composition of flowering plants shift over time, but so did species diversity and evenness, which followed a parabolic trajectory through the season.

When species diversity and evenness was highest (Figure 8A) during the first half of the observation period, *B. vancouverensis* used five species out of the 28 flowering species available. Of these, two species (BT, and YBT) were used at higher probabilities than predicted by abundance. The use of *Lupinus* and *Penstemon* species by *B. vancouverensis* during the course of this study are supported by other research with well-documented use by *B. vancouverensis* and other species (e.g. Harder & Barclay, 1994; Williams et al., 2014). Both genera of flowers have multi-flower inflorescences in the form of spikes, allowing multiple flowers to be visited at one stalk, minimizing flight distances. Additionally, *Lupinus* is known to provide large pollen rewards per visit (Rasheed & Harder, 1997). Thus, the use of *Lupinus* species allows workers to collect large quantities of pollen for little energetic cost.

In the late season when fewer species were available, flower diversity and evenness decreased, and a few taxa began to dominate (Figure 1). The impact of late season abundance shifts is apparent in Figure 8B, where diversity declines resulted in increased PU in the AB model. During that time, *Centaurea stoebe* (KN), an invasive species, had the highest PU of all flowering plants indicating that it was selected most by workers, new queens, and drones over many other species when it was present. *C. stoebe* dominated the site at the end of the season (76% flower coverage by week 5), and was the only species used by new queens and drones. For drones that mainly require the energy provided by nectar, *C. stoebe* may be an excellent source as it is known to provide substantial nectar to honeybees (Urbanowicz et al., 2020). However, for new queens that must also sequester lipids, proteins, and minerals to survive winter and initiate new broods, the quality of *C. stoebe* pollen should be important. If the pollen is high quality regarding the needs of new queens, this invasive may be beneficial to the species. However, if it is attractive but nutritionally deficient it may actually reduce bumble bee fitness. Thus, single plant foraging by post-hibernation queens and drones raises some interesting questions and concerns. These results further indicate a need to not only track foraging preferences but also to relate preference and use to how well different plants support bee needs.

While I investigated the effects of species richness on the degree of selective foraging, I found no evidence of an effect. The relationship between range of PUs and Shannon's Diversity Index did not result in a linear relationship ($R^2 = 0.133$, F (1, 572), $p > 0.05$). Therefore, I rejected my second hypothesis that *B. vancouverensis* exhibits greater selectivity in foraging during times of high resource selectivity because they can select the highest quality resources. Rather, selectivity for some species did not attenuate when the bee was presented with a greater choice range. Similar results were found by Fründ et al., 2010, whose analyses found while all species demonstrated specialization (in this study termed preference), it was not significantly correlated with flower diversity. Increased preference during times of high resource diversity could have negative implications in complex food webs whereby increased individual preference overall decreases the availability of resources despite the diversity. Instead, theoretical predictions related to ecological networks suggest increased consumer (pollinator) diversity increases the degree of specialization not increased resource diversity (Montoya & Yvon-Durocher, 2007).

B. vancouverensis castes foraged differentially among species of flowering plants, some of which appears to be driven by seasonal abundance. Post-hibernation queens foraged only on *Arctostaphylos uva-ursi* (KK), which only flowers in the very early season. Ericaceous species have documented relationships with *Bombus* pollinators, owing to their poricidal anther that only releases pollen by a process of buzz pollination, a method employed by *Bombus* species (Moquet et al., 2016). Additionally, Roulston et al. (2000), found buzz-pollinated species to have higher protein content pollen, suggesting that the use of *A. uva-ursi* by queen bees early in the season may provide protein-rich pollen to aid in larval development (Moquet et al., 2016; Vaudo et al., 2016). Interestingly, workers present at the same time were not observed using this species, instead using *Taraxacum officinale* (DL), a slightly less available alternative. *T. officinale* provides high sugar content nectar, and given the ubiquity of the species, it's use is unsurprising (Hicks et al., 2016; Mosquin, 1971). The preference for *T. officinale* over *A. uva-ursi* may be explained by the low number of flowers which at this time and their dispersed distribution on the landscape requires higher energetic costs for newly emerged workers. The broad spatial distribution of resources at this time, and the energetic costs of newly emerged workers, suggest that the use of *T. officinale* over *A. uva-ursi* may be due to high energetic demands. *Taraxacum officinale* is an introduced species that has become ubiquitous in most of North America. Its blooms are long-lived and, with two peaks in bloom periods, in early spring and again in fall, its effect on pollinators is of interest (Hicks et al., 2016; Lázaro & Totland, 2010a, 2010b; Mosquin, 1971). Two periods of tenuous floral availability, very early and very late season, raise questions about the role of introduced species with different flowering times in plant communities. Similar to the use of *C. stoebe* by new queens and drones, regardless of native or exotic status, *T. officinale*, *C. stoebe*, and other species may play a vital role during transition periods (Vitt et al., 2020).

Finally, my data supports a view that the temporal component of resources available may provide extra information related to their use. The middle of June marks the emergence of the first workers that primarily forage on *T. officinale* before shifting to *Lupinus* (LU) (Figure 12, 13). Since bumble bees should optimize foraging to provide nutrients for themselves and a growing brood (Goulson, 2002; Ruedenauer et al., 2015; Woodard & Jha, 2017), it is likely that during this time the active foraging is to provide nutrients for a second cohort of workers. The peak in workers was four weeks after the first workers were observed, matching the estimated brood development period of 3-5 weeks (Crone & Williams, 2016; Sarro et al., 2021). After this peak in workers, the nests shifts to producing reproductives. The first drones were observed at the end of July and the first new queens the following week. It is during this time floral resource availability dropped at the site, with only a handful of species still blooming. Of those, *C. stoebe* dominated both sites and became the sole foraging resource for new queens and drones. My data are inconclusive with respect to my final hypothesis that shifts in *B. vancouverensis* foraging are due to the production of different castes because of each caste's different nutrient requirements. While there were differences in caste preferences, these may be due to differences in either caste needs or flower availability. Further research on pollen nutrient content and the nutrient requirements of each caste is needed.

