

UNIVERSITY OF CALGARY

How Landscape Filters Local Abundance:

A Test of the Body Size-Foraging Range Hypothesis in Bumble Bees

by

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## Abstract

For central place foragers, foraging range increases with body size. This is true for eusocial pollinators such as bumble bees, for whom body size dictates the maximum distance to which foragers can travel from their nest. Body size should therefore influence the size of landscape over which floral resources are accessible, and indirectly affect local abundance. Given this dispersal constraint, landscape should be an environmental filter for bees based on their body size, resulting in a size-based distribution of abundances in the local bee community reflecting the distance-based availability of resources. In this way, the abundance of bumble bees should reflect landscape composition. I found that the abundance of queens in Southern Alberta was related to an interaction between the amount of semi-natural land cover (a measure of foraging resources for bees) at two spatial scales: near the nest (local; 0 – 500 m) and further afield (broad; 500 – 2000 m). Small queens were more abundant when local availability of semi-natural land was moderate or high, and broad availability of semi-natural land was at low or moderate. The converse was not true: large queens were not more abundant when local resources were poor, and broad resources high. Worker abundance increased with local semi-natural land cover, but surprisingly showed no sign of this relationship being mediated by body size, suggesting that landscape composition influences the body size composition of bumble bee communities primarily during the nest establishment phase by queens. I conclude that the body size-foraging range hypothesis is generally unsupported in my system, but the hypothesis received partial support in the case of small-bodied queen bumble bees being more abundant when amount of local semi-natural habitat was high.

## Acknowledgements

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## **Dedication**

This work is dedicated to my parents, Yvonne and Bart, as well as my brother Logan and sister-in-law Maddie, and my husband Philip. My family has always given me the encouragement to pursue new experiences, the freedom to dream of heights well beyond my capabilities, support when I failed, and the perseverance to keep moving forward. For your love and support I have eternal gratitude.

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## **Epigraph**

Aerodynamically, the bumble bee shouldn't be able to fly, but the bumble bee doesn't know it so it goes on flying anyway.

Mary Kay Ash

## Introduction

### ***Body size and foraging distance***

Much of an organism's biology is a consequence of its body size. Body size is a functional trait that imposes physiological and biophysical constraints, creating limits on an organism's response to environmental and ecological conditions (Blueweiss et al. 1978). In mammals, home range increases with body size for both carnivores and herbivores (Lindstedt et al. 1986; Swihart et al. 1988). This pattern also holds for birds (Schoener 1974, Brown and Maurer 1989) and may hold generally across taxa. In mammals, after statistically controlling for foraging constraints (such as stomach capacity), and daily food consumption, we find that foraging distance and daily movement distance scale similarly to one another with respect to body size (Garland 1983). This suggests that body size is positively correlated with both foraging range and daily movement (Garland 1983).

The relationship between body size and movement may be observed across a broad range of taxa. In central place foragers, such as birds, many mammals, and social insects, body size can determine the distance that individuals move from the central place (Swihart et al. 1988). Thus, the body size of central place foragers may be an important determinant of which organisms or taxa are present in a local community, because it defines which resources are reachable and which are too remote.

The argument that local community may be structured by a functional trait, body size, because of its influence on realized foraging distance, may also be true for bumble bees (genus *Bombus*). Nesting bees are central place foragers whose body size correlates with foraging

distance (Gathmann et al. 1994; Gathmann and Tscharrntke 2002; Greenleaf et al. 2007), and their communities may be structured based on distance-based access to resources.

As a consequence of foraging distance, the body size composition of a community may reflect landscape sorting or selection (which I will call “filtering”) of species (Urban et al. 2008), creating communities where the related trait (body size) is correlated to an aspect of the environment (in this case, availability of habitat at relevant spatial scales) (Vellend 2016). One way to examine communities is to ignore species, and examine the distribution of the traits of individuals relative to environmental variables such as habitat or food availability, also known as composition-environment relationships (Carmona et al. 2016, Vellend 2016). Instead of species richness, examining distributions of functional traits has been proposed as an effective way to examine ecosystem functioning as it emphasizes the value of trait driven processes, while avoiding overemphasis of species responses that may obscure overall ecosystem service responses due to the variability of outcomes related to species loss or gain (Díaz et al. 2006). Likewise, examination of trait based responses may allow for better understanding and prediction of landscape impacts on wild pollinators (Carrié et al. 2017). Landscape structure appears to filter functional groups (Petchey and Gaston 2006). For example, diversity, diet breadth and habitat use in bird communities differ between agricultural and forest landscapes, and the diversity of pollinating bees decline with agricultural intensification according to their functional traits (Tscharrntke et al. 2008). My study extends this work by examining how resource availability at different distances from a location filters bumble bees, based on their body size.

### ***Body size in bumble bees***

Body size varies widely among species of bumble bees (Appendix B, Figure B3), and also varies within species (Alford 1975, Harder 1985, Ramalho et al. 1998, Roulston and Cane 2000, Waddington and Herbst 2013). The queen is largest, typically three times the size of the smallest worker, and the other females in the colony will range between these two sizes (Knee and Medler 1965). Worker size generally increases over the season (Sladen 1912, Frison 1927, 1928, Plath 1934, Richards 1946). Likewise, body size may be conserved for each species (Pellissier et al. 2013), where each species has a range of body sizes (bees from my study appear in Appendix B, Figure B3).

Body size is one important factor in the success of bumble bee colonies (Goulson et al. 2005, Williams et al. 2010), because body size determines the distance that bees can forage from their nest (Gathmann et al. 1994, Gathmann and Tschardt 2002, Westphal et al. 2006a, Greenleaf et al. 2007, Ricketts et al. 2008, Garibaldi et al. 2011), foraging speed (Pyke 1978, Harder 1985) and foraging efficiency (Harder 1983, Spaethe and Weidenmüller 2002, Araújo et al. 2004, Kuhn-Neto et al. 2009, Garibaldi et al. 2013). Larger bees have higher foraging efficiency because they can fly faster between sites, extract nectar from deep flowers faster, and have a larger foraging radius. They also have a better ability to forage earlier in the day, because they can thermoregulate at lower temperatures than smaller bees (Spaethe and Weidenmüller 2002). Larger bumble bees may be less affected by landscape quality as they are able to explore a greater area for patchy food resources (Greenleaf et al. 2007, Williams et al. 2010) and may therefore be less affected by poor food resources available locally (Osborne et al. 2008).

Thus, it would seem that large bees have in all circumstances a clear competitive advantage over smaller bees, but its consequences are deceiving. Smaller bodied bees should have a narrower breadth of diet, and be more spatially constrained to local food (Lindstrom et al. 1994). But small bees are less costly to the colony to produce than large bees (Pyke 1978), so that more can be produced from the same, limited food resources. Hence, when food is locally abundant, smaller bees can be favoured by a numeric (“demographic”) advantage over large bees: the collective foraging gain of many smaller bees can exceed that of fewer larger bees, because each individual larger bee has only a slightly higher foraging gain than each individual smaller bee, relative to its investment costs. Body size can therefore be favoured under different conditions, where high-quality local resources should favour the production of many, smaller bees, and high-quality distant resources should favour the production of fewer, larger bees.

### ***Impacts of differences in body size***

As introduced above, the capacity to travel further for food may allow large-bodied bumble bees to overcome the effects of low habitat quality near their nests, as would happen following disturbances created by agricultural practices such as mowing. Areas with poor local foraging resources may, therefore, favour bumble bees of larger body size, because they can potentially gain access to resources at greater distances. Bumble bees should be sensitive to distance when making decisions about where to forage (Carvell et al. 2012, Westphal et al 2006b), thus large bees should use distant foraging options when the foraging gain of local habitat is poor relative to the travel-discounted benefits of foraging in better, more distant (broad) habitat. For a few species of *Andrena*, a solitary bee genus, body size appears to increase in response to

habitat fragmentation locally (Warzecha et al. 2016). However, it is unclear whether landscape filters in favour of larger body size in social bees (Williams et al. 2010), despite the importance of body size in predicting responses to landscape for other taxa (Henle et al. 2004).

Landscapes can filter (or select) composition of organisms that live within the community, where the distribution of a trait is related to (or reflects) aspects of the niche or habitat (Vellend 2016) within which they reside. Thus, traits favoured by natural selection become locally abundant (Cornwell et al. 2006). In agricultural landscapes, feeding and nesting habitats are provided by (remnant) semi-natural land, such as native prairie, pasture, wetland and forest. These habitats often provide diverse and abundant floral resources that may sustain bumble bee populations across a season (Fussell and Corbet 1991, Corbet 1995, Wray et al. 2014, Wray and Elle 2015). Here, I use the availability and proximity of semi-natural areas as a measure of floral and nesting resources. I assume that semi-natural habitat can be a limiting resource for bees, because it contains food and nest sites both of which are limiting resources for bees (Roulston and Goodell 2011), and thus semi-natural habitat becomes the filter that may affect the relative body sizes present under competition. I examine how landscape composition (at two different spatial scales), in which semi-natural habitat is assumed to provide limiting resources, and therefore the spatial distribution of semi-natural habitat filters communities of bumble bees. This is expected to result in a community-wide distribution of individuals with the relevant traits for the surrounding landscape.

How might a landscape filter work? Omniscient bees should choose to nest at sites that have resources at distances that are appropriate for their body size, and will provide the highest overall net benefit for their colony. For this reason, the availability of resources at

different distances from the nest may filter presence and abundances of bumble bees of different sizes through the mechanism of nest site selection. Foraging areas of large bumble bees are disproportionately larger than those of small bumble bees (Greenleaf et al. 2007), a simple consequence of area increasing as the square of foraging distance, and this means that foraging opportunities increase as a square of each increment in foraging distance. The environmental grain (*sensu* Levins 1968) experienced by larger bees will therefore be finer (with many more choices) than that experienced by smaller bees, (i.e., larger bees experience a much larger portion of the surrounding environment than do smaller bees). Conversely, the environmental grain for small bees will be coarser with fewer choices, given their shorter foraging distances. I expect filtering of bumble bee communities to be based on limiting resources available within shorter foraging distances for bumble bees of all sizes (with small bees responding more strongly, because of their lower costs of production), and on resources available within longer foraging distances for large-bodied bumble bees. A similar hypothesis has been tested in ants, finding that body size dictates the environmental experience (i.e., the environmental grain or scale of their environment) for ants based on body size, but using the landscape's physical characteristics, not distances, as the metric of environmental experience (Kaspari and Weiser 1999). Kaspari and Weiser showed that body sizes mediated the response of ants to their environments, determining the trait composition favoured for communities in varying landscapes.

Using functional traits is a promising approach to explain community responses to an environmental driver such as resource availability (e.g. floral resources), and the effect such responses may have on an ecosystem function or services (e.g. pollination ecosystem services)

(Lavorel et al. 2013). Studies find that the evaluation of functional traits can determine the outcomes for ecosystem functioning more fully than those that focus on species diversity or richness (Díaz et al. 2006), and thus is it of value to examine how the patterns of functional traits shift in response to important environmental drivers.

I propose to examine semi-natural landscape as a filter to explain the distribution of body size in communities of bumble bees in prairie croplands. Body size of bumble bees is linked to habitat amount and fragmentation (Carrié et al. 2017). Landscape amount and proximity therefore may also be important in structuring the body size distributions of communities of bumble bees in an agro-ecosystem. I hypothesize that the environmental driver will be competition for the semi-natural habitat available within foraging range, given that such habitat provides the nesting opportunities and floral resources necessary for bumble bee populations, and that bee populations are most strongly determined by food resources (Roulston and Goodell 2011).

***Context: agro-ecosystems with semi-natural habitat***

The landscape (semi-natural land availability), at multiple spatial scales, may impact bee abundances, depending on their body sizes. What are the relevant spatial scales? For large bees such as bumble bees, landscape within ~1500 m better explains abundance than does a smaller, more “local” landscape (< 300 m) (Benjamin et al. 2014). Thus, access to foraging resources (semi-natural habitat), as determined by body size (and the competitive benefits that differing body sizes present), should act as the environmental filter. This will, in turn, influence the local abundances of bees of different sizes, and therefore the relative composition of body sizes in the community (Fig. 1).

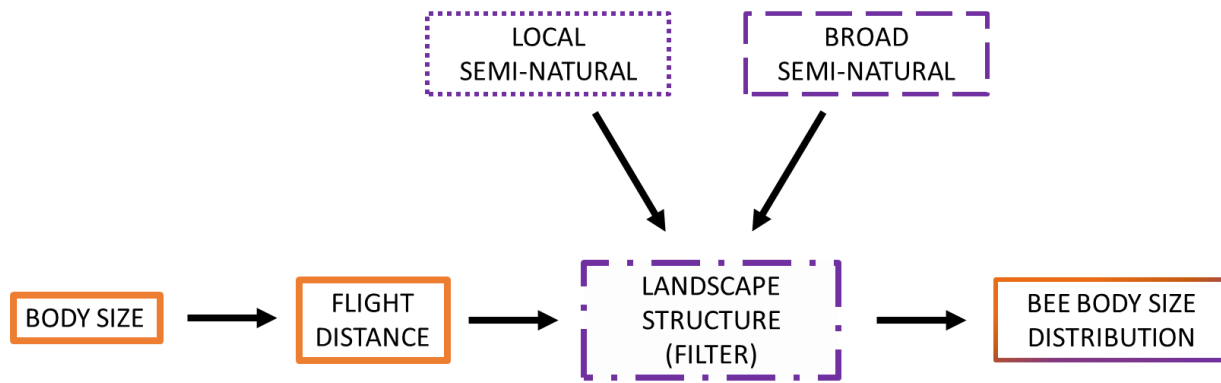


Fig. 1. Abundance of bees can be filtered by the availability of appropriate floral resources, semi-natural (purple boxes) at the local (0-500 m) and broad (500-2000 m) scales, and this relationship is likely mediated by a functional trait: body size (orange boxes), resulting in a landscape-dependent distribution of body size within the community of bumble bees.

Large bumble bees, with large foraging range ( $\geq 1500$  m) can persist in a world of crop heterogeneity and ephemeral flower patches, while other, smaller bumble bees with smaller foraging ranges might not, resulting in higher success related to location for those larger bees (Osborne et al. 2008). The managed honey bees (*Apis mellifera*) and leaf-cutter bees (*Megachile rotundata*) fly further when the distance to a highly-rewarding floral resource increases (Bacon et al. 1965, Beekman and Ratnieks 2000) or when resources are low locally (Steffan-dewenter and Kuhn 2003). Hence, broadly-available food is likely to be important for large-bodied bees, and a shift in body sizes towards larger bees should be detected when broad habitat is better than local habitat (Fig. 2b). Under conditions where bees of large size benefit from being able to access forage that smaller bees are unable to reach, their body size should be selected for and the community filtered towards having relatively more individuals with large body size. Conversely, foraging range declines when floral resources are high locally (Redhead et al. 2016), suggesting that all bees will be successful when there is good quality local habitat, as competition for resources is reduced. However, small-bodied bees should be

more strongly filtered by local habitat quality, given that their environment is a much coarser grain, and they will therefore have fewer choices than large-bodied bees. When local habitat is good, colonies should produce more small-bodied bees, to benefit from having more workers without the cost of investing in a larger body size that is of little dispersal value (Fig. 2a). In this manner, smaller body size is selected for by the local landscape context, where bees of all sizes can benefit from local habitat, but where many smaller bees produce a higher collective foraging gain than do fewer larger bees, resulting in a relative shift in body sizes towards smaller bees. Decoupling the effects of foraging at different spatial scales, based on body size, may help us understand bumble bee abundance across a heterogeneous landscape.

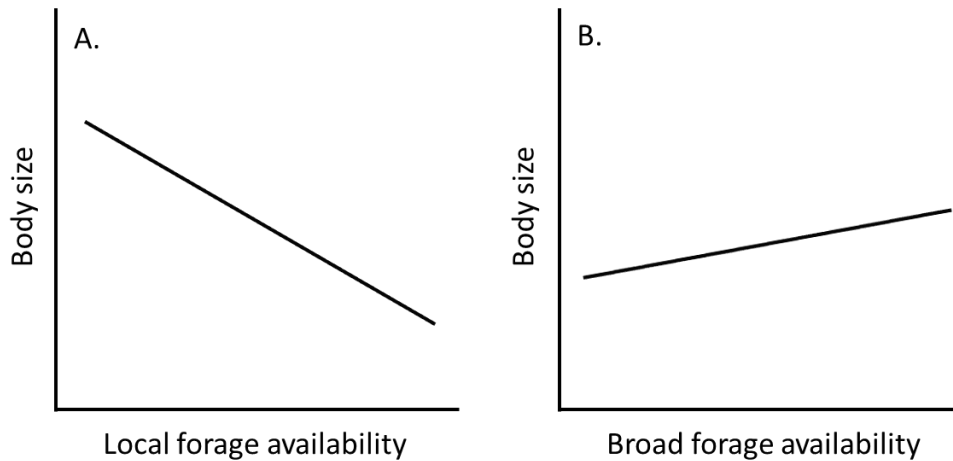


Fig. 2. General predictions for the selection strength of landscape (semi-natural) at the local (0-500 m) and broad (500-2000 m) scales. Strength of the filtering relationship is indicated by the steepness of the slope, where local semi-natural should more strongly filter small bees based on a size-number trade-off (panel A), and larger bees are expected to be filtered less strongly by broad semi-natural based on a size-distance trade-off (panel B).

Over the past century, croplands have experienced significant agricultural intensification intended to increase crop yields, replacing most natural and semi-natural areas (Ollerton et al. 2014). Increases in fertilizer and pesticide inputs have been coupled with spatial intensification

of crop areas intended to maximize the land area available for planting crops. In many areas, for example, the margins of fields, that may have supported floral resources used by bees, have been cultivated to increase production. In some cases, the crops offer an abundant, homogenous floral resource for pollinators, but of short duration (e.g. canola, alfalfa). However, a mass-flowering pulse can also support unsustainably high population densities that may contribute to bee population declines long term (e.g., Galpern et al. 2017). The intensification of agriculture, and the associated loss of natural habitat, may lower the abundance and diversity of pollinators (Hines and Hendrix 2005a; Gixti et al. 2008). Such declines are evident under extreme habitat loss, but community responses to moderate habitat loss are less clear (Winfree et al. 2009; Winfree et al. 2011; Cariveau and Winfree 2015). Conversely, the area of semi-natural landscapes, as well as their configuration and fragmentation contribute to the diversity and abundance of wild bees (Carrié et al. 2017). In Alberta, the conversion of native lands to agricultural production is sufficiently intensive that, for a colony of bumble bees, the landscape within 500 m may have virtually no forage available. Given the uncertainty in floral resources at this small radius, small-bodied bumble bees should be strongly selected to choose nest sites based on the local habitat/forage quantity. Selection should be correspondingly more relaxed on the nest site selection of large-bodied bumble bees.

To understand the importance of body size and its filtering by landscape conditions, I conducted a study in southern Alberta croplands. I use information on land cover composition to relate the size-structured abundance of bumble bees and semi-natural land cover measured at two scales: near (0 – 500 m, henceforth referred to as “local”) and far (500 – 2000 m, henceforth referred to as “broad”) from the point of sampling. I use amount of semi-natural

habitat (quantity), as a measure of habitat and forage quality, to assess how the local size-abundance distribution of bumble bees responded to differences in food availability at local and broad distances from the sampling location.

### ***Hypotheses and predictions***

The body size-foraging range hypothesis, coined by me, posits that the local bumble bee community is structured by body size, a functional trait that should influence the foraging area of a central place forager. Assuming competition exists for a limiting resource (likely flowers) in semi-natural habitat, bees will benefit from increasing amounts of semi-natural land, but the benefit (reflected in relative abundance of bees), should vary by body size. Small bumble bee abundances should be influenced by local habitat availability, due to their short foraging distances (and thus more constrained foraging choices) and the ability of a colony to produce more small individuals given a set amount of resources compared to producing large bodied bees. This means that under conditions where local habitat is highly available, a numerical response with increasing numbers of small bees should be detected, but not necessarily for large bees whose relative advantage is capacity for broad-scale foraging. The larger foraging ranges of large bees allow them to choose among a larger variety of habitat patches (and to more likely to encounter suitable habitat). Given that their likelihood of success will increase given more options and that the gain of far forage may outweigh their extra flight costs, larger bees should be selected for when local habitat is poor because they can access (and will choose to access) habitat further afield. Small bees are simply unable to access resources at greater distances and will not be favoured under these conditions. The hypothesis predicts that relative

abundances of individuals of different sizes should be filtered by, and thus reflected in the quantity of both local and broad habitat availability due to the above mentioned mechanisms.

The predicted interactions are depicted in Fig. 3, which partitions each of two continuous traits (quantity of local landscape, quantity of broad landscape) into 3 levels, producing a 9 panel interaction (i.e., the essence of the body size-foraging range hypothesis). These cells can be arranged according to whether: 1) local habitat quantity is higher than broad habitat quantity (Fig. 3, green panels A, B, and D), 2) local habitat quantity is equal to broad habitat quantity (Fig. 3, orange panels, C, E, and G), and 3) local habitat quantity is less than broad habitat quantity (Fig. 3, purple panels F, H, and I). I predict more large-bodied bumble bees as the proportion of semi-natural is high broadly, and low locally (Fig. 3. purple panels F, H, and I). In this world, local foraging is poor, so the only successful bees would be those with the ability to fly to distant semi-natural habitats, and thus the community should be filtered toward having relatively more large bodied bees who have the competitive advantage of being able to fly further. Bumble bees fly further when local forage is low (Heinrich 1976; Bowers 1985; Osborne et al. 2008), and thus be less affected by habitat quality locally. I predict only the large-bodied bees can accomplish this outcome and are thus filtered for by the landscape under these conditions.

I expect the abundance of small-bodied bees to increase most strongly when semi-natural land cover is higher locally and low broadly (Fig. 3, green panels A, B, and D), because their foraging radius is much smaller, and are able to produce more offspring for a given amount of resources in comparison to large-bodied bees (e.g., Montague et al. 1981 for fruit flies). Thus, I predict a stronger abundance response by small bees than large-bodied bees, since large bees

have more potential choices in forage due to their larger flight distances and are more costly to produce than smaller bodied bumble bees. Of course, large bees can also utilize local habitat, and abundance of all sizes of bees should increase when local semi-natural land is available, with small bees increasing most strongly.

Finally, when local and broad are available in similar amounts at low, moderate, and high levels across the landscape, the filtering for bumble bee size will reflect that seen in typical size-structured communities: log-normal, and the frequency distribution of body size having a unimodal distribution (Preston 1948, 1962, May 1986, Chown and Gaston 2010). Under these conditions, no body size will have an advantage over one another, and thus no filtering will occur. Due to the binned nature of the body size variable (where every body size bin is equally likely when all body sizes are combined across years) in the predictive figure and forthcoming analyses, the expected abundance distribution will be wider, and lower in amplitude across body sizes (Fig. 3, orange panels C, E, and G) than would be an un-binned frequency distribution of body sizes, as the data are evenly dispersed across the x-axis instead of being aggregated around the mean body size value (See Appendix B, Fig B1 and B2).

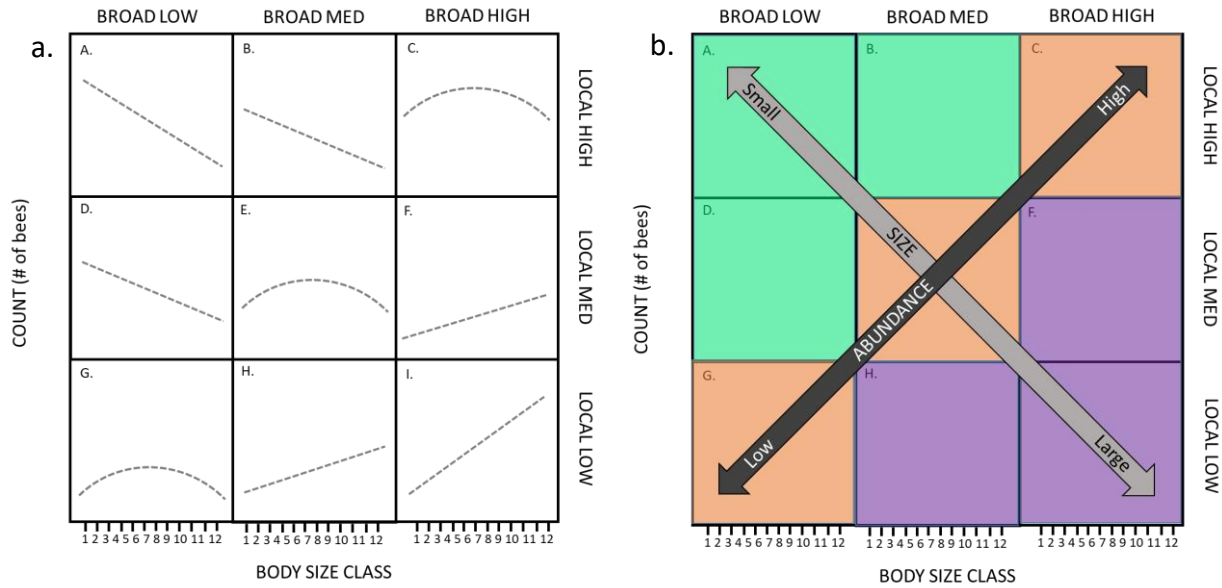


Fig. 3. a: The predicted influence of local semi-natural availability on counts of worker bumble bees (genus *Bombus*) within body size classes. Gray dotted lines represent predicted trends between counts (#bumble bees) of a given body size (bin) with varying conditions of local and broad semi-natural land proportions. Local and broad semi-natural land cover area were held constant when producing these predictions at low (-1), medium (0) and high (1). b. Regions of selection orange (local = broad), green (local > broad), purple (local < broad). Double ended arrows are characterizations of the expected patterns, black (over all abundances), and gray (shifts in body distribution).

I test these predictions in prairie croplands of Southern Alberta, an extensively cultivated area which is dominated by large, regularly spaced crop monocultures, interspersed with semi-natural areas such as pasture, native prairie, wetland, and shrubby/tree covers (Appendix D, Table D1).

## Methods

### Site selection

In the summers of 2015 and 2016, I sampled one hundred sites selected across a gradient in landscape composition of semi-natural, canola, and other land cover types (Fig. 4). About 50% of sites were sampled during both seasons to allow comparison between collection years (Fig. 5), resulting in a total of ~150 sampling sites. Within each year, all sites were  $\geq 2$  km apart to reduce spatial non-independence created by sampling bees from the same colony at the different sites, or overlapping landscapes. Collection data from both years were used for all analyses.

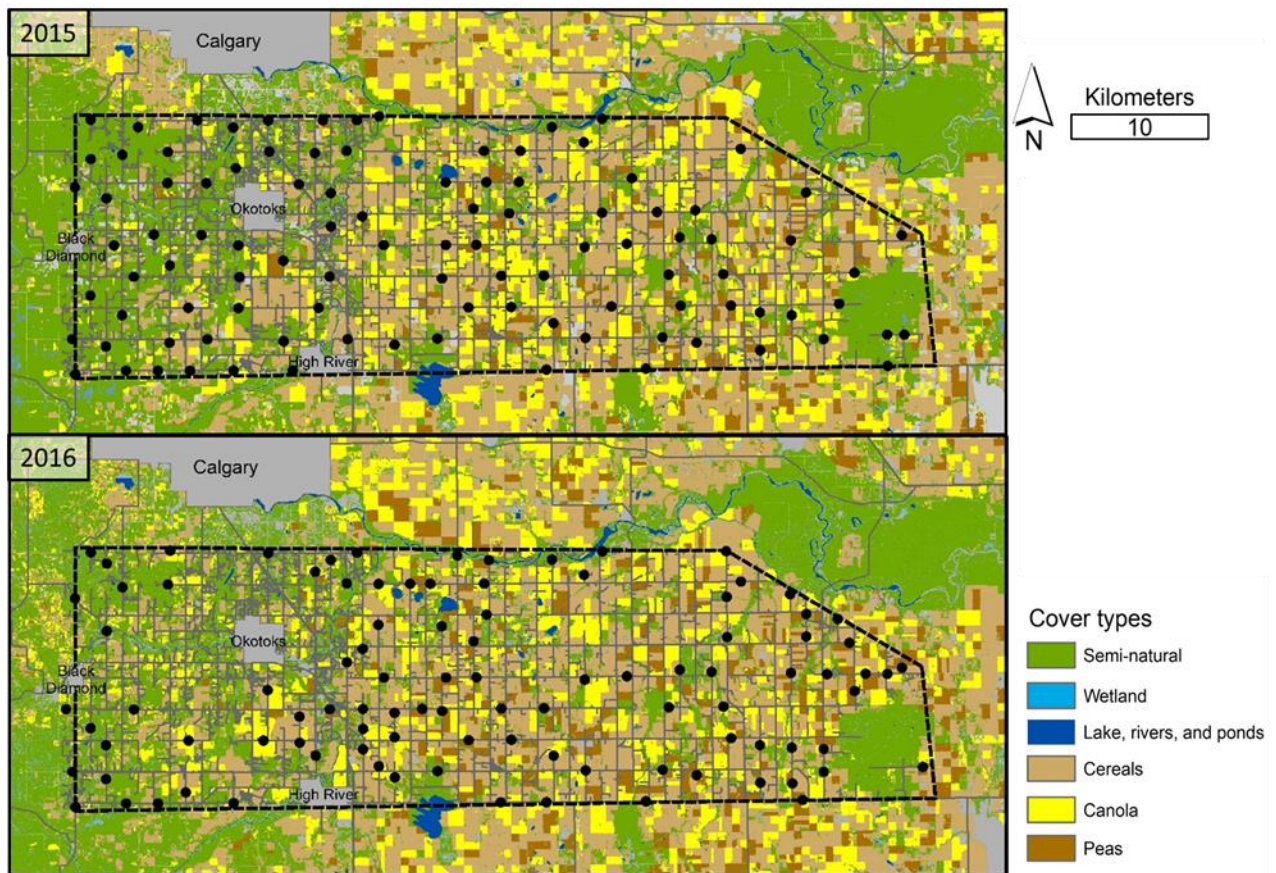


Fig. 4. Map of study area showing semi-natural habitat (green) and other habitat (various colours). Sampling locations indicated by black dots (all are  $\geq 2$  kilometers apart). Study area is delimited by a dashed line. Major municipalities are noted.

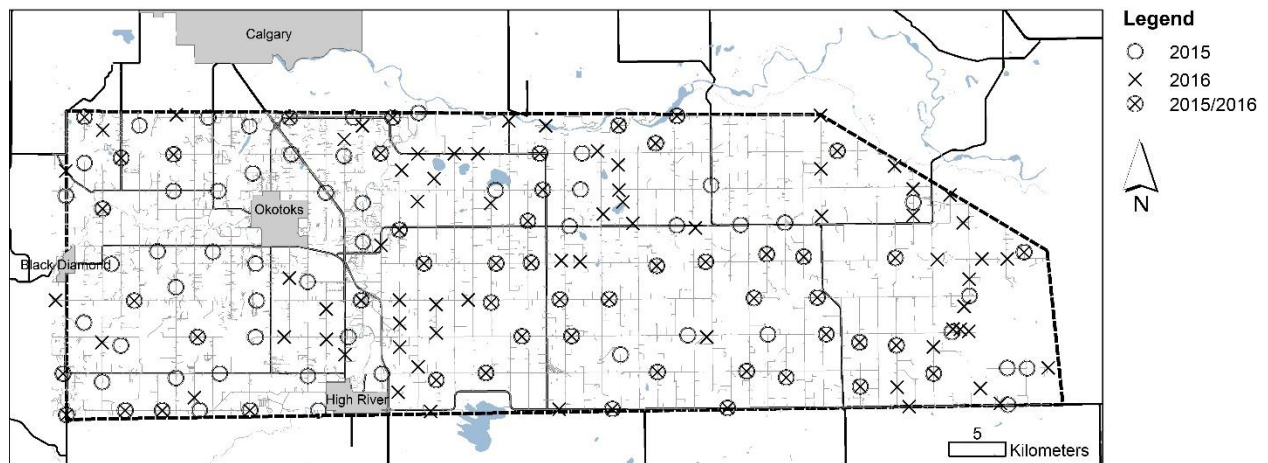


Fig. 5. Map displaying study area of interest with sites sampled in 2015 (O), 2016 (X) and those sampled in both years (both symbols). Major roads and municipalities are noted.

### ***Land cover data***

Land covers surrounding each trap have been recorded by classification of land covers on medium resolution Landsat imagery (e.g. Agriculture and Agrifood Canada Crop Inventory). The AAFC annual crop inventory has an overall accuracy of  $\geq 85\%$  at a spatial resolution of 30 metres overall (AAFC Annual Crop Inventory 2015). To simplify the analysis, only 2016 land cover data were used as it is highly correlated with the availability of semi-natural land in the previous year at the same sites.

Proportion of semi-natural habitat was summarized at two distances from the trap (i.e., from 0 to 500 m, and from 500 to 2000 m) (Fig. 6). I chose the local (0 – 500 m) and broad (500 – 2000 m) annuli based on existing information about foraging distances of bumble bees. There are differences in foraging range between species (Goulson et al. 2005; Osborne et al. 2008) and one reason for this variation may be due to the differences in body size (Benjamin et al. 2014). For large sized species of bumble bees, 1500 m represents an average flight distance (Greenleaf et al. 2007; Osborne et al. 2008; Benjamin et al. 2014), but may forage as far as 1750

m (Walther-Hellwig and Frankl 2000), and much further than small bees (who forage less than 500 m);(Westphal et al. 2003). This local versus landscape dichotomy has been used to compare bumble bee abundance (Hines and Hendrix 2005, Benjamin et al. 2014) and has been proposed as a useful tool for evaluating not only the habitat patch but also landscape level resource availability (Westphal et al. 2003). There is some variability in the definitions of local and broad landscape in previous studies. In one, local was defined by a radius of 300 m and landscape defined as 1500 m (Benjamin et al. 2014), another used 500 m and 700 m (Hines and Hendrix 2005); both studies used land cover radii instead of annuli, an important contrast with my study, where local landscapes were not nested within broad landscapes.

Because my largest bee species (*B. nevadensis*) is much larger than the European bee *B. terrestris* that foraged at 1.5 km, I extended my broad landscape scale to 2 km. These annuli can be used to represent areas that may be considered to characterise local or broad landscape from a central place (Fig. 6). This was done to test the correlation of land covers locally (0 – 500 m) and broadly (500 – 2000 m) with abundance of bumble bees of various sizes. These annuli were then standardized by subtracting the mean and dividing by the standard deviation to allow comparison between them. For comparison of standardized values with actual land cover values, see Appendix D, Tables D2 and D3.

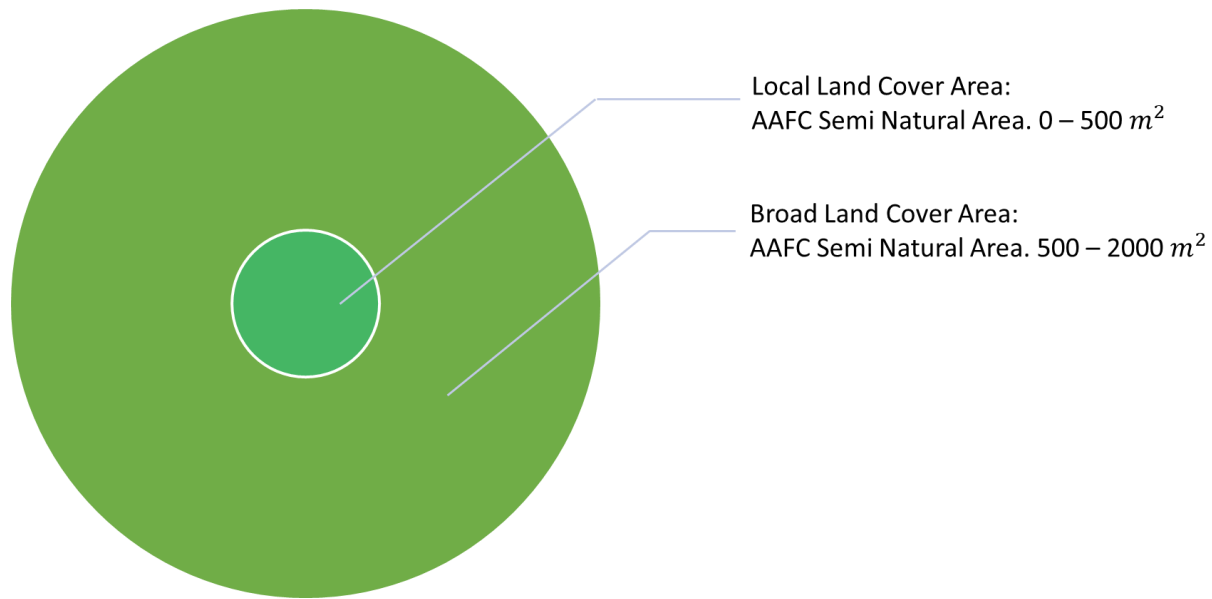


Fig. 6. Visualization of the calculation of land cover, where the broad annulus subtracts the area of the local annulus. Trap was positioned at the center of the diagram.

The amount of semi-natural land within the study area was similar between years 2015 and 2016 (Pearson's  $r = 0.97$  locally,  $0.98$  broadly). Higher variation among years is found in the data at smaller radii (0 – 100/250 m), and is due to the low resolution of data points available within the area.

### ***Insect sampling and processing***

At all sites, traps were placed in ditches between fence lines and roads (Fig. 7). Blue vane traps were used as they are attractive to native pollinators such as bumble bees (Schmidt et al. 2006; Stephen and Rao 2007). Diluted food grade propylene glycol (70%) was used as a trapping fluid as it is effective both for resisting desiccation and enhancing preservation of invertebrates (Schmidt et al. 2006). Traps were emptied every 7-10 days, and set continuously from 29 June until 14 August in 2015 and 27 June until 28 August in 2016. The period was chosen to capture *Bombus* throughout its phenology, while missing as many of the earliest spring nest-establishing queens as possible. Once retrieved, samples were stored in 125 mL mason jars with 70% diluted ethanol to clean and preserve the specimens until further



processing.

Fig. 7. Photograph showing typical set up of sampling location with Blue Vane trap and sign located in ditch approximately 1-2 meters from the fence. Traps are placed in 3-4 inch holes to prevent toppling by weather or interference. Photo by Sarah Johnson.

Following each field season, bumble bee specimens were curated and incorporated into the University of Calgary's invertebrate museum. Each bee was cleaned, prepared, pinned, labelled with the procedure recommended by Sam Droege (2015) and identified to species. Body size of each pinned specimen was measured as intertegular distance (ITD) using digital calipers (World Precision Instruments™). Intertegular distance has been widely used as a correlate of overall body size in many bee genera (Cane 1987, Hagen and Dupont 2013). Bumble bees were divided into castes (i.e., males, workers and queens). Among female bumble bees, the ITD and body length (vertex to distal tip of the abdomen) was used to determine if the bee was a worker or a queen, as we expect a bimodal distribution of body size within each species due to differences in caste size among female bumble bees. Length was used a second estimate of caste (Allen et al. 1978), and these two metrics were inspected to ensure bimodal separation of the two castes.

### ***Statistical Analysis***

Analysis was performed in R v. 3.4.2 (R Development Core Team 2017). Model assumptions were met for all models including checking for homogeneity and normality of variance of residuals, collinearity of predictors, over dispersion, and outliers. Response variables are presented as the count of bumble bees for a given trapping location, body size, and year. Only female bees were analysed in this study, as only they are central place foragers.

Within a female caste, body size was approximately normally distributed (For examples, see Appendix B, Fig. B4). To maximize statistical power relative to body size, this variable was subdivided into bins with equal numbers of observations for a given caste and year (Appendix B, Table B3). This resulted in body size bins that were broad at the body size extremes, and

narrow near the median body size, with the consequence that each body size bin was equally likely occur. However, it is important to realize that an equi-probable distribution of body sizes from a summed sample (i.e., my entire summer's catch) is not the same as an equi-probable body size distribution from individual sites. Appendix E shows some of the body size distributions observed at particular site-year combinations, which were never equi-probable (i.e., flat).

I analysed abundance of worker and queen bumble bees using the MASS package in R (Venables and Ripley 2002). Abundance data were analyzed separately by female caste (workers, queens), to allow for testing of caste-specific responses to environment. Generalized linear models assuming a negative binomial distribution of counts were used to explore the relationship between abundance and size bin, year, and the interaction of the two landscape variables (semi-natural habitat at local or broad scales), using the length of the trapping period as covariate to account for variations among sites in the total length of trap deployment. Semi-natural land is a composite variable that summarizes pasture, native prairie, wetlands, trees, and shrub area (Appendix D, Table D1). Species with low total abundance (<35 individuals) were removed from the data set. Model fits were visualized using the visreg package in R (Breheny and Burchett 2017).

I predict that when local habitat is more or less available than broad habitat (Fig. 3b; green and purple panels), this will result in abundance by body size trends. After fitting models using body size bins as a predictor, in order to quantitatively describe trends in the model fits, I estimated the correlation between the mid-body size in a bin, and the predicted count of bees at that body size at various combinations of local and broad landscape levels (low, medium, and

high) using JMP (v. 13 ). I used Spearman's correlation because it is useful for illuminating relationships that are not necessarily linear. I use this approach to evaluate the evidence for body size and abundance predictions in Fig. 10.

## **Results**

### ***Abundances from sampling***

Blue vane trapping yielded 20726 native bees in 2015, and 25,523 in 2016. 10,954 or about 24% of these were bumble bees, of which 9,557 were females and the focus of my subsequent analyses (Appendix A, Table A1). There were 6,706 females trapped in 2015, and 2,851 in 2016, yielding 23 species of bumble bee (14 of which were common enough to be used for analysis);(Appendix A, Table A2). The most common species caught were *B. rufocinctus* (red-belted bumble bee) and *B. borealis* (northern amber bumble bee), representing 42% and 37% of all bumble bees collected in 2015 and 2016 respectively (Appendix A, Table A2). Uncommon bumble bees captured included *B. terricola* (yellow-banded bumble bee) which is currently listed as vulnerable, with much conservation effort focusing on this species in eastern Canada, and *B. suckleyi* (Suckley's cuckoo bumblebee), a parasitic bumble bee species currently listed as critically endangered (Hatfield et al. 2015).

### ***Body size patterns***

Body size in bumble bees varied within and among species, as well as between and within female castes (Appendix B, Fig. B3). Since there is more variation among species than within species and this would mask total variation as deviations from a species mean, I will not include species in subsequent analyses. In my analysis, I focused on a trait based approach (Vellend 2016), looking at body size-abundance trends among queens and workers.

### ***Abundance of workers***

Abundance of workers increased with local (0 - 500 m) proportion of semi-natural landscape (Fig. 8), and was higher in 2015 than in 2016 (Table 1). Neither body size, nor broad

semi-natural landscape were related to worker abundance (Table 1). While there are significant differences in worker abundances due to locally available habitat and among years, these have no interaction with body size. Hence, for workers, the body size-foraging distance hypothesis is unsupported.

Table 1. Analysis of worker abundance using a type III ANOVA to test the importance of terms in the model. McFadden’s pseudo  $R^2 = 0.048$  for whole model fit. Landscape variables in the model are local (standardized proportions of semi-natural from 0 – 500 m from trap) and broad (standardized proportions of semi-natural from 500 – 2000 m from trap).

	Df	$\chi^2$	P
bodySizeClass	11	6.78	0.82
local	1	5.45	0.0196 *
broad	1	1.75	0.19
year	1	14.28	<0.0001***
bodySizeClass:local	11	4.73	0.94
bodySizeClass:broad	11	4.88	0.94
bodySizeClass:local:broad	12	5.31	0.95

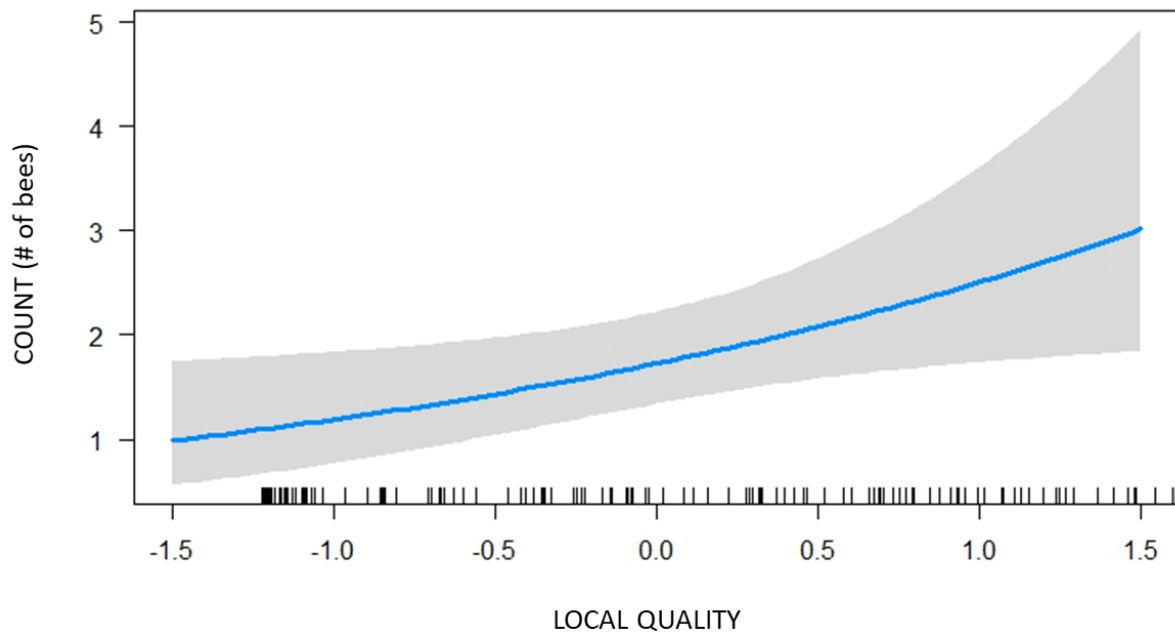


Fig. 8. Partial regression plot showing the influence of local semi-natural availability (quantity) on abundance of worker bumble bees (for model presented in Table 1). Line represents mean and bands represent the 95% CI. Local semi-natural is standardized, see Appendix D for actual values. Tick points on axes show data points.

### ***Abundance of queens***

Body size interacted with broad proportions of semi-natural landscape and local proportions of semi-natural landscape (Table 2, Fig. 9 and 10) to explain queen abundance. This result begins to illuminate patterns that are otherwise unclear from inspecting unadjusted abundances across, years, caste, or season (Appendix C).

Table 2. Analysis of queen abundance using a type III ANOVA to test the importance of terms in the model. McFadden's pseudo  $R^2 = 0.069$  for whole model fit. Landscape variables in the model are local (standardized proportions of semi-natural from 0 – 500 m from trap) and broad (standardized proportions of semi-natural from 500 – 2000 m from trap).

	Df	$\chi^2$	P
bodySizeClass	11	7.41	0.76
local	1	6.91	0.0085 **
broad	1	2.90	0.088
year	1	285.6	<0.0001***
bodySizeClass:local	11	19.80	0.0481 *
bodySizeClass:broad	11	8.86	0.64
bodySizeClass:local:broad	12	37.72	<0.0001***

Overall, queen abundance was higher when local semi-natural availability was high (Table 2, local term, Fig. 9).

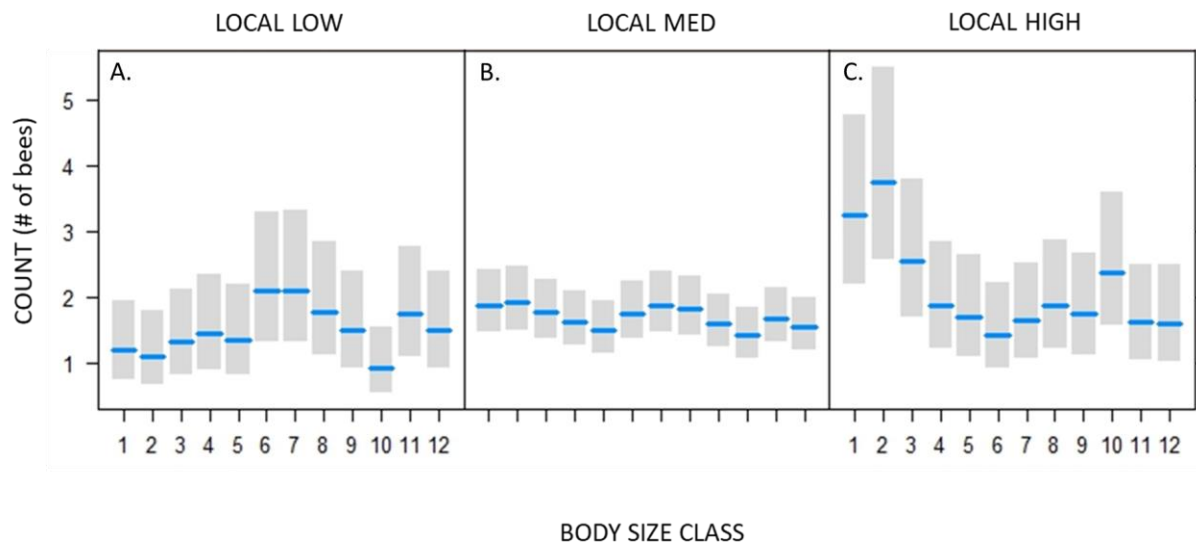


Fig. 9. The influence of local semi-natural availability on counts of queen bumble bees (genus *Bombus*) within body size classes. Blue lines represent the least square mean count and bars represent the 95% confidence intervals. Local semi-natural land cover area was held constant when producing these predictions at low (-1), medium (0) and high (1) standardized values (corresponding to actual values of 5.98 Ha, 32.65 Ha, and 59.31 Ha), and broad semi-natural was held constant at a moderate level (0);(actual value of 448.03 Ha). Also see Appendix D. The figure visualizes the 2-way interaction term in the model reported in Table 2.

Most importantly, larger bees were not more abundant in conditions where broad landscapes were better than local ones (Fig. 10, panels F, H, and I). This result does not support the body size-foraging distance hypothesis. In contrast, smaller bees were more abundant when local conditions were better than broad ones (Fig. 9, panel C and Fig. 10, panels A, B, and D), supporting the hypothesis. Finally, in cases where local and broad landscapes were equivalent, and where I predicted a unimodal (log)normal distribution of body sizes, where this pattern would manifest itself as a gently unimodal pattern due to the binning of the body size variable (Fig. 3, orange panels C, E, and G). We see such a pattern (weakly) in a single circumstance (both local and broad of low quantity, Fig. 10, panel G), contrasting with unadjusted body sizes that were unimodal (For examples see Appendix B, Fig. B4). Indeed,

moderate local and broad landscapes also appear to tilt the body size distribution in favour of small bees (Fig. 10, panel E). Overall, the body size-foraging distance hypothesis was unsupported in favourable broad conditions, but supported in favourable local conditions.

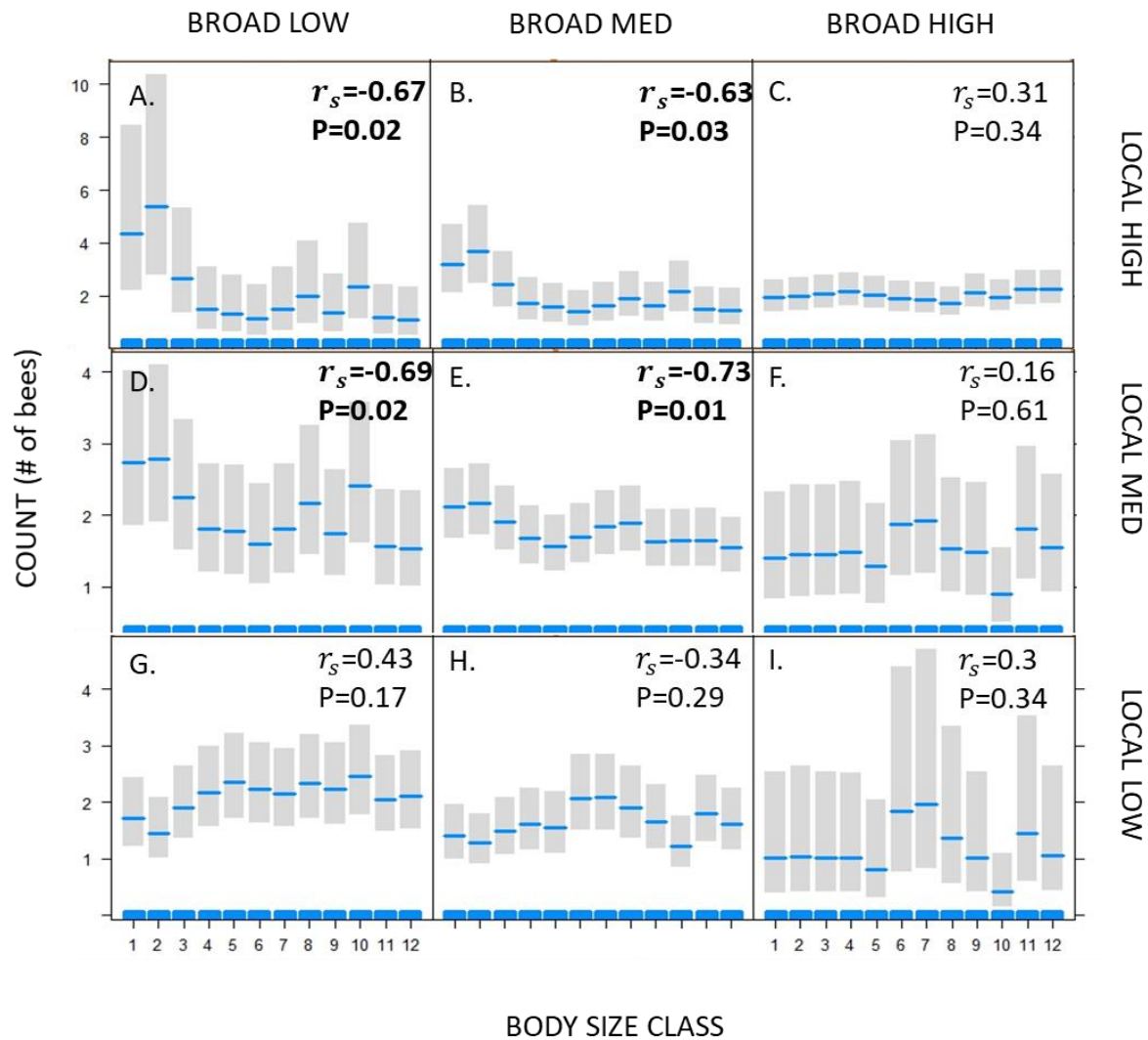


Fig. 10. The influence of local and broad semi-natural availability on counts of queen bumble bees (genus *Bombus*) within body size classes. Blue lines represent the least square mean count and bars represent the 95% confidence interval. The areas of local and broad semi-natural land cover were held at specified values when producing these predictions, namely at low (-1), medium (0) and high (1) standardized values. These standardized values correspond to 5.98 Ha, 32.65 Ha, and 59.31 Ha of the local variable, and 169.34 Ha, 448.03 Ha, and 726.71 Ha of the broad variable. See also Appendix D. Spearman's correlations and their P values appear in the upper right of each box (n=12 for each correlation), significant correlations are in bold text. The figure visualizes the 3-way interaction term in the model reported in Table 2.

## Discussion

The body size-foraging distance hypothesis predicts that the distribution of bee size will reflect habitat amount at local and broad scales in particular patterns. I predicted that there will be more large bodied bees when there was more semi-natural habitat at greater distances from a central place than it was nearer to the point of sampling (i.e., broad > local);(Fig. 3, purple panels F, H, and I). And, I predicted the opposite when semi-natural habitat was more available nearby than it was further away (i.e., local > broad);(Fig. 3, green panels A, B, and D). Finally, when availability of semi-natural habitat was similar at both scales (i.e., local = broad), the body size distribution was expected to be unimodal (Fig. 3, orange panels C, E, and G). For queens, I found no evidence that broad habitat availability favoured larger bees, but, at the other end of the distance continuum, local habitat availability selected for small bees, and that under homogenous conditions (when local = broad), the predicted log-normal distribution appears to be weak or missing. For workers, availability of semi-natural habitat had no effect on size, but local semi-natural habitat significantly affected abundance. I will now discuss the support for the hypothesis overall, followed by each prediction and result in turn.

### ***General support for landscape as a filter for bumble bee abundance***

The general question motivating this work was whether the landscape in southern Alberta is a filter for bumble bee size. The question was addressed by asking if landscape shapes the size distribution of a community, by mediating the distance-based accessibility of resources. For queens, but not workers, body size interacted with landscape conditions (at both local and broad). This result was detected through landscape-associated changes in the relative abundances of bees of different sizes (i.e., the body size shape distribution). Other

research has also found that landscape filters the body size distribution of bees (Benjamin et al. 2014), and other Hymenoptera (Kaspari and Weiser 1999; Warzecha et al. 2016), and that body size depends on habitat (and therefore resource availability), likely because it mediates foraging distance (Warzecha et al. 2016; Carrié et al. 2017). Local and broad semi-natural availability were not equally important in filtering body size of bumble bees. Local habitat was more important than broad habitat, because local always impacted abundance, while broad semi-natural alone never influenced the abundance of bees, and showed a minor influence in the local by broad interaction in queens. I conclude that local semi-natural has a stronger filtering effect than broad has, and that broad has at best a weak filtering effect, but only for very large bees (queens).

My thesis contributes uniquely to the understanding of bee size response to habitat availability by explaining the *distribution* of body sizes instead of the change in mean value (as done in Kaspari and Weiser 1999 and Benjamin et al. 2014). I suggest this as a better method for explaining functional traits, as it more powerfully describes the entire breadth of a community, instead of portions of this relationship as done in previous literature. Recent studies similarly propose that studying trait distributions is a better method for understanding community trait responses to environments that are heterogeneous in nature because it accounts for the probability of observing a given trait value under a set of conditions (Carmona et al. 2016). In essence, this approach described by Carmona and colleagues captures the multidimensional nature of functional trait ecology, is useful for understanding impacts of changing environmental conditions, and predicting community outcomes across spatial scales. Other studies support this finding, suggesting that it allows for robust prediction of how traits

respond to landscape impacts in wild pollinators specifically (Carrié et al. 2017). Because of this novel approach, I've been able to demonstrate a new response that contrasts with results of other work for bees, a local response, and little to no broad response of body size to landscape.

### ***Study predictions***

The first prediction that relatively larger bees when broad semi-natural landscape was more available than local (Fig. 3, purple panels F, H, and I), was unsupported. This non-support was surprising, considering previous findings that large bees responded more strongly to broad scale landscape composition than to local or field scales (Benjamin et al. 2014). Similar to my result, Benjamin et al. also found that the local x broad interaction term explained bee abundance, but the outcome for large bees differed between our studies. They found that semi-natural habitat measured at similarly broad scales had a strong, positive effect on large bodied bee abundance, while I found no such effect. One difference between this study and my own is that they used semi-natural radii instead of annuli for their landscape variables; i.e., their broad variable is a sum of all area within the broad distance. I instead used annuli, which subtracted the local distance from the broad distance to ensure any response was specifically due to landscape further away from the trap. I think the response Benjamin et al. found may be an artefact of local semi-natural land occurring twice in their model, in both the local and broad variables, making the two variables non-independent. Local habitat is always important for central place foragers (Carrié et al. 2017), and thus by including it in their broad landscape variable, the fit of the model will be tighter as the variables are correlated (for an example of this phenomenon in studies of self-thinning, see Weller 1987).

Another important contrast is that the definition of semi-natural differ between our studies. Benjamin and colleagues define semi-natural land as all non-agricultural land and is largely comprised of forested areas. However, non-agricultural land is much more heterogeneous in my study area, where it is composed of forest and shrub lands, wetland, pasture, and native prairie that provide a greater variety of floral resources (Table 1), which I quantified independently (instead of using a proxy measure, the inverse of agricultural land, as used by Benjamin et al.). This heterogeneity may result in semi-natural land differing in quantity across the landscape, producing variation in its foraging value for large bees that may weaken the power to statistically detect its filtering effect. Lastly, I used a different maximum distance for broad semi-natural; if this was an inappropriate distance for the largest bees (i.e., the biggest bees routinely flew further than 2 km), then the lack of trend would be a logical result. Benjamin et al. used 1500 m as their maximum radius, while I used 2000 m because the largest forager in my study area is bigger than the largest forager they considered (and thus has a potentially greater foraging distance). To consider this issue, I ran models with various thresholds (1000 m, 1500 m, and 3000 m), and none provided better fit for the data or clearer trends.

The result is also surprising because the likelihood of finding better forage is higher when the organism has more choices, the so-called “sampling effect” (Tilman et al. 1997), which should be the case for large foragers. Given that foraging range increases with body size in bees (Gathmann et al. 1994, Gathmann and Tschardtke 2002, Greenleaf et al. 2007, Ricketts et al. 2008, Garibaldi et al. 2011), we expect that as the choices of accessible forage increase, the probability of finding high quantity food increases, although the cost of traveling further

and the physical difficulty of sampling among more distant alternatives constrains the potential value of distant foraging. Stochasticity in foraging success of individual bees should lessen when they can sample from larger areas, which may matter if colonies have a requirement whose probability of their not meeting motivates their foraging (Cartar 1991). Under conditions where broad is better than local, large-bodied bumble bees should be more successful as they have more forage choices, at these scales, than small-bodied bees, potentially allowing for higher foraging gain or more predictable foraging gain, or both.

An explanation for finding no effect of broad landscape on large bees may be that traps capture large bumble bees nesting far away who are at the limit of their foraging range, and thus the broad landscape experienced by its nest is different from the one I have categorized around the trap. In this study, the trap was the unit of sampling, and thus the landscape as I have defined it is the trap landscape, not that of a particular colony or nesting site. I expected the sample of bumble bees captured to be largely representative of the local community from that area, however, it is possible that a greater number of large bees from distant areas were caught in the trap, experiencing slightly different landscapes, and weakening the landscape effect for large bees.

The second prediction of my study, that small bees will be favoured when local habitat was better than broad (Fig. 3, green panels, A, B, and D) was supported for queen bumble bees. Local habitat interacted with both broad habitat and body size to affect abundance of queen bumble bees, but not workers. For queens, local semi-natural conditions favoured small bumble bees under moderate and high local conditions, when broad semi-natural landscape was of low or moderate quantity (Fig. 10, panels A, B, D, and E). Small bees are less costly to

produce than large bees, and should therefore be favoured under high-quality local conditions (i.e., local > broad), based on size-number trade-offs (Smith and Fretwell 1974, Montague et al. 1981). Thus, size in bumble bees should trade off the superior foraging intake of larger bees against the numerical benefits of smaller bees, and will likely result in changing distributions of bee size as colonies will allocate energy to more numerous, small bees, so long as the forage they can access is sufficient (Pyke 1978). Under these conditions, a demographic advantage of more small offspring should outweigh the foraging advantage of large offspring in shaping community structure for bumble bees.

I found evidence that local (0 – 500 m) semi-natural land explained the abundance of both workers and queens, regardless of their body size. Bumble bees, as central place foragers, are expected to be sensitive to distance in making decisions about where to forage (Carvell et al. 2012, Westphal et al 2006b). As such, distant foraging options should be used only when the foraging gains offered in local habitat are poor relative to the travel-discounted benefits of foraging in more distant (broad) habitat. Bumble bees have reduced how far they forage when resources are high locally (Redhead et al. 2016), and semi-natural habitat at the local scale is also correlated with bumble bee abundances in commercial agricultural areas of the Eastern USA (Benjamin et al. 2014). Thus, local resources should be most important in filtering abundance, and my results for local bees entirely fit these expectations, now with an additional element: body size.

Under homogenous conditions, and thus no predicted filtration by the landscape for specific bumble bee sizes, I expected abundance distributions to be slightly unimodal in shape (Fig. 3, orange panels C, E, and G). Across a community, individual body size should also be

normally distributed, meaning relatively higher numbers of average sized bees, and a few with very large or small sizes, in absence of selection by other factors (Chown and Gaston 2010). My expectations under homogeneous conditions did not hold. For queens at high or low, and equal levels of semi-natural land (Fig. 10, panels C and G), the abundance has no clear trend. Under moderate and homogenous levels semi-natural (Fig. 10, panel E), with opposite influences by the landscape for body size (a local-small body size effect, and no effect of broad), there is filtering for small-bodied bees. One reason may be that bumble bees, as central place foragers, are strongly filtered by local habitat, and thus small bees have the advantage, regardless of broad semi-natural conditions of equal quality. It may be that that homogenous conditions are not representative of balanced filtering from local and broad habitats, since broad habitat had no discernable signal. This inequality of filtration by the landscape could result in distributions that tilt toward small body size, as observed (Fig. 10, panel E). Regardless, these cases where local semi-natural habitat is equivalent to global semi-natural habitat is not pertinent to my central issue: testing the foraging range-body size hypothesis.

### ***Drawing inference from an uneven distribution of landscape conditions***

One reason why there was no increase in large-bodied bees in cases of high levels of semi-natural habitat at the broad scale may be because there were little to no data available for conditions where local semi-natural locally is low, and broad is high (Appendix D, Fig. D1). The converse was also true, meaning that a part of the parameter space (Figure 4, panel A), remain unexplored. While the study design pre-selected sites that spanned a range of landscape features, it was difficult to avoid positive local-broad correlations in a world where landscape conditions are likely to exhibit spatial auto-correlation at the scales I am examining. In other

words, if semi-natural availability at the local scale increases, it is likely that broad availability will also increase, confounding the effect of the broad scale impact on trapping rates (Appendix D, Fig. D1). In future work, choosing a set of sites where local and broad semi-natural conditions were uncorrelated in aggregate (see for example, Fahrig et al. 2011) would likely improve the power to detect this relationship; such site selection has been used previously in smaller, manipulation-based pollinator studies with a focus on body size (Benjamin et al. 2014).

### ***Caste differences in body size responses to landscape***

The landscape filtering of body size in bumble bees differed strikingly between castes. Previous studies of bumble bee foraging range, landscape influences, and body size often disregard caste (Benjamin et al. 2014), generalize across bumble bees as a single taxon (Carvell et al. 2012; Benjamin et al. 2014), consider only one caste (Spaethe and Weidenmüller 2002; Redhead et al. 2016), or assess only a few common species, not the entire community (Walther-Hellwig and Frankl 2000; Redhead et al. 2016). In this section I discuss the ecology of each caste briefly, and reflect on my findings in this light.

The abundance distribution of queen bumble bees may be attributable to behaviour during nest establishment, as they are highly mobile and may respond to features of the landscape during this phase. Queens trapped during this study are those who successfully overwintered, and searched for a suitable nesting location, or performing the first bouts of foraging before producing their first brood. Beyond these activities, queens remain in their nests to produce and tend to their offspring (Heinrich 1979). Given the importance of choosing areas with sufficient foraging resources, bumble bee queens should choose locations with resources at distances that are appropriate to their size (or at least foraging resources that are

detectable or predicted at the environmental grain they operate within). My study demonstrates that landscape filtration has acted on queens, with the implication that the abundance of bees of different sizes reflects the relative success they had in finding nest sites and establishing nests given the surrounding habitat.

The abundance distribution of worker sizes did not appear to be the result of landscape filtering. Worker size is determined by the amount they are fed as larvae (Sutcliffe and Plowright 1988, 1990; Pereboom et al. 2003; Pelletier and McNeil 2003). Given my finding that queens are filtered by local habitat quantity, not by broad, it follows that the workers produced will have no body size relationship with broad habitat. Logically, worker abundance should be largely structured by local habitat quantity, with a weaker influence of body size, which is what I found for this caste (Table 1).

However, local is a relative term. As mentioned above, another explanation for the lack of landscape signal in size-based abundance of worker bumble bees may be that my definition of local and broad with respect to foraging radii were not meaningful to workers, who are smaller than queens. Smaller bees should forage more locally, and my local – broad breakpoint of 500 m may have been too large to detect landscape filtering of workers. I designated variables based on *a priori* knowledge of bumble bee foraging ecology and methodology from previous literature. *Post hoc*, I explored alternative models (with a series of different scales for the landscape variables), and found none of the models to be significantly better fitting, had similar AICs, and similar patterns to the model outcomes I present in this paper.

### ***Body size as a functional trait***

Mechanisms underlying this work have individually been supported in previous studies. For example, body size determines foraging range for bumble bees (Gathmann et al. 1994; Gathmann and Tschardtke 2002; Greenleaf et al. 2007; Williams et al. 2010). Landscape quality at differing scales determine bee abundance (Benjamin et al. 2014), and heterogeneity in forage patches locally can determine colony success for bees of small size (Osborne et al. 2008). Studies prior to my thesis have not teased apart the influence of body size and distance-based habitat availability, with feeding resources ultimately influencing abundance of bumble bees (Roulston and Goodell 2011).

However, conceptual frameworks have been developed that similarly propose to link multiple trophic systems (e.g. plant-pollinator interactions) via trait-based approaches. These frameworks propose that functional traits (that directly respond or correlate to environmental drivers) mediate the environmental impacts on the ecosystem services provided by plants. This has specifically been proposed as an effective way to study pollinator responses (Lavorel et al. 2013) to habitat disturbance and management. My study mirrors the approach suggested in this framework, where the environmental driver is semi-natural land amount and configuration, body size the functional trait directly associated with semi-natural habitat, and the abundance of bumble bees a proxy measure of the ecosystem service (more bumble bees = more pollination).

Finally, this study examines a single functional trait, body size, but it is important to recognize that other traits potentially structure communities of bumble bees. While my study focused on body size, this work can easily be expanded to include other traits across gradients of conditions. Data on other traits such as tongue length can easily be acquired. Tongue length is an important functional trait for determining a bee's ability to feed on flowers. Bumble bees tend to exhibit strong matching between floral depth and their tongue length, a match that is important for maximizing foraging gain (Plowright and Plowright 1997). This trait has potential for exploring similar relationships to body size, but through the lens of foraging gain (flower access) instead of movement (foraging distance).

## **Conclusion**

The intention of this study was to evaluate whether abundance is filtered by the landscape at two different scales which I have called local (0 m – 500 m) and broad (500 m – 2000 m), and to determine the importance of body size in mediating this relationship. By testing the body size-foraging range hypothesis, I wanted to decouple the effects potentially favouring different body sizes foraging at different spatial scales, to better understand bumble bee abundance across a heterogeneous landscape. I expected: 1) increased semi-natural land availability at broad scales would filter bumble bee community assemblages such that there were relatively more bees of large body size, when local forage availability is low, 2) high local semi-natural land would filter for more bumble bees with small body size, when broad availability is low, and 3) the abundance-body size distribution would be unimodal when local and broad semi-natural conditions are similar. Overall, the body size-foraging range hypothesis was only partially supported. Increases in local semi-natural land appears to consistently filter for small queen bumble bees, but not workers. This suggests that landscape filtering of body sizes occurs when queens are searching for and establishing nests. Surprisingly, broad semi-natural land did not appear to select for larger bees of either caste. Local semi-natural increases numbers of worker and queen bumble bees overall. Overall, the body size-foraging range hypothesis received only partial support, specifically for the case of small body-bodied queens who were more abundant when local resources were high. This thesis exhibits a new application for examining the importance of body size in bumble bees, and provides unique insight into the response of body size distributions to habitat quality that has not previously been demonstrated.

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## Appendices

### Appendix A.

This section provides information about insect collection, detailing species that were collected during this study.

Table A1. All species documented across sampling years (2015 and 2016), separated by caste (male, queen, workers), and species. Species with less than 35 individuals indicated by \*.

species	male	queen	worker	total
<i>B. balteatus*</i>	0	0	1	1
<i>B. griseocollis*</i>	0	0	1	1
<i>B. appositus*</i>	0	1	1	2
<i>B. flavidus*</i>	1	1	0	2
<i>B. melanopygus*</i>	0	0	2	2
<i>B. sylvicola*</i>	1	4	1	6
<i>B. suckleyi*</i>	7	1	0	8
<i>B. cryptarum*</i>	4	0	6	10
<i>B. terricola*</i>	9	6	15	30
<i>B. frigidus*</i>	7	4	22	33
<i>B. insularis</i>	25	23	0	48
<i>B. huntii</i>	22	5	34	61
<i>B. flavifrons</i>	4	13	62	79
<i>B. fervidus</i>	6	29	53	88
<i>B. mixtus</i>	4	9	103	116
<i>B. occidentalis</i>	17	14	101	132
<i>B. nevadensis</i>	13	101	58	172
<i>B. bifarius</i>	48	17	155	220
<i>B. vagans</i>	68	25	163	256
<i>B. centralis</i>	285	95	491	871
<i>B. ternarius</i>	178	161	925	1264
<i>B. borealis</i>	520	1785	1484	3789
<i>B. rufocinctus</i>	200	861	2763	3824

Table A2. Counts of bumble bees distributed across sampling years (2015 and 2016), caste (male, queen, workers), and species. Species with less than 35 individuals removed.

species	Year					
	2015			2016		
	Caste					
	male	queen	worker	male	queen	worker
<i>B. bifarius</i>	6	8	56	42	9	99
<i>B. borealis</i>	375	1253	955	145	532	529
<i>B. centralis</i>	130	71	319	155	24	172
<i>B. fervidus</i>	1	18	38	5	11	15
<i>B. flavifrons</i>	3	6	40	1	7	22
<i>B. frigidus</i>	7	1	14	0	3	8
<i>B. huntii</i>	7	5	14	15	0	20
<i>B. insularis</i>	9	12	0	16	11	0
<i>B. mixtus</i>	3	7	77	1	2	26
<i>B. nevadensis</i>	10	90	44	3	11	14
<i>B. occidentalis</i>	9	7	69	8	7	32
<i>B. rufocinctus</i>	135	640	2167	65	221	596
<i>B. ternarius</i>	76	130	549	102	31	376
<i>B. vagans</i>	30	14	101	38	11	62

## Appendix B

This section contains descriptive information pertaining to bumble bee body sizes including how the data was partitioned into bins, and the distribution of body size within species.

Table B1. Description of body size bin data for bumble bee castes.

Body Size Class	Queens		Workers	
	Min (mm)	Max(mm)	Min (mm)	Max(mm)
1	3.32	4.05	2.42	3.04
2	4.06	4.39	3.04	3.14
3	4.39	4.53	3.14	3.23
4	4.53	4.65	3.23	3.30
5	4.65	4.76	3.30	3.37
6	4.77	4.88	3.37	3.44
7	4.88	5.00	3.44	3.51
8	5.00	5.18	3.51	3.59
9	5.18	5.32	3.60	3.74
10	5.32	5.49	3.74	3.98
11	5.49	5.65	3.98	4.26
12	5.65	6.77	4.26	6.30

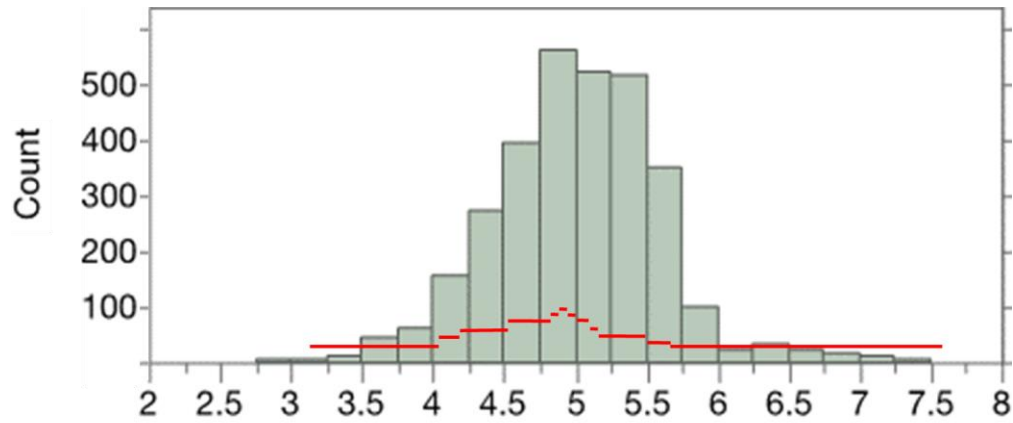


Figure B1. Histogram displaying raw counts of body sizes for queen bumble bees. Red bars indicate approximate binning used for data analyses, as outlined in Table B1.

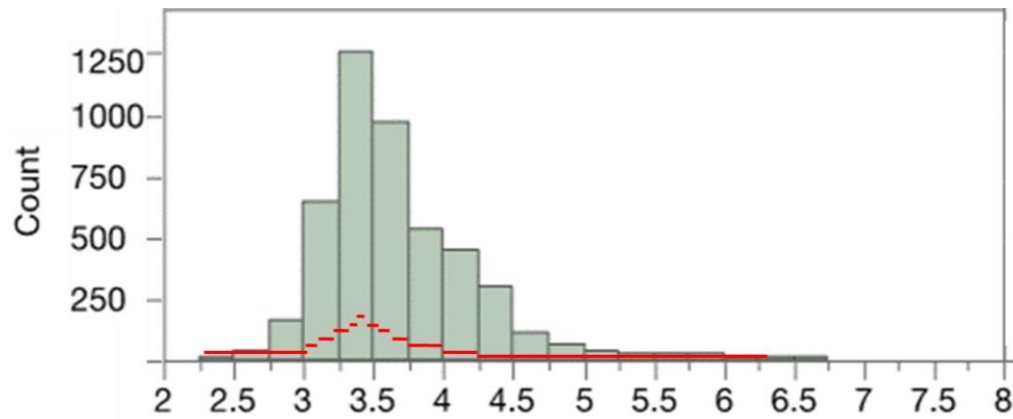


Figure B2. Histogram displaying raw counts of body sizes for worker bumble bees. Red bars indicate approximate binning used for data analyses, as outlined in Table B1.

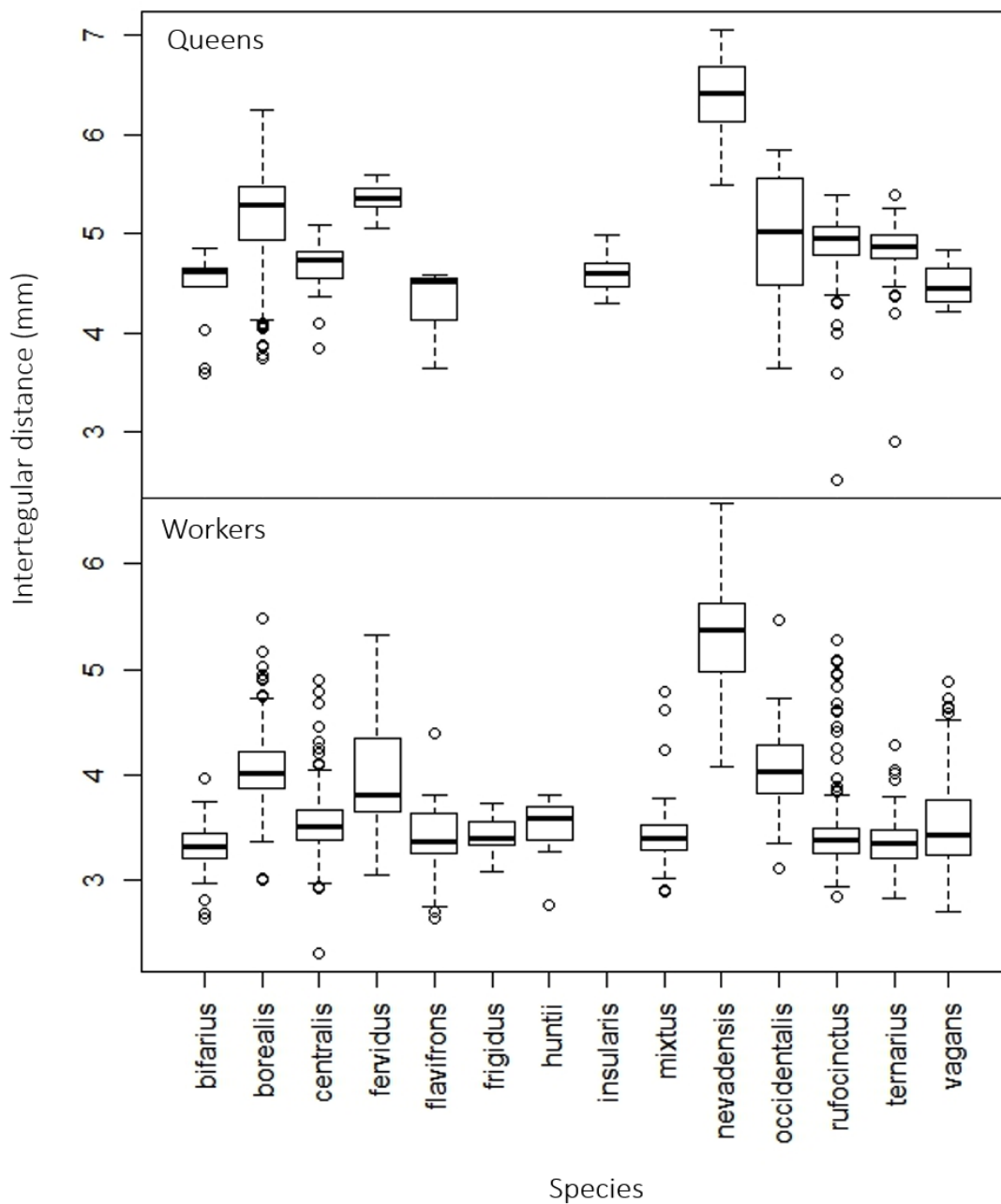


Figure B3. Intertegular distance (mm) box plots for 14 study species, separated by caste. The thick bar represents the median, and the upper and lower ends of the boxes show 75<sup>th</sup> and 25<sup>th</sup> percentiles, respectively. The typical range is indicated by the whiskers, and the open circle points show outliers.

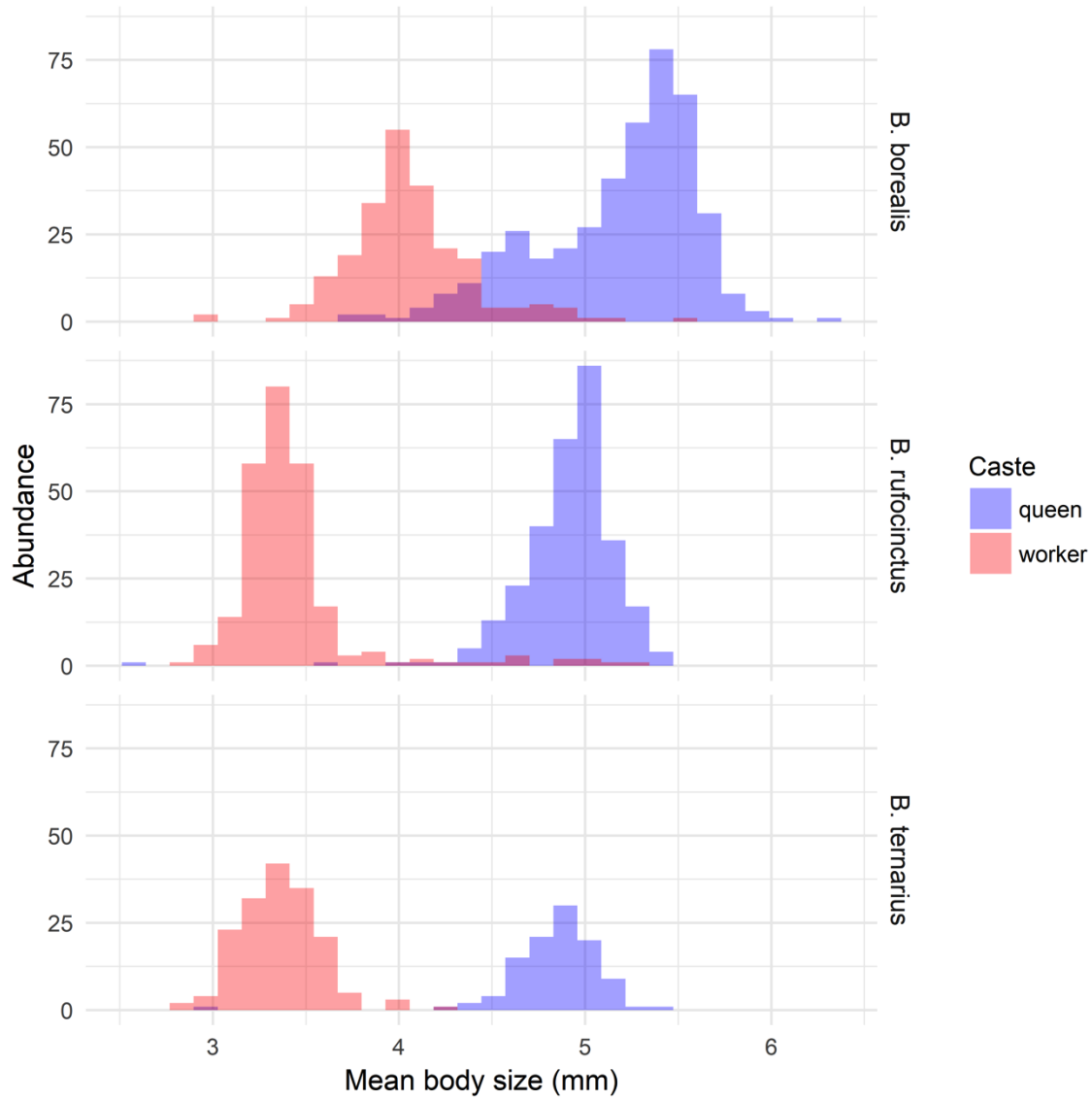


Figure B4. Histogram displaying raw abundance of body sizes separated by caste for three highly abundant bumble bee species: *B. borealis*, *B. rufocinctus*, and *B. ternarius*.

Appendix C.

This section provides multiple visualizations of raw density distributions of bumble bee body size in relation to landscape variables, useful for inspection to determine whether obvious visual patterns are discernable.

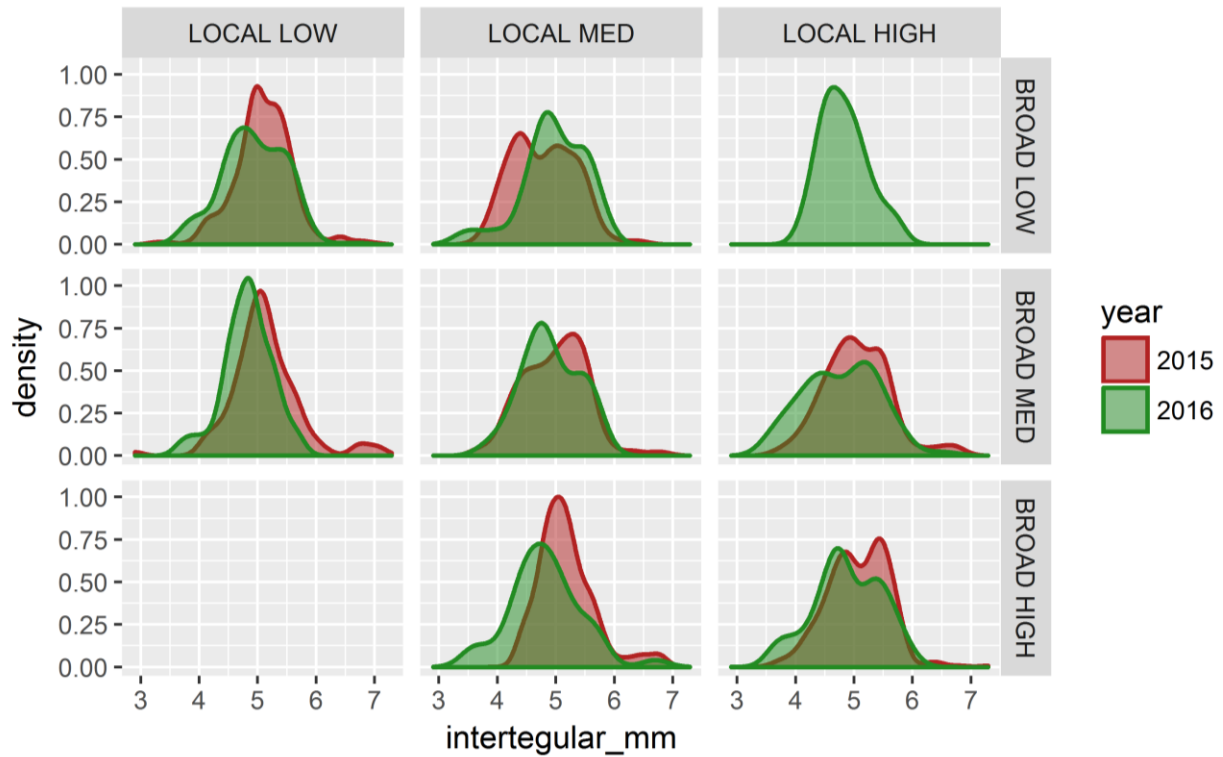


Fig. C1: Raw data distributions for density as a function of intertegular length for queen bumble bees at different levels of local and broad semi-natural availability. Data from 2015 and 2016 included.

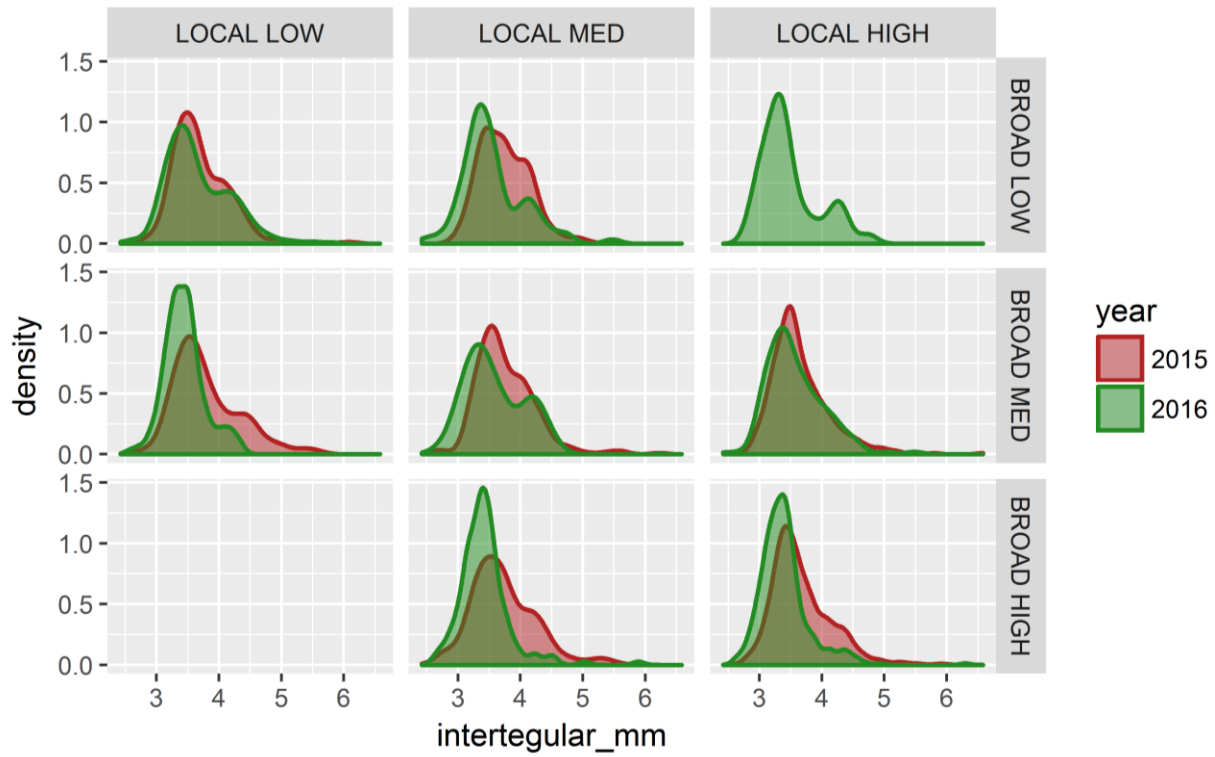


Fig. C2: Raw data distributions for density as a function of intertegular length for worker bumble bees at different levels of local and broad semi-natural availability. Data from 2015 and 2016 included.

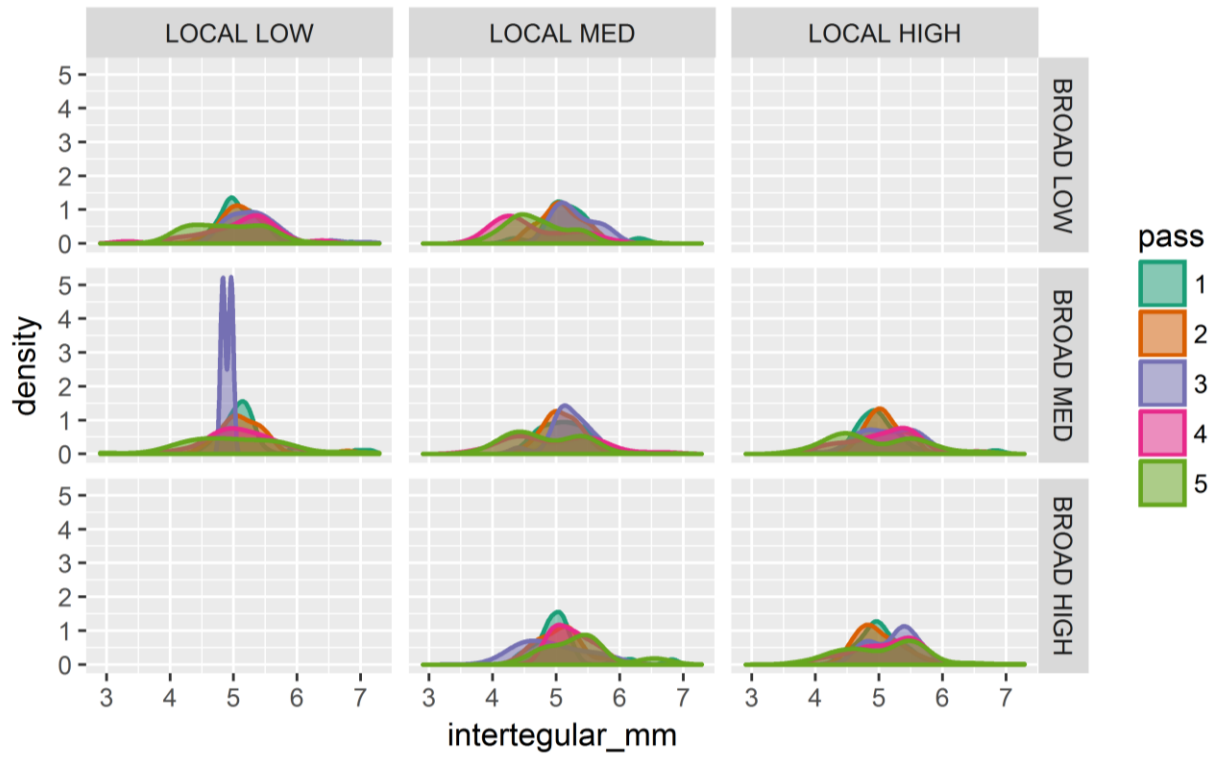


Fig. C3: Raw data distributions for density as a function of intertegral length for queen bumble bees at different times during the sampling season, as a function of local and broad semi-natural availability. Data from 2015 included.

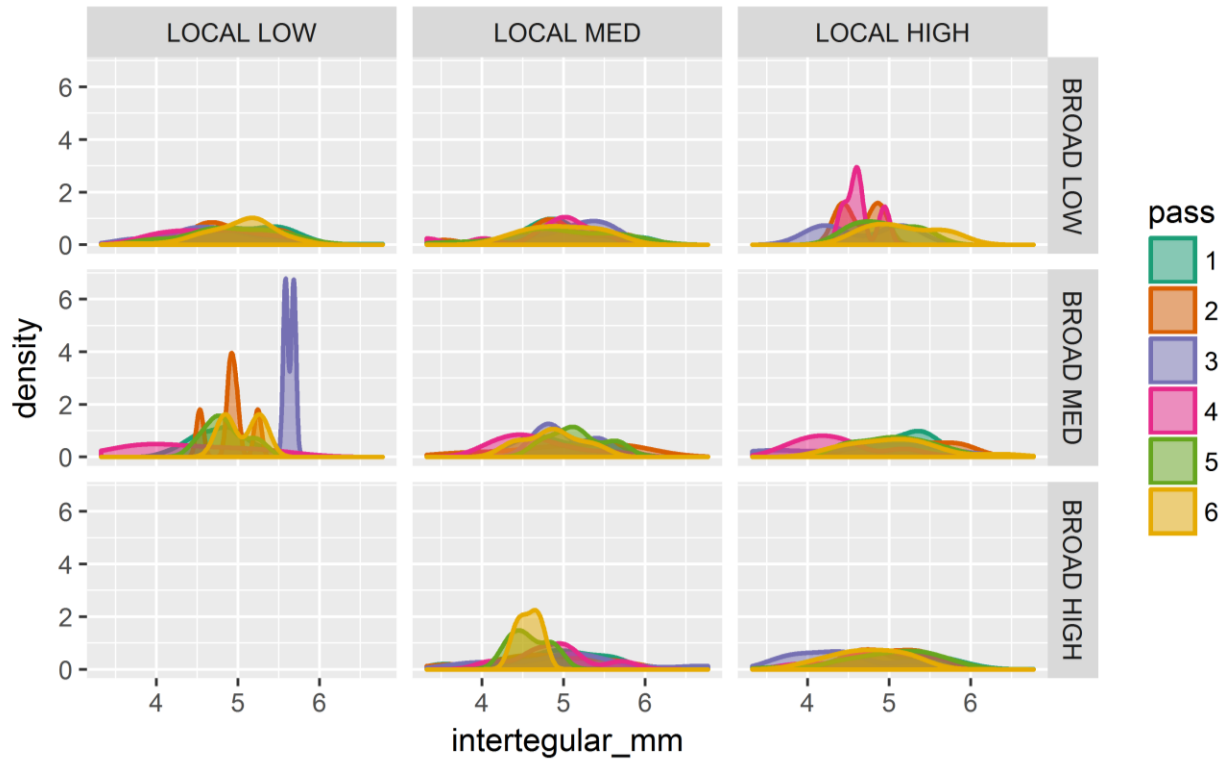


Fig. C4: Raw data distributions for density as a function of intertegral length for queen bumble bees at different times during the sampling season, as a function of local and broad semi-natural availability. Data from 2016 included.

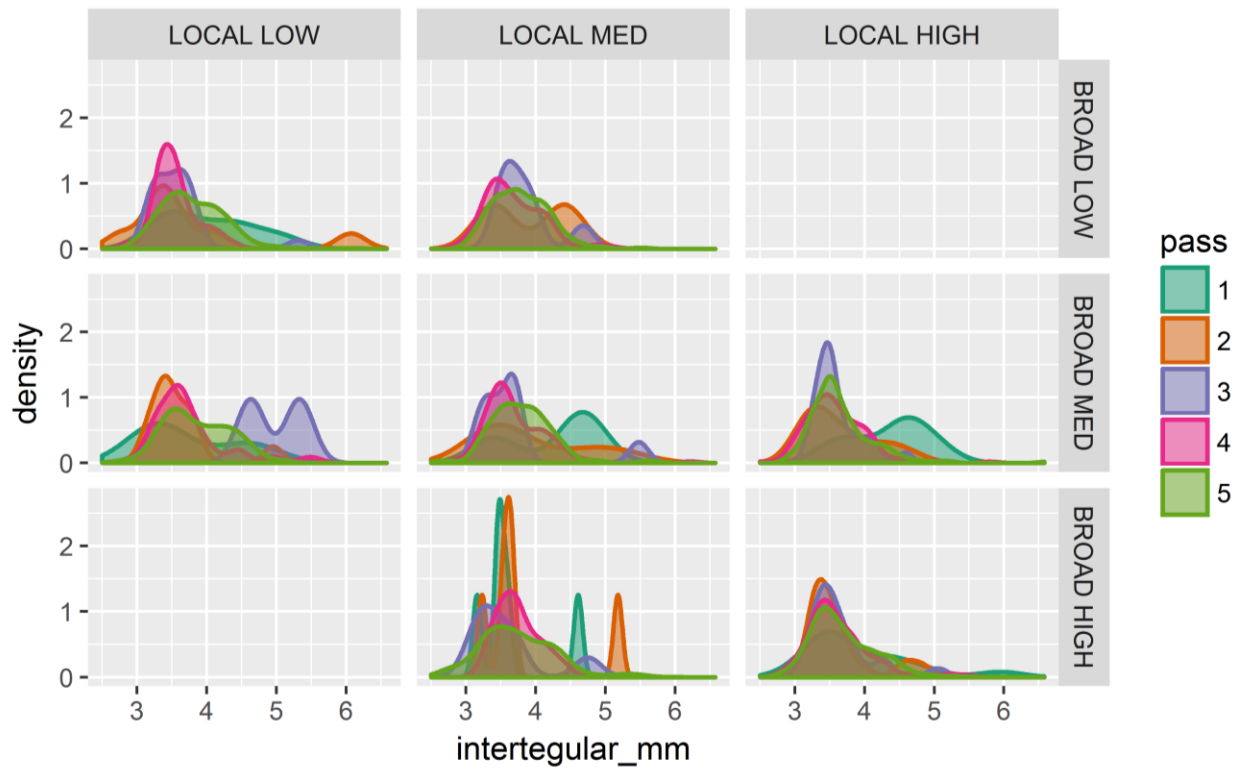


Fig. C5: Raw data distributions for density as a function of intertegular length for worker bumble bees at different times during the sampling season, as a function of local and broad semi-natural availability. Data from 2015 included.

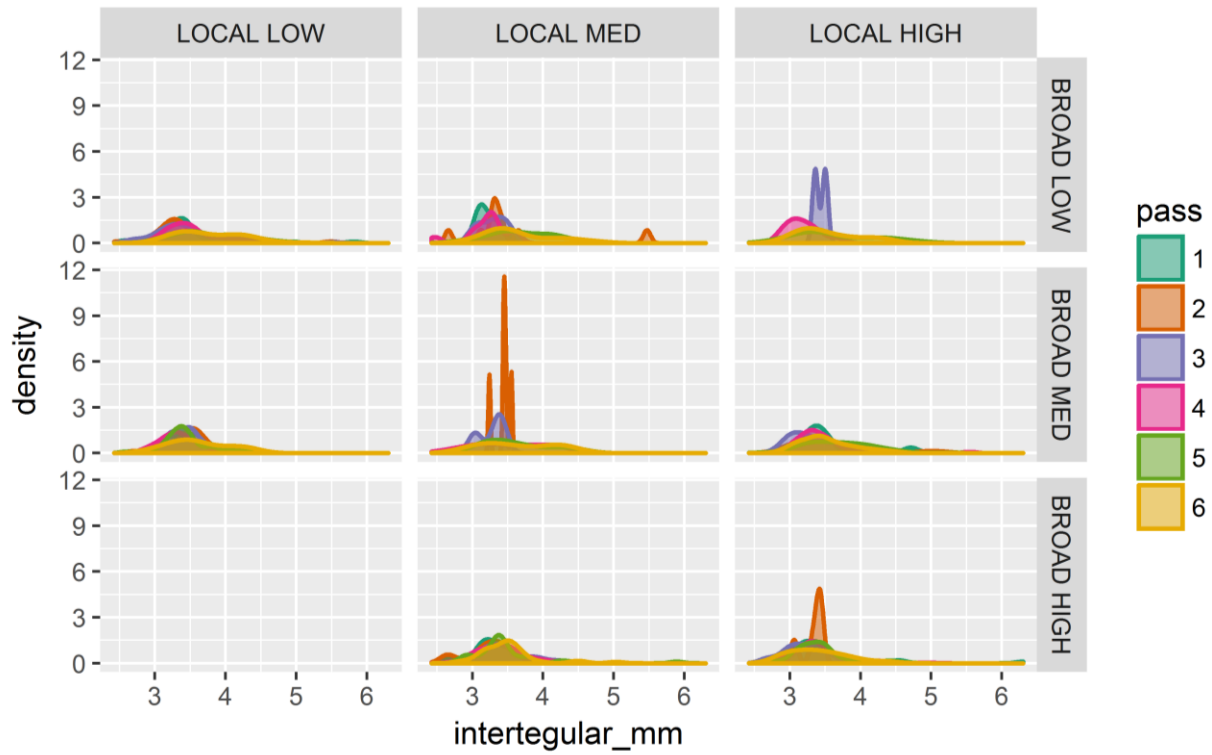


Fig. C6: Raw data distributions for density as a function of intertegular length for worker bumble bees at different times during the sampling season, as a function of local and broad semi-natural availability. Data from 2016 included.

## Appendix D

This section contains descriptive information about habitat types and land cover areas.

Table D1. Semi-natural land contains multiple types of natural habitats, including native prairie, pasture, forests, shrublands, and wetlands. Each habitat type differs in its floral community, and contains different flower species, species richness, and phenology. Each land cover was assessed during each site pass of the study at ten sites per cover type, using 100 m long, 3 m wide transects, measured 25-27 July 2016.

Land Cover Type	Mean Richness	Max Richness	Std Richness	Mean Density	Std Density
Native Prairie	29.43	36.00	4.58	2.34	1.26
Pasture	14.86	20.00	4.06	7.71	4.62
Tree and Shrub	20.14	28.00	5.34	0.81	0.52
Wetland	16.00	24.00	6.06	4.51	4.08

Table D2. Standardized local landscape variable with corresponding area values for local semi-natural (0 – 500m).

Local 0 - 500 m <sup>2</sup> - Total area available: 785,398.16 m <sup>2</sup>			
Standardized Value	Area (m <sup>2</sup> )	Area (Hectares)	% of Total Area
-1	59,793.41	5.98	7.6131
-0.5	193,128.19	19.31	24.5898
0	326,462.96	32.65	41.5666
0.5	459,797.74	45.98	58.5433
1	593,132.51	59.31	75.5200
1.5	726,467.29	72.65	92.4967

Table D3. Standardized broad landscape variable with corresponding area values for broad semi-natural (500 – 2000 m).

Broad 500 - 2000 m <sup>2</sup> - Total area available: 11,780,972.45 m <sup>2</sup>			
Standardized Value	Area (m <sup>2</sup> )	Area (Hectares)	% of Total Area
-1.5	300,023.05	30.00	2.5467
-1	1,693,441.70	169.34	14.3744
-0.5	3,086,860.35	308.69	26.2021
0	4,480,279.00	448.03	38.0298
0.5	5,873,697.65	587.37	49.8575
1	7,267,116.30	726.71	61.6852
1.5	8,660,534.95	866.05	73.5129
2	10,053,953.60	1,005.40	85.3406

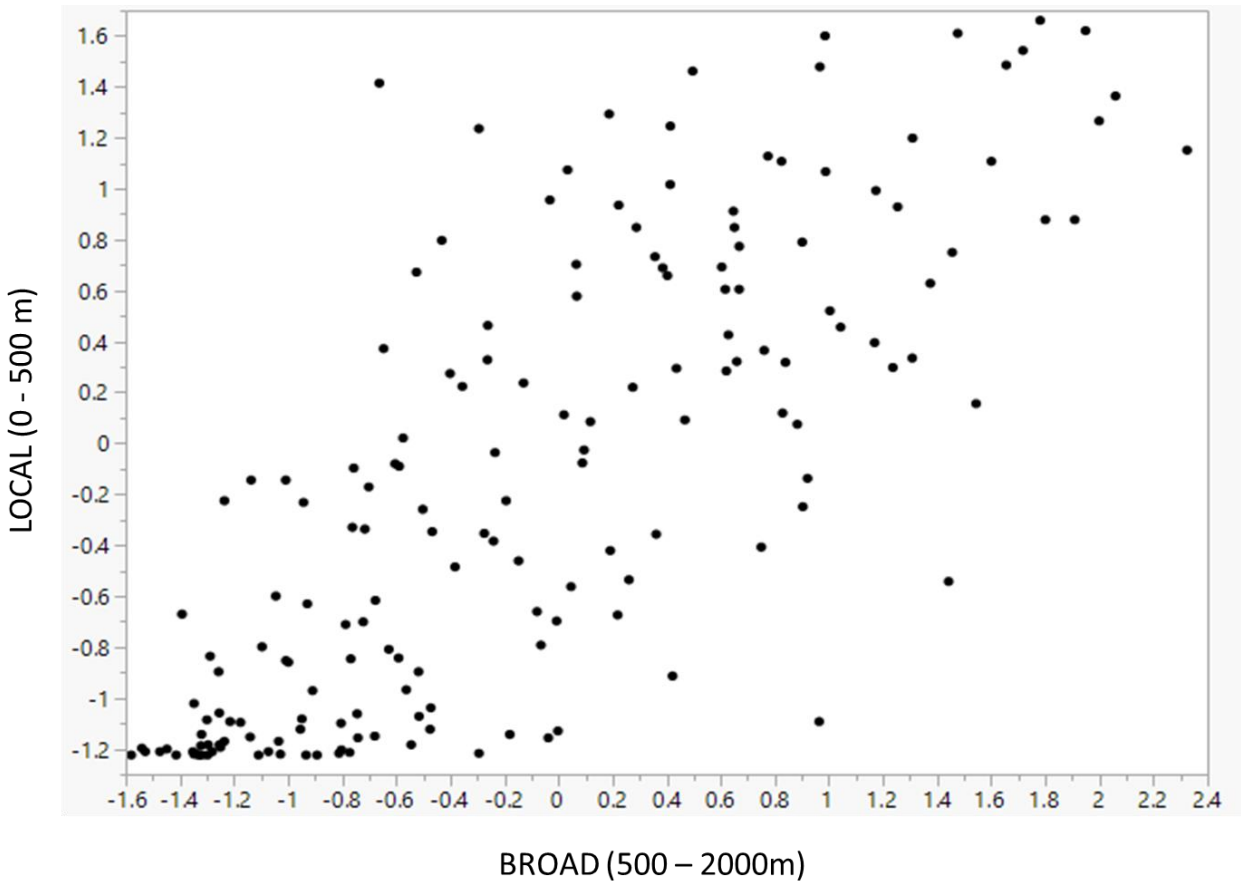


Figure D1. Scatterplot displaying bivariate fit of local semi-natural land with broad semi-natural land. Both variables are standardized for comparison. Pearson's correlation = 0.81.

## Appendix E

This sections contains examples of count distributions of body sizes bins for various locations for queens and workers, displaying the variation in response that can be observed that is site specific.

### Queens

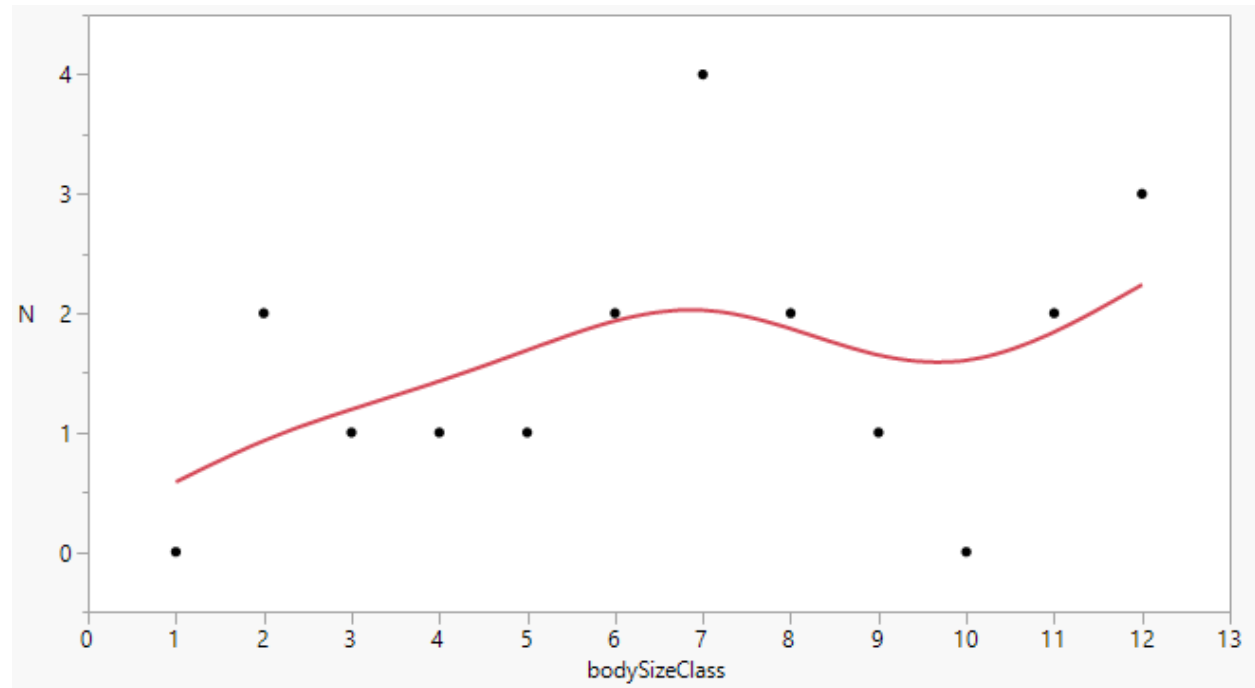


Figure E1. Scatterplot of queen abundance by body size (binned variable) for site 10092 in 2015. Splined fit displayed where lambda=10.

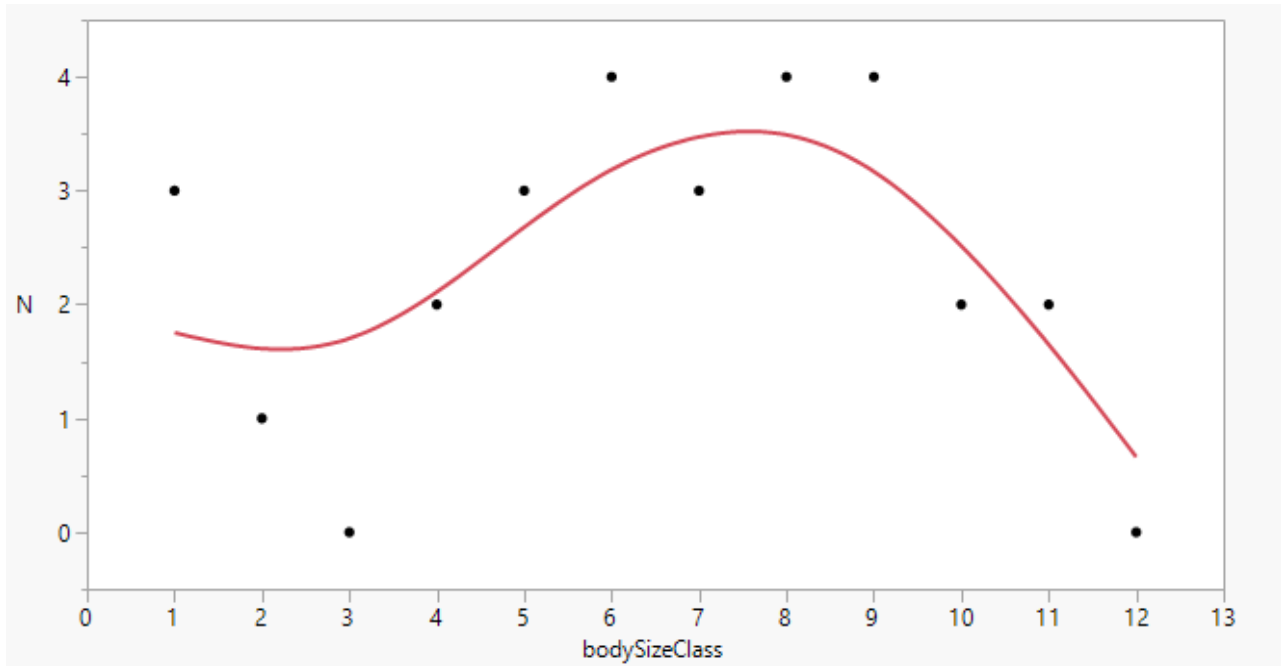


Figure E2. Scatterplot of queen abundance by body size (binned variable) for site 10832 in 2015. Red line shows spline fit ( $\lambda=10$ ).

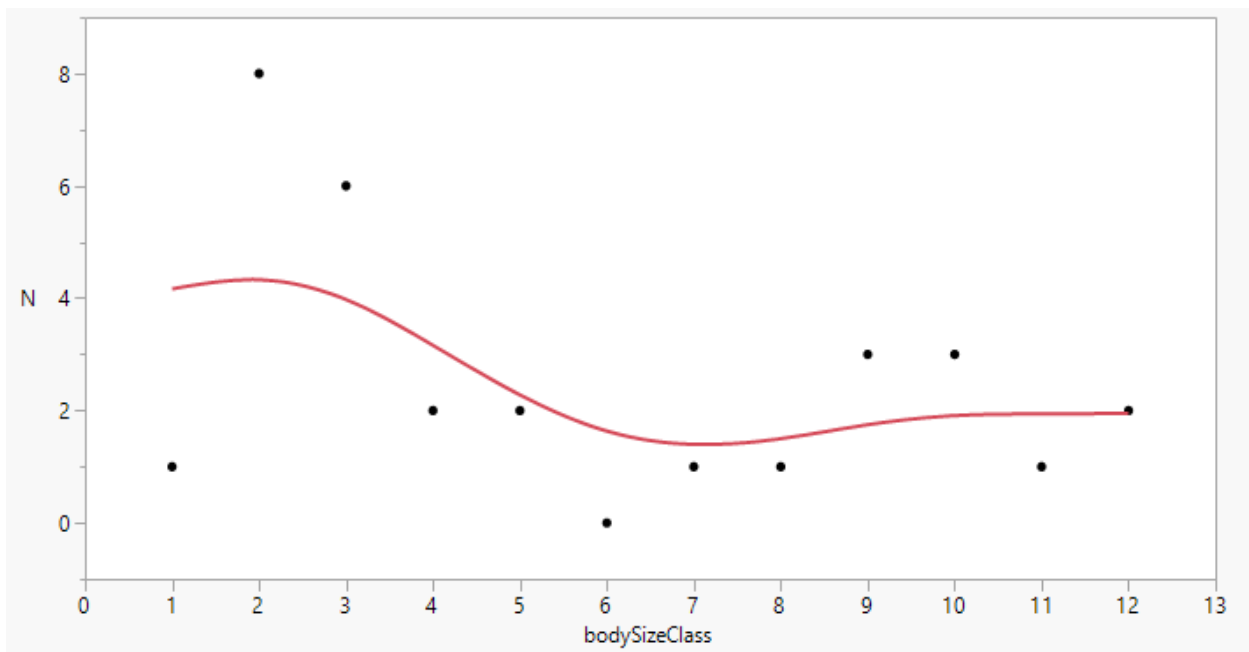


Figure E3. Scatterplot of queen abundance by body size (binned variable) for site 11794 in 2015. Red line shows spline fit ( $\lambda=10$ ).

Workers

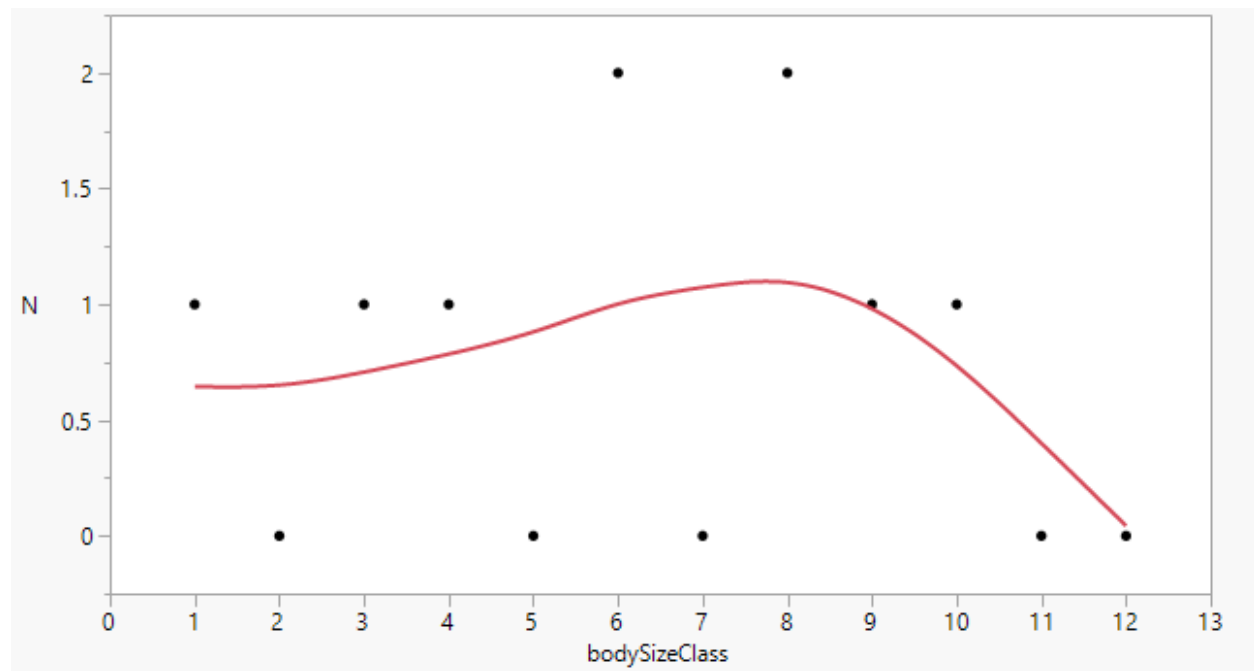


Figure E4. Scatterplot of worker abundance by body size (binned variable) for site 10092 in 2015. Red line shows spline fit ( $\lambda=10$ ).

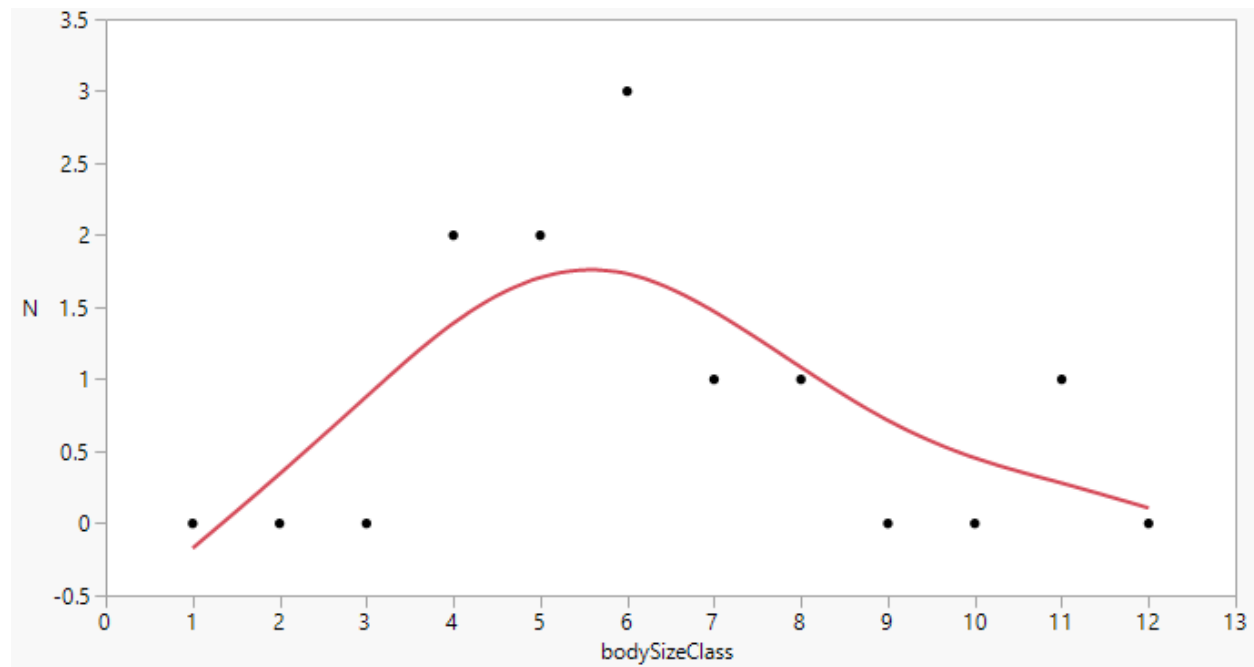


Figure E5. Scatterplot of worker abundance by body size (binned variable) for site 10832 in 2015. Red line shows spline fit ( $\lambda=10$ ).

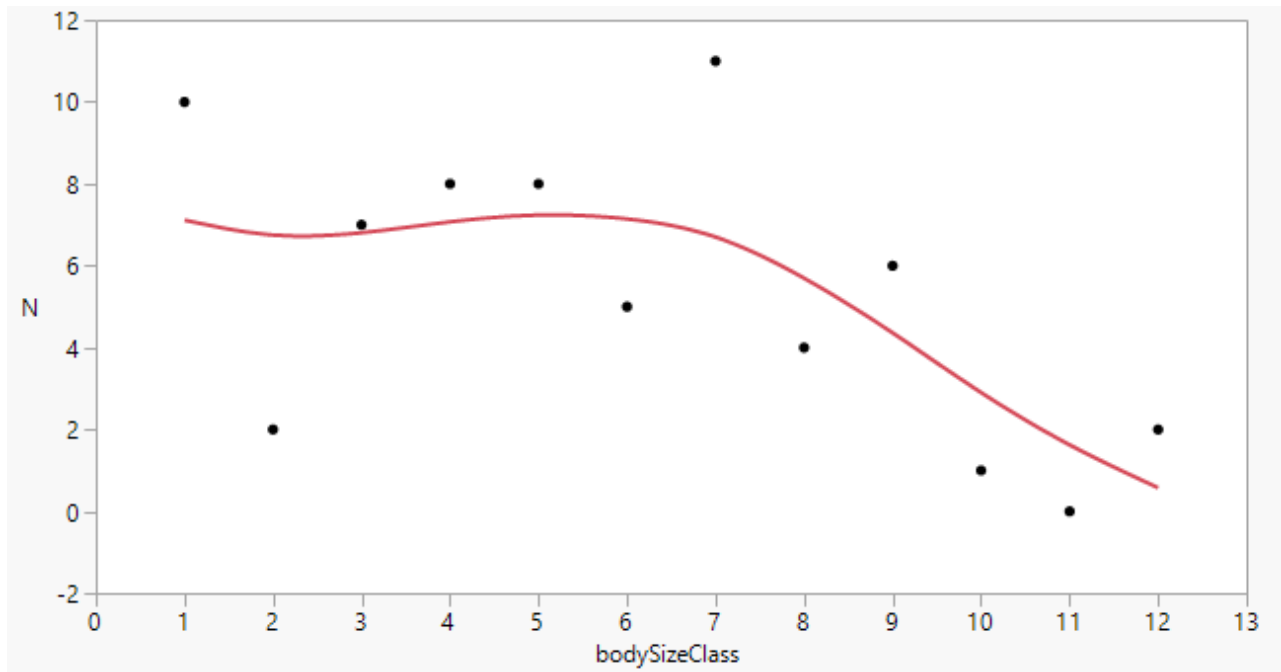


Figure E6. Scatterplot of worker abundance by body size (binned variable) for site 11794 in 2015. Red line shows spline fit ( $\lambda=10$ ).