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Central-place foraging, crop yield, and population change in bees: A study in canola agroecosystems

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Central-place foraging, crop yield, and population change in bees:
A study in canola agroecosystems

by

Samuel Victor Joseph Robinson

A THESIS

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Abstract

Canola (*Brassica napus* L.) is a valuable crop that occupies a large part of the Canadian prairies, and is visited by wild and managed bees. However, the distribution of foraging bees in mass-flowering crops (MFCs), the value of bee visitation, and how MFCs and semi-natural land (SNL) affect wild bee populations in the context of canola agro-ecosystems is unclear. Using three separate studies, I related pollination and yield to bee visitation, and landscape composition and canola abundance to wild bee abundance. The first study examines honey bee (*Apis mellifera* L.) visitation in commodity canola fields using a simulation model, and reveals that honey bees most closely followed predictions for solitary efficiency-maximizers, valuing nearby flower sources much more than distant ones. The second study relates visitation rates of honey bees and alfalfa leafcutting bees (*Megachile rotundata* (Fabr.)) to pollen deposition and seed production using a structural equation model. Leafcutter bee visitation strongly increased pollen deposition, but not honey bee visitation, and extra pollen deposition increased seed production in seed canola, but not in commodity canola. The final study uses solitary bee abundance data from a set of landscapes across southern Alberta, and relates bee abundance to landscape composition from the current and previous year. While the overall response of bee abundance to SNL was positive, individual species' response to SNL ranged from positive to negative, and canola had little effect on any species' abundances. These results reveal that insect visitation in flowering crops decay rapidly with distance, that the plant growth context of canola is equally important as the pollination context, and that while the effect of SNL on wild bee abundance is generally positive, it likely varies depending on the traits of individual bee species. This work provides mechanistic insight into the foraging behaviour and contextual value of pollination by managed bees, and sheds light on how agro-ecological landscapes shape wild bee communities.

Preface

This thesis is an original work by the author. No part of this thesis has been previously published.

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who showed me that the natural world is a beautiful, fascinating place

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who showed me that the world of music is an equally beautiful, fascinating place,

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who gave me the first glimpse into the world of research

Sally Otto

who made matrix inversions interesting at 8 AM

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Epigraph

The pale flowers of the dogwood outside this window are saints. The little yellow flowers that nobody notices on the edge of the road are saints looking up into the face of God.

- Thomas Merton, *New Seeds of Contemplation*

Chapter 1

Introduction

1.1 Space, time, and ecological processes

All ecological processes, either biotic or abiotic, are embedded in space and time, and have characteristic length scales at which they operate. Environmental heterogeneity occurs at multiple spatial scales (Kotliar and Wiens, 1990; Kolasa and Pickett, 2012), influencing their associated biodiversity. Therefore, identifying the relevant spatial scales and the mechanisms of action that determine patterns observed in local communities is a fundamental question in ecology (Wiens, 1989; Levin, 1992). Similarly, ecological processes change over time (Preston, 1960). Seasonal changes in resources, disturbance, succession, and climate change can all add temporal variation to the resource supply in a given environment. Simultaneous heterogeneity in space and time is likely to produce complex effects, depending on the extent, frequency, and intensity of the spatial and temporal changes (Petchey et al., 1997; Bissonette and Storch, 2007; Yang et al., 2010). Accordingly, there is a rich history of spatial and temporal models in ecology that attempt to understand these effects (Huffaker, 1958; Hutchinson and MacArthur, 1959; Connell and Orias, 1964; MacArthur and Pianka, 1966; Wright, 1983; Holling, 1992).

Because space and time are important related concepts in ecology, the spatial arrange-

ment of a given environment is equally important. The concept of a “landscape” stems directly from the concept of distance, and in particular, relates the composition and arrangement of ecosystem elements within a heterogeneous area (Wiens, 1989; Addicott et al., 1987; Turner, 1989). Early models, such as the theory of island biogeography (MacArthur and Wilson, 1967), treated the environment as “islands” of suitable habitat surrounded by a matrix of unsuitable habitat. However, the matrix in many environments is not completely unsuitable (Ricketts, 2001), and many organisms can gain valuable resources from the matrix, or use the matrix for movement. While landscapes are typically thought of in spatial terms, they also have a temporal component that can outpace the importance of the spatial component (Fahrig, 1992). Temporal changes in resource availability can change organismal fitness at higher trophic levels (Yang et al., 2008), resulting in “echos” of bottom-up effects into higher trophic levels. Organisms with long generation times will experience a delayed increase in fitness, by virtue of the longer scale at which they translate resources into fitness (Fahrig, 1992; Ostfeld and Keesing, 2000). Therefore, the landscape that an organism experiences during their lifetime, and how an organism chooses to use the landscape, can have a large impact on their fitness.

Foraging is a singularly important activity for an organism (Stephens and Krebs, 1986), and exists within a spatio-temporal framework. Foraging strategies affect fitness, either at the individual or the group level, so foraging strategies that efficiently gather resources and translate them into fitness will be selected for. How organisms sense and use their environment depends on their body size, but also on their behaviour within a given part of the foraging environment. For example, decisions for moving between habitat patches may depend on patch arrangement as well as organismal traits (With et al., 1999). Spatially separate foraging environments may increase foraging costs by increasing the distance travelled by the organism, and increasing time energy, and predation risk when moving among the foraging environment. This means that understanding how landscapes affect groups of mobile organisms also requires an understanding of both their behavioural ecology, the landscape

structure, and how these two components interact (Lima and Zollner, 1996).

1.2 Agriculture and ecology

Agriculture has been a part of human history for over 10,000 years, and has played an enormous role in shaping human societies, religions, and political ideologies (Vasey, 1992). 37% of the world's ice-free surface area is involved in agricultural production, and agriculture contributes about one-third of global gross domestic product (Ramankutty et al., 2018). The study of ecology ultimately arose from the studies of agriculture and forestry, as both are interested in the relation of sets of organisms to one other in their physical environment, as well as how they collectively shape with their environment (Harper, 1974). Both use similar conceptual models of pools and fluxes of nutrients, energy, and individuals, and are ultimately interested in the functioning of the components of an ecosystem. Agriculture deliberately directs energy and nutrients into and out of various pools, with the goal of maximizing productivity or income (but see Ch. 6 in Altieri, 1996), while ecology is largely concerned with “self-sustaining”, unmanaged systems. The division between agriculture and ecology exists, in part, because agriculture is typically thought of as “practical” and ecology as “theoretical” (Levins, 1973). However, both fields share similar underlying goals: the understanding of physical processes occurring among the components of a complex biological system, that is embedded in the underlying genetic structure brought about by natural or artificial selection and the underlying landscape that they exist in.

Insects represent the largest component of terrestrial biodiversity ($\sim 50\%$, Stork et al., 2015), and are important contributors to global ecosystem functioning (Yang and Gratton, 2014). Insect pollination is important to the reproductive success of many species of wild flowering plants, but is also essential for fruit and seed set in many crop plants. Globally, 35% of food production comes from crops that depend on animal pollination (Klein et al., 2007), and pollinating insects can significantly increase crop yield (Garibaldi et al., 2013, 2014) and

crop value (Bommarco et al., 2012). Diversity of pollinating species, as well as abundance can also increase yield (Hoehn et al. 2008; Martins et al. 2015, but see Winfree et al. 2015), highlighting the value of a diverse pollinator assemblage. While most cereal and starchy crops do not depend on insect pollination, many of the essential nutrients in the human food supply are derived from insect-pollinated plants. Therefore, changes in pollinator abundance have important implications to agricultural productivity, food commodity prices, and ultimately, to human health (Klein et al., 2007; Gallai et al., 2009).

Canola (*Brassica napus* L.) is a group of cultivars of oilseed rape, and is a singularly important crop in western Canada. Hybrid “commodity” canola makes up close to 99% of the Canadian canola market, and is produced by the cross-breeding of two separate lines of plants. Cross-breeding takes place in “seed canola” (or “pedigreed hybrid seed”) fields between bays of male-sterile and male-fertile plants, and large numbers of European honey bees (*Apis mellifera* L.) and alfalfa leafcutting bees (*Megachile rotundata* Fabr.) are used to ensure adequate cross-pollination between the two plant lines (Clay, 2009). The male-fertile line has hermaphroditic flowers, and carries a nuclear fertility-restoring trait, meaning that seeds sired on the male-sterile line will produce hybrid offspring with hermaphroditic flowers, resulting in greater plant vigour due to heterosis. Commodity canola was planted across 20.7 million ha of farmland in 2016 (roughly equivalent to the area of the United Kingdom), and contributed C\$26.7 billion to the Canadian economy (Statistics Canada, 2019; LMC International, 2016), making it the most valuable cash crop in Canada, while seed canola occupies a fraction of this area ($\approx 20,000$ ha, Gregory Sekulic, *pers. comm.*). Commodity canola fields are often stocked with honey bees for honey production (typically 20–60 hives per apiary). Canola flowers can produce several kilograms of pollen and sugar per hectare per day during the summer (Szabo, 1985; Westcott and Nelson, 2001), and canola honey makes up about 80% of all Canadian honey (Clay, 2009). Therefore, canola production depends, either directly or indirectly, on pollination services, and is a large potential resource to both wild and managed pollinators.

Historically, many agricultural systems relied on the services of wild pollinators from the surrounding landscape. Many agricultural practices still rely on pollinator services from wild pollinators, such as almond (Klein et al., 2012) or mango plantations (Carvalho et al., 2010). High losses and instabilities in the availability of managed honey bee populations in North America and Europe (vanEngelsdorp et al., 2009), coupled with increasing demand for pollination services, have led to a renewed interest in the use of wild pollinators for crop pollination. However, facilitating wild pollinators is a complex problem involving both ecological and economical elements (Tschardt et al., 2012). As the scale of agricultural production has increased in North America, wild pollination services have declined, primarily due to habitat loss (Potts et al., 2010). Simultaneously, the amount of agricultural land requiring pollination services in North America has expanded by over 300% since the 1950s, leading to increased demands for pollination services (Aizen and Harder, 2009). Beekeepers may be unable to supply managed bees to these large areas of cropland, or the high demand may make the cost of doing so prohibitive. Like many aspects of agriculture, this can no longer be simply treated as a purely “agricultural” problem, as it involves the relation between multiple components of a complex agroecosystem (Figure 1.1), and requires a deeper understanding of the ecological principles underlying it.

1.3 Knowledge gaps

1.3.1 Distance-based foraging

We require a mechanistic model of foraging behaviour that accurately reflects the energetic constraints that foragers experience in a given landscape. Despite the importance of distance in ecological processes, many models of how organisms distribute themselves across a heterogeneous environment do not explicitly account for it, meaning that our understanding of the ways in which organisms use their environment is incomplete. Organisms should distribute themselves across a landscape in a way that maximizes their fitness (ideal-free distribution;

Fretwell and Lucas, 1969), but central-place foragers are constrained by distance to their nest or aggregation, meaning that they will be limited in their use of a landscape (Orians and Pearson, 1979). Bee foraging has been studied at length (Eckert, 1933; Free and Williams, 1973; Heinrich, 1976; Pyke, 1978b), but rarely at larger scales in the agricultural context (Free and Nuttall, 1968; Langridge and Goodman, 1982; Picard-Nizou et al., 1995), making findings difficult to generalize to other situations. Bees are central-place foragers, so their choice of foraging patch will be constrained by distance to their colony or nest, but many studies of patch choice are done in artificial environments (Marden and Waddington, 1981; Schmid-Hempel and Wolf, 1988), or are largely descriptive and non-mechanistic (Núñez, 1982; Reynolds and Rhodes, 2009; Olsson and Bolin, 2014). Mechanistic models represent a codified set of assumptions about a given system that can be further built upon or tested, where parameters are related to individual behaviour (Geritz and Kisdi, 2012). Some of the best studies have a firm mechanistic basis (Dukas and Edelman-Keshet, 1998; Cresswell et al., 2000), but are not tested in the field, making their results difficult to apply to different landscapes. This points to a need for an integrated, mechanistic model of central-place foraging behaviour that incorporates realistic foraging behaviour, is analytically feasible, and is tested in the field.

1.3.2 Connecting ecosystem services to seed production

In addition to how foraging insects use their environment, management of insect pollination in agroecosystems requires an understanding of how visitation relates to pollination, and how this affects crop production. Pollination is important for seed production in many annual flowering plants, but increased pollen deposition has a saturating effect on fruit production (Ashman et al., 2004) that also depends on the available resources that a plant is able to devote to making flowers, fruit, and seeds (Tamburini et al., 2019). Much research has linked landscape composition to pollinator abundance in agricultural systems (Hoehn et al., 2008; Jauker et al., 2009; Arthur et al., 2010; Albrecht et al., 2010; Morandin and Kremen, 2013;

Nayak et al., 2014), but few make the connection between species richness, landscape diversity, and the actual measurement of visitation (Greenleaf and Kremen, 2006b,a), while some suggest that the relation is generally weak (Davila et al., 2012). Others studies demonstrate that yield is increased by visitation (Fries and Stark, 1983; Kevan and Eisikowitch, 1990; Sabbahi et al., 2005; Isaacs and Kirk, 2010; Perrot et al., 2018), but few studies examine the entire chain of visitation to pollination services to yield (Ricketts et al., 2008; Sáez et al., 2017). Annual plants have a limited amount of time and resources to produce seeds during the growing season, meaning that poorly pollinated plants may produce larger seeds rather than more of them, resulting in a size-number tradeoff (Smith and Fretwell, 1974; Silvertown, 1989; Venable, 1992). However, pollination may not matter as much as the resource context, as plants with an indeterminate growth strategy can respond to low pollen deposition by simply producing more flowers (Hurd et al., 1979). These plants can achieve equivalent seed yield to those under high pollinator abundance (Clarke, 1979; Sabbahi et al., 2006; Bos et al., 2007), depending on their available resources for growth and the amount of time left in the growing season (Marini et al., 2015; Tamburini et al., 2016). Predictions derived from pollination experiments in greenhouse studies or experimental fields often feature flower visitation that is unrealistically high (Eisikowitch, 1981; Durán et al., 2010; Jauker et al., 2012), as well as unlimited water and fertilizer (but see Marini et al., 2015; Tamburini et al., 2016). In field studies, cage-excluded plants are assumed to be direct analogues for unvisited plants, but these often alter wind pollination, humidity and pest pressure (Neal and Anderson, 2004). There are few studies in agroecosystems that systematically examine how pollinator density decreases from their source (but see Manning and Wallis 2005; Farwig et al. 2009), how distance-based foraging is related to the energetics of pollinator movement, and pollinator density (Cresswell et al., 2000; Cresswell, 2000), and ultimately how distances affect pollination service and yield. In other words, we need a model of crop yield that links all of the components of pollination to yield within a realistic growing environment, rather than treating each piece independently.

1.3.3 Landscape effects

Ecosystem services in a crop field are typically thought of as a one-way process, with pest-control, pollination, or other services flowing from the surrounding semi-natural matrix into the field (Öckinger and Smith, 2007; Bommarco et al., 2012; Peisley et al., 2015; Woodcock et al., 2016). However, the flows of energy and materials between crop fields and the surrounding landscape matrix operate in both directions (Figure 1.1), and crop fields can alter the amount of ecosystem services within the surrounding matrix. Managing and protecting ecosystem services in fragmented environments with a loss of natural habitat requires more complete understanding of the novel landscapes we are creating, and the processes that drive them (Wiens, 2009).

Undeveloped semi-natural land (SNL) can increase the diversity and abundance of wild pollinators in crop fields by increasing the abundance of nest sites and floral resources (Morandin et al., 2007; Öckinger and Smith, 2007; Ricketts et al., 2008; Jauker et al., 2009; Bommarco et al., 2012; Chateil and Porcher, 2015). Mass-flowering crops (MFCs) can also alter the abundance of wild pollinators during the next year, both positively (Rundlöf et al., 2014), negatively (Holzschuh et al., 2011), or positively but only for some species (Le Féon et al., 2013; Galpern et al., 2017; Dainese et al., 2018). MFCs tend to have a negative effect on bumble bees (*Bombus*), as their colonies require more prolonged periods of sustained forage to produce new gynes (Westphal et al., 2009; Riedinger et al., 2015; Galpern et al., 2017), but there may be a positive effect (Diekötter et al., 2014, but see Rollin et al., 2013) in quasi-social non-*Bombus* bees (hereafter, “solitary” bees). For example, Crone (2013) found that solitary *Anthophora* responded positively to biennial pulses in mass-flowering *Astragalus*, with increased abundance in the year following a bloom, while *Bombus* did not. However, we have very little idea as to why some solitary pollinator species benefit from MFCs while others do not. Most solitary bees are univoltine (Michener, 2007), so any benefits from additional foraging will be seen in increased population during the next year (Crone, 2013; Holzschuh et al., 2012; Dainese et al., 2018), meaning that the effect of the resource

pulse is temporally lagged (Bissonette and Storch, 2007; Yang et al., 2010). MFCs can also act to dilute pollinators during the bloom (Westphal et al., 2003; Kovács-Hostyánszki et al., 2013; Riedinger et al., 2014; Holzschuh et al., 2016) or cause spillover into adjacent areas (Montero-Castaño et al., 2016). Therefore, nearby flowering crops can further increase habitat value for wild bees, but only some species, and this effect may be seen during the bloom (behavioural response), or during the next year (numerical response).

How pollinators respond to increases in food availability depends on the density-dependence of the insect population (Turchin and Taylor, 1992; Roulston and Goodell, 2011), but we have little idea of whether growth of pollinator populations is density-dependent. Nest sites and food sources are finite, so pollinator populations must be density-dependent at some level, but they seem to be largely density-independent because they seldom reach levels where they are limited by food. Alternatively, parasite abundance and nest site availability, may be the forces driving pollinator abundance (Steffan-Dewenter and Schiele, 2008; Dainese et al., 2018), with food only occasionally limiting their growth. We need a better understanding of how pollinator populations vary year-to-year, and how they interact with semi-natural land and mass-flowering crops to maintain their populations, over time spans of more than one season. Finally, we need to compare these effects among a suite of species with varying traits, including nest preferences and floral specializations, to assess *a*) whether this pattern is general and *b*) to understand how these traits influence persistence in the landscape (Williams et al., 2010). Food resources can increase the abundance of wild pollinators, but this tends to be for only a few pollinator species (Wood et al., 2015, 2017), so in the face of increased crop development alongside SNL, we require knowledge of these systems in order to manage for pollinator diversity as well as abundance.

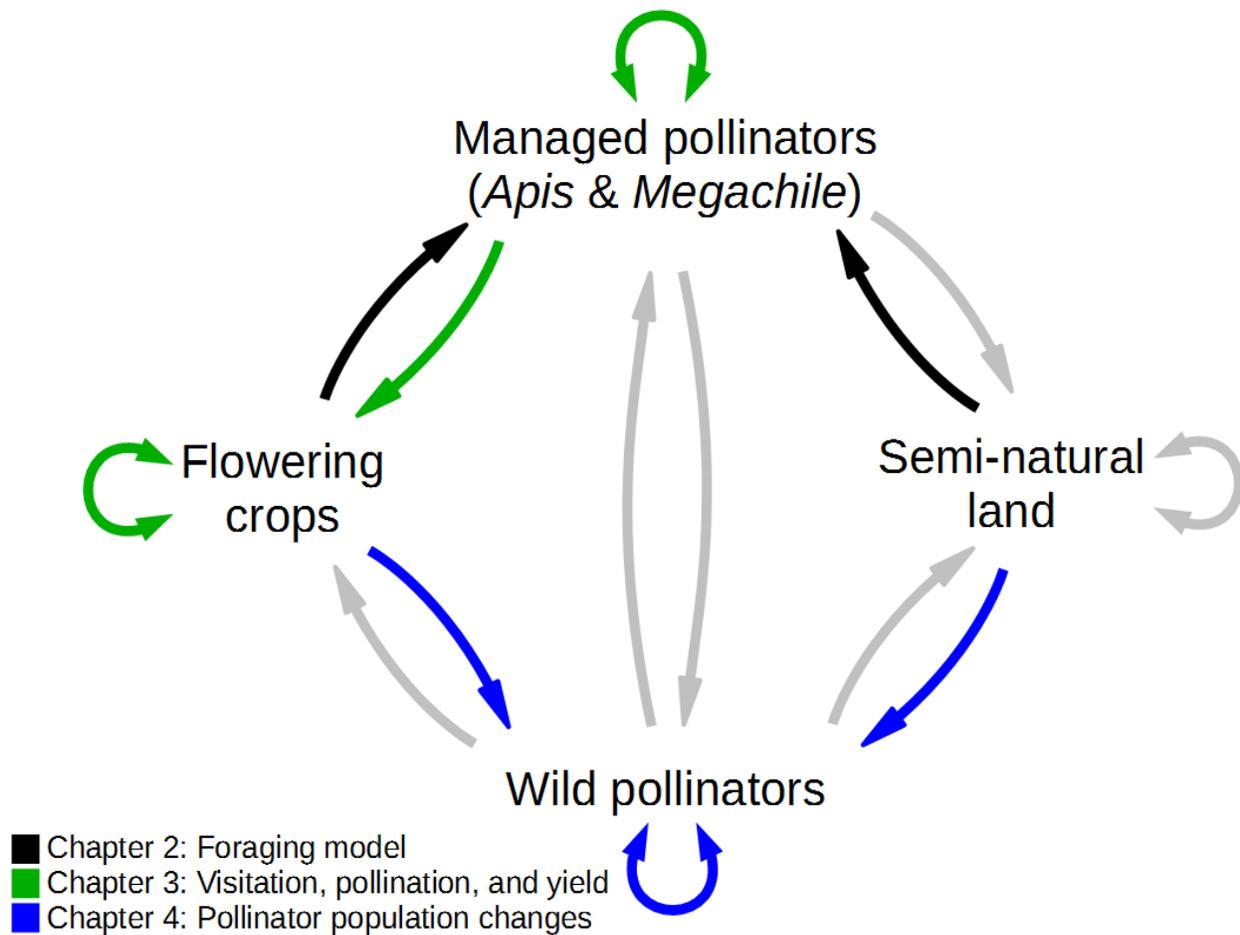


Figure 1.1: Conceptual model of ecosystem components and scope of my three studies, with arrows representing flows of nutrients, energy, and individuals between each part. Circular arrows represent dynamics within each component (*e.g.* interactions between *Apis* and *Megachile*). Transparent gray arrows are implied in my work, but were not directly studied.

1.4 Scope of thesis

This thesis examines the effect of canola agroecosystems on wild and managed pollinators, and assess the ecosystems services provided to canola by managed pollinators, combining aspects of landscape ecology, behavioural ecology, and plant ecology (Figure 1.1). In chapter two, I address how central-place foraging organisms should distribute themselves across a heterogeneous landscape, and relate this to observed visitation in the field. I build on the concept of the ideal-free distribution (Fretwell and Lucas, 1969) using central-place foraging theory, incorporate a realistic model of competition within patches of flowers (Possingham,

1988), and test the model using honey bee visitation in canola fields. In chapter three, I examine how seed production relates to pollination and visitation, all within the context of resources and size-number tradeoffs within plants. I develop a causal model relating yield to pollen deposition and visitation, parameterize it for two canola production systems, and show how seed production depends on resources and pollination. In chapter four, I ask how landscape composition affects pollinator populations, how persistent they are year-to-year, and how resource pulses are subject to lags. I use trap data for 20 solitary wild bee species collected during two years along a semi-natural landscape gradient, model how abundances change in response to semi-natural land and canola bloom, and model the year-to-year stability of populations.