Understanding plant use and selectivity by bumble bees can aid not only in understanding their behavior and nutritional ecology but inform conservation aimed at slowing population declines and in restoration. Many factors have contributed to bumble bee declines including changes in land-use. The use of RSPF models in this study provide insights into resource by a common western bumble bee by considering use versus the availability of flowering species on the landscape over a foraging season. For bumble bees that have seasonal shifts in caste production, understanding use in relation to temporal availability of resources may be crucial to understanding how they meet their nutritional needs. As climate change and invasive species proliferations alter plant communities and predictability of resource presence, it is crucial to understand which plants support or limit bee fitness in a given environment. In this study, I elucidated use and temporal selectivity for a generalist bumble bee, *B. vancouverensis*. In a companion study I analyzed the nutrient content of pollen produced by available plants. While this combined approach will help us understand use and needs in this generalist bee, additional studies on other bees, including specialists, will help us understand bumble bee ecology more generally. Currently, little is known about nutrient quality of pollen of wild plants, and this should be a major focus in new research.

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Figures and Tables

Table 1. Community composition of flowering species observed at the study sites and abbreviations used in the text and subsequent tables and figures. Bolded species are classified noxious and invasive by the USDA.
***notes species found in both ES and LS models**

Family	Abbreviation	Species
Apiaceae		
	BR*	*Lomacium* sp.
	TBR	*Lomatium foeniculaceum*
Asparagaceae		
	FS	*Smilacina racemosa*
Asteraceae		
	AL	*Balsamorhiza sagittata*
	AR	*Arnica cordifolia*
	DA	*Agoseris* sp.
	DL*	*Taraxacum officinale*
	FA	*Aster* sp.
	GO	*Solidago canadensis*
	GR	*Hieracium* sp.
	HK	*Crepis* sp.
	HW	*Senecio* sp.
	KN	***Centaurea stoebe***
	OD	***Leucanthemum vulgare***
	PE	*Anaphalis margaritacea*
	PT	*Antennaria* sp.
	PW	*Matricaria discoidea*
	ST	*Centaurea macrocephala*
	TH	*Carduus nutans*
	YS	*Tragopogon dubius*
	YW	*Achillea millefolium*
Berberidaceae		
	OG	*Berberis repens*
Boraginaceae		
	HT	***Cynoglossum officinale***
	SW	*Phacelia hastata*
	WES	*Lithospermum ruderale*
Campanulaceae		
	HA	*Campanula rotundifolia*
Caprifoliaceae		
	SN	*Symphoricarpos albus*
Caryophyllaceae		
	CW*	*Cerastium arvense*
	PI	*Dianthus armeria*
Ericaceae		
	H	*Vaccinium membranaceum*
	KK	*Arctostaphylos uva-ursi*

Table 1. Cont.

Family	Flower abbreviation	Scientific name
Fabaceae		
	CO	*Trifolium repens*
	LU*	*Lupinus* sp.
	VE	*Hedysarum boreale*
	YCL	*Trifolium campestre*
Geraniaceae		
	SG	*Geranium viscosissimum*
Lamiaceae		
	SH	*Prunella vulgaris*
	WB	*Monarda fistulosa*
Liliaceae		
	GL	*Erythronium grandiflorium*
	ML	*Calochortus apiculatus*
	NO	*Allium cernuum*
Melanthiaceae		
	DC*	*Zigadenus venenosus*
Montiaceae		
	BI	*Lewisia rediviva*
Orobanchaceae		
	OC	*Orthocarpus tenuifolius*
	PB	*Castilleja* sp.
	YPB	*Castilleja cusickii*
Plantaginaceae		
	BT*	*Penstemon albertinus*
	KTT	*Besseya rubra*
	LB/SE	*Veronica sp.*
	YBT*	*Penstemon confertus*
Polygonaceae		
	BW	*Erigonium* sp.
	ERI	*Erigonium* sp.
Primulaceae		
	BS	*Dodecatheon conjugens*
Ranunculaceae		
	CL	*Clematis occidentalis*
	LP*	*Delphinium bicolor*
Rosaceae		
	AN	*Purshia tridentata*
	OS	*Holodiscus discolor*
	PS	*Geum triflorum*
	SA	*Amelanchier alnifolia*
	SB	*Fragaria californica*
	SP	*Spiraea betulifolia*
	SU	*Potentilla recta*
	WR	*Rosa woodsii*
Saxifragaceae		
	AU*	*Heuchera cylindrica*
	WS	*Lithophragma parviflorum*

Table 1. Cont.

Scrophulariaceae		
	MU	*Verbascum thapsus*
Violaceae		
	V	*Viola adunca*

Table 2. Model covariates and AIC values for early season (ES) and late season (LS) models predicting foraging selectivity of *Bombus vancouverensis*.

Model covariates	AIC	
	ES	LS
Flowering Resource Only (FL)	173.89	200.99
Abundance Only (AB)	175.65	199.71
Abundance : Flower (FL:AB)	178.36	195.88

Table 3. Flowering species with the highest probability of use (PU) for foraging by *Bombus vancouverensis* in early season (ES) and late season (LS) models. Species abbreviations defined in Table 1.

Scientific Name	Average Probability of Use	Abbreviation
ES		
Lupinus sp.	0.255 (±0.05)	LU
Penstemon confertus	0.195 (±0.11)	YBT
Penstemon albertinus	0.118 (±0.05)	BT
Heuchera cylindrica	0.173 (±0.06)	AU
Arctostaphylos uva-ursi	0.132 (±0.05)	KK
LS		
Centaurea stoebe	0.953 (±0.09)	KN
Holodiscus discolor	0.765 (±0.47)	OS
Trifolium repens	0.300 (±0.11)	CO
Verbascum thapsus	0.215 (±0.11)	MU
Orthocarpus tenuifolius	0.157 (±0.05)	OC

Table 4. Mean comparisons of floral resource probability of use (PU) using Tukey's HSD between floral resource only model (FL) and abundance only model (AB). Significance set at p<0.05.

Comparison by flower species	Mean difference	P-value
FL: BR x AB: BR	-0.048	0.0035
FL: BT x AB: BT	0.194	<0.000001
FL: BW x AB: BW	-0.074	0.0024
FL: CO x AB: CO	0.230	<0.000001
FL: CW x AB: CW	-0.052	0.000012
FL: KN x AB: KN	0.188	0.000003
FL: LP x AB: LP	-0.058	<0.000001
FL: LU x AB: LU	0.060	<0.000001
FL: MU x AB: MU	0.223	<0.000001
FL: OC x AB: OC	0.114	<0.000001
FL: OS x AB: OS	0.938	<0.000001
FL: YBT x AB: YBT	0.110	<0.000001
FL: YR x AB: YR	-0.058	<0.000001

Table 5. Mean probability of use by flowering phenology stage and Tukey's pairwise comparison of stage 2 (more flowers than buds) with stage 1 (more buds than flowers) and 3 (more seeds than flowers). Significance set at p<0.05.

Flowering Stage	Mean Probability	Mean Difference (Against Stage 2)	P-value
1	0.0430	-0.048	0.0222019
2	0.0920	-	-
3	0.0407	-0.051	0.0000591

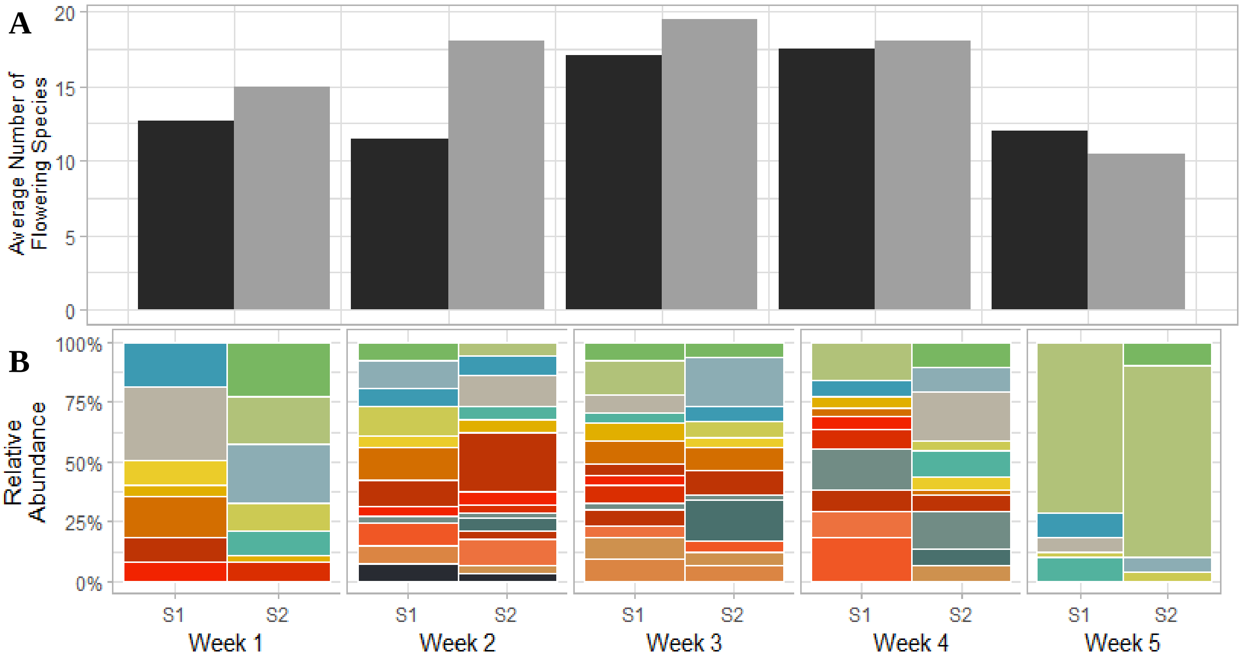

Figure 1. Diversity and community composition of flowering species at the study site over a five-week observational period (June 3-August 10, 2022). (A) Mean number of flowering species (species diversity) in the 50 m plots [black = Plot 1 (S1), grey = Plot 2 (S2)]. (B) Stacked bar chart of community composition of flowering species (evenness) in the 50 m plots by plot (S1 and S2). Each color represents a different species each weeks. Species comprising <5% within a week are grouped into a single category (color).

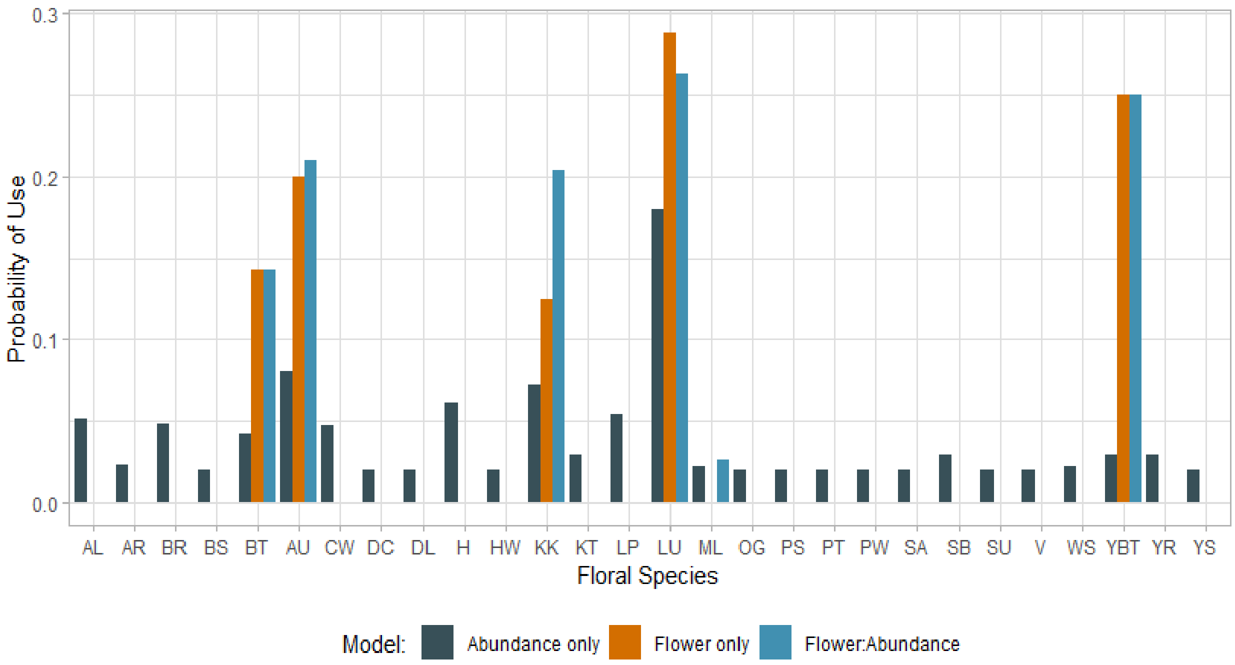

Figure 2. Mean probability of use (PU) for each floral species as estimated by early season (ES) models: flowering abundance only (AB), flower species only (FL) and combined floral resource and abundance interaction model (FL:AB). Plant species abbreviations defined in Table 1.

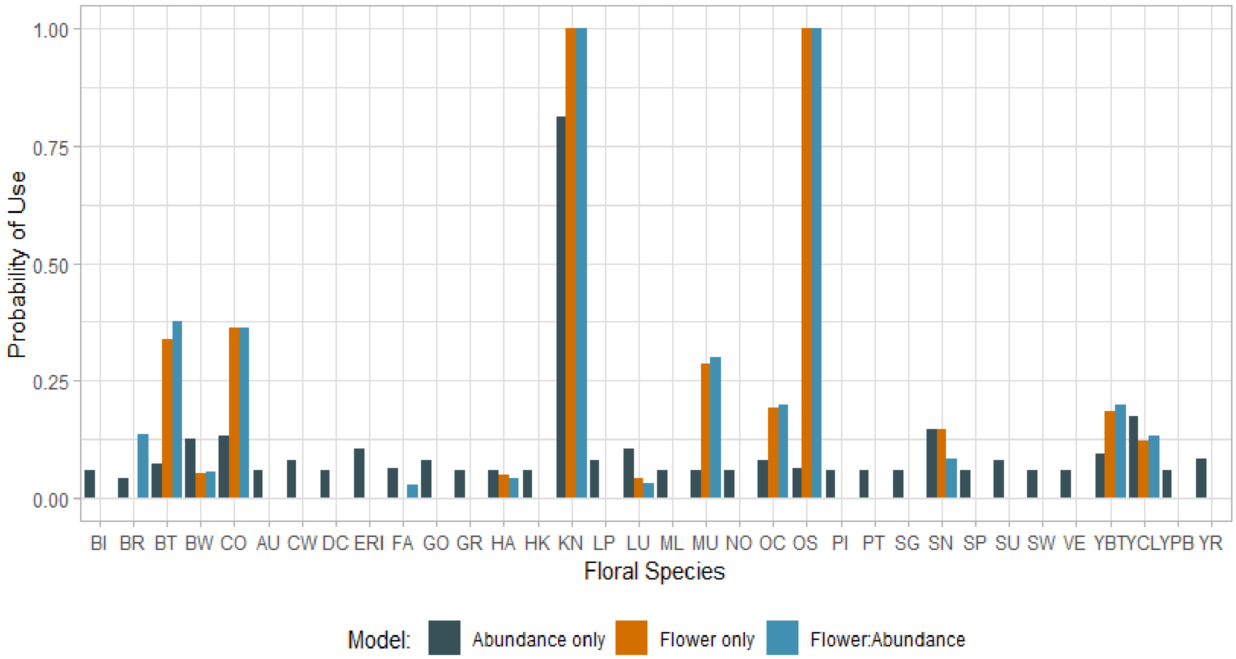

Figure 3. Mean probability of use (PU) for each floral species as estimated by late season (LS) models: flowering abundance only (AB), flower species only (FL) and combined floral resource and abundance interaction model (FL:AB). Plant species abbreviations defined in Table 1.

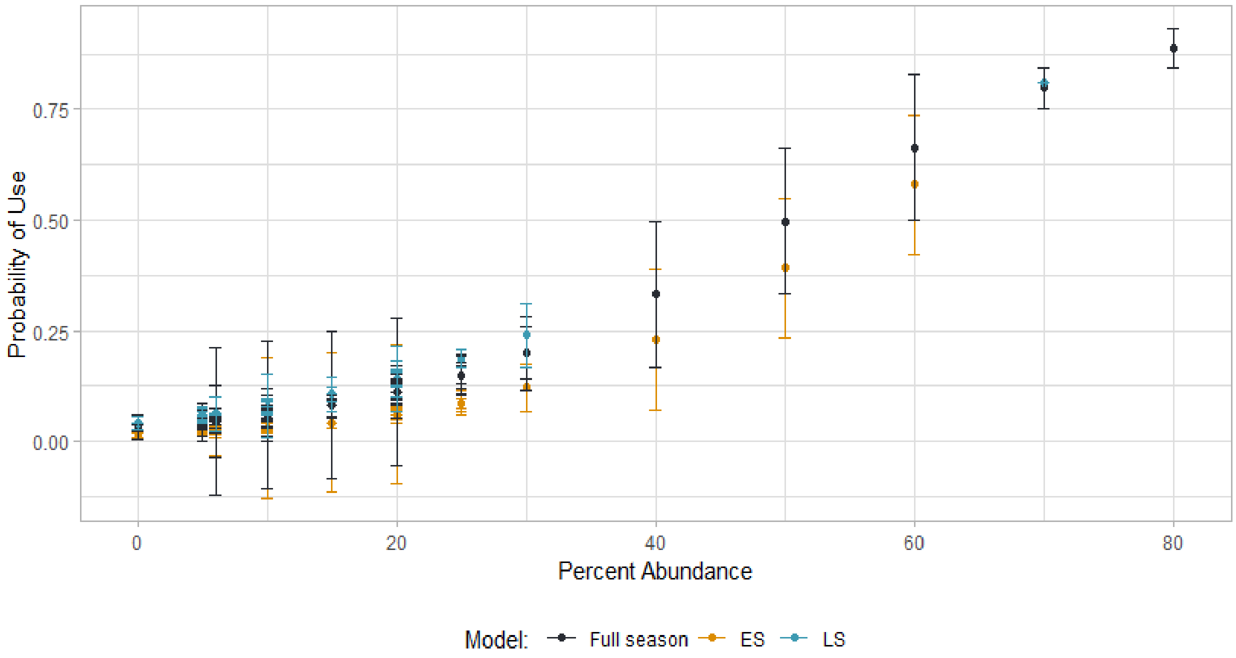

Figure 4. Relationship between probability of use (PU) and percent abundance using abundance only models (AB) for early season (ES), late season (LS) and full season (ES +LS combined). Error bars show standard deviation of mean PU.

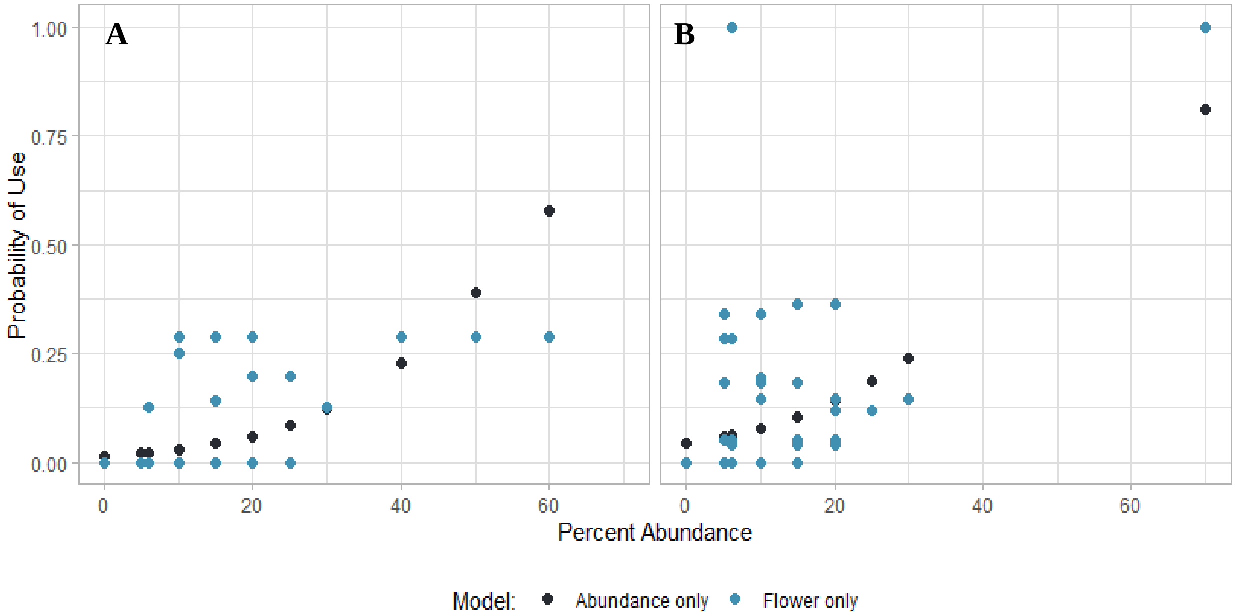

Figure 5. Comparison of early season (ES) (A) and late season (LS) (B) probability of use (PU) of flowering species by *Bombus vancouverensis* and percent abundance of flowering species as predicted by abundance only model (AB) and flowering species only model (FL).

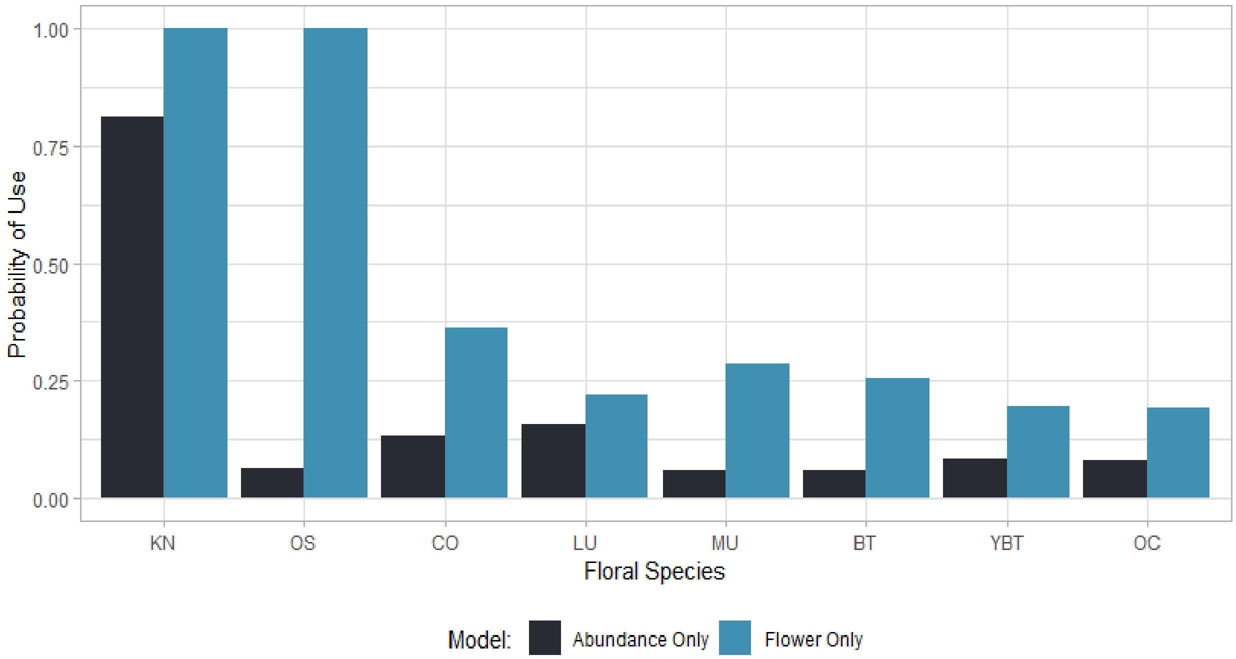

Figure 6. Mean probability of use (PU) for floral resources as predicted by flowering abundance only model (AB) and flower species only model (FL). The eight resources shown had a mean difference >0. Plant species abbreviations can be found in Table 1.

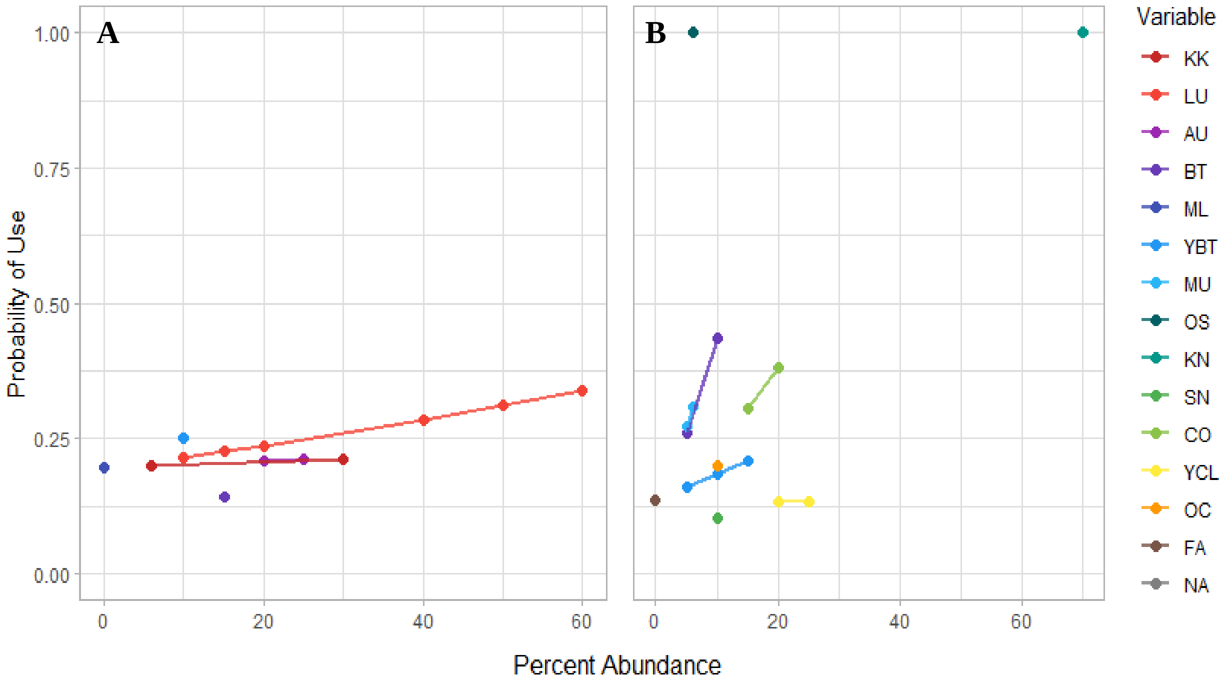

Figure 7. Probability of flowering species use (PU) by percent abundance over the observation period. (A) Probability of use (PU) compared with percent flowering species abundance for early season (ES) observations as predicted by flowering species and abundance interaction model (FL:AB). Species presented surpassed 0.06 PU threshold as determined by ES data distribution. (B) Probability of use (PU) compared with percent flowering species abundance for late season (LS) observations as predicted by flowering species and abundance interaction model (FL:AB). Species presented surpassed 0.1 PU threshold as determined by LS data distribution. Plant species abbreviations defined in Table 1.

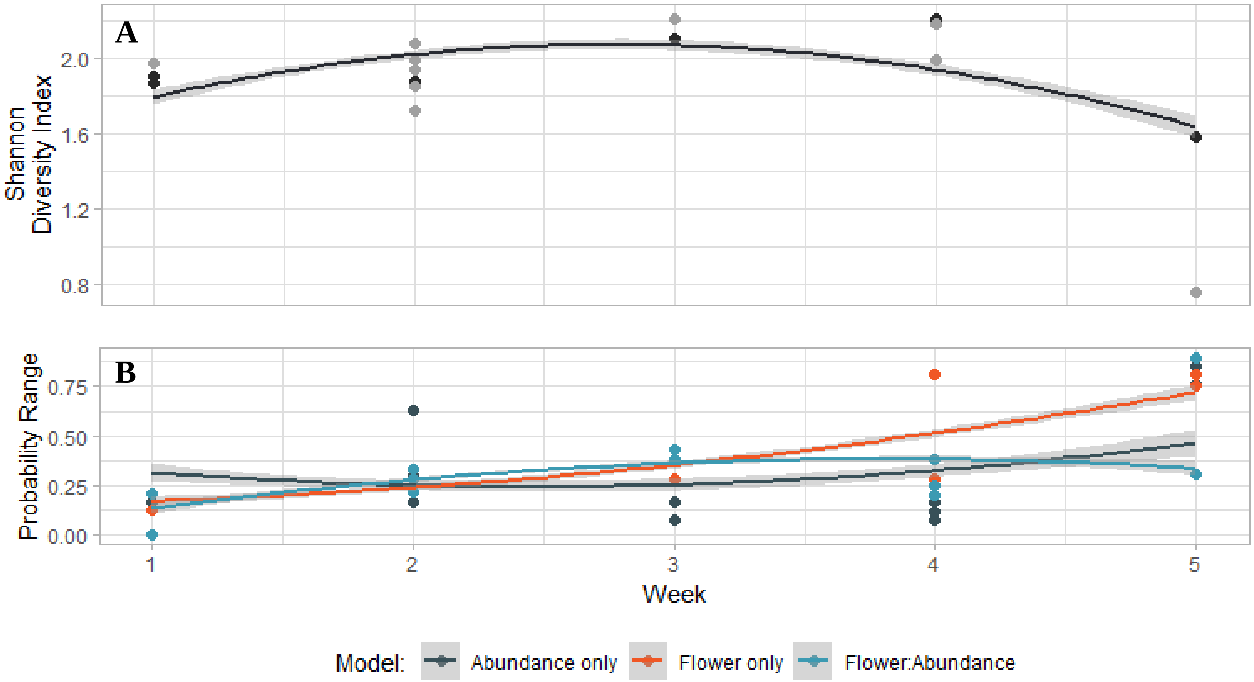

Figure 8. Mean Shannon's diversity index on a daily timestep, averaged by week, per site (June 3-August 10) and range of probability of use (PU) for each model with a polynomial smoothing function and standard error (shading). (A) Shannon's diversity index by week for each site (black = Site 1, grey = Site 2). (B) Calculated range of PU for each model, abundance only (AB), flower species only (FL), and flower species and abundance interaction model (FL:AB).

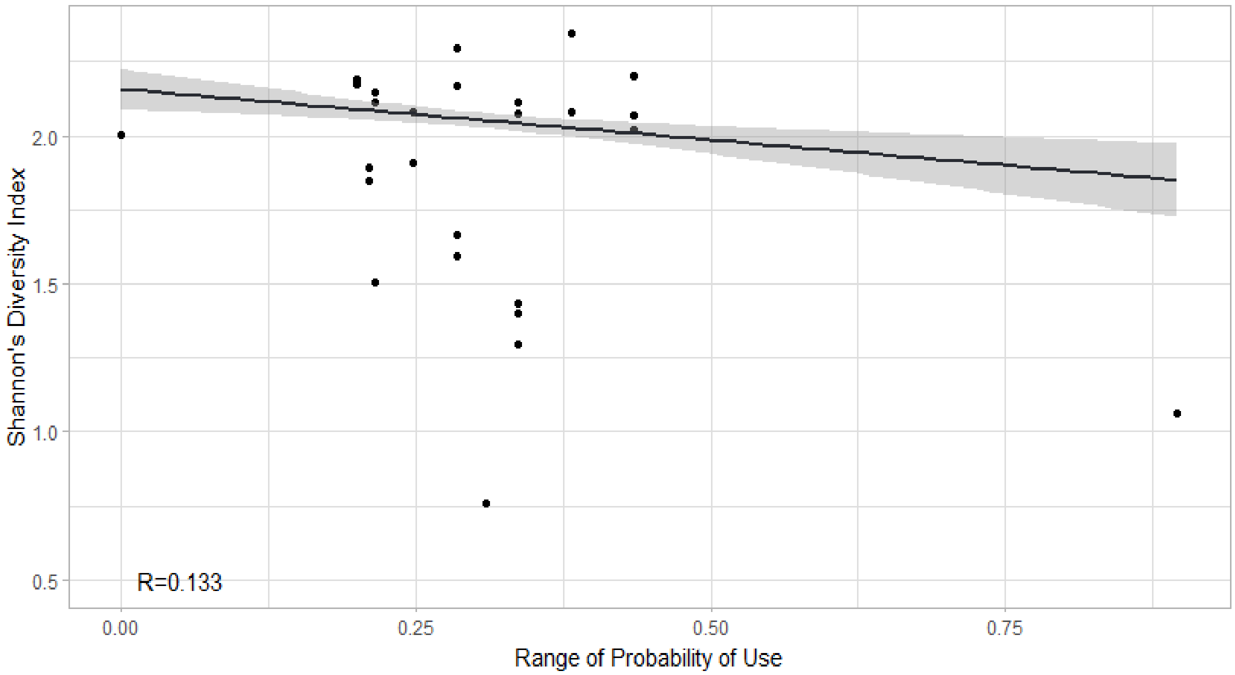

Figure 9. Relationship between daily Shannon's Diversity Index and the range of probability of use (PU) as predicted by the floral species and abundance interaction (FL:AB) model. $R^2 = 0.133$.

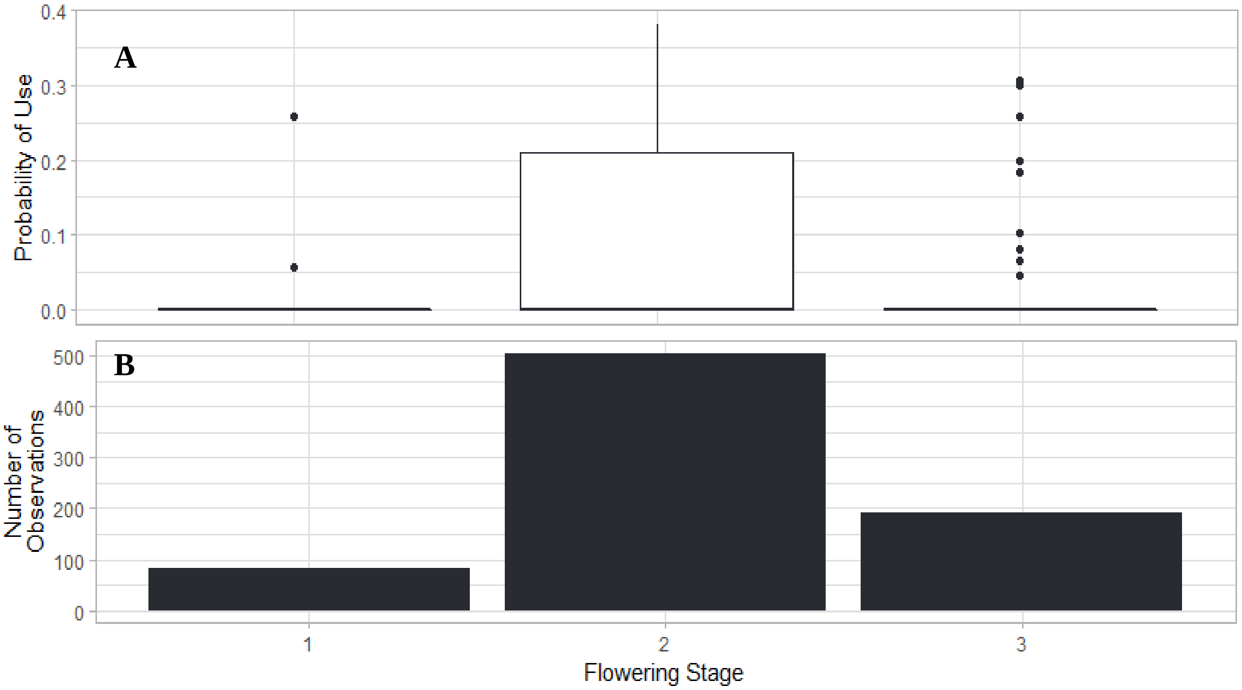

Figure 10. Probability of use (PU) by stage (stage 1= more buds than flowers, stage 2 = more flowers than buds, stage 3= more seeds than flowers). (A) Histogram of the PU with the bolded line as the mean, the box is standard deviation and the points are outliers. An outlier at stage 2 with a PU of 1.0 was removed to allow better graph scaling. Different letters denote statistical significance among means using Tukey's HSD and *p*<0.05. (B) shows the total number of observations of flowering species at each stage.

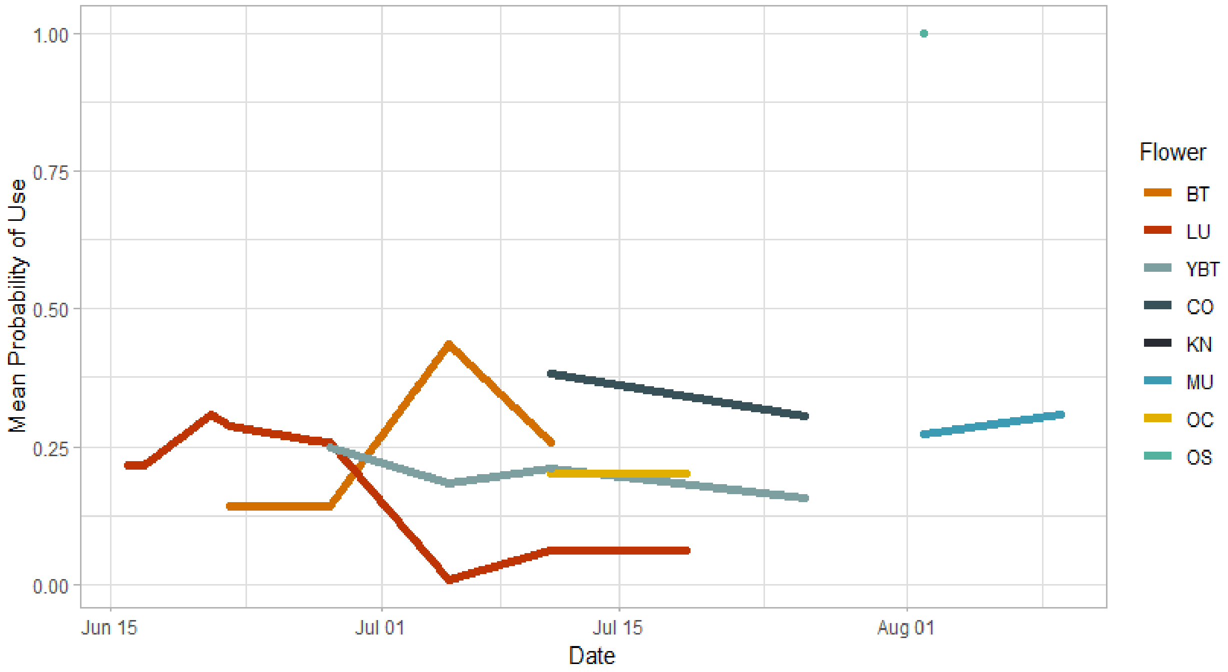

Figure 11. Mean probability of use (PU) of *Bombus vancouverensis* over time for flowering species with the highest mean difference in pairwise comparisons in abundance only (AB) and floral species (FL) models. Mean PUs calculated from flower and abundance model (FL:AB) to account for changes in abundance over time. Species OS and KN overlap with 1.0 PU. Plant species abbreviations defined in Table 1.

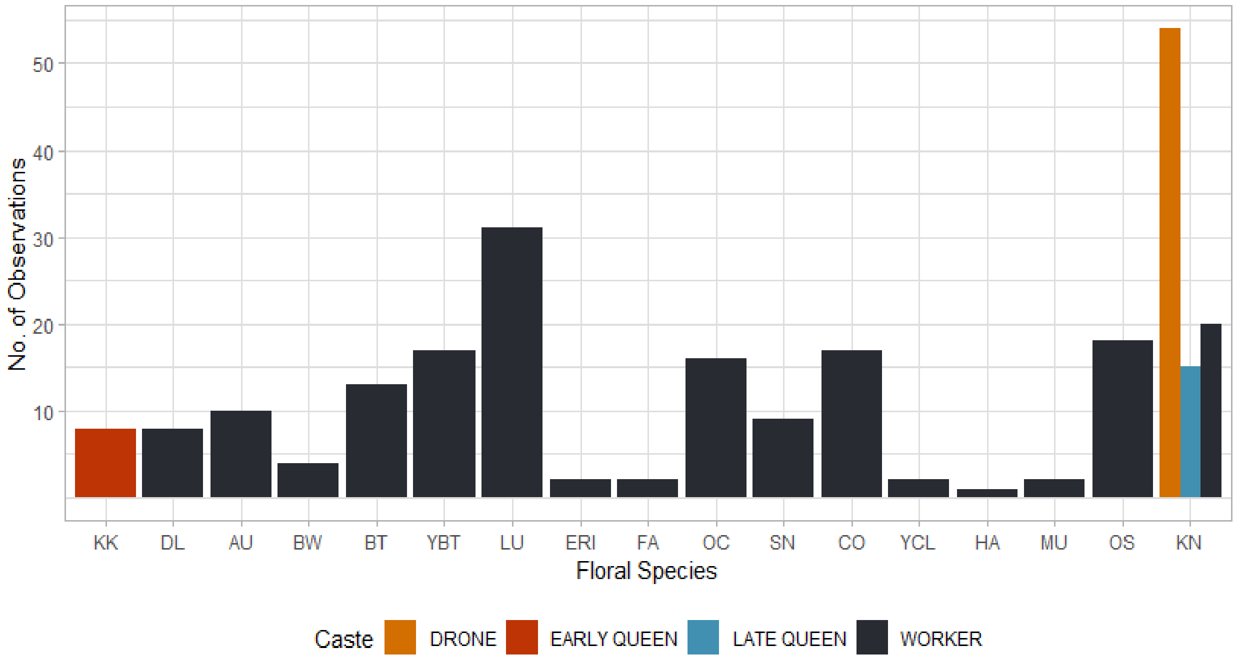

Figure 12. Number of observations of each caste of *Bombus vancouverensis* over the observation period (June 3-August 10, 2022. Castes observed were: post-hibernation queen (early queen June 3-June 6), workers (worker, June 3-August 10), drones (July 26-August 10), and new queens (late queen, August 2-August 10).

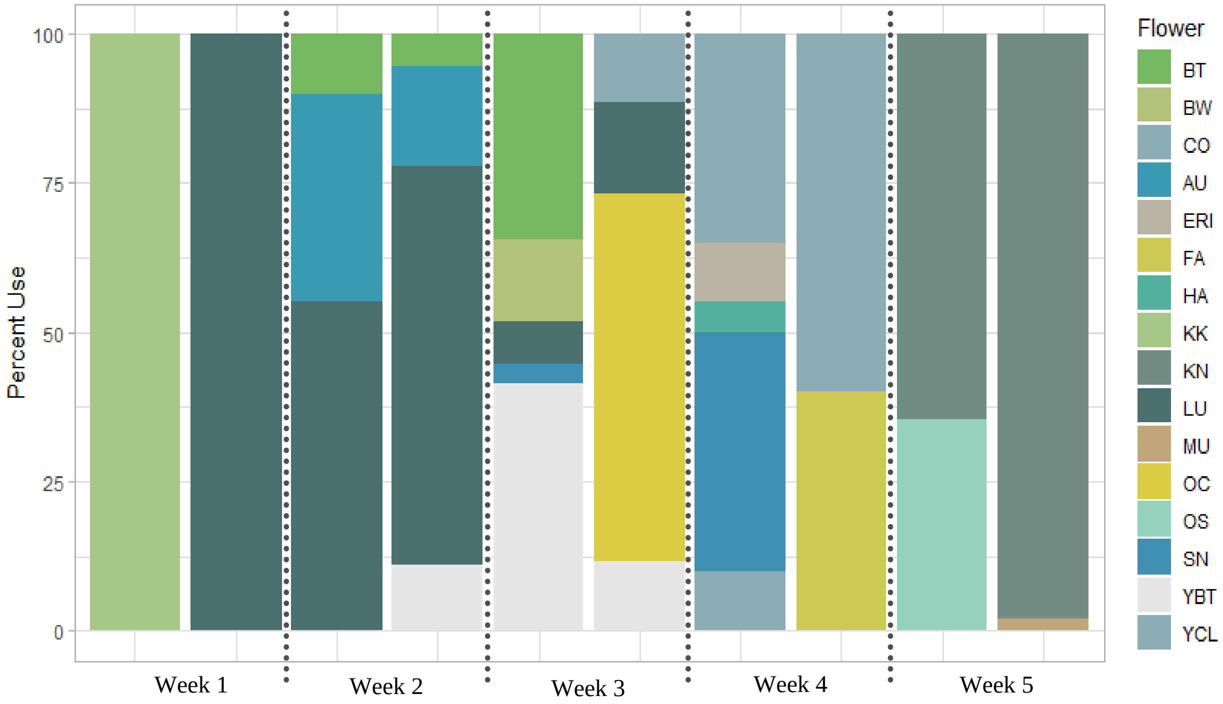

Figure 13. Percent of each flowering species used by B. vancouverensis (all castes combined) by week (June 3-August 10, 2022).