My work is novel for a few reasons: *a)* no other studies have built and tested a large scale central-place foraging model based on first-principles, *b)* no other studies have combined multiple spatial scales of analysis to model pollination and yield of agricultural crops, and *c)* few studies have examined multi-year interactions between agroecosystems and wild pollinators, and none have done it across individual species within the overall communities. Chapter two demonstrates that honey bees operate as solitary efficiency-maximizers, visit largely within 200 m from the edge of canola fields, and also revealed that trip times for efficiency maximizers are peaked in relation to distance. These results could be used to construct appropriate buffer distances for honey bee foraging, in order to avoid gene transfer between crops, or to avoid competition with wild pollinators. Chapter three shows that honey bee visitation does not directly alter pollen deposition or seed production in commodity or seed canola, and that leafcutter bees are the main agents of pollen transfer in seed canola. It also shows that leafcutter bees likely drift to the edge of the field, but only at high forager densities, and suggests strategies to mitigate this. Finally, chapter four shows that population growth in solitary wild bee populations is largely density-independent across a variety of taxa, and that the effect of SNL is not uniformly positive for all of them. Canola bloom had little effect on solitary wild bee populations, regardless of nesting habitat or foraging preferences, but this

may also have been due to lack of temporal overlap between bloom and emergence. Overall, this thesis identifies factors contributing to canola yield (an applied ecology problem), tests alternative models of spatial competition (a behavioural ecology problem), and examines the effects of landscape and mass-flowering crops (MFCs) on the solitary bee community in an intensive agro-ecosystem (a community ecology problem). Ultimately this research will help to inform policy makers and land managers about how wild and managed pollinators behave in complex landscapes, how they relate to crop production, and how land uses changes alter pollinator abundance.

Chapter 2

The ideal free distribution of central-place foragers: a model of honey bees foraging in canola

2.1 Introduction

Explaining the distribution of organisms over space and time is an important goal of ecology (Brown and Orians, 1970; Gaston et al., 2000). The spatial distribution of organisms can be influenced by many factors, such as abiotic factors, such as temperature or moisture (Parmesan et al., 2005), or biotic factors, such as risk of predation (Lima and Dill, 1990; Grand and Dill, 1999). However, foraging for food is a singularly important activity for most organisms, and can strongly limit the distribution of an organism because the risk of starvation is usually more immediate (Stephens and Krebs, 1986). Foraging can involve decisions about what types of food to eat, where and for how long to forage, and how to interact with heterospecific or conspecific competitors (Waite and Field, 2007). Foraging takes place across landscapes that vary in their value to a given organism, so foragers should choose areas of the landscape that maximize their fitness. In this way, behavioural ecology

and landscape ecology are inexorably linked (Lima and Zollner, 1996), and merging the two disciplines is important to our understanding of how changes to landscapes affect both species distributions and behaviour (Knowlton and Graham, 2010).

Since foraging landscapes are not homogeneous, organisms should distribute themselves among parts of the landscape in a manner that equalizes their access to resources, therefore equalizing their fitness. This outcome results from an ideal-free distribution (IFD, Fretwell and Lucas, 1969), which is commonly used to explain the distribution of competitors among habitat patches. An IFD arises when organisms are *ideal*, in that they can perfectly assess patch quality, and *free*, in that they are free to forage wherever they want. If organisms are identical competitors, they distribute themselves between patches in a manner that equalizes individual fitness across all patches, meaning that organisms are more numerous in resource-rich patches, but have the same fitness as organisms in resource-poor patches. Refinements of the model involve relaxing assumptions to include despotic behaviour, interference competition, movement costs between patches, information deficits, unequal competitors, and other aspects of behaviour (Tregenza et al., 1996). Real foragers are not omniscient, but non-omniscient animals using simple learning rules can also assume an IFD, at least in fine-grained spatial environments (Bernstein et al., 1988, 1991).

However, the choice of a patch by an organism is not simply based on competitor number and resource density, but also includes a spatial aspect. Central-place foragers (CPFes) must return to their central place (nest, burrow, breathing hole, etc.) after each bout of foraging, meaning that the cost of travel will make nearby resources more valuable than far-away resources (Orians and Pearson, 1979). The single-prey-loading model of central-place foraging is a special case of optimal diet choice (Lessells and Stephens, 1983), and predicts that larger prey should be selected in far-away patches. If foragers can obtain multiple prey items and travel between patches while foraging, this yields models that are similar to the marginal value theorem of Charnov (1976), in that load sizes are predicted to increase with distance from the central place. These models predict that resources further away from

the central place will be less valuable than nearby resources, due to the time, energy, and predation risk caused by longer bouts of travel (Ydenberg et al., 1986).

Foragers should choose patches that maximize a given energetic currency (a measure of fitness), either individually or at the level of their social group. Net-rate maximization, whereby organisms maximize their energetic profit per unit time ($\frac{\text{Joules}}{\text{second}}$), is a commonly-used foraging currency that performs well when time is limited to a forager (Pyke et al., 1977; Ydenberg et al., 1994). However, other currencies appear to do equally well, depending on the rate of self-feeding (Ydenberg et al., 1994; Ydenberg and Schmid-Hempel, 1994), or the mortality risks in patches (Higginson and Houston, 2015). Efficiency maximization, or maximizing the ratio of energetic profits to losses ($\frac{\text{Joules}}{\text{Joules}}$), appears to explain load sizes of foraging bees (*Apis* and *Bombus*) better than net rate (Schmid-Hempel et al., 1985; Schmid-Hempel, 1987; Charlton and Houston, 2010), possibly because it entails lower costs, or prolongs the life of individual foragers (Schmid-Hempel and Wolf, 1988). Social circumstances may also influence the currency that a CPF should maximize. Some CPFs, such as seabirds, share a nesting aggregation and forage on the same resources (Ashmole, 1963), but are not related to other individuals in the aggregation, meaning that they should maximize their individual foraging currency. For social CPFs such as honey bees (*Apis mellifera* L.), foragers cannot reproduce, so they maximize their inclusive fitness, leading to a group (colony-level) currency. Maximizing a colony-level currency requires information about the foraging success of other foragers, which can be transmitted to other foragers via dancing (Seeley, 1994). However, this information may be ignored if the foraging environment is relatively uniform (Dornhaus and Chittka, 2004), or if foragers are unable to simultaneously gather information from the entire foraging force (Richter and Waddington, 1993).

Both the IFD and CPF models are incomplete, because they ignore important elements of foraging. Models of the distribution of central place foragers are often spatially-explicit, but omit competition (Cresswell et al., 2000; Olsson et al., 2015), or apply a distance-based “rule-of-thumb” (Lonsdorf et al., 2009), rendering them largely descriptive. Other models of

CPF behaviour assume that the foraging landscape is uniform (Charnov, 1976; Andersson, 1978), or alternatively, assume a small number of discrete patches (Křivan et al., 2008). Some spatial-competition models do exist (Ydenberg et al., 1986), but are usually restricted to simple 2-patch scenarios. The most comprehensive synthesis of the IFD and CPF models to date is by Dukas and Edelman-Keshet (1998), who created a competitive CPF model to predict distributions of honey bees. They modeled a single CPF aggregation that distributed foragers between two patches of equal value with differing distances, and compared the optimal distribution between these patches using two currencies (net-rate versus efficiency maximization) and two levels of sociality (solitary versus eusocial foragers). They showed that different energetic currencies across different socialities can lead to very different spatial distributions for CPFs. While patch usage declined with distance from a CPF aggregation, social foragers dispersed further away from their central place to avoid competing with nearby conspecifics, and this effect was even stronger for efficiency-maximizers. However, their model remains untested; it has not been applied outside a set of simple conditions (choices between 2 patches), and it does not account for differences in competition across a range of distances. Their model also assumed that load size was close to the maximum except at nearby patches ($<100\text{m}$, similar to Schmid-Hempel et al., 1985), but does not consider how load size alters patch value. For example, foragers collecting large loads from a patch will reduce the patch value more than foragers taking small loads, so social foragers may gather a smaller load than predicted by non-competitive models, simply to reduce patch depletion for colony mates.

In this chapter, I present and test a simulation model of the distribution of flower-visiting foragers from a single aggregation. This model builds on the model of Dukas and Edelman-Keshet (1998), using the model of Possingham (1988) as a mechanistic model of nectar competition at the patch level. I use simulation results from a simplistic foraging environment to demonstrate how optimal forager distributions are strongly influenced by currency and sociality. I then test model predictions against observations of honey bees conducted in

stocked canola fields (*Brassica napus* L.), using remotely-sensed landscape data to model the surrounding foraging landscape. Solitary CPFs optimize individual foraging success, so they should use close resources at the expense of the aggregation, meaning that only solitary foragers will assume an ideal-free distribution (Fretwell and Lucas, 1969). Efficiency-maximizers minimize costs by taking on smaller loads when foraging at short distances from their aggregation (Schmid-Hempel et al., 1985), while rate-maximizers take similar-sized loads at all distances, so efficiency-maximizers should take shorter, but more numerous trips to nearby patches. Finally, honey bee foragers maximize their fitness by maximizing colony-level fitness, and behave similar to predictions of efficiency-maximizers (Schmid-Hempel et al., 1985). Therefore, honey bee distributions in a field should match predictions made for social efficiency-maximizers.

2.2 Methods

2.2.1 The model

Foraging behaviour

To represent the behaviour of foragers using patches surrounding their central place, I used the following model. During a foraging bout, foragers travel d m from their nest to a foraging patch, gather nectar from flowers within that patch until they reach a volume of nectar L μL (up to a maximum crop volume of L_{max}), then return directly to their aggregation, spend H s within their nest unloading, and begin another foraging bout. Foragers spend f s to fly between flowers within a patch, h s to handle a flower, and p s per μL of standing crop to gather nectar from the flower. Foragers fly at a speed of v (m/s), using c_f (J/s) as the energetic cost of flying, while the cost of non-flying activity (handling a flower, licking, or unloading nectar at the aggregation) is c_i (J/s). As in the model of Schmid-Hempel et al. (1985), larger load sizes decrease the flight speed (α) and increase the cost of flight (β),

depending on the proportion of maximum load carried, L/L_{max} . All foragers within a patch have identical L , meaning that their energy gains and losses within a patch are all identical.

The energy gathered by a forager during a given trip is the volume of nectar L times the energetic value of the nectar e ($J/\mu L$):

$$\mathbf{Energy\ gathered\ (J)} = Le \quad (2.1)$$

The time and energy a forager spends to gather nectar is comprised of three parts: *travel*, *foraging*, and *hive*. *Travel costs* and *travel time* represent the energy and time required to travel to and from a given foraging patch:

$$\mathbf{Travel\ costs\ (J)} = \text{Inbound Cost} + \text{Outbound Cost}$$

$$= c_f \frac{d}{v} + c_f \frac{d}{v} \frac{\alpha L}{L_{max}} = c_f d \frac{\left(\frac{L\alpha}{L_{max}} + 2\right)}{v} \quad (2.2)$$

$$\mathbf{Travel\ time\ (s)} = \text{Inbound Time} + \text{Outbound Time}$$

$$= \frac{d}{v} + \frac{d}{v} \left(\frac{1}{1 - \beta \frac{L}{L_{max}}} \right) = \frac{d}{v} \left(\frac{2L_{max} - \beta L}{L_{max} - \beta L} \right) \quad (2.3)$$

Foraging costs and *foraging time* represent the energy and time required to travel between flowers within a patch and gather the nectar load L :

$$\begin{aligned} \mathbf{Foraging\ costs\ (J)} &= \sum \text{Flower Handling costs} + \sum \text{Inter-flower Flying costs} \\ &= \frac{Lc_i(Slp + h)}{Sl} + \frac{Sc_{cf} \sum_{i=1}^{\frac{L}{Sl}} i}{L_{max}} = \frac{L(Sc_{cf}l\alpha + Lc_{cf}\alpha + 2L_{max}Sc_i l p + 2L_{max}c_i h)}{2L_{max}Sl} \end{aligned} \quad (2.4)$$

$$\begin{aligned}
\text{Foraging time (s)} &= \sum \text{Flower Handling time} + \sum \text{Inter-flower Flying time} \\
&= \frac{L(Slp + h)}{Sl} + \frac{Lf}{Sl} = \frac{L(Slp + h + f)}{Sl}
\end{aligned} \tag{2.5}$$

Finally, *hive costs* and *hive time* represent the energy and time taken to unload nectar within the hive:

$$\text{Hive costs (J)} = c_i H \tag{2.6}$$

$$\text{Hive time (s)} = H \tag{2.7}$$

Foraging currency calculations

Honey bee foragers cannot reproduce in this model, so I assume that they maximize their fitness by maximizing their foraging currency. I compared outcomes for foragers maximizing two foraging currencies: net rate (Equation 2.8, Pyke et al., 1977) and efficiency (Equation 2.9, Schmid-Hempel et al., 1985).

$$\begin{aligned}
\text{Net Rate (J/s)} &= \frac{\text{Energy Gain} - \text{Energy Loss}}{\text{Time taken}} \\
&= \frac{\text{Energy Gain} - \text{Flight Loss} - \text{Foraging Loss} - \text{Hive Loss}}{\text{Flight Time} + \text{Foraging Time} + \text{Hive Time}} \\
&= \frac{\text{Eq.2.1} - \text{Eq.2.2} - \text{Eq.2.4} - \text{Eq.2.6}}{\text{Eq.2.3} + \text{Eq.2.5} + \text{Eq.2.7}} \\
&= \frac{Le - c_f d \left(\frac{L\alpha}{L_{max}} + 2 \right) - \frac{L(Sc_f fl\alpha + Lc_f f\alpha + 2L_{max}Sc_i lp + 2L_{max}c_i h)}{2L_{max}Sl} - c_i H}{\frac{d}{v} \left(\frac{2L_{max} - \beta L}{L_{max} - \beta L} \right) + \frac{L(Slp + h + f)}{Sl} + H}
\end{aligned} \tag{2.8}$$

$$\begin{aligned}
\text{Efficiency (J/J)} &= \frac{\text{Energy Gain} - \text{Energy Loss}}{\text{Energy Loss}} \\
&= \frac{\text{Energy Gain} - \text{Flight Loss} - \text{Foraging Loss} - \text{Hive Loss}}{\text{Flight Loss} + \text{Foraging Loss} + \text{Hive Loss}} \\
&= \frac{\text{Eq.2.1} - \text{Eq.2.2} - \text{Eq.2.4} - \text{Eq.2.6}}{\text{Eq.2.2} + \text{Eq.2.4} + \text{Eq.2.6}} \\
&= \frac{Le - c_f d^{\left(\frac{L\alpha}{L_{max}} + 2\right)} - \frac{L(Sc_f fl\alpha + Lc_f f\alpha + 2L_{max}Sc_i lp + 2L_{max}c_i h)}{2L_{max}Sl} - c_i H}{c_f d^{\left(\frac{L\alpha}{L_{max}} + 2\right)} + \frac{L(Sc_f fl\alpha + Lc_f f\alpha + 2L_{max}Sc_i lp + 2L_{max}c_i h)}{2L_{max}Sl} + c_i H} \tag{2.9}
\end{aligned}$$

I used two types of foraging socialities: solitary and social foraging. Solitary foragers maximize the energetic currency C_i at patch i , such that:

$$C_{individual} = C_1 = C_2 = \dots = C_i \tag{2.10}$$

In this situation, all foragers experience the same C_i , and no forager can gain a higher currency by moving to another patch, making this parameterization similar to the predictions of the IFD (Fretwell and Lucas, 1969). Social foragers maximize the currency summed over all foragers in all occupied patches:

$$C_{colony} = \sum_{i=1}^I n_i C_i \tag{2.11}$$

This leads to slightly different distributions of foragers, as social foragers tend to forage farther from their nest so that nearby foragers can have a higher currency. In other words, they maximize the success of the entire aggregation at the expense of some of their foragers.

Foraging landscape

To represent the distribution of resources across the foraging environment, I used a 2D matrix of discrete patches located d m from a single nesting aggregation, allowing simulation of landscapes of arbitrary arrangement and complexity. Each patch contained a fixed number

of N_{Flws} identical flowers that all produce nectar with an energetic value of e_i (J/ μ L) at a secretion rate μ (μ L/s) up to a maximum standing crop per flower of l (μ L). S represents the proportional reduction of nectar standing crop from visitation (standing crop = $S \times$ maximum standing crop = Sl), using the equilibrium model from Possingham (1988) (Equation 2.12, see Equation S5 for the full solution). For example, a patch with a maximum standing crop of 2 μ L/flower with an S value of 0.5 would have a standing crop of 1 μ L/flower. *B. napus* produces more nectar when continuously drained, meaning that nectar production ceases in the absence of visitation (noted by Mohr and Jay, 1990).

$$\text{Standing crop } (\mu\text{L}) = Sl = \frac{l}{D_\lambda l + 1}, \text{ where } D_\lambda = \frac{\text{Visitation rate per flower}}{\mu} \quad (2.12)$$

During a simulation, foragers all start in the patch in which the aggregation is located, and are distributed to the rest of the landscape based on their energetic currency. Given that patch-level parameters are fixed (see Table 2.1), foraging currency within a patch is a function of load size L and the number of foragers using the patch N_{Frggr} , so the model maximizes C by optimizing L within that patch, given N_{Frggr} . In each step, the model finds the lowest-value and highest-value (by calculating potential currency if a forager was to be moved there) patches of the given foraging currency, and moves a forager to that patch. If the change in foraging currency from moving a forager is ≤ 0 , then no better distribution of foragers is possible (Nash Equilibrium), and the model has converged on the optimal distribution and load sizes of foragers. In this way, the model optimizes both L and N_{Frggr} across all cells within the foraging landscape, such that currency of the aggregation is maximized (as in Equations 2.10 and 2.11).

Two major caveats apply to this model. First, it does not deal with predation risk, but Dukas and Edelman-Keshet (1998) found that predation risk had only minor effects on the predicted distribution of competitors. In their model, increased predation slightly decreased

the number of solitary foragers and slightly increased the number of social foragers at distant patches. The influence of predation depends on the amount of risk experienced while flying versus while at the patch, which is poorly studied and difficult to estimate (but see Dukas, 2005; Higginson and Houston, 2015). Second, the model does not consider competition between different nests, which requires a game-theory approach that is beyond the scope of this study.

I wrote the model in R version 3.6.0, and compiled it into the package *CPForage*, available at the Github repository <https://github.com/samuelVJrobinson/CPForage>.

Table 2.1: Parameters used in foraging model. “Patch” indicates terms that are unique to each patch, whereas “Aggregation” indicates terms that are common to all foragers from an aggregation. Terms in red are variables that were optimized by the model. Parameter values for different land cover classes are described in Table S2.

Level	Parameter	Definition	Value	Source
Patch	L	Load size (μL)	-	-
	N_{Frgr}	Number of foragers at patch	-	-
	S	Proportion reduction in l	Eq. S5	-
	N_{Flws}	Number of flowers at patch	-	From data
	d	Distance to patch (m)	-	From data
	e	Energetic value of load (J/ μL)	7.5	From data
	h	Handling time per flower (s)	1.5	From data
	l	Standing crop under no visitation (μL)	0.82	From data
	f	Flight time between flowers (s)	0.86	From data
	μ	Per-flower nectar production ($\mu L/s$)	0.000039	From data; Mohr and Jay 1990
	p	Max licking rate on flower ($\mu L/s$)	1	Schmid-Hempel et al. 1985; Harder 1986
Aggregation	v	Unloaded flight speed (m/s)	7.8	Wenner 1963
	v_l	Loaded flight speed (m/s)	7.0	Wenner 1963
	α	Increase in cost of flight with load (J/sJ)	$\frac{c_f + L_{max}e_i(5 \times 10^{-5})}{c_f} - 1$	Schmid-Hempel et al. 1985
	β	Reduction in flight speed at maximum load	0.102	$1 - v/v_l$
	L_{max}	Maximum load size (μL)	59.5	Schmid-Hempel 1987
	c_f	Unloaded flight energetic cost (J/s)	0.05	Dukas and Edelman-Keshet 1998
	c_i	Cost of non-flying activity (J/s)	0.0042	Schmid-Hempel et al. 1985
	H	Time spent unloading in hive (s)	100	Seeley 1986

2.2.2 Field data collection

To compare the foraging model to actual honey bee visitation, I observed honey bee visitation in 28 stocked commodity canola fields in the Lethbridge and Grande Prairie regions of Alberta, Canada during the summers of 2014 and 2015 (Grande Prairie, 2014: 6 fields, 2015: 9; Lethbridge, 2014: 5, 2015: 8). Each canola field was stocked with a range of honey bee colonies (mean: 31.7, SD: 8.8, range: 20–40 hives per apiary), and field sizes ranged from 30.6 to 680 hectares (mean: 132.2 ha, SD: 162.8). I surveyed fields at plots along a linear transect, at 5, 20, 100, and 500 m into the crop, beginning at the edge of the field nearest to the apiary (Figure 2.2). At each distance, I observed the visitation rate of honey bees (as well as wild insect visitors) for 10 min in a 1 m² area using a square quadrat, and counted open, visitable canola flowers. During 2015, I also counted the number of foragers. A “visitable” flower was open (not in bud) but not yet senescent (petals had not yet started to dehisce, and style had not elongated more than 3-4 mm beyond the anthers). Bumble bees (*Bombus*) and other wild bees (*Halictus*, *Andrena*) were present in both regions (Table S4), but were rare compared to honey bees, so I excluded them as a source of nectar competition. Muscid, Syrphid, and Anthomyid flies were common flower visitors, but their nectar-feeding habits are not well-known, and these flies mainly basked on flowers or ate pollen (personal observation), so I also excluded them from analysis. I surveyed the areas surrounding my observation plots for hidden apiaries to ensure that the focal apiary was the only one in the area (feral colonies of honey bees are rare in both Lethbridge and Grande Prairie). All surveys occurred on fair-weather days with no rain and minimal wind (less than 30km/hr).

Since I did not measure canola nectar production over time, I estimated it using visitation rates and nectar standing crop. During the field observations, I sampled the standing crop of nectar in 5 visitable flowers from each plot using a 5 μ L microcapillary tube, and measured nectar concentration using an Atago HSR-500 refractometer (mean: 58.3% brix, 0.74 mg sugar/ μ L, see Bolten et al., 1979). I used the model of Possingham (1988), which describes the distribution of nectar standing crop values, given an arrival rate of flower visitors and

a nectar secretion rate. The nectar secretion rate was $0.146 \mu L/hr$ (SE: 0.025), which is about half of the value reported by Mohr and Jay (1990) ($0.32 \mu L/hr$), but is reasonable for field conditions rather than greenhouse conditions. Maximum nectar per flower was $0.823 \mu L$ (SE: 0.022), but there was high variation in the measured values (Figure S2), as nectar production can vary with both time of day and the stage in crop phenology (Pernal and Currie, 1998).

To account for the influence of flowers in non-crop (semi-natural) areas surrounding each field site, I constructed maps of floral landscapes within a 4 km radius around the sampled fields using Agriculture and Agri-Food Canada land cover data (Figure 2.2) from 2014 and 2015 (Agriculture and Agri-Food Canada, 2018), divided into 15 x 15 m patches. I did not gather floral abundance data from outside the canola fields during my study, so I used floral data collected by Galpern et al. (unpublished) to estimate flower abundance in non-canola patches. Flowers were counted using a 25 x 2 m transect and identified to species at 116 sites surrounding Vulcan, Alberta (approximately 110 km north-east of canola fields sites in Lethbridge). Sites were sampled multiple times during the summer of 2016 (mean: 6.9 visits per site, start day: June 26, end day: August 28). Most transects were located in road-side ditches and field margins, but flowers were also counted for native prairie, pasture, forests, and wetland areas. For the 20 most-abundant flower species at these sites, I collected estimates of nectar production, concentration, and maximum volumes from literature (Table S1), which allowed estimation of the average nectar values of flowers in the different cover classes (Table S2). I used the between-flower flight time (f) and handling time (h) of honey bees foraging on canola (using video footage from Waytes, 2017, unpublished) to estimate the between-flower flight speed (0.03 m/s), then scaled this up to the average densities of flowers in each cover class, using the foraging distance results from the earlier random foraging simulation. This likely differs from actual conditions experienced by foragers during 2014 and 2015, and potentially over-estimates the travel time between flowers (Marden and Waddington, 1981), but serves as an approximate level of wild flower abundance.

Table 2.2: Number of foragers used in the model

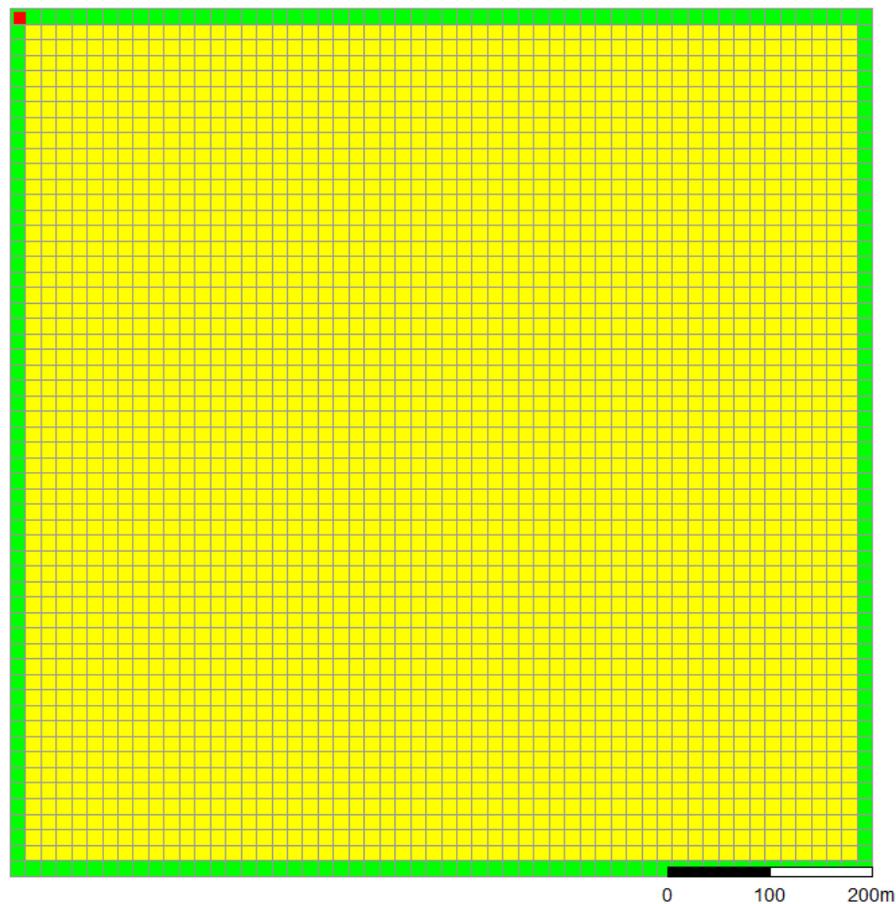
Colony size	% foragers	Forager number	Colony class
5000	10	500	Small
10000	20	2000	Medium
40000	30	12000	Large

2.2.3 Simulations

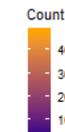
Simple simulations - quarter-section of canola, with surrounding buffer of semi-natural land

To generate predictions for forager distributions in a simple, closed system, I constructed a model of a single quarter-section of canola (840 x 840 m, see Figure 2.1), surrounded by a 15 m buffer strip containing a semi-natural flowering area (same nectar conditions as “ditch” class from Table S2), similar to uncultivated ditches or fence lines at the edges of canola fields. 40 honey bee hives were located in the patch of semi-natural habitat near the corner of the canola field, similar to arrangements used in honey-producing yards in southern Alberta (Clay, 2009). To assess the effect of aggregation size, I used small, medium, and large colony sizes (Table 2.2), based on published estimates of forager and colony demography from honey bee colonies (Roubik, 1980; Seeley, 1985; Beekman et al., 2004). I ran simulations using the same spatial arrangement for all combinations of sociality (social or solitary), foraging currency (net rate or efficiency), and aggregation size (small, medium, and large), for a total of 12 simulations. Finally, I ran a sensitivity analysis using only large colonies, where I varied all patch and aggregation parameters (Table 2.1) by 10% of their value to see what terms most strongly affected predicted visitation.

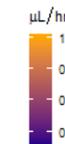
a) Simple model - quarter section of canola



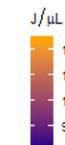
b) Input parameters

Flowers per m^2 

Nectar production per flower



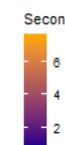
Nectar energy value



Maximum nectar capacity



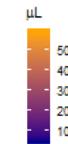
Inter-flower flight time



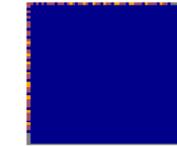
c) Output parameters

Foragers per m^2 

Load size



Efficiency



Standing crop

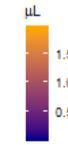
Visits per m^2 per hr

Figure 2.1: Cover classes (a), model input (b) and output (c) parameters for a single quarter section of canola, surrounded by buffer zone of grassland (see “ditch” values in Table S2). Cells are 15 x 15 m. The location of 40 bee hives is marked with a red point in the top left. Output shows model results for solitary efficiency-maximizing foragers with a large colony.

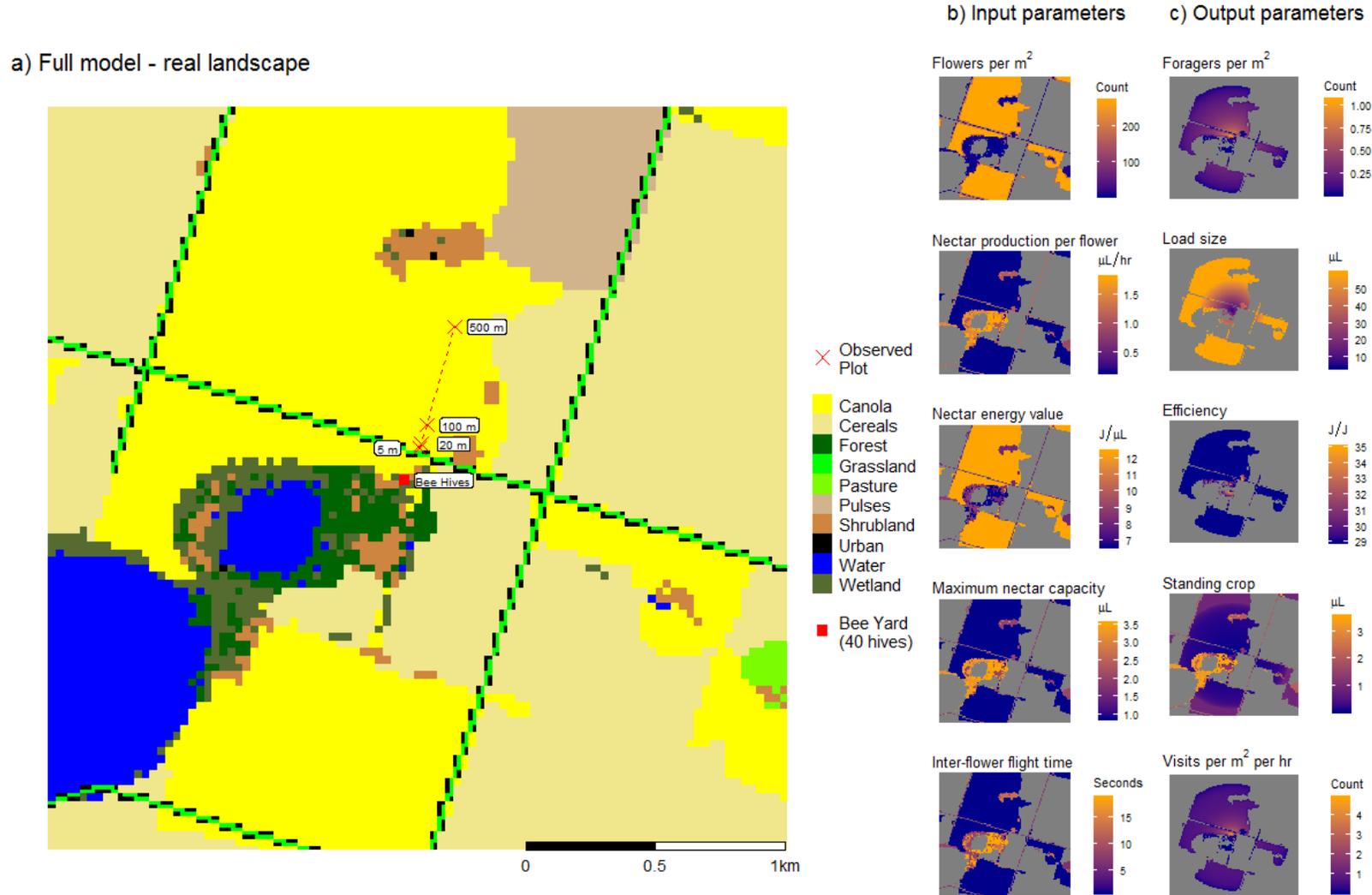


Figure 2.2: Cover classes (a), model input parameters (b) and output variables (c) for a single canola field near Grande Prairie in 2014. Location of bee hives is marked with a red point, location of observed plots along transect line (dashed line) are marked with a red X. Output shows predictions for efficiency-maximizing solitary foragers with a large colony size. Visitation declined quickly away from the bee hives, and was limited to within a 2 km radius.

Full simulations - real landscapes, including adjacent fields and semi-natural land

I simulated visitation at each of the 28 observed fields, using the number of honeybee hives that were located at each field, but used the real floral landscape maps derived from the AAFC data, instead of using the simple quarter-section scenario. As in the simple simulation, I used the foraging parameters for honey bees (Table 2.1), but used the nectar production values and flower density for the canola and all non-cropped areas (Table S2) in a 4 km radius around each field. I used each of the combinations of foraging currencies and foraging socialities, for a total of four possible foraging behaviours (Solitary Net-Rate, Solitary Efficiency, Social Net-Rate, Social Efficiency), and using three colony sizes (Table 2.2). This resulted in a total of 12 model runs for each of the 28 fields, for a total of 336 model runs (3 colony sizes \times 4 foraging behaviours \times 28 fields), on the Cedar computing cluster (<https://docs.computecanada.ca/wiki/Cedar>).

To convert the number of foragers and load size from the patches in the simulation (15 \times 15 m patches = 225 m²) into a simulated visitation rate at the observed 1 m² plots, I used data from 2015 when I recorded visits per forager within the observed plots. I used the predicted number of foraging bouts per hour for a given patch from the model divided by relative size of the plot as the number of foragers predicted to visit the observed 1 m² plot. I calculated the predicted visits per hour by multiplying predicted bouts per plot by visits per plot (4 flowers visited per plot, Figure S3), and compared predicted to actual visits in in-field plots using a linear mixed-effects model, with a random intercept and slope term for each field. I compared the slope of the predicted visits:actual visits relationship to a value of 1 to assess which combination of foraging currency, sociality, and aggregation size best predicted the visits seen in-field (all intercepts overlapped zero, $p=0.27$). All linear models were fit using Bayesian methods, with a diffuse normal prior for the main effects ($\mu=0$, $\sigma=5$) and an inverse-Wishart prior for the variance and covariance estimates ($V=1$, $\nu=1$), as recommended by Hadfield (2010). The upper and lower 95% quantiles of the posterior distribution were used to construct credible intervals (CIs) for each slope estimate, using a

minimum of 1000 independent Markov Chain Monte Carlo samples. All models were run in R 3.4.1 using `MCMCglmm` (Hadfield, 2010). I calculated R^2 to assess the relative explanatory power of the fixed and random effects using marginal and conditional R^2 (Nakagawa et al., 2013; Johnson and O’Hara, 2014).

2.3 Results

2.3.1 Simple model - quarter-section of canola

The predicted distribution of foragers from the simple model depended on both their sociality and their foraging currency (Figure 2.3). Predicted visitation by rate-maximizing foragers declined gradually with distance (Figure 2.3), both in number of foragers and visits per hour by each forager, but for large colonies of social rate-maximizers, the number of foragers per patch gradually increased with distance from the colony. Predicted visitation by solitary efficiency-maximizers declined with distance more quickly than social efficiency-maximizers, but neither showed the increase with distance shown in the social rate-maximizers. For efficiency maximizers, predicted visitation declined with distance from the hives, and most visitation occurring within 200m (Figure S4), indicating that they prioritize closer patches compared to rate-maximizers, even in the absence of predation. Both social and solitary efficiency-maximizers were predicted to use the field margin as well as the field itself, but rate-maximizers used field margins only at large colony sizes (see field margins in Figure 2.1c). Most simulated foragers used the canola crop rather than the field margin (sol-RM: 100%, sol-eff: 99.8%, soc-RM: 99.3%, soc-eff: 99.6%, all using large colony sizes).

Predicted load size, trip duration, and currency all varied with the foraging currency and sociality of the foragers. When foraging close to the colony, efficiency-maximizers were predicted to return with unfilled crops, but rate-maximizers foraging close to the colony returned with unfilled crops only when large colony sizes were large. The predicted increase in load with distance was linear for both rate- and efficiency-maximizers (Figure 2.3, row 2),

until they reached their maximum crop size. Predicted nectar standing crop also increased away from the hives, and was driven mainly by visits per hour and load size (Figure 2.3, rows 4 and 5). For example, standing crop for rate-maximizers roughly followed visits per hour, except for large-sized colonies, where reduction in load size allowed a higher visitation rate at the same standing crop. Predicted trip duration of social rate-maximizers increased with distance from hives, but was constant for solitary foragers, at least those from small- and medium-sized colonies. However, predicted trip length by efficiency-maximizers varied in a hump-shaped manner, with long trips occurring at the point where load size was maximized (bottom row of Figure 2.3) but shorter trips to near and far-away patches. The hump-shaped curve was more pronounced for solitary efficiency-maximizers, as the decline in trip duration with distance occurred more gently in social foragers, except in large-colony situations. Finally, solitary foragers were predicted to have the same value of foraging currency across all foraging distances (i.e. they assumed an ideal-free distribution). Social foragers did not, and predicted foraging currency declined with distance from their hives, but the decline with distance was small at large colony sizes.

Maximum nectar standing crop (l) was the most important term affecting predicted visitation rate within patches, but net-rate and efficiency-maximizers responded differently to changes in l . Predicted visitation rate at 100 m was most sensitive to variation in l (Table 2.3, Figure S5), especially for efficiency-maximizers. Interestingly, net-rate maximizers increased their predicted visitation rate if l was higher (greater dispersion away from the central place), while efficiency maximizers' visitation rate decreased (lower dispersion). Predictions for rate-maximizers were very sensitive to loaded flight speed (v_l), while predictions for efficiency-maximizers were somewhat sensitive to flowers per patch (N_{Flws}), nectar energetic value (e), nectar secretion rate (μ), and increase in flight costs with loading (α).

Table 2.3: Percent sensitivity (% difference from original) of visitation rate to 10% variation in model parameters, measured at 100 m from apiary, using a large colony size. Results for most influential parameters (maximum nectar standing crop, l , and loaded flight speed, v_l) are in bold text. See Table 2.1 for a description of all parameters.

Level	Parameter	Rate-maximization				Efficiency-maximization			
		Solitary		Social		Solitary		Social	
		-10%	+10%	-10%	+10%	-10%	+10%	-10%	+10%
Patch	N_{Flws}	-1.69	1.07	0.52	-0.09	-5.92	5.60	-5.58	5.15
	e	-0.33	0.27	-0.30	0.82	-6.04	5.74	-5.99	5.59
	h	3.88	-3.54	4.51	-3.58	3.80	-3.52	4.51	-4.20
	l	-12.03	36.78	-8.60	42.34	21.91	-16.53	22.09	-16.67
	f	-3.41	2.57	-3.41	3.70	-3.87	3.45	-4.38	3.90
	μ	-1.69	1.07	0.52	-0.09	-5.92	5.60	-5.58	5.15
	p	0.18	-0.18	0.77	-0.20	0.06	-0.20	0.09	-0.09
	Aggregation	v	-1.66	0.89	-2.20	2.56	-3.32	2.89	-3.64
v_l		18.37	-20.51	20.52	-23.65	-0.17	0.02	-0.04	0.04
α		-3.30	2.73	-3.23	3.80	-6.04	5.74	-5.99	5.59
L_{max}		2.41	-2.51	0.81	-0.40	0.14	-0.14	-0.46	0.01
c_f		-0.23	-0.29	0.26	0.30	3.74	-3.50	3.52	-3.26
c_i		0.01	-0.01	0.58	-0.01	2.34	-2.22	2.62	-2.42
H		3.95	-4.04	4.55	-3.55	0.96	-0.94	0.90	-1.11

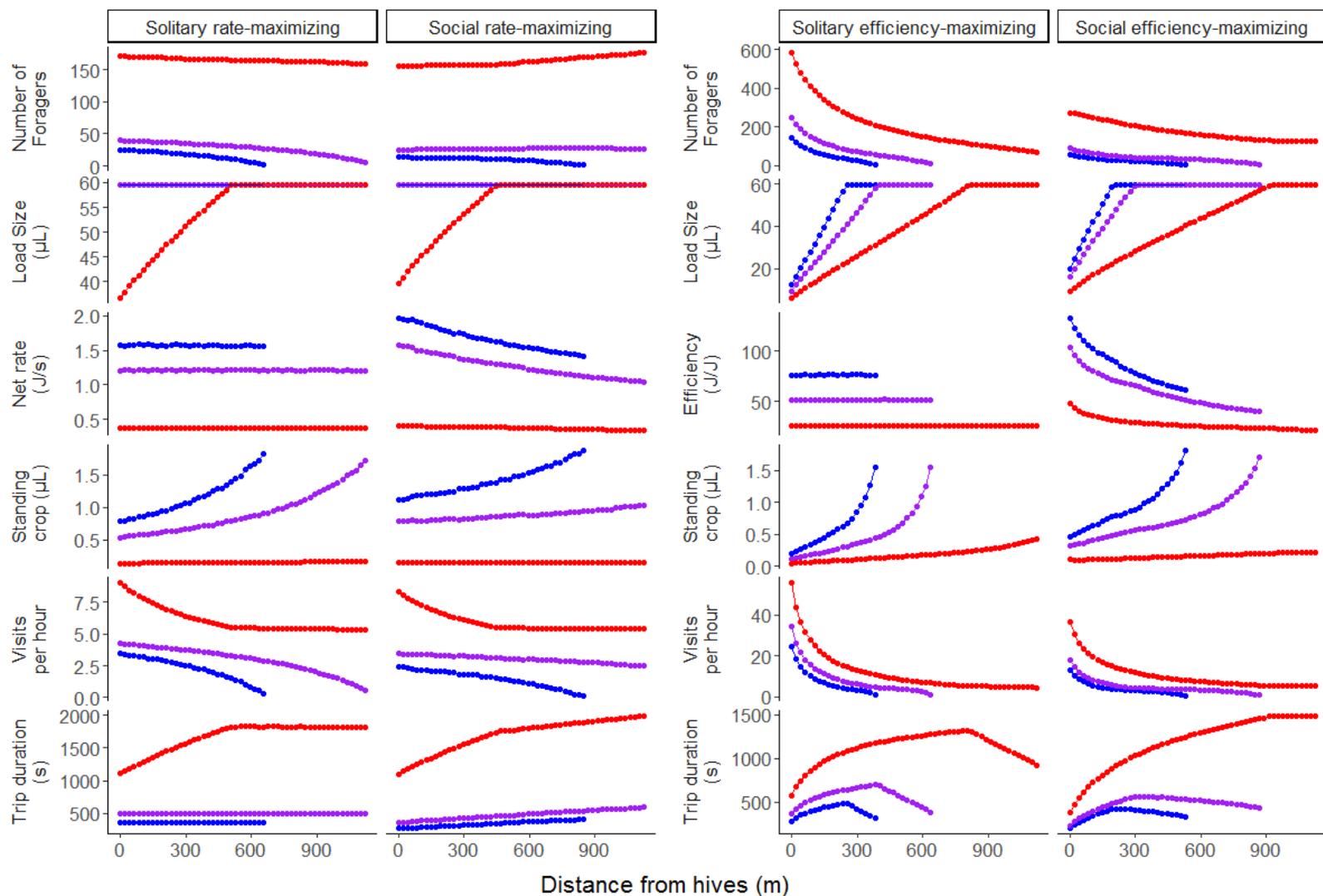


Figure 2.3: Predicted foraging responses to distance from hive, measured along the main diagonal of a square field of canola (visits in semi-natural habitat not shown), for foragers from 40 small (blue), medium (purple), and large (red) colonies. Number of foragers represents the number of foragers using the patch. Visits per hour is the predicted number of visits to a 1m^2 plot within a patch. “Standing crop (μL)” refers to nectar standing crop. A map of the foraging circumstance is depicted in Figure 2.1.

2.3.2 Full model - real landscapes, including adjacent fields and semi-natural landscape

The honey bee visitation rates observed in the 28 fields most closely matched the predicted visitation rates of solitary efficiency-maximizing foragers with a large colony size. This currency combination was the only regression fit for which the observed:predicted slope overlapped 1 (median: 0.88, 95% CI: 0.30-1.42, Figure 2.4), indicating that honey bees appear to maximize individual efficiency, and that forager forces were large during the period of my observations. Observed visitation rates were lower in the Lethbridge region in 2015 than in 2014 or in Grande Prairie alone (Figure 2.5, see also Chapter 3), but removing that combination of year and region did not change which currency-sociality combination best fit the data (Figure 2.6). The predicted visitation rates explained 16.8% of the variance in observed visitation, with among-site variation explaining 49%, indicating large field-to-field variation that was not accounted for in the simulation, possibly due to changes in off-field forage or in numbers of nectar foragers per colony. Like the simple simulation, very few predicted foragers used the surrounding non-canola resources, indicating that floral resources in nearby semi-natural land likely had little effect on visitation (Table S3).

2.4 Discussion

My results show that different currencies and socialities cause strong differences in predicted foraging of central-place foragers, and show support for honey bees foraging as solitary efficiency maximizers in real landscapes. Both the simple and the full model predicted very different distributions of foragers among currency types and socialities. However, my work extends the predictions of the two-patch model of Dukas and Edelman-Keshet (1998), and shows that these predictions can be applied to field situations. This model has theoretical and practical implications, as it allows comparisons of CPF distributions to be made across landscapes of arbitrary complexity, using energetic values derived from literature. This will

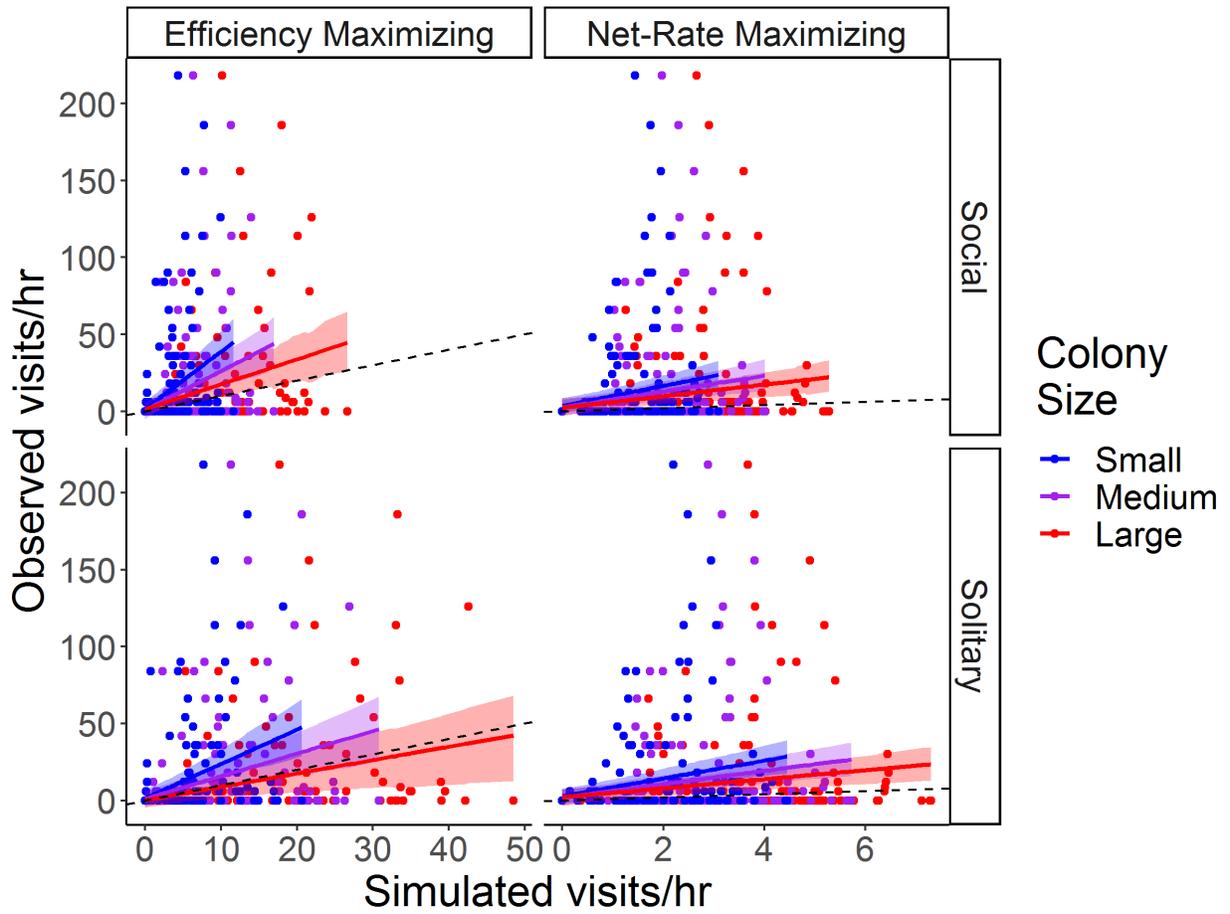


Figure 2.4: Simulated and observed visits per hour for all 4 foraging styles and 3 colony sizes. Simulated visitation rates for solitary efficiency-maximizing foragers with large colonies most closely matched the observed visitation rates from the field (slope was closest to dashed 1:1 line). Shaded areas represent 95% credible intervals. See Figure 2.6 for slope coefficients.

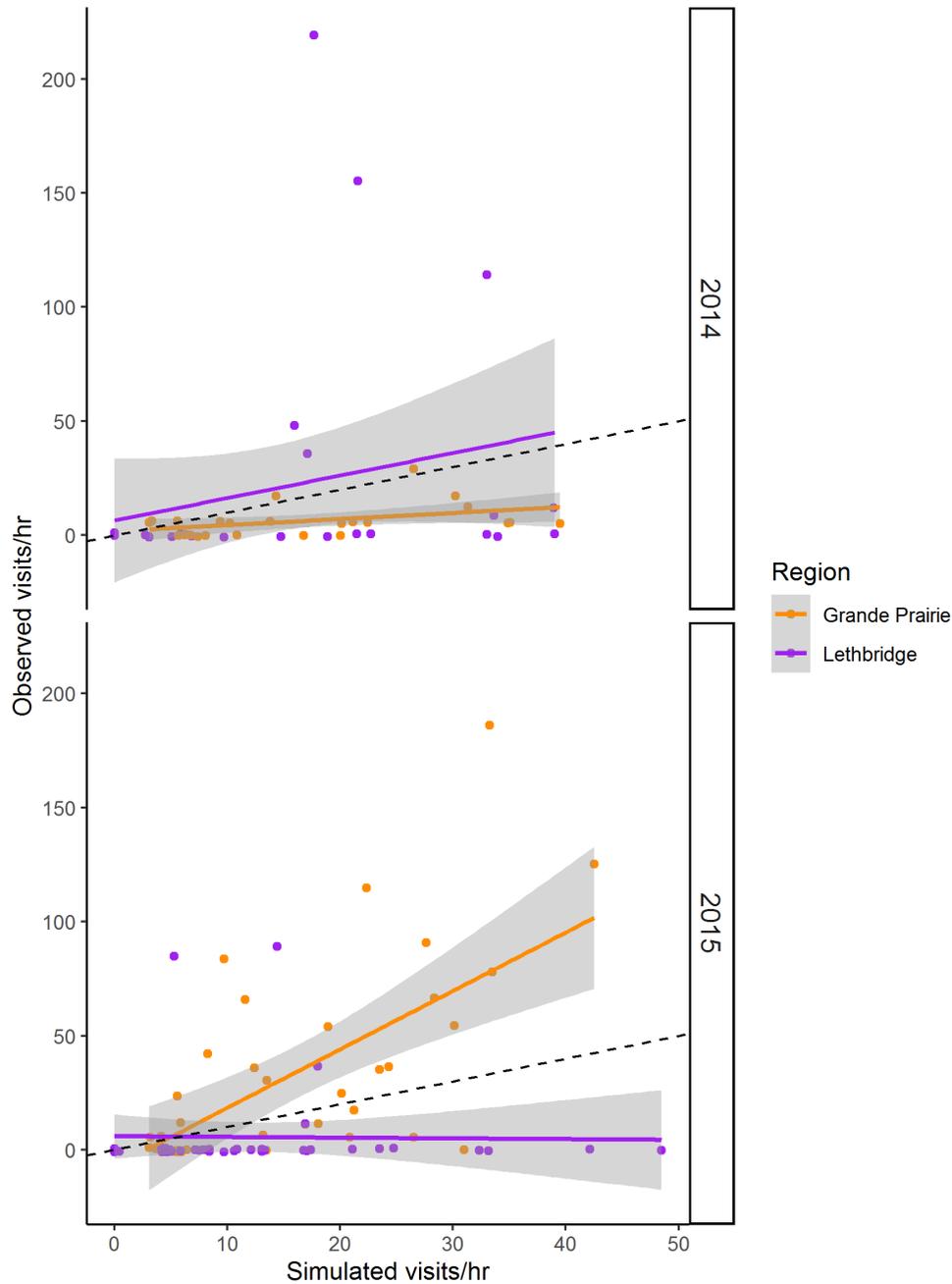


Figure 2.5: Simulated and observed visits per hour for solitary efficiency-maximizing foragers, using a large colony size, for each combination of region and year. The slope coefficient for Lethbridge in 2015 was much lower than other years (-2.23 ± 2.30 , $p=0.05$), indicating that actual visitation was much lower compared to the predicted values. Shaded areas represent 95% credible intervals. Dashed black line is 1:1.

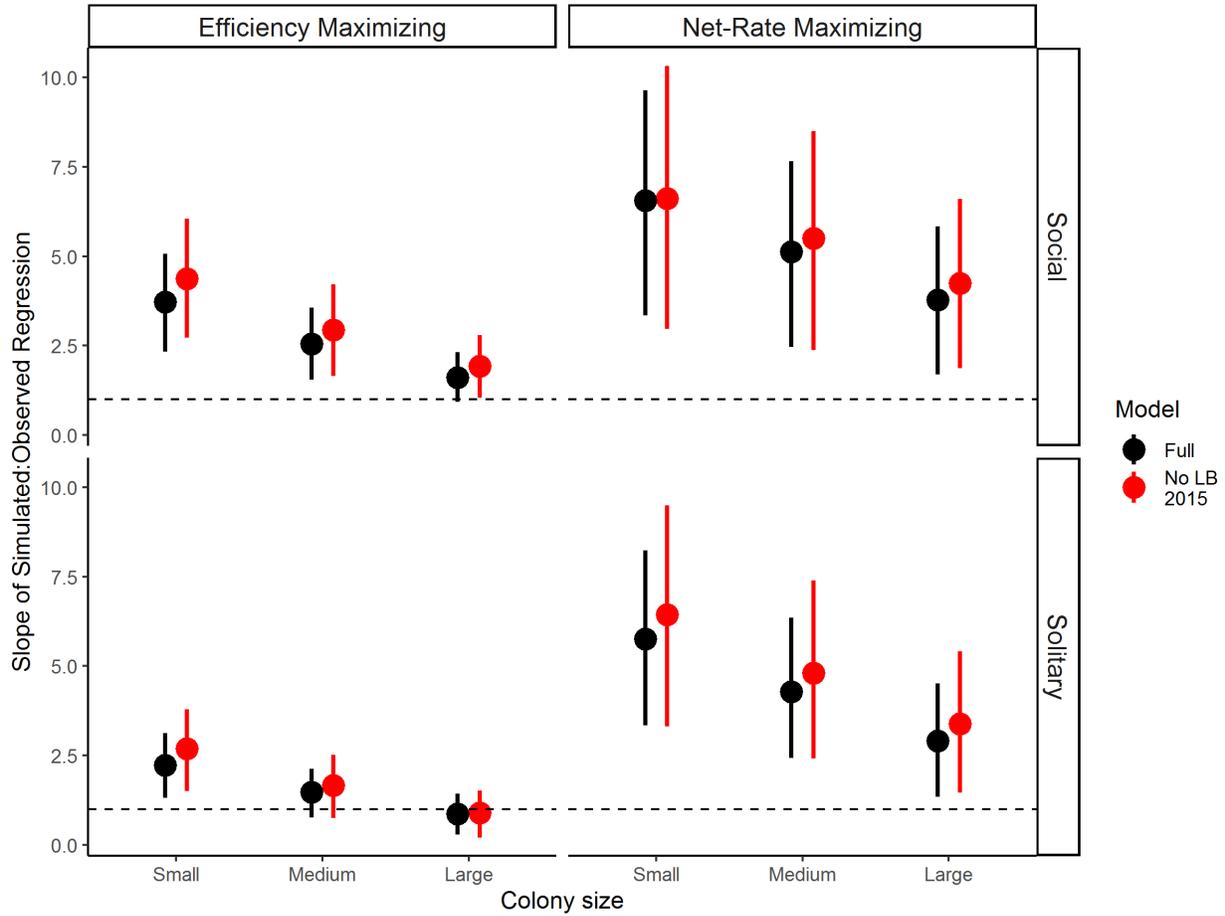


Figure 2.6: Regression slopes of simulated vs actual visits, using all field visitation data (black), and data with sites in Lethbridge from 2015 removed (red). Social efficiency-maximizers with a large aggregation size had the slope closest to the 1:1 line (dashed horizontal line), and removing the low-visitation sites from Lethbridge in 2015 did not make any large difference in the results of the model. Dots and lines represent the median and 95% quantiles (credible intervals) of the posterior distribution.

be useful to both landscape ecologists and beekeepers, as it allows simulations of CPF success under a range of simulated landscapes, and it has the potential to provide information on optimal hive placements for honey production (if linked to honey yield data) or crop visitation.

2.4.1 Simple model

Rate-maximizing foragers should fill their crops to capacity, while efficiency-maximizers may return to their colony with smaller loads, at least on shorter trips (shown by Schmid-Hempel et al., 1985). However, I found that the reductions in load sizes at short distances were much larger than the 7% reduction in load size predicted by Dukas and Edelman-Keshet (1998). For example, solitary efficiency-maximizers at 100 m were predicted to carry about half of a full load when colony sizes were small, but only 25% of a full load when colony sizes were large (Figure 2.3). I also found that simulated net-rate maximizers did not fill their crop to capacity when colony sizes were large (Figure 2.3). At large load sizes, further increases in load size delivered little additional net-rate, so simulated foragers chose smaller load sizes than the theoretical optimum size (which is the maximum crop capacity for net-rate maximizers, Schmid-Hempel et al., 1985), yet experienced a similar currency. This is similar to what foragers with a perceptual limit may do, as they are unable to map the precise shape of the net-rate:load size curve, but this only occurred in the presence of a large numbers of competitors (i.e. large colony size). As this occurred in a limited area, net-rate maximizers in the real world may simply choose increasingly distant patches, beyond the limited selection from the simple simulation (40 hives x 12000 foragers per hive = 480000 foragers in a 70.5 ha area).

Predicted trip lengths of efficiency maximizing foragers were hump-shaped with respect to distance from their aggregation, as they took more time to forage in patches at an intermediate distance than nearby or distant patches. This was shown empirically by Núñez (1982), although his results showed a much gentler curve of trip length with distance (see Figure 5 of Núñez, 1982), possibly because real foragers may have trouble estimating the precise threshold for taking on a full load of nectar. Since this was a unique feature for simulated efficiency maximizers, this also potentially presents an novel test of foraging currency, if researchers were to record duration of trip time and the distance to the chosen foraging patch for a given set of foragers. However, distinguishing between solitary and social efficiency-

maximizers may be difficult, as the decline in trip length with distance (after maximum load size is reached) was not predicted to be as steep for social efficiency-maximizers (Figure 2.3, bottom row).

The sensitivity analysis showed that the maximum nectar standing crop (l) was the most influential term on predicted visitation rates, with loaded flight speed (v_l) also being influential for rate-maximizers. However, predicted visitation responded differently to l : net-rate maximizers increased their visitation rate as l increased, while efficiency maximizers decreased their visitation rates. Changes in predicted visitation rates were caused by changes in load size (L) for net-rate maximizers, but efficiency maximizers distributed their number of foragers differently instead of altering their load size (Figure S5, compare row one to row two). This is consistent with bee behaviour under natural competitive scenarios, as well as behavioural models. In the Possingham (1988) nectar model, standing crop is positively related to maximum standing crop at a given visitation rate (Equation S2), so an increase in l causes an increase in nectar standing crop. Patch value is ultimately driven by nectar standing crop, but foraging bees still tend to visit flowers that secrete nectar more quickly (Pedersen, 1953; Klinkhamer and de Jong, 1990; Williams, 1997) because they use turning behaviour (Heinrich, 1979) or scent-marking (Stout and Goulson, 2001) to avoid previously-visited flowers. Dukas and Edelman-Keshet (1998) found that loading rate and patch size (nectar production) were both highly influential on visitation rate (see their Fig. 1), and similarly, this model predicts that for patches with higher nectar production rates, bees should increase their forager force but maintain approximately equal load sizes.

2.4.2 Full model

Honey bees most closely followed the predicted foraging of efficiency maximizers (Schmid-Hempel et al., 1985), but why do honey bees appear to maximize one type of energetic currency over another? Efficiency may be a better currency than net-rate because honey bee workers may be constrained by lifetime foraging activity (Neukirch, 1982; Kacelnik et al.,

1986, but see Visscher and Dukas, 1997). Ydenberg et al. (1994) and McNamara and Houston (1997) suggested that all foragers are net-rate maximizers, and that the net-rate versus efficiency dichotomy is related to the rate of self-feeding versus provisioning by foragers. They predicted that *provisioning* net-rate maximizers will maximize efficiency to achieve a high daily delivery rate, but when *self-feeding*, then digestive constraints will cause their behaviour to resemble net-rate maximizers. By this definition, honey bees should usually act as efficiency maximizers, since self-feeding rates are low, nectar will almost always be limited, and travel time between flowers will be relatively high in natural situations. Other foraging currencies, such as intake per wingbeat (Higginson and Gilbert, 2004) or lifetime profit (Higginson and Houston, 2015), may also provide good proxies of fitness in central-place foragers, but modeling these currencies requires estimates of relative forager predation risk during flight and within patches. Both Higginson and Houston (2015) and Dukas and Edelstein-Keshet (1998) found that the ratio of flight to in-patch risk can make lifetime profit-maximizers behave as either rate-maximizers (if both risks are equivalent) or efficiency-maximizers (if patch risks are higher). I did not include predation risk in the model, as I did not assess predation risks within different environments, but future work could attempt to estimate relative risks by recording departures to and from hives and patches (Dukas, 2008), allowing for a test of lifetime profit as a candidate currency.

Solitary foraging is similar to the ancestral behaviour of quasi-social bees and wasps (Michener, 2007), which form nesting aggregations but do not share labour or form distinct castes. So why did honey bees follow predictions for solitary rather than social efficiency, given that their fitness is maximized at the colony level? This may be because *true* social foraging requires a level of communication and information processing of which they are not capable. Foragers can map their foraging environment and update it based on information from other foragers (Sherman and Visscher, 2002), but they likely cannot integrate simultaneous information from tens of thousands of other foragers into their own foraging experience (Richter and Waddington, 1993). Whether information from other foragers is

used by a forager also depends on the relative value of the information; if the environment is either highly predictable or unpredictable, extra information has little value (Stephens, 1993). For example, Dornhaus and Chittka (2004) manipulated honey bee hives to obscure information from foraging dances, and found that non-dancing hives in temperate areas (non-patchy forage) had no difference in foraging success, while non-dancing hives in dry tropical forests (patchy forage) had lower success. This does not imply that honey bees do not gather information from other foragers, but simply that they may not use this information if their foraging sources are more evenly distributed in space and time (as in the case of mass-flowering crops). Finally, even if they could track information from their hive-mates perfectly, social foraging would still require foragers to choose patches of *lower quality* in order that other foragers may profit. There is no behavioural mechanism that could cause this; foragers are either recruited to patches by dancing (Seeley, 1989; Seeley et al., 1991) or ignore the information from dancing (Dornhaus and Chittka, 2004), but are never *repelled* by it. Since the predicted distributions of solitary and social efficiency maximizing foragers are qualitatively similar (Figure 2.3), solitary foraging may be the closest approximation of social foraging, in the absence of a central communication mechanism.

The simulation results from large-sized colonies (30000 foragers) most closely matched the field observations, which makes sense qualitatively, as honey bee hives in central Alberta typically contain approximately 45000 (± 1500) workers during the time of the observations (range: 20 - 75000 during July 10 - 31, SE: 1500, Szabo and Lefkovitch, 1989). The model assumed a fixed number of nectar foragers, but a bee colony can also increase its nectar foraging effort by a) having individual foragers work harder or b) switching workers from other tasks to nectar foraging (Ydenberg and Schmid-Hempel, 1994). Individual foragers tend to work harder when colonies are small or food is limited (Fewell et al., 1991; Cartar, 1992). For example, Fewell and Winston (1992) showed that honey bees increase pollen foraging in response to pollen demand, but pollen-forager numbers explained only 20% of the increase. This model predicted that both social and solitary foragers tend to work

harder with greater distances from the nest (greater flight time and foraging time), but did not account for changes of work pacing related to colony size. Fewell and Winston (1992) suggested that these changes in foraging represent homeostatic feedbacks related to pollen storage, whereby colonies increase their individual and collective foraging to maintain pollen stores at a given threshold. My model treated time spent in the hive (H) as a fixed value, but since honey bees may spend different amounts of time resting in the hive as a function of availability or competition (Núñez, 1982), future work could consider optimization of time spent in the hive in order to examine how hard foragers should work under different landscape scenarios (Becher et al., 2014).

A honey bee colony also can change the number of nectar foragers by redirecting them to other tasks. Workers can revert to other in-colony tasks, such as nursing or defence, if large losses of workers occur in the colony (Winston, 1991). Nectar foragers can switch to pollen collection in response to brood and pollen storage conditions (Fewell et al., 1991; Higo et al., 1992), but can also switch to water collection or fanning under hot and dry conditions (Lindauer, 1955; Ohguchi and Aoki, 1983; Kühnholz and Seeley, 1997), or collection of propolis.. Pollen foraging ultimately contributes to making workers and reproductives, and water foraging can reduce thermal stress on the colony. These activities contribute to the overall fitness of the colony, but are difficult to quantify from a purely energetic perspective (Rasheed and Harder, 1997; Cresswell et al., 2000). Foragers with dilute nectar are preferentially received during hot periods (Lindauer, 1955), and foragers avoid highly-concentrated nectar in favour of forager plants with more dilute nectar (e.g. *Trifolium*, *Medicago*, 0.34 mg/ μ L nectar, Szabo, 1985), which may be an energetically worse choice, but maximize the overall fitness of the colony. Canola flowers are a source of both pollen and nectar, so a switch to pollen foraging seems unlikely to explain the scarcity of foragers in some years (Figure 2.5). However, some of the field-to-field variance in observed visitation may be explained by preference for more dilute nectar types, especially in hot weather, as *Brassica* nectar is very concentrated (0.74 mg/ μ L). Accounting for this phenomenon would be difficult to do in a

purely foraging-focused model, as it would require a sub-model of hive-level thermodynamics where foragers can cool the colony by foraging for water, which is beyond the scope of this study.

One of the central assumptions of the IFD is that organisms have perfect information regarding the quality of foraging patches (Fretwell and Lucas, 1969). While foragers are not omniscient, Bernstein et al. (1988) showed that non-omniscient animals using a simple learning rule can approach the IFD. The same authors also found that in variable environments, animals tended to not match IFD predictions in coarse-grained environments (Bernstein et al., 1991), due to the difficulties of learning about other foraging opportunities. Both of the above models were based on non-CPF animals, but this mismatch may become even more intense with distance from the central place, as both patch value *and* information about the patch decrease with distance. Within the large-scale, coarse-grained environment of flowering crops (typical quarter-section fields are $\sim 800 \times 800$ m), this may mean that foraging honey bees have difficulty matching IFD predictions, simply based on incomplete information about the entire foraging landscape (Ranta et al., 2000). Even though returning workers dance to communicate forage locations (von Frisch, 1967; Wenner et al., 1967), the shared information from these dances may have little value if the size of the flowering patches is very large (Dornhaus and Chittka, 2004; Beekman and Lew, 2008), or if foragers prioritize private information over group information (Grüter and Farina, 2009). Landscape homogeneity, which is commonly seen in agricultural fields such as canola, may also reduce the value of information (Sherman and Visscher, 2002). Finally, Wells and Wells (1983) showed that individual foragers forage less efficiently when presented with a choice of forage types, and prefer flowers they were trained on (floral constancy). This may have led to flowers that were in bloom earlier than canola being selected, despite the higher energetic value of canola. However, my model and observations suggest that overall, honey bee distributions do approach an IFD (Dreisig, 1995; Cartar, 2009).

2.4.3 Future directions

This model makes the prediction that solitary efficiency-maximizing CPFs have a hump-shaped distribution of trip times, but data to test this prediction are scarce, aside from Núñez (1982). Others report average trip times (Schmid-Hempel and Wolf, 1988; Eckert et al., 1994), but what is needed for this is a comparison of trip lengths among foragers using patches of varying distances (Schmid-Hempel et al., 1985) with realistic levels of competition. A test of this would involve marking foragers at patches of a known distance from a honey bee colony, then comparing average trip lengths among patches. Since competition is one of the key features driving this hump-shaped distribution of trip times, realistic nectar competition should be a key feature of this test. Núñez (1982) used a feeder with an intermittent flow rate that simulated competition, but ideally this should be done using patches of flowering plants with a known nectar secretion rate, or a nectar feeder that can secrete nectar in a saturating manner (Possingham, 1988; Stout and Goulson, 2002).

The model only considered the behaviour of a single CPF aggregation, but in reality, multiple aggregations may be present in a landscape. A foraging landscape may have a) many CPF aggregations distributed across it (e.g. eusocial honey and bumble bees; quasi-social mining bees and sweat bees), and b) non-CPF foragers that do not use a central place (e.g. nectar-feeding flies). One potential way to address this would be a game-theory approach (Křivan et al., 2008) to distribute foragers to the highest-currency patch *given* that other foragers may be present in the same patch, choosing patches either by maximizing potential benefits or minimizing potential risks (both in terms of the foraging currency). Adding non-CPF foragers would require an additional layer of “mobile” foragers that choose the best available patch in the landscape, or a layer of “static” foragers that cannot move from their assigned habitats, and act as constant competitors. The model did not consider interference competition, where foragers actively reduce the benefit for heterospecific foragers by harassing, attacking, or other direct attempts at interfering with foraging (Sutherland et al., 1988). Since the value of a patch appears different depending on the competitive

ability of their neighbour as well as distance, interference with heterospecifics is beneficial close to the CPF, but not far away (Ydenberg et al., 1986). This means that the distribution of mobile foragers would be reduced near the CPF aggregations, in order to avoid indirect (scramble) or direct competition (interference) from CPFs, or in the case of two CPFs with overlapping ranges, would determine the shapes of the forager distribution within the overlapping range.

Chapter 3

Bee visitation, pollination services, and plant yield in commodity and hybrid seed canola

3.1 Introduction

Animal pollination of agricultural flowering plants is an important ecosystem service that contributes to about 10% of total crop production value worldwide (Gallai et al., 2009), and animal-pollinated plants produce a large number of important micronutrients in the human diet (Eilers et al., 2011). Therefore, understanding the process of animal pollination in crops is economically and ecologically important. Agricultural pollination, however, is largely treated as a single process, even though there are many links in the chain of events that result in the production of a fruit. Visitation of flowers by animals, typically bees and other insects, can result in pollen deposition on the stigma of the flower, followed by the growth of pollen tubes into the style and fertilization of ovules (Erbar, 2003). After fertilization, the plant may provide resources to fertilized fruits (or ovules within a fruit) to mature them into fruit (Goldberg et al., 1994). Each step has many other underlying processes (*e.g.* stigma

receptivity, pollen tube growth, ovule abortion, fruit maturation, reviewed in Real, 1983; Giovannoni, 2001; Erbar, 2003; Takayama and Isogai, 2005, and others), but even at the level of this coarse approximation, most studies of agricultural pollination fail to account for important underlying processes. Pollinating animals rarely visit equally on all flowers in a blooming crop field (Currie, 1997; Brosi et al., 2008; Isaacs and Kirk, 2010), but some agronomic studies implicitly make this assumption (Jr. and Simpson, 1989; Bommarco et al., 2012; Bartomeus et al., 2014). Pollen deposition from visitors depends on a number of factors (*e.g.* behaviour on flowers, size of pollinator), and whether this deposited pollen from visitors results in increased fruit production depends on the pollination context (*e.g.* self-pollination) and the life history and resource contexts of the plant (*e.g.* annual vs. perennial, determinate vs. indeterminate growth, light, soil nutrients and moisture). Moving beyond the “black-box” model of agricultural pollination requires accounting for these steps, and is necessary for understanding the contextual value of pollination services, as well as optimizing crop yield in novel circumstances.

Pollinator visitation is not spatially uniform within fields, as most pollinators are central-place foragers, meaning that visitation rates decline with distance away from their nest, and the bloom of flowering crops is not uniform. Smaller bees fly shorter distances than larger bees (Greenleaf et al., 2007; Zurbuchen et al., 2010), so their presence at the centre of large fields can be limited (Isaacs and Kirk, 2010). Hence, managing the location and density of managed pollinators in relation to their target crops is important for optimal yield of pollinator-dependent crops (Fries and Stark, 1983; Cresswell and Osborne, 2004). Foraging insects will often specialize on certain species or morphs of flowers in order to forage more efficiently (Heinrich, 1976; Goulson et al., 1997). However, pollination of hybrid seed crops requires movement of pollen between spatially separated lines of plants, so floral specialization can reduce the pollination services in these systems (Waytes, 2017; Gaffney et al., 2019). Competition between different species of foraging insects can occur if they deplete floral resources, but foragers can spatially or temporally separate their foraging to reduce compe-

tition (Schaffer et al., 1979; Thomson et al., 1987, but see Steffan-Dewenter and Tschardt, 2000), thereby increasing their fitness. Both resource depletion or interference competition can motivate visitors to reduce competition by increasing their foraging distance, switching between floral morphs more often, or visiting less frequently (Heinrich, 1979; Greenleaf and Kremen, 2006b). Thus, variation in visitation is driven by both distance from their nest (see Chapter 2), as well as competition with foragers from other aggregations, and increased competition can benefit plant fitness.

Insect visitation of flowers can enhance fruit production in flowering plants by increasing either the quantity or quality of pollen deposited on the stigma (Stephenson, 1981; Burd, 1994; Aizen and Harder, 2007), providing a larger range of female mate choice for each flower. Many flowering plant species are capable of self-pollination, but typically produce more fruit or seeds from outcrossed pollen (Knight et al., 2005) transported from conspecific plants by wind or an animal vector, but not all animal visitors are equal from a flowering plant's perspective. For example, large-bodied insects can deposit more pollen per visit on the stigma of the flower because they have a greater chance of contacting the stigmatic surface (Sahli and Conner, 2007). Pollinator behaviour is also important, as flower-visiting insects may steal nectar, clean off pollen between visits, or travel mainly between flowers on the same plant (Thomson, 1986; Herrera, 1987). Finally, the benefit of extra pollen deposition is diminishing (Plowright and Hartling, 1981), with very high numbers of pollen grains causing less and less of an increase in fruit production (Ashman et al., 2004; Harder et al., 2016).

Seed production can be limited by plant resources as well as pollen (Galen et al., 1985; Haig and Westoby, 1988; Campbell and Halama, 1993), meaning that the benefits of insect pollination depend on the resources available to the plant (Stephenson, 1981; Tamburini et al., 2017). Pollen limitation can also occur at multiple levels within a plant, reducing the number of seeds per fruit, the number of mature fruit, or both (Burd, 1994). Low pollen deposition may reduce the number of mature fruit via flower abortion (Knight et al., 2006), where poorly-pollinated flowers are cut off from the plant. Plants with an indeterminate

growth strategy may compensate for a high flower abortion rate by simply making more flowers, resulting in similar seed production to pollinated plants (Lovett-Doust and Eaton, 1982; Lawrence, 1993; Sabbahi et al., 2006; Bos et al., 2007). Whether individual plants can compensate for low pollination depends on the time remaining in the season, as well as the resources available to create extra shoots and flowers. Pollen limitation may also reduce the number of seeds per fruit, so additional pollen may result in a greater number of seeds per fruit (Knight et al., 2006), which in turn may result in a reduction in the size per seed (Free and Nuttall, 1968; Mazer, 1987) due to competition between ovules. Seed size can vary strongly among plants, and can be affected by resources available to the plant (Mazer, 1987; Venable, 1992). For example, Maddox and Antonovics (1983) observed a negative size-number tradeoff in *Plantago* seeds, but only after accounting for the positive effect of plant size, indicating that larger plants were better able to provision their seeds. Since the size and number of offspring are direct determinants of a given plant’s fitness, and the yield of the plant in an agricultural setting, allocation strategies that plants use under situations of pollen or resource deficits are important both theoretically, and in the context of food production (Bos et al., 2007; Tamburini et al., 2019).

Insect pollination is especially important in the production of hybrid canola crops (*Brassica napus* L.). Hybrid “commodity canola” (used for oil and meal production) is the offspring of two parental “seed canola” breeding lines, a male-sterile “female” line and a hermaphroditic “male” line (Westcott and Nelson, 2001; Steffan-Dewenter, 2003; Clay, 2009). Seed canola production requires a large number of pollinators to ensure pollination of the female line (seed from the male line is not harvested), and extra pollination may also increase the yield of commodity canola (Morandin and Winston, 2005; Rader, 2010; Bommarco et al., 2012; Bartomeus et al., 2015; Perrot et al., 2018). However, many studies of commodity canola pollination suffer from either a lack of realistic context, have a number of potential confounding variables, or infer plant-level outcomes from flower-level treatments. Greenhouse experiments typically involve unrealistically high pollination, nutrient availabil-

ity, and water, all of which can influence yield (Bartomeus et al., 2015; Marini et al., 2015). Field studies often relate yield to indirect measures of pollination services, such as insect abundance, species richness, or distance from sources of potential pollinators (Morandin and Winston, 2005; Ricketts et al., 2008), rather than direct measures, such as visitation rates or pollen deposition per stigma. These pollination proxies are then related to measures of yield, such as grams of seed per m^2 , which may be useful to growers, but provide limited information about how plants dynamically respond to pollen exclusion or addition (but see Sabbahi et al., 2005). Net- or cage-treatments exclude insect visitation from certain plants or flowers, but can alter wind pollination, humidity, light, or pest pressure (Olsson, 1960; Neal and Anderson, 2004; Jauker and Wolters, 2008), meaning that the sole effect of lower insect visitation is confounded by other factors. These methods offer an incomplete picture of how pollination relates to yield in canola crops (Ouvrard and Jacquemart, 2019), and obscure estimates of pollinator value in a globally valuable crop species (Melathopoulos et al., 2015). Thus, whether pollination impacts commodity canola production (or if not, why not) is poorly understood.

Fruit production in plants involves a sequence of processes (visitation \rightarrow pollen deposition \rightarrow fruit production \leftarrow plant resources), that determine the magnitude of the link between pollination and the components of crop yield. However, most studies of how pollination relates to crop yield either examine each process independently, or omit intermediate steps in the sequence of events (but see Sáez et al., 2018), meaning that the relative importance of visitation and plant resources are unresolved. Structural equation models (SEM) provide a framework for empirical analysis of this sequence, as they allow underlying causal assumptions to be formally stated and tested (Shipley, 2009; Grace et al., 2012), provide insight into alternative mechanisms that may be at play, and are flexible in many of their assumptions (Clough, 2012). SEMs represent an intermediate class of statistical models, occupying a space somewhere between regression-style models and dynamic or agent-based models, making them ideal for generating and testing sets of mechanistic hypotheses (Grace, 2006;

Kline, 2013). Using both commodity and seed canola provides an opportunity to compare two plant varieties that differ strongly in their pollination requirements, using a similar type of structural model, while accounting for agricultural differences between varieties (spatial arrangement, planting density, irrigation).

In this study, I modeled how distance influences pollinator visitation, which in turn influences pollen deposition and seed yield, using commodity and hybrid seed canola crops in Alberta, Canada. My five main hypotheses are outlined as follows:

1. Foraging honey bees and leafcutter bees are sensitive to distance due to cost of flight (Schmid-Hempel et al., 1985), and deplete floral resources with visitation. Therefore, insect visitation should decline with distance from their hive or shelter to achieve equivalent rewards (Dukas and Edelman-Keshet, 1998; Cresswell et al., 2000).
2. Visiting bees can deposit pollen on stigmas, so areas with high rates visitation should have more pollen deposition on stigmas than areas with low rates of visitation (Mesquida et al., 1988; Hoyle et al., 2007), depending on foraging behaviour of the bee (Free and Ferguson, 1983).
3. Seed production for a given plant is limited by the resources it is able to sequester. Therefore, large plants should have more resources at their disposal, and should produce more fruit per plant and produce a higher number of larger seeds per fruit (Galen et al., 1985; Lawrence, 1993; Marini et al., 2015).
4. Seed production in resource-rich plants is also limited by pollination. Plants in areas with high pollen deposition should have a higher proportion of successful flowers (Sabbahi et al., 2005), and a higher number of seeds per pod (Morandin and Winston, 2005).

This study assesses the strength of the connections between visitation, pollination, and yield, in a globally important crop species, and identifies the relative importance of bee pollination for seed production, using in-field data from two distinct cropping systems. Other

studies of crop pollination focus on individual components, such as visitation and pollination (Cresswell, 1999; Thomson and Goodell, 2001), or visitation and yield (Steffan-Dewenter, 2003; Manning and Wallis, 2005; Hudewenz et al., 2013), but have not incorporated the links in a single framework (but see Sáez et al., 2018, and few have used realistic field data (Morandin and Winston, 2005; Isaacs and Kirk, 2010). This work adds to the body of literature examining the resource context of pollination services (Haig and Westoby, 1988) within cropping systems (Marini et al., 2015; Tamburini et al., 2016; Fijen et al., 2018; Tamburini et al., 2019), and identifies directions of future research in seed production systems.

3.2 Methods

3.2.1 Data collection

From June through August of 2014 and 2015, I surveyed 29 commodity canola fields (14 in 2014, 15 in 2015) near Beaverlodge, Alberta and 31 fields (17 in 2014, 14 in 2015) near Lethbridge, Alberta. Commodity canola fields were selected based on the proximity of honey bee apiaries and site access. 28 of the 60 fields were stocked with an average of 0.6 hives/hectare (range: 0.03 - 3.1, SD: 0.58) while 32 fields were not stocked. I assumed similar numbers of workers per colony at both localities. Apiaries were typically stationed at the corners of fields, often near to shrubs or tree-lines to act as a wind break. Growers were asked for canola variety information, but there was not enough replication to test for difference between varieties. 14 of 31 commodity fields near Lethbridge (but no fields in Beaverlodge) were irrigated. Fields with central-pivot irrigation were mostly circular, but dryland (non-irrigated) fields were usually square or rectangular.

During 2015 and 2016, I also surveyed 35 hybrid canola seed fields (15 in 2015, 20 in 2016) near Lethbridge, Alberta, again from June through August. Seed fields were consistently stocked with honey bee hives at a rate of 3.6 hives/ha, and apiaries were stationed in the corners of fields. Seed fields were also stocked with leafcutter bees, and used either “standard”

or “double” leafcutter bee stocking rates ($\approx 50,000$ vs. $100,000$ cocoons/ha), and “standard” or “double” shelter densities (1.3 vs. 2.6 shelters/ha). Double stocking rates were only used in fields with double shelter density. All seed fields had central-pivot irrigation, and were mostly circular or semi-circular in shape.

At each commodity canola field, I used a GarminTMeTrex20 GPS to establish plots at 5, 20, 100, and 500m along a transect into the field, starting at the field edge nearest to the set of honey bee hives (271 total plots). In fields without honey bee hives, I began the transect at a field edge close to potential sources of natural pollinating insects, such as forests or grasslands, but I observed very few wild pollinators (Table S5). In seed canola fields, the male and female lines were planted in 1- and 6-m wide bays, respectively, and leafcutter bee shelters were placed in the female bays (Figure 3.1, 3.2). I established plots at 5, 20, 100 (250 in 2016), and 400m into the field along a transect from the nearest set of honey bee hives. I made paired observations in adjacent male and female plots at each distance from the edge of the field (Figure 3.2). At the edge and centre of the field (5m and 400m) I established another plot in the centre of the female bay to examine the effect of distance from the male bay. Additionally, I used plot-level leafcutter and honey bee visitation data from Waytes (2017, and unpublished; same years and locations) to more accurately estimate the effect of distance from shelter on visitation rates (647 total plots). Distances between leafcutter bee shelters were not constant within a field, so I used a NikonTMLaser 800S Rangefinder to measure the distance from each plot to the nearest shelter. All surveys occurred on fair-weather days (median air temperature: 24.5°C ., range: $17\text{--}33$) with no rain and as minimal wind as possible (less than 30km/hr). Mean air temperature was similar between years in Grande Prairie ($\approx 22^{\circ}\text{C}$), but Lethbridge was warmer in 2015 (23 vs. 28°C). Plots were marked with coloured stakes driven into the soil to locate them later in the season.

Within each 1m^2 plot, I recorded the number of insect visits during 10 min (5 min for seed fields during 2015), and recorded the taxonomic identity of visitors contacting the stigmas and anthers. During 2015, I also recorded whether honey bees were top-working or side-



Figure 3.1: Hybrid seed field near Rainer, AB, showing the outlines of male and female bays in the foreground, with orange leafcutter bee shelters stationed throughout the field. The linear structure on the horizon is the central-pivot irrigation sprinkler.

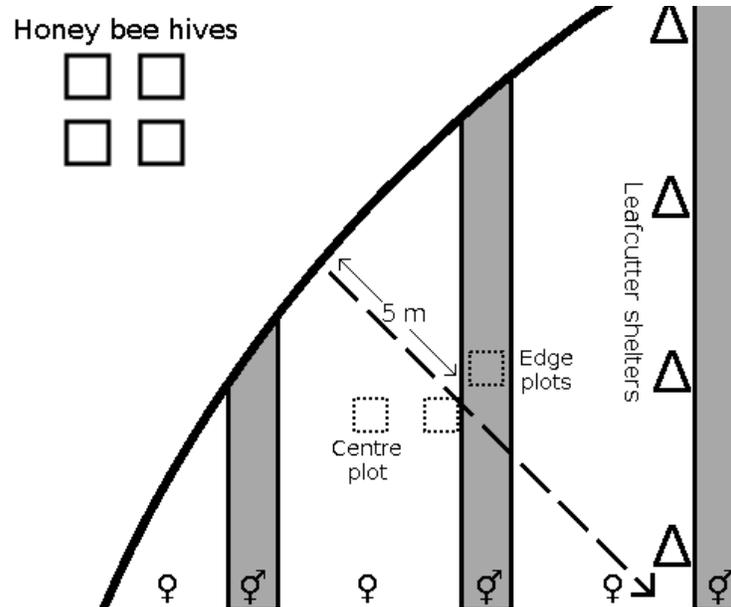


Figure 3.2: Plot arrangement for surveys in hybrid seed fields, showing hypothetical arrangement of leafcutter shelters (Δ), and male-fertile ($\♂$) and female bays ($\♀$) at 5m from the edge of the field. Plots were placed 5, 20, 100, and 400m along a transect (dashed line) from the field edge nearest to the set of honey bee hives. Plots were placed side-by-side in the male bay and edge of the female bay (“edge” plots), and at the 5m and 400m distances, a plot was placed in the centre of the female bay (“centre” plots).

working flowers (see also Free and Williams, 1973; Free and Ferguson, 1983; Mohr and Jay, 1988). Top-working bees landed on the top of the flower and inserted their proboscis down between the petals to access the nectaries of the flower, while side-working bees landed on the side of the flower and stole nectar by inserted their proboscis between the petals, avoiding contact with the stigma or anthers. Additionally, I recorded whether honey bees were pollen or nectar foragers (pollen foragers had a visible pollen load on their corbicula, while nectar foragers had none). I counted visitable flowers in each plot, where “visitable” was defined as an opened flower (not in bud) but not yet senescent (petals had not yet started to dehisce, and the style had not elongated more than 3-4 millimeters beyond the anthers). To assess pollen deposition at the plot level, I collected stigmas from five random open, receptive flowers at each plot, mounted them in fuchsin gel (Beattie, 1971) on depression slides, and counted the pollen on each stigma using a LeicaTMDME 13595 light microscope under 100x magnification (1294 commodity and 1050 seed canola stigmas). Each field was visited once

during the main canola bloom (late June - late July), and again before harvest (mid - late August) to collect plant samples. I collected three plants and recorded the density of plants per m² at the same plot where I conducted the visitation observations, collecting a total of 789 commodity canola plants and 582 seed canola plants. After drying the plants in a drying oven, I weighed the entire plant, counted mature pods, and counted the number of remaining flower pedicels to estimate total flower production. I sampled five pods at random from each plant, and counted and weighed the seeds from each pod, for a total of 3872 commodity canola and 2885 seed canola pod measurements. Finally, I threshed all the pods for each plant by hand, winnowed them using an air separator, and weighed the total mass of cleaned seeds in order to calculate the harvest index (seed mass \div above-ground biomass).

3.2.2 Analysis

To examine how yield is ultimately related to insect visitation, I used a piecewise structural equation model framework (pSEM, Shipley, 2009). Structural equation models are comprised of a set of underlying (usually) linear models arranged in a causal network, and provides a framework for formulating and testing hypotheses about a complex system (Grace et al., 2012; Lefcheck, 2015). Starting with a simple model (visitation \rightarrow pollen deposition \rightarrow fruit production \leftarrow plant resources), I built larger models that related measured variables within a causal framework (Figures 3.3 and 3.4). This allowed me to infer the relative strength of the main terms (e.g. pollen deposition, plant size) while controlling for other confounding factors (e.g. distance into field). Fruit set can suppress future vegetative growth and flower production (Stephenson, 1981), but pSEMs do not allow for causal loops (Grace et al., 2012), so I included a path from fruit set to flower production to approximate the process of fruit set suppressing future vegetative growth and flower production. The direction of the path could be reversed (large number of flowers reduces the proportion of fruit set), but I considered only the first scenario, as Sabbahi et al. (2006) showed that removing pods from canola plants causes an increase in later flower production.

I used generalized linear mixed-effects models (GLMMs) as the underlying linear models of each pSEM (see Equation sets S1 and S2 for model specifications). Hierarchical (mixed or random effects) models used in pSEMs can include processes that occur at different levels; for example, seed size-number trade-offs were modelled at the pod level, whereas pollen deposition was modeled at the flower level. Normal random effects were used to model variance between fields, between-plot (pollen, flower survival, seed count & size), and between-plant (seed count & size); if the lowest-level variance term was inestimable, I fit the model without it. Continuous responses were modeled using log-normal (plant density, plant size), square-root normal (flower density), and exponential-normal distributions (weight per seed), while counts were modeled as a negative-binomial (honey bee visits, pollen grains per stigma, flowers per plant, seeds per pod) or zero-inflated negative-binomial distribution (leafcutter bee visits), both using a log-link function. Each insect visitation model used a $\log(\text{exposure})$ term with a slope of 1 (i.e. an “offset” variable) to account for differences in observation times. Fruit set (fraction of flowers that matured into pods) was modeled using a beta-binomial distribution with a logit-link function. Independent variables were centred and log-transformed as necessary. Interactions between predictors were evident in honey bee visitation rate (Year:Locality interaction) and plant density (Irrigation:Year) in commodity canola, and for leafcutter bee visitation (Tent Stocking:Distance from edge) in seed canola, and were included in each model (represented as Y-shaped path in Figures 3.3 and 3.4). Finally, I created bivariate partial-effect plots of relevant terms within each model to aid in visualising each relationship, as well as any interaction terms (see below).

All structural equation models can contain non-included paths between variables (slope implied to be zero), but this can bias the model results if the assumption is not true. Therefore, I checked for non-included paths (“basis set”) by evaluating independence claims using Fisher’s C statistic from Shipley’s d-separation criteria (Shipley, 2000, 2009). Several missing paths were identified for the initial commodity model (Fisher’s $C=202.1$, $df=100$, $p<<0.001$), meaning that the model was misspecified, but the subsequent model that included the miss-

ing paths was adequate (C=81.6, df=86, p=0.62). Similarly, the initial seed field model also had several missing paths (C=37.54, df=56, p=0.027), which I corrected (C=58.10, df=64, p=0.68). D-separation criteria sets were generated using the `dagitty` library in R 3.5.1.

All component GLMMs of the pSEM were written in Stan 2.17.1 (Gelman et al., 2015), and run using `rstan` 2.18.1, and `cmdstan`. I used informative normal priors ($\mu = 0, \sigma = 5$) for the fixed effects terms, and gamma priors ($\alpha = 1, \beta = 1$) for the variance components. I ran three separate chains with an adaptive phase of 2000 iterations, and a sampling phase of 2000 iterations, then checked for convergence of the chains ($\hat{R} \approx 1$) and low autocorrelation within chains (high N_{eff}). I assessed the adequacy of the underlying probability distribution functions of each model using posterior predictive checks (Gelman et al., 2013), and found that the probability distributions were specified correctly (p~0.5) for all components except seed count. This means that while the average seed counts (per plant) were unbiased, the variance within a plant was not; however, the negative binomial distribution had the closest posterior predictive checks. p-values listed below (also in Tables S3 and S4) are *posterior* p-values, which represent the proportion of the posterior distribution that overlapped zero, with Z-scores (mean/standard deviation of posterior) showing the effect size. Predictions from models are median values of the posterior, representing the median prediction, while intervals displayed in figures are credible intervals (CIs), representing 95% of the samples drawn from the posterior distribution (analogous to confidence intervals, see Gelman et al. 2013).

3.3 Results

The SEMs revealed that plant size and pollen deposition were the main drivers of yield in seed canola, while only plant size mattered in commodity canola. Distance from the field edge had a negative effect on honey bee visitation in commodity and seed canola (Z=-3.7, -2.5, respectively), and unexpectedly, had a negative effect on leafcutter bee visitation (Z=

-4.4), showing that overall visitation decreases with distance into the field. The path from leafcutter bee visitation to pollen deposition was strong in seed canola ($Z=3.2$), but there was no path from honey bee visitation to pollen deposition in either crop type. Pollen deposition increased fruit set ($Z=3.1$) and seeds per pod ($Z=2.3$) in seed canola, but was not present in commodity canola, showing that yield in seed canola, but not commodity canola, is strongly dependent on pollination. Both crop types had strong negative paths from flower survival to flowers per plant (commodity $Z=-12.5$, seed $Z=-12.1$), indicating that high flower survival suppressed future flower production. Commodity canola had a similar weight per seed, regardless of the plant size, but in seed canola, plant size had a strong influence on seeds per pod ($Z=5.6$) and weight per seed (4.6). Finally, in both crop types, the paths leading from plant size were the dominant signal influencing fruit set (commodity $Z=5.8$; seed $Z=19.9$), but the path from pollen deposition to fruit set was only present in seed canola, showing that plant resources matter strongly for both crop types, but that increased pollen deposition only benefits seed canola.

The results of the underlying components of each pSEM are shown below:

3.3.1 Prediction 1: Decline in visitation with distance

Bee visitation strongly declined with distance away from the hives and shelters, in both commodity and seed canola fields. In commodity canola, honey bee visitation sharply declined with distance into the field ($Z=-3.7$, $p=0.0002$, Figure 3.5), decreasing from 8.5 visits/hr at the edge of the field to 3.1 visits/hr at 100 m into the field (at a stocking level of 20 hives). Visitation rates were higher in both years in Lethbridge (2014: 9.3 visits/hr, 2015: 7.1), but were higher in 2015 than 2014 at Grande Prairie ($Z=2.3$, $p=0.02$), rising from 5 visits/hr at the field edge in 2014 to 17 visits/hr in 2015. Honey bee visitation increased with the number of hives used for stocking ($Z=5.3$, $p<0.0001$); plot-level visitation at the edge of the field increased from 14.5 visits/hr with an apiary of 20 hives to 22.7 visits/hr with an apiary of 40 hives, while unstocked field edges had 1.8 visits/hr. In seed canola fields, honey bee

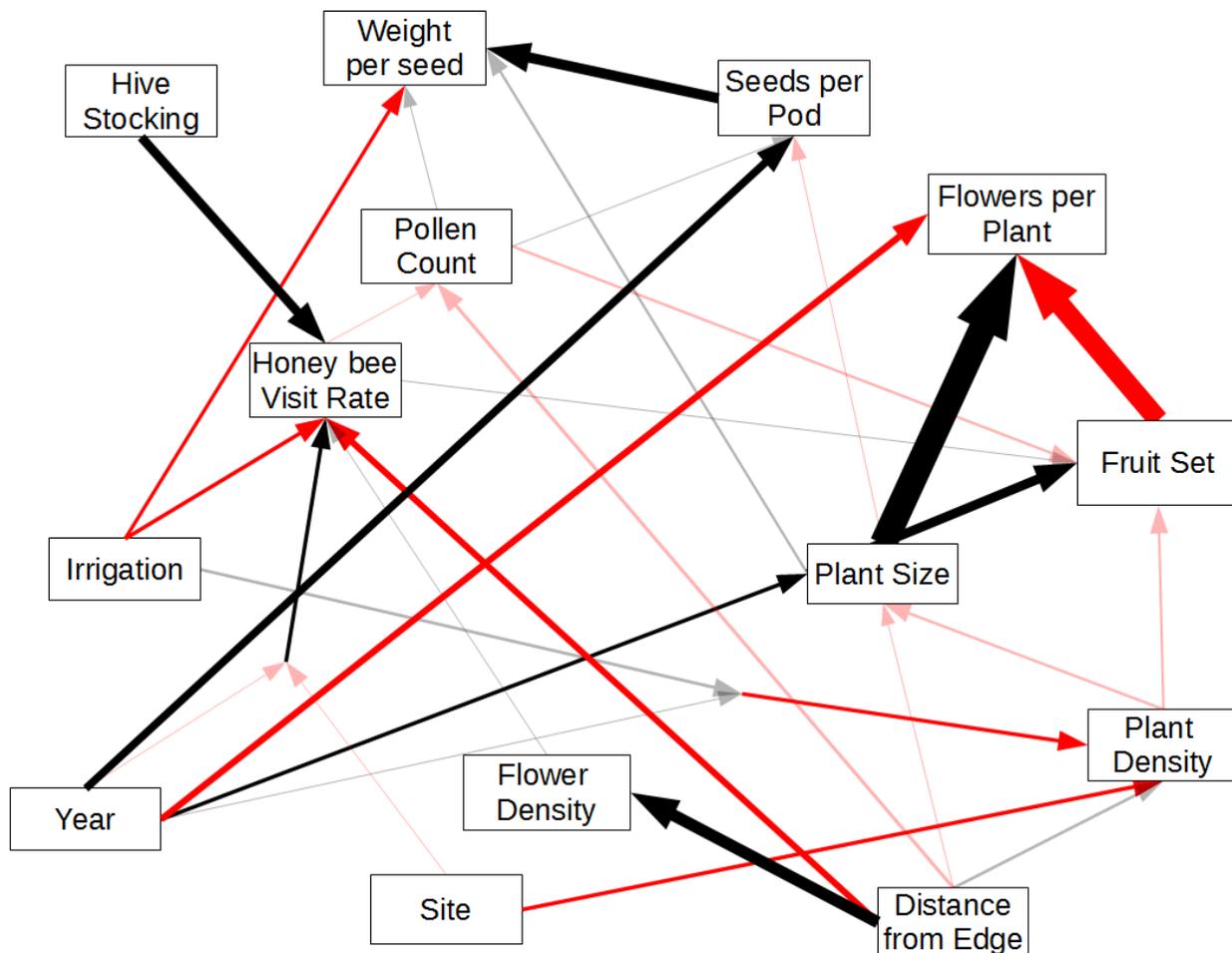


Figure 3.3: Path diagram for the commodity canola model, with positive and negative terms shown in black and red, respectively. Line thicknesses are proportional to effect size (mean/SD) of coefficients. Coefficients with 95% posterior quantiles overlapping zero are shown with a transparent line. Interactions are shown as an inverse Y-shaped path, with the two branches representing main effects, and the final branch representing the interaction term (*e.g.* effect of site and year on honey bee visitation rate). Year:site interaction is also shown in Figure 3.5. “Year” indicates the year effect of 2015, and “Site” indicates the site effect of Grande Prairie.

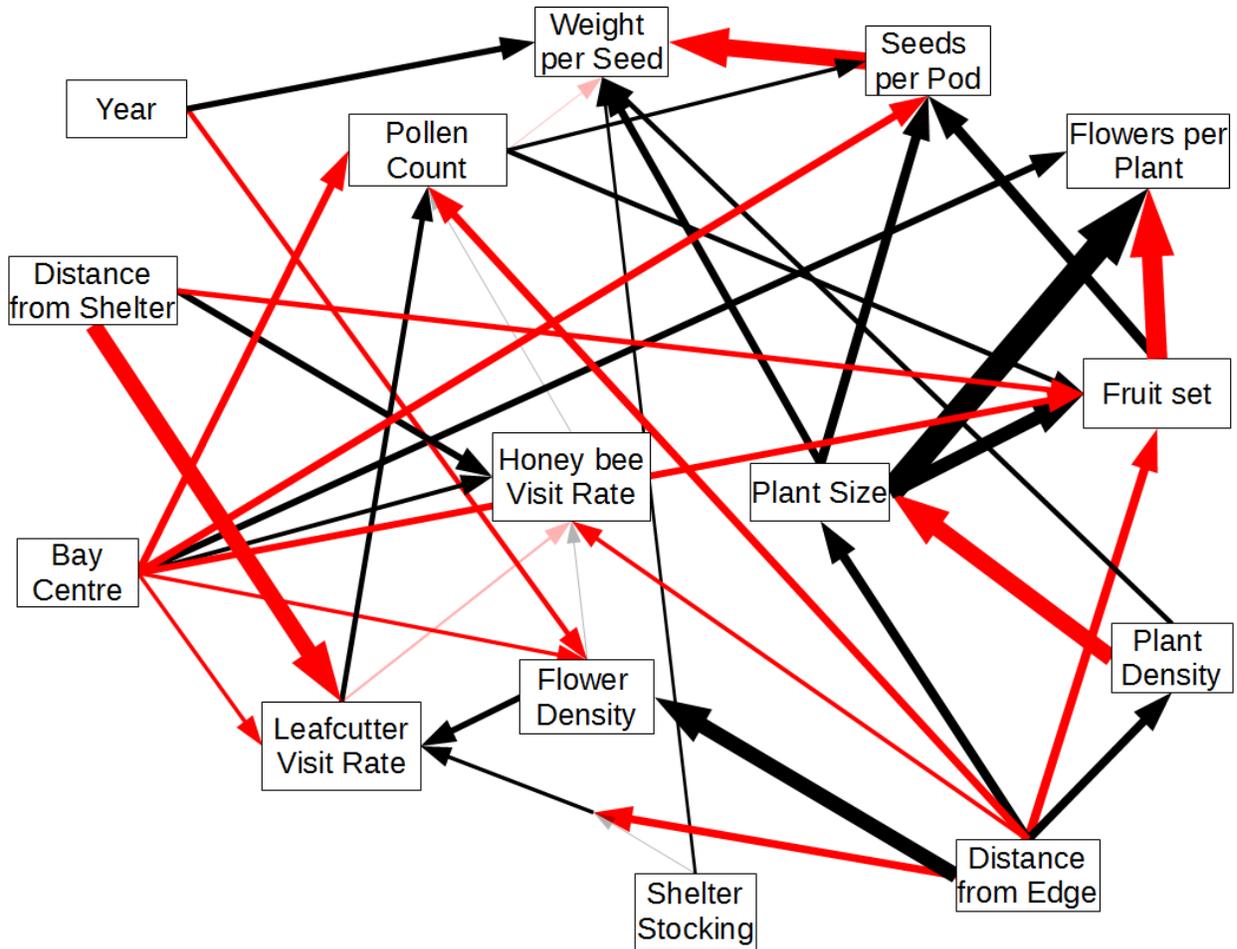


Figure 3.4: Path diagram for the seed canola model with positive and negative terms shown in black and red, respectively. Line thicknesses are proportional to effect size (mean/SD) of coefficients. Coefficients with 95% posterior quantiles overlapping zero are shown with a transparent line. Interactions are shown as an inverse Y-shaped path, with the two branches representing main effects, and the final branch representing the interaction term (*e.g.* effect of distance from edge and shelter stocking rate on leafcutter bee visitation rate). Stocking:Distance interaction is also shown in Figure 3.6. “Year” indicates the year effect of 2015.

visitation also declined with distance into the field ($Z=-2.5$, $p=0.01$), but not as strongly as in commodity fields (126 visits/hr at edge of field vs. 78 visits/hr at 100 m). Honey bee visitation was lower near leafcutter shelters ($Z=3.9$, $p=0.001$), dropping from 60 visits/hr at 10 m to 34 visit/hr at 2 m, likely due to competition with leafcutter bees (Figure 3.6, 3.7).

Leafcutter bees were much more sensitive to distance from their shelter than honey bees. Leafcutter bee visitation sharply declined with distance from their shelters ($Z=-11.4$, $p=0.0001$, 350 visit/hr at 2 m to 83 visit/hr at 10 m), and unexpectedly, was higher at the edge of the field than the centre ($Z=-4.4$, $p=0.0001$, 114 visits/hr vs 28 visits/hr). However, there was no difference in visitation rates when the stocking rate of cocoons per shelter was lower ($Z=2.2$, $p=0.028$), indicating that leafcutters at high stocking densities may migrate to shelters close to the edge of the field (Figure 3.6). Both leafcutter bees and honey bees visited at similar rates in the male and female bays (leafcutter bee: $p=0.72$, honey bee: $p=0.32$), but within the female bay, leafcutter bee visitation was lower in the centre of the bay ($p=0.04$, 51 vs. 29 visits/hr), while honey bee visitation was higher at the centre of the bay ($p=0.008$, 71 vs. 117 visits/hr, Figure 3.8).

Pollen- and nectar-foraging honey bees had very different patterns of side-working, both on commodity canola, and the male and female lines of seed canola. Side-working was common in nectar foragers, but was more common in commodity canola (64%) than in the male (36%) or female bays (2.8%) of seed canola, indicating that a large proportion of honey bees foraging on canola flowers may never come in contact with the stigmas. Pollen foragers were almost uniformly top-foragers in both commodity and seed fields (Table 3.1), and pollen foragers were much less common in the female bays (1.4%) than in the male bays (15%), or in commodity fields (18%). Therefore, foraging honey bees in seed canola fields tend to treat male-fertile flowers similar to commodity canola flowers, but seem to top-work flowers more in commodity canola than seed fields. Leafcutter bee foraging behaviours were not recorded, but seemed to almost exclusively top-work flowers in seed canola fields.

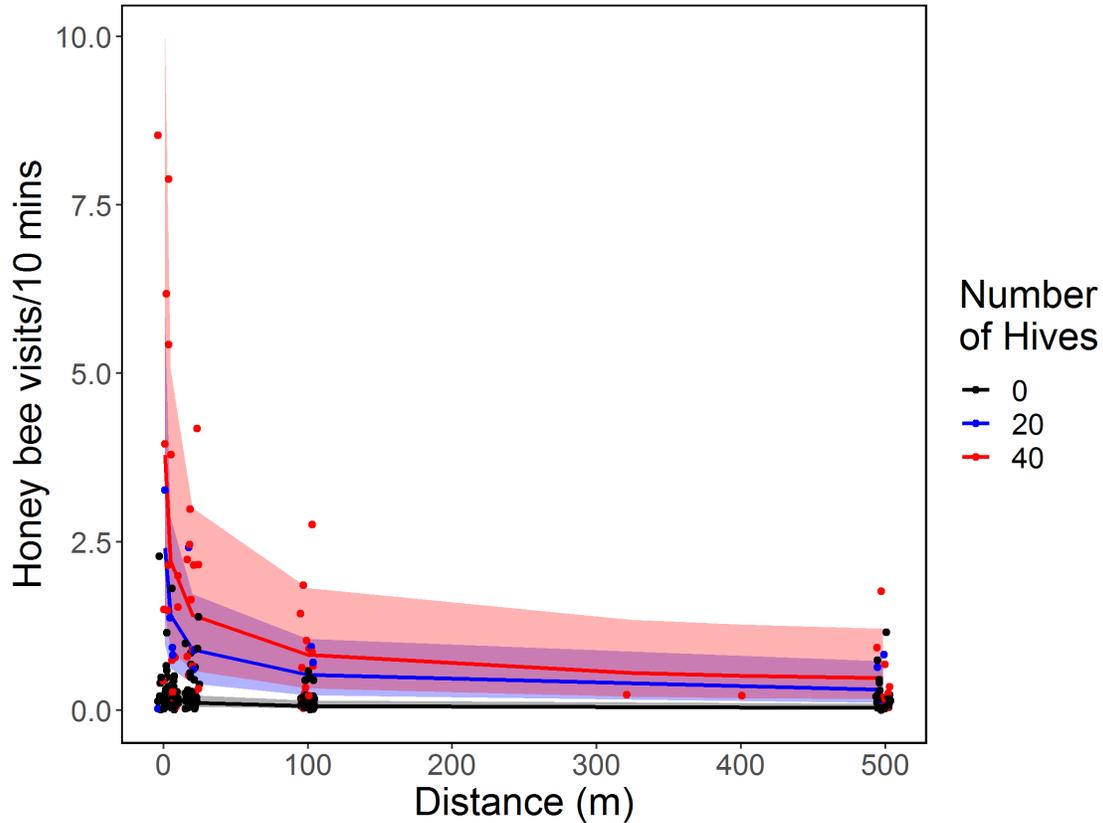


Figure 3.5: Partial effect of distance away from field edge and stocking on honey bee visitation in commodity canola fields. Solid lines represents median, and shaded areas represent 95% CIs. Red line represents overall slope (controlling for region and year).

	Commodity fields		Seed fields (female bay)		Seed fields (male bay)	
	Top	Side	Top	Side	Top	Side
Pollen forager	44	2	12	0	115	0
Nectar forager	75	138	832	24	428	242

Table 3.1: Foraging behaviours of honey bees on commodity and seed canola flowers, recorded during 2015. “Top” (top-working) indicates that the bee inserted their proboscis down between the petals from the top of the flower, while “side” (side-working) indicates that the bee fed from the side of the flower and did not contact the anthers or stigma. Pollen foragers had pollen visible on their corbicula, while nectar foragers had none.

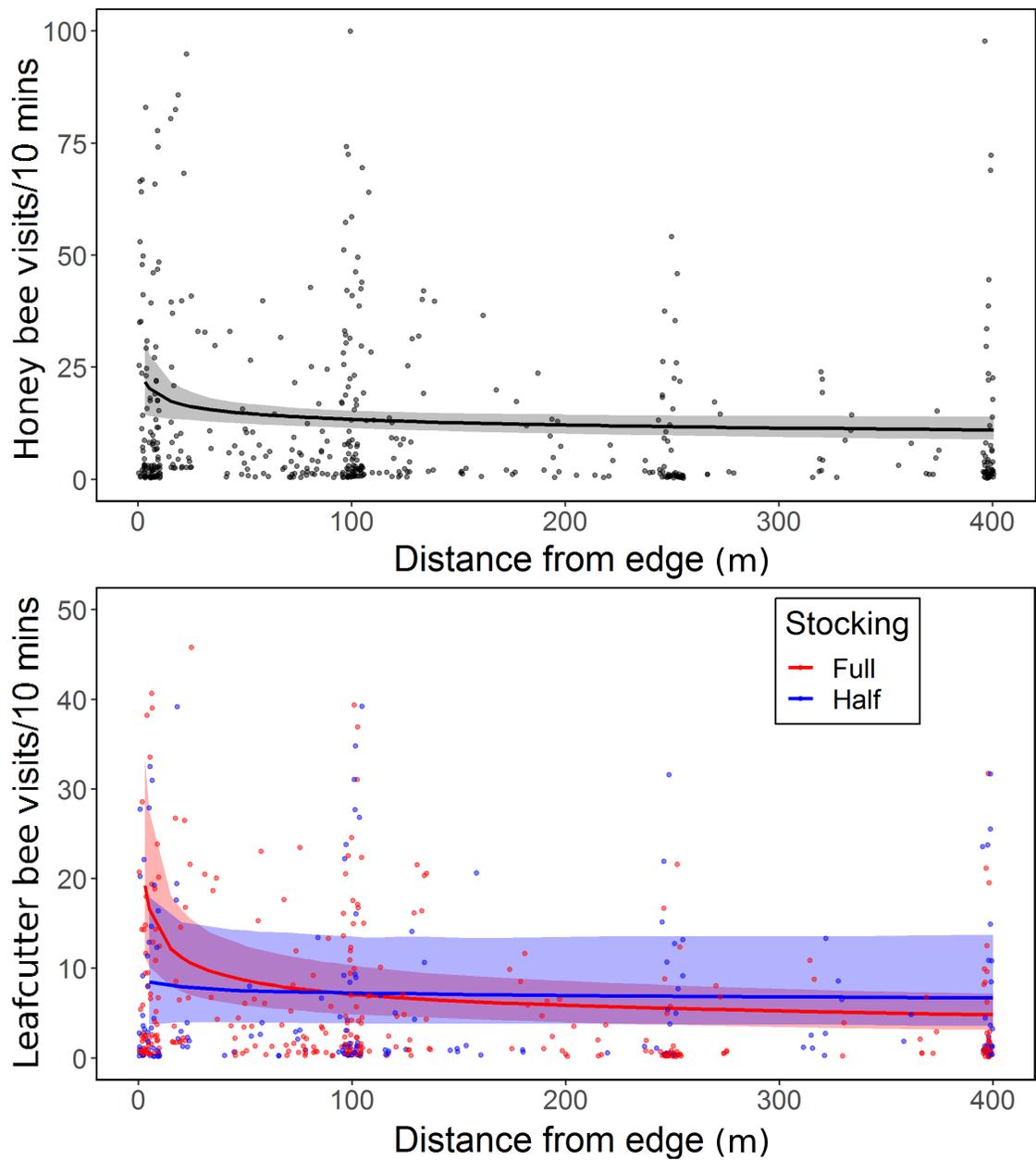


Figure 3.6: Partial effect of distance from field edge on honey bee and leafcutter bee visitation in seed canola fields. Solid lines represent medians, and shaded areas represent 95% CIs.

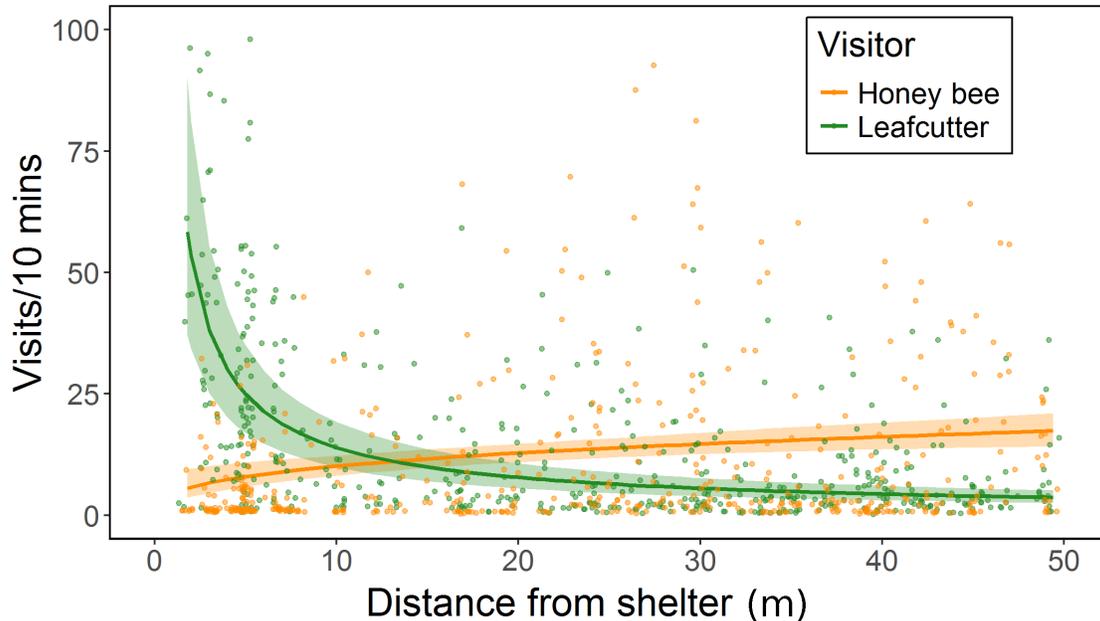


Figure 3.7: Partial effect of distance from leafcutter shelter on honey bee and leafcutter bee visitation in seed canola fields. Solid lines represent medians, and shaded areas represent 95% CIs.

3.3.2 Prediction 2: Pollen deposition increased by bee visitation

Pollen deposition was enhanced by bee visitation in seed canola, but not in commodity canola. In commodity canola, pollen deposition on stigmas was high (mean: 293 grains per stigma, SD: 385, range: 0–3981), but honey bee visitation did not affect deposition ($p=0.77$, Figure 3.9). Pollen grains per stigma weakly declined with distance from the edge of the field ($p=0.07$), but this only amounted to an average decrease of 290 grains per stigma at the edge compared to 240 at the field centre (6% decrease), meaning that distance did not strongly affect pollen deposition either. Flies were common visitors in commodity fields (Table S5), but had no detectable effect on pollen deposition ($p=0.577$), and other flower visitors were rare, so only honey bees and leafcutter bees were considered as potential pollinators. In seed canola, overall pollen deposition was much lower (mean: 22 grains per stigma, SD: 43, range: 0–578), was strongly increased by leafcutter bee visitation ($Z=3.2$, $p=0.002$, Figure 3.10, 12 grains/stigma at 6 visits/hr vs. 16 pollen grains at 60 visits/hr), and also decreased with distance from the edge of field ($Z=-4.4$, $p=0.0001$, Figure 3.11, 23 vs. 11 grains/stigma).

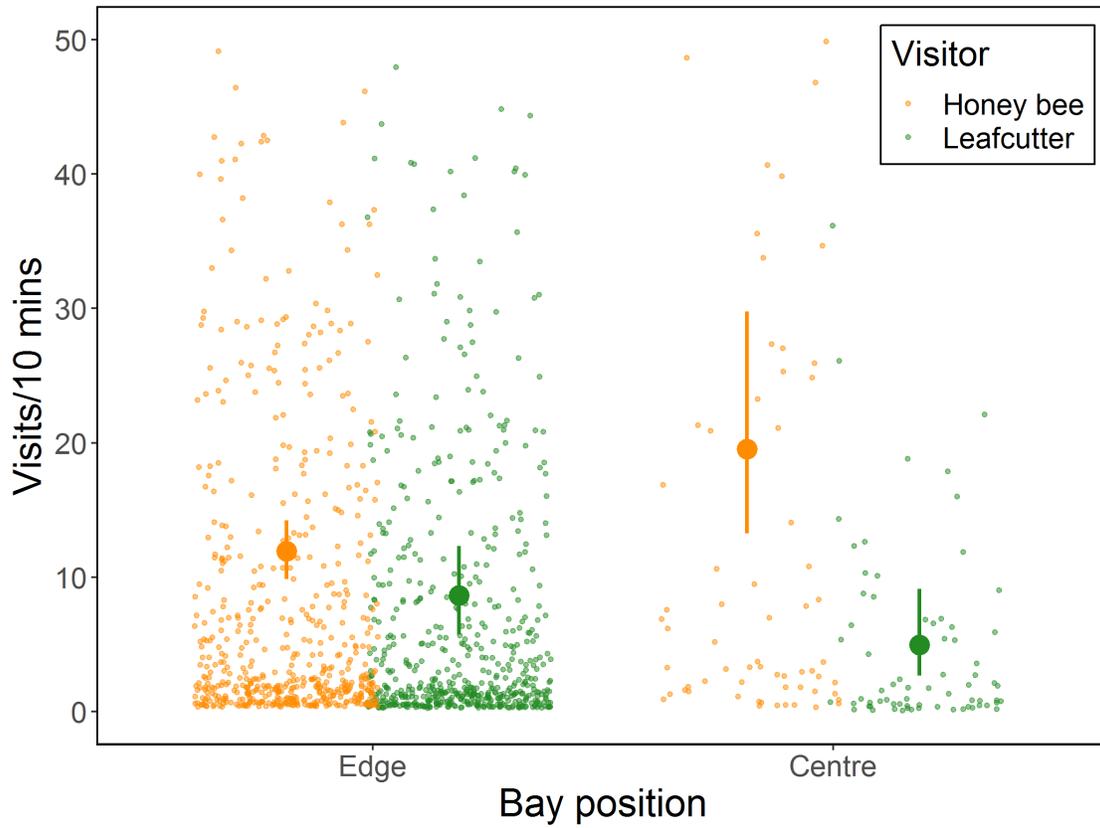


Figure 3.8: Partial effect of bay position (edge or centre of female bay) on honey bee and leafcutter bee visitation. Coloured points represents median value, and vertical bars represent 95% CIs.

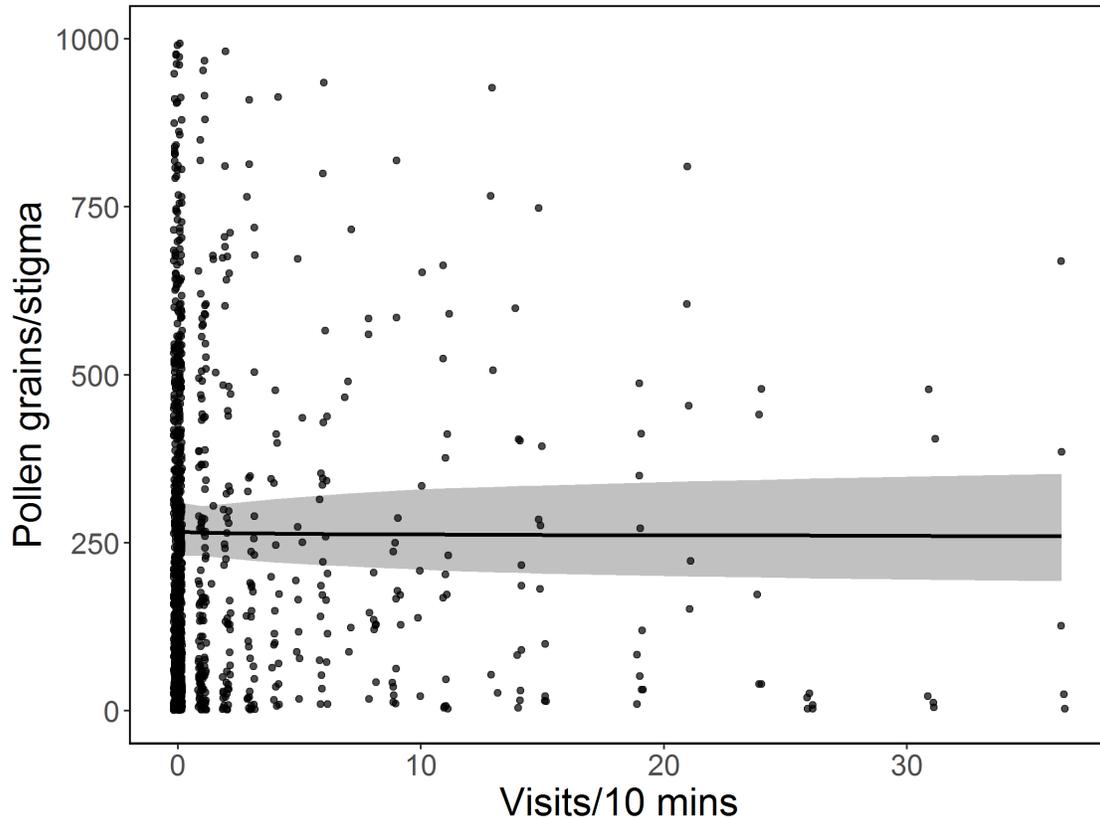


Figure 3.9: Partial effect of honey bee visitation on pollen deposition in commodity canola. Solid line represents median, and shaded areas represent 95% CIs.

Pollen deposition was lower in the centre of the female bay ($Z=-4.5$, $p=0.0001$, 23 vs. 13 grains/stigma) independent of visitation rate, suggesting that pollen is lost from bees crossing from male bays, who likely visit flowers at the edge of the bay first (Pinnisch and McVetty, 1990). There was no direct effect of honey bees on pollen deposition ($Z=0.98$, $p=0.33$), implying that most of the pollen deposition occurs via leafcutter visitation.

3.3.3 Prediction 3: Larger plants produce more seeds

Plant size was largely influenced by plant density, but this differed between commodity and seed canola crops. Plant density was higher overall in commodity fields (mean: 48.5 plants/m², SD: 22.9, range: 6–151) than seed fields (mean: 39.4 plants/m², SD: 17.0, range: 11–89), and commodity canola plants were smaller on average (mean: 18.2 g, SD: 14.4, range:

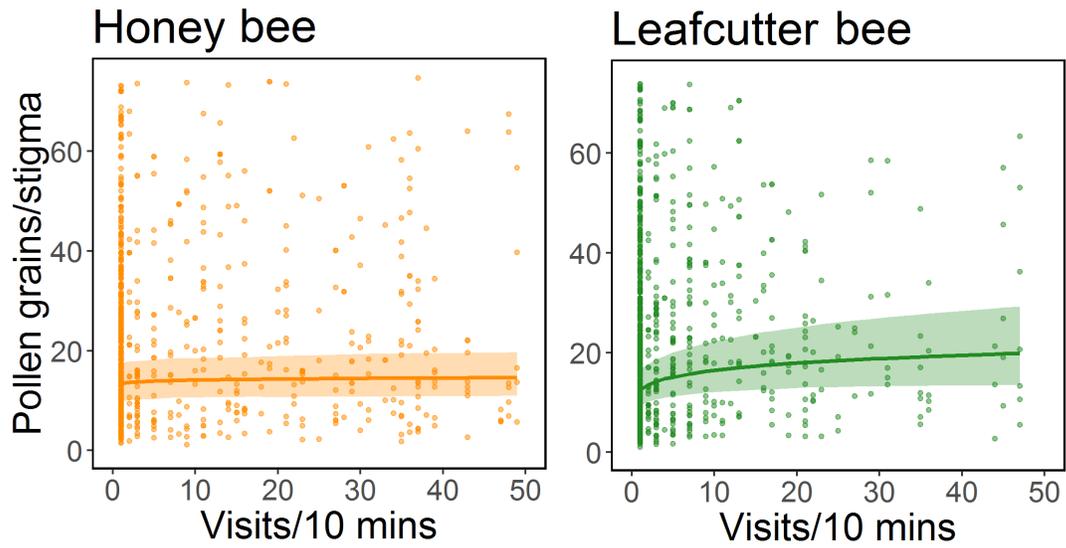


Figure 3.10: Partial effects of honey bee and leafcutter bee visitation on pollen deposition in seed canola. Solid lines represent medians, and shaded areas represent 95% CIs.

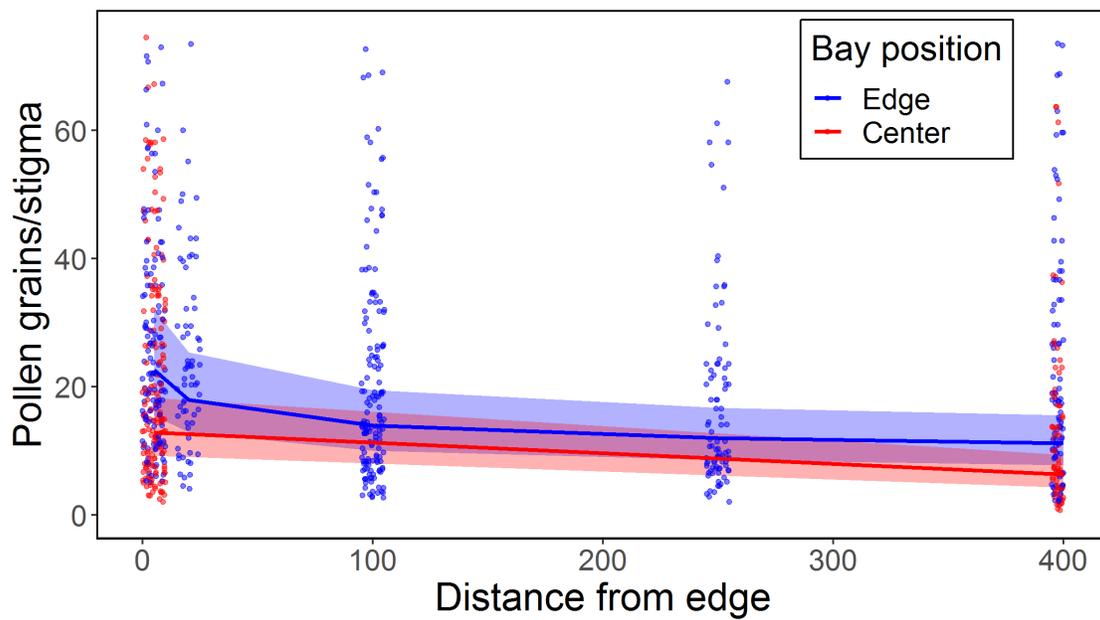


Figure 3.11: Partial effect of distance from field edge and bay position on pollen deposition in seed canola. Coloured points represents median, and shaded areas represent 95% CIs.

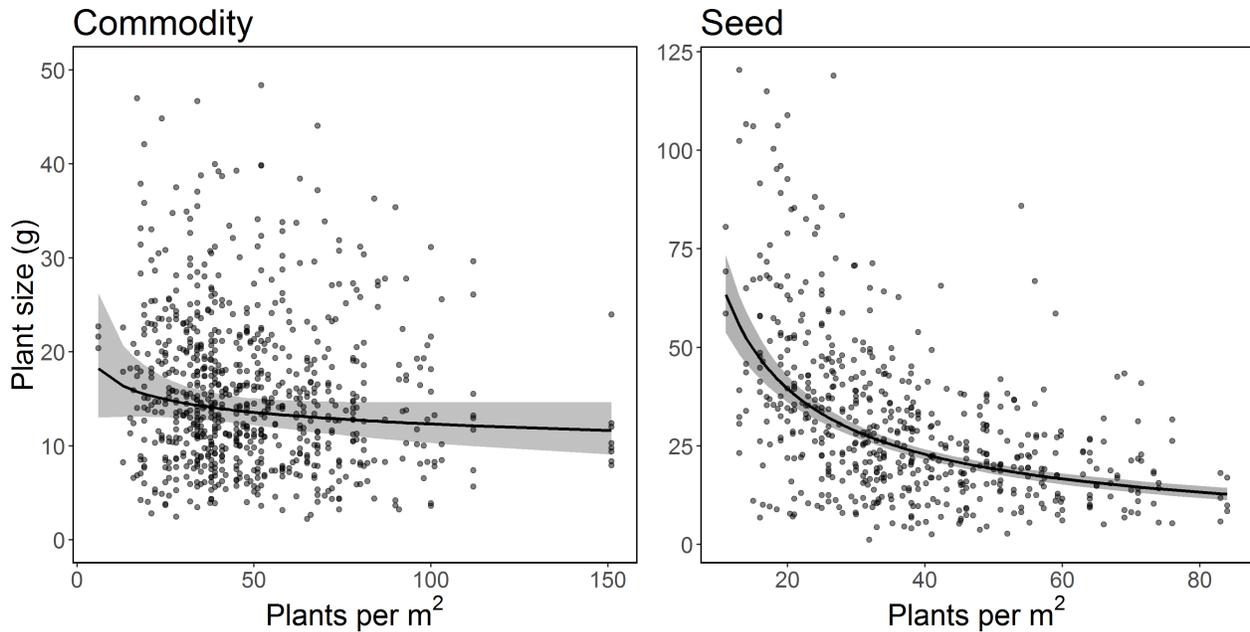


Figure 3.12: Partial effects of plant density on plant size, for commodity and seed canola plants. Solid lines represents median, and shaded areas represent 95% CIs.

0.8–110.2) than seed canola plants (mean: 30.7 g, SD: 21.2, range: 1.2–144.3). However, commodity canola plant size was not influenced by plant density ($Z=-1.62$, $p=0.10$, Figure 3.12), indicating that any density-dependence was overwhelmed by other factors, but plant size in seed canola was negatively influenced by planting density ($Z=-13.2$, $p<0.0001$), and plants were larger at the centre of the field independent of density ($Z=5.4$, $p<0.0001$). Plant density was slightly lower at the edge of commodity canola fields ($Z=1.68$, $p=0.09$), but was much lower in seed canola ($Z=5.2$, $p<0.0001$), indicating lower seedling survival or seeding density at the edges of the field. Neither irrigation ($p=0.76$), site ($p=0.86$), nor distance from field edge ($p=0.70$) directly influenced commodity canola plant size, but plants were larger in 2015 ($Z=2.5$, $p=0.01$).

Plant size had a strong effect on the number of pods produced, and there was evidence of fruit set suppressing future flower production. Commodity canola plants produced fewer flowers per plant (mean: 198, SD: 157, range: 13–1419) than seed canola plants (mean: 468, SD: 328, range: 26–2712), and also produced fewer pods per plant (mean: 143, SD: 114, range: 5–892) than seed canola plants (mean: 303, SD: 208, range: 10–1410). In both

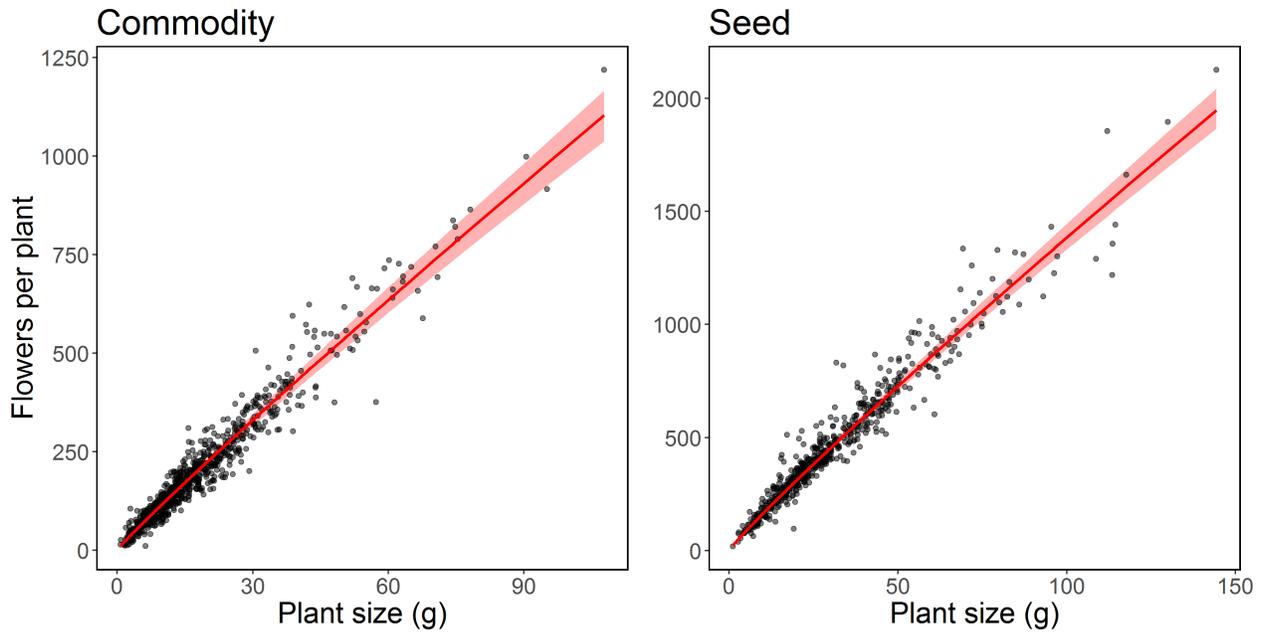


Figure 3.13: Partial effect of plant size on number of flowers per plant, for commodity and seed canola plants. Solid lines represent median, and shaded areas represent 95% CIs.

commodity and seed canola, plant size had a strong positive effect on the total number of flowers per plant (commodity: $Z=92.4$, $p<0.0001$, seed: $Z=82.7$, $p<0.0001$, Figure 3.13), as well as fruit set (commodity: $Z=5.5$, $p=0.0002$, seed: $Z=19.9$, $p<0.0001$, Figure 3.14). Fruit set had a strong negative influence on total flowers per plant ($p<0.0001$) in both commodity ($Z=-12.5$) and seed canola ($Z=-12.1$), indicating that high levels of fruit set suppressed future flower production. Finally, commodity plants were also lower-yielding (mean: 6.8 g of seeds per plant, SD: 6.0, range: 0.01–47.9) than seed canola plants (mean: 9.6, SD: 7.9, range: 0.02–60.8). However, the harvest index of commodity canola (mean: 0.26, SD: 0.08, range: 0.005–0.65) was higher than seed canola (mean: 0.23, SD: 0.09, range: 0.003–0.55), meaning that commodity plants produced more seeds per gram of biomass than seed canola plants, likely due to the lack of pollen limitation (see below).

Plant size had a positive effect on seed size and seeds per pod in seed canola, but not in commodity canola, and the relationship between seed size and number was negative in seed canola but positive in commodity canola. Commodity canola plants produced more seeds per pod (mean: 23.0 seeds per pod, SD: 7.4) than seed canola (mean: 16.3 seeds per pod,

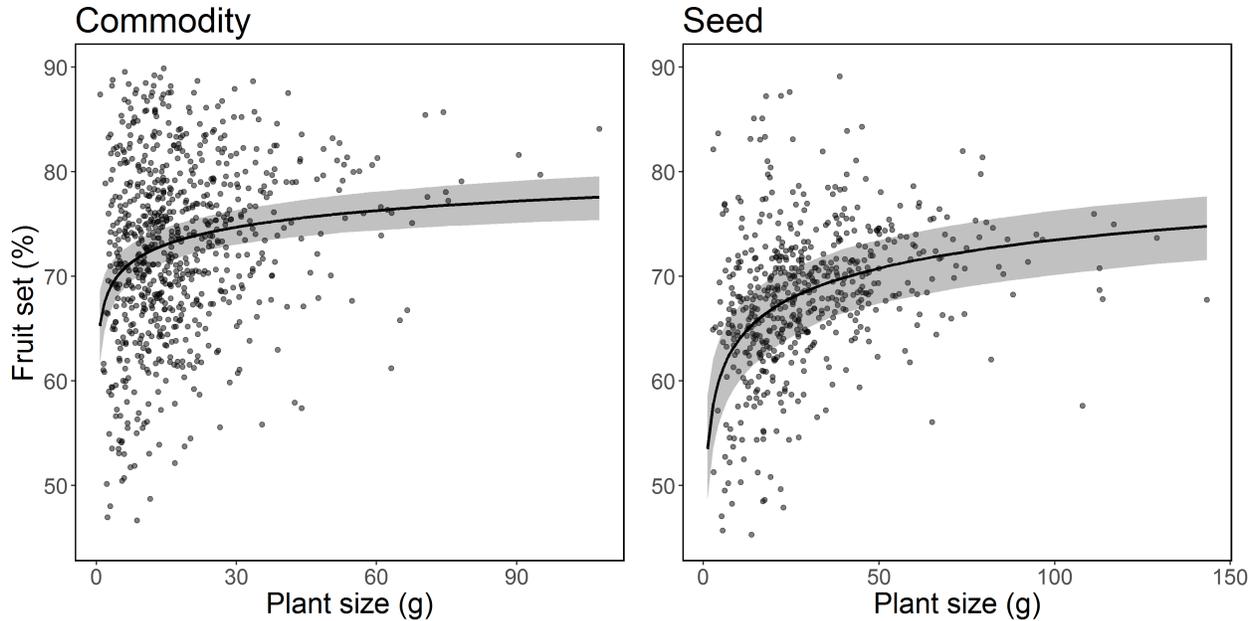


Figure 3.14: Partial effect of plant size on fruit set (% of flowers that became pods), for both commodity and seed canola. Solid lines represent median, and shaded areas represent 95% CIs.

SD: 9.1), but seed mass was lower in commodity canola (mean: 2.74 mg/seed, SD: 1.04) than seed canola mean (mean: 3.59 mg/seed, SD: 1.33). In commodity canola, plant size did not impact seeds per pod ($Z=1.00$, $p=0.32$) or seed size ($Z=-0.40$, $p=0.69$, Figure 3.15), but seed size was positively related to seeds per pod ($Z=6.1$, $p<0.0001$, Figure 3.15). In seed canola, however, seed size increased with plant size ($Z=4.7$, $p<0.0001$, Figure 3.15), decreased with seeds per pod ($Z=-13.1$, $p<0.0001$), and interestingly, increased with plant density ($Z=2.9$, $p=0.004$), suggesting resource limitation at both the pod and the plant level. There were also between-year differences in seeds per pod (commodity canola only: $Z=4.7$, $p<0.0001$, 21.7 seeds per pod in 2014, 24.6 in 2015) and seed size (commodity canola: $Z=2.2$, $p=0.031$, 2.04 mg/seed in 2014, 2.31 mg/seed in 2015; seed canola: $Z=3.6$, $p=0.0003$, 3.11mg/seed in 2015, 3.59mg/seed in 2016), pointing to differences in overall growing conditions between years.

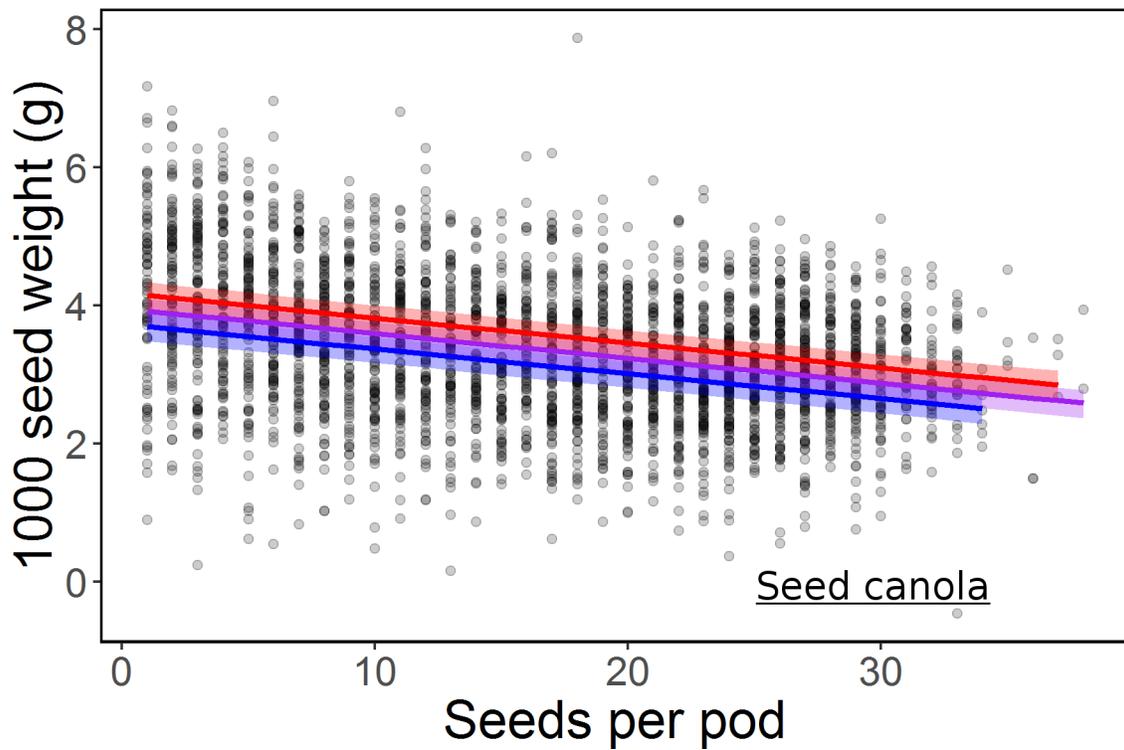
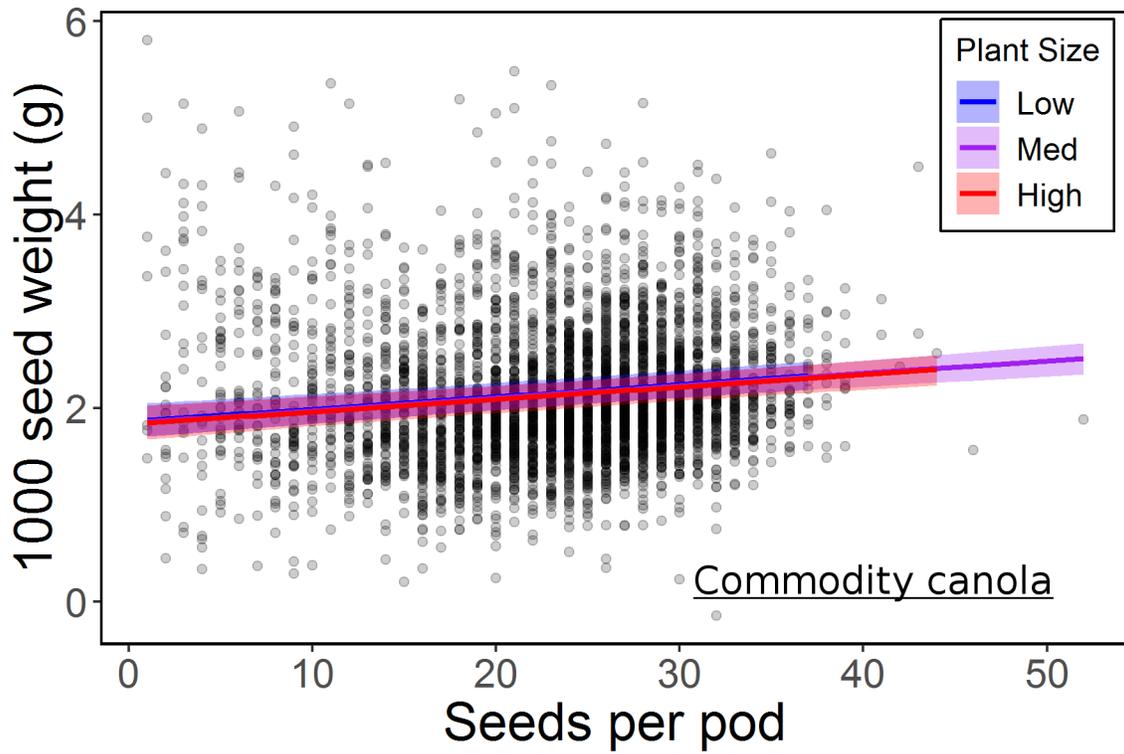


Figure 3.15: Partial effects of seed count and plant size on seed size, for both commodity and seed canola. Solid lines represent median, and shaded areas represent 95% CIs.

3.3.4 Prediction 4: Pollinated plants produce more seeds

Pollen deposition increased fruit production and seed production in seed canola, but not in commodity canola. Pollen deposition had no effect on fruit set ($p=0.12$), seeds per pod ($p=0.94$) or seed size ($p=0.56$) in commodity canola, and there was also no direct effect of honey bee visitation on fruit set ($p=0.38$), seeds per pod ($p=0.55$), or seed size ($p=0.34$). Seed canola, in contrast, was highly dependent on pollen deposition. Pollen deposition increased fruit set ($Z=3.1$, $p=0.002$), and seeds per pod ($Z=2.3$, $p=0.02$), but had no direct effect on seed size ($p=0.35$). Fruit set also decreased with three types of distance: distance into the field ($Z=-5.3$, $p<0.0001$), distance from leafcutter shelters ($Z=-3.2$, $p=0.002$), and distance from the edge of the female bay ($Z=-4.0$, $p=0.0001$). Seeds per pod decreased in the centre of the female bay ($Z=-4.6$, $p<0.0001$), and was higher in plants with high fruit set ($Z=6.0$, $p<0.0001$).

3.4 Discussion

This study examined the relative strength of the path between visitation, pollination, and yield, in two types of canola crops, and showed a strong path between visitation and yield in seed canola, but not in commodity canola. First, honey bee and leafcutter bee visitation decreased with distance from their hive or shelter, but unexpectedly, leafcutter bees visited more frequently at the edge of the field. Secondly, honey bees had little (direct) influence on pollen deposition in either crop type, leafcutter bees had a positive effect on pollen deposition in seed canola. Finally, the model revealed that commodity canola production is largely limited by plant size, while seed canola production is limited by both pollen and plant size.

Bee visitation

Honey bee visitation in both field types declined with distance into the field, but overall visitation was much higher than commodity fields, due to the higher honey bee stocking rate used in seed fields (3.6 vs. mean 0.6 hives/ha). Since honey bees travel from their hive outside the edge of the field, this decline was not surprising, but I did not expect the similar decrease observed in leafcutter bee visitation with distance into the field, as their shelters are located *within* the field. This decrease with distance into the field may have been caused by leafcutter bees migrating from shelters at the centre of the field to the edge (Goerzen et al., 1995). Like honey bees, female leafcutter bees are central-place foragers, and tend to not forage far from their nests (Peterson and Roitberg, 2005; Pitts-Singer and Cane, 2011; Brunet et al., 2019). However, leafcutter bees are not as constrained to their nest site as honey bees, and can drift between shelters in a given field (Goerzen et al., 1995; Pitts-Singer, 2013). Leafcutter bees must also forage for leaf materials to create cocoons, but they prefer to build cocoons out of thinner, non-canola leaf types, mainly plants in the families Fabaceae and Rosaceae (Sinu and Bronstein, 2018). Seed canola fields have very few weeds within the area of the crop, meaning that leafcutter bees at the centre of the field may have few choices of leaf material, or alternative pollen and nectar sources. Therefore, leafcutter bees likely move from the shelters at which they were released in the centre of the field to the shelters at the edge of the field, so as to gain access to better leaf material (Horne, 1995a), which is more available off-field, or to better forage for off-field pollen or nectar (Horne, 1995b). This would explain why greater visitation occurred at the edge of the field, and may also explain why this pattern was not seen in fields with half-stocked shelters. To test this, a mark-recapture study of female leafcutter bees could be done to see if bees migrate to shelters at the edge of the field, or if visitation is higher due to other reasons (*e.g.* feral populations migrating to edge of field, long-distance foraging from centre of field as in Peterson and Roitberg, 2005). It would be interesting to see if there is a critical threshold of leafcutter bee density per-shelter that causes them to move to shelters at the edge of the

field (similar to Pitts-Singer, 2013).

Honey bee visitation in hybrid seed fields was lower at areas near to leafcutter shelters. This may have been driven by avoidance of nectar and pollen competition near shelters, as areas close to leafcutter shelters may become depleted in nectar and pollen, deterring honey bee visitation (similar to Currie, 1997). Honey bees also suffer from direct interference by leafcutter bees near to their shelters. Several times during the study, *M. rotundata* females and males directly harassed honey bees during the plot-level observations, tackling honey bees both on the flowers and in the air (also seen by Batra, 1978 and Waytes, 2017). Honey bees were never the aggressor in these interactions, so interference between leafcutter bees and honey bees may be unidirectional, at least in areas near leafcutter bee shelters. For this reason, I treated high leafcutter visitation as causing lower honey bee visitation in my SEM (Figure 3.4, arrow from leafcutter visit rate to honey bee visit rate).

Honey bee visitation and foraging behaviour varied strongly between the male and female bays of seed fields, as well as within the female bays. Visitation rates of honey bee foragers were almost twice as high in the centre of the female bay, and conversely, leafcutter bee visitation was almost twice as low. This could be due to leafcutter bees avoiding competition for nectar with honey bees, but more likely reflects a stronger need for pollen among leafcutter bees than honey bees (Cane et al., 2011). Only 1.4% of the honey bees in the female bay were pollen foragers (Table 3.1), meaning that foragers who have (recently) come into contact with pollen rare. Both Waytes (2017) and Gaffney et al. (2019) showed that honey bees exhibit floral fidelity during foraging trips, with minimal crossing between male and female bays ($\sim 5\%$ of observations, Waytes, 2017), limiting pollen transfer between the male and female flowers. Side-working was a very common behaviour among honey bees in commodity fields (65% of the total visits from honey bees during 2015 were side-working), as well as the male bays of seed fields (36%), but not in the female bays (3%, Table 3.1). This behaviour is relatively common on male-fertile flowers of *Brassica* (Free and Williams, 1973; Free and Ferguson, 1983; Delbrassine and Rasmont, 1988; Mohr and Jay, 1988) as well

as other flowering crop flowers (Thomson and Goodell, 2001), and may be due to honey bees avoiding contact with the stigmas to increase ease of access to nectar, or to reduce the amount of grooming needed during a nectar foraging bout. The foragers who were side-working tended to not switch to top-working (personal observation), so this is likely a consistent individual behaviour (at least in experienced foragers). Therefore, honey bees pollen foragers in seed canola fields appear to avoid flowers in the female bay, and commonly engage in side-working behaviour in both commodity and seed canola fields, limiting their opportunities for pollen transfer (see below).

3.4.1 Pollen deposition

Honey bee visitation did not increase pollen deposition in commodity canola fields compared to unstocked fields, meaning that wind and/or self-pollination are the likely agents of pollen transfer. The stigmas and flowers of *Brassica* are not aligned for optimal dispersal and deposition from the wind, so cross-pollination likely occurs mainly via insects (Mesquida and Renard, 1982; Cresswell et al., 2004). However, wind-induced self-pollination (plant shaking) can increase yield in *Brassica* (Williams et al., 1986; Mesquida et al., 1988), and fields without bee pollination have outcrossing rates of about 20% within the field (Rakow and Woods, 1987; Becker et al., 1992). The style of *Brassica* grows past the anthers during maturation, allowing deposition of large amounts of self-pollen, suggesting that self-pollination is the dominant mode of pollination. Honey bees can assist in deposition of self-pollen, as Ali et al. (2011) found that *Apis dorsata* and *Apis florea* can both deposit 100-200 grains of pollen per visit on a canola flower (*B. napus* var. *Bulbul*). However, Waytes (2017) used male-sterile flowers and found that *A. mellifera* deposit far less outcrossed pollen (~ 2 grains per visit), suggesting that much of the pollen deposited by honey bees on canola stigmas is self-pollen. Because the overall pollen deposition rates found in this study were so high (mean: 293, SD: 385), honey bee visitation seems to have made little difference in the amount of self-pollination. The typical lifetime of a canola flower is approximately 3 days, and the

stigmatic surface is receptive for 24–36 hours within this period (Eisikowitch, 1981; Hoyle et al., 2007), so it may be that 10-minutes of observing flower visitors was too short of a time interval to relate to pollen deposition. This is unlikely, however, as large amounts of pollen were present on commodity canola stigmas even at the centre of unstocked fields (average plot-level visitation rate was 0.23 visits/hr). These results suggest that stigmas are largely saturated with self-pollen, swamping any extra pollen deposition by honey bees.

Honey bee behaviour in seed fields made pollen transfer between male and female plants unlikely, and this was also reflected in the measurements of stigma deposition. Deposition was not affected by honey bee visitation, but was strongly increased by leafcutter bee visitation. Leafcutter bees tend to switch between male and female flowers more frequently than honey bees do (Waytes, 2017), transport more viable pollen between flowers (Parker et al., 2015), and tend not to side-work canola flowers (Soroka et al., 2001, personal observation), which may explain their increased pollination efficacy. I also found that pollen deposition also decreased with distance from the edge of the field, was lower in the centre of the female bays, and that this was not solely explained by leafcutter bee abundance (Figure 3.4). During foraging bouts, leafcutter bees may travel further between flowers than honey bees do; Brunet et al. (2019) found that leafcutter bees foraging in alfalfa (*Medicago sativa* L.) travelled an average of 21 cm between flowers, while honey bees only travelled 16 cm. However, pollen carryover (Thomson, 1986) to the middle of the bay female is likely reduced, as leafcutters likely visit the edge of the female bay before venturing into the centre. The decrease of pollen deposition with distance into the field (independent of visitation rates) also suggests that the same visitation rate of pollinators in the centre of the field results in less pollen deposition. This may be due to lower levels of competition at the centre of the field, leading to a higher nectar (or pollen) standing crop. Foraging *Bombus* take smaller trips between flowers and will forage in smaller areas under nectar-rich conditions (area-restricted search, Pyke, 1978b; Heinrich, 1979), so leafcutter foraging may follow a similar pattern, causing lower pollen deposition at the centre of the field where competition is lower.

Honey bees may have an indirect positive effect on pollen deposition, as they may cause leafcutter bees to travel farther by lowering overall nectar and pollen standing crop, or release airborne pollen from male-fertile flowers. Pierre et al. (2010) showed that honey bees can increase the amount of airborne pollen by foraging on male-fertile flowers and releasing pollen from the anthers, causing increased yields in nearby male-sterile flowers; therefore, honey bees may indirectly contribute to a higher rate of wind pollination. Honey bees may also cause leafcutter bees to forage at further distances away from their shelters. Bumble bees move further between flowers when foraging in *Trifolium* fields that have been depleted by honey bees Heinrich (1979), so a similar process could occur in canola seed fields. Leafcutter bees do not appear to use area-restricted search (Brunet et al., 2019), but I expect that the foraging range of leafcutter bees around their shelters would still decrease, because if honey bees lower pollen and nectar levels at the edge of the field, then leafcutter bees should travel shorter distances to gather the same reward (according to the predictions of Chapter 2). I also expect that foraging leafcutter bees would make shorter trips between flowers (similar to Heinrich, 1979), and possibly may switch between bays less frequently (Waytes, 2017; Gaffney et al., 2019), due to a greater floral fidelity on higher-rewarding flowers in the male bay (Mesquida and Renard, 1978). If this is true, this would result in a lower rate of (overall) pollen deposition by leafcutter bees during the same period. However, testing this would require observations of seed canola fields that were only stocked with leafcutter bees, which is extremely rare in southern Alberta.

3.4.2 Pod production

Fruit set (i.e. pod production) in commodity canola was positively affected by plant size, but not by pollen deposition or honey bee visitation. Both pod production and seeds per pod can increase with extra pollination (Jauker and Wolters, 2008; Sabbahi et al., 2005, 2006; Durán et al., 2010), so this lack of effect may be due to a high overall level of pollen deposition (Figure 3.9), even in fields without honey bees. There was no effect of honey bee

visitation on fruit set, seeds per pod, or seed size, indicating that visitation did not seem to cause either *a*) a greater quantity of pollen (see above) or *b*) higher quality (outcrossed) pollen. Self-pollination (geitanogamy) in canola can result in similar fruit production as outcrossing (Rosa et al., 2011), implying that pollen quality is not likely a limiting factor in canola fruit set, at least in some varieties. Flower number was negatively related to fruit set, which implies a response to pollination (high flower fertilization suppresses further flower production) and/or a reproductive trade-off (greater pod development rate means more competition among pods for resources). I considered the first scenario to be the stronger effect, as Sabbahi et al. (2006) and Mesquida and Renard (1981) both found that canola plants compensated for experimental removal of flowers by increasing branch and flower production, until the plant reached about 170 pods. Their final number of pods is similar to the plants from my study (median: 112, range: 5–892), but I found that larger plants also had greater fruit set, in addition to higher flower production, presumably caused by the larger pool of resources that large plants are able to invest into reproduction.

Pollination increased pod production in seed canola, but not in commodity canola, meaning that extra pollination is valuable for seed canola crops, but not commodity canola. This is similar to the findings of Mesquida and Renard (1981) and Steffan-Dewenter (2003), who found that fruit set in male-sterile plants responded positively to visitation, while male-fertile plants (“male” plants in seed fields, all plants in commodity fields) had no response (but see Adegas and Nogueira Couto, 1992). Pod production in seed canola increased with both pollen deposition and plant size, suggesting that both pollen availability and plant resources constrain pod production. However, the effect size of pollen deposition ($Z=3.1$) was much smaller than that of plant size ($Z=19.9$), indicating that the factors controlling plant size (fertilizer, plant density, and soil quality) likely constrain pod production more strongly than pollination alone, in both commodity and seed canola plants. There were also effects of distance on fruit set, independent of pollen deposition: pod set decreased with distance from the edge of the field and distance to leafcutter shelters independent of pollen deposition, and

was lower in the centre of the female bays. Mesquida and Renard (1978) also found that fruit set in male-sterile canola declined quickly with distance from the male-fertile plants (due to wind pollination), but the effect I found is likely related to the earlier effect of lower pollen carryover at the centre of the female bays, and possibly the centre of the field. However, my analysis points to the strong relative importance of plant resources, as well as pollination services (Marini et al., 2015), mediated through the effect of leafcutter bee visitation, to the production of hybrid seed canola.

3.4.3 Seed number and size

In commodity canola plants, the number of seeds per pod was only affected by between-year variation, and was unaffected by plant size and pollination. In contrast, the number of seeds per pod in seed canola was increased by pollen deposition, flower survival, and plant size, and was reduced in the centre of the female bay. Position in the female bay influenced pollen deposition, both by wind and insects, indicating that the decrease in seed number at the centre of the bay is ultimately caused by reduced pollen deposition from lower visitation (Mesquida and Renard, 1981, 1982). Seeds per pod also increased with pollen deposition and plant size, but the effect size of pollen deposition ($Z=2.3$) was smaller than that of plant size ($Z=5.6$), suggesting that plant resources limit seed production more strongly than pollen deposition in seed canola. Mesquida and Renard (1982) found that in seed canola, pod production, rather than seeds per pod, was the main variable that was reduced by low pollen deposition. Interestingly, plant density had a positive effect on seed size in seed canola, pointing to a possible reduction in seed count because of shading or crowding, causing an increase in seed size (but see Angadi et al., 2003).

Plant size was one of the dominant factors controlling seed size in seed canola, while in commodity canola, plant size did not influence seed size. Plant size can positively influence seed size in some plant species (Maddox and Antonovics, 1983), and this appears to be true in canola (Riffkin et al., 2012) as well as other Brassicaceae (Mazer, 1987). Similarly, seeds per

pod and seed weight varied positively in commodity canola, this pattern was reversed in seed canola (Figure 3.15). These differences likely occurred because of variation in available seed resources among the parts of the plant (van Noordwijk and de Jong, 1986), which can cause a positive size-number relationship even in resource-limited plants. In commodity canola, pollen is readily available, and there seems to be little difference between outcrossed- and self-pollen (Steffan-Dewenter, 2003; Rosa et al., 2011). Canola plants produce flowers from the bottom up, and produce fewer, smaller seeds at the ends of the branches because the younger pods have access to fewer resources at the end of the season (Sabbahi et al., 2006), resulting in an increased rate of seed abortion (Clarke, 1979). Pods with low resources at the end of the season are forced to abort more ovules (Wang et al., 2011), causing a positive relationship between seed number and size. Thus, in commodity canola, variation in resources with plant size is masked by resource variation over time. In seed canola, pollen is much rarer (median: 7 grains/stigma vs. 155 in commodity), but plant sizes are similar (or larger) than commodity canola, such that plant resources are still available to developing pods at the end of the season. This causes a size-number trade-off within pods that is mediated by plant size. Most studies on commodity canola report a seed size-number trade-off at the level of plant (Angadi et al., 2003; Koltowski, 2005), I found a positive relationship at the pod level (but see Sabbahi et al., 2005). Perhaps within-plant resource variation is a more likely driver of seed number than pollen deposition, as pollination did not appear to be limiting (Figure 3.3, weak paths from pollen to yield metrics).

3.4.4 Summary

This study assesses the relative importance of pollination and plant resources for the production of canola crops, using field-realistic data from central and southern Alberta. First, it shows that insect visitation changes across small spatial scales (meters for leafcutter bees, tens of meters for honey bees), and are at odds with the large scales of Albertan crop fields (Fritz et al., 2015). Visitation of both honey bees and leafcutter bees in canola fields is

concentrated at the edge of fields, and is lower at the centre of the female bays in seed canola. Second, honey bees have little direct influence on pollen deposition in either crop system, likely due to a high background level of pollen deposition on stigmas in commodity canola, whereby extra pollen deposition is of little benefit to plant reproduction. Seed canola plants, in contrast, have much lower levels of pollen deposition overall, and leafcutter bees deliver a large direct benefit to fruit and seed production. The centre of the female bays illustrates this effect: honey bees have a higher visitation rate, but pollen deposition, fruit set, and seed set are all lower. Finally, both plant size and pollination limit seed production in seed canola, but only plant size limits commodity canola production, showing the relative importance of both pollination and plant resources using in-field data.

Several future lines of work could be followed based on this study. First, other factors besides total seed yield are important for commodity canola production, such as green seed and oil content (Tautorus and Low, 1994; Abbadi and Leckband, 2011; Ghazani and Marangoni, 2013). My work identified the effect of bee pollination on seed production in terms of total weight, but may have overlooked these aspects of yield valuation (Bommarco et al., 2012). Secondly, I found that honey bees appear to add little pollination value for seed canola crops, but since I did not use fields that had no honey bees, there may be unobserved indirect benefits that honey bees add. For example, they may contribute to better pollination by leafcutter bees by reducing the nectar and pollen standing crop, causing leafcutter bees to forage further away from their shelter (Pyke, 1978b; Heinrich, 1979), or by increasing the amount of airborne pollen (Eisikowitch, 1981; Mesquida and Renard, 1982). Third, while the random-intercept model that I used accounts for field-to-field variation in growing conditions, this also means that I may have marginalized across other factors that were not accounted for by plant size, such as nutrients, soil moisture, crop pests, and variety. Pollination benefits to all flowering crops are contextual, even in highly-pollination dependent crops (Tamburini et al., 2017, 2019); that is, the effect of additional pollination depends on the levels of other plant resources available during growth (Marini et al., 2015; Bartomeus

et al., 2015; Gagic et al., 2017). Finally, SEMs cannot model causal loops (Grace, 2006), which is closer to the method by which plants respond to lack of pollination (*i.e.* pollination failure \rightarrow plant growth \rightarrow flower production). My model serves as an approximation of this process, but could be built upon by using dynamic linear programming techniques (Iwasa, 2000; Nord et al., 2011) to examine how plants dynamically respond to pollen failure. These would lend greater understanding to the process of hybrid seed production, and could be used to more accurately predict crop yields in novel scenarios.

Chapter 4

Effects of canola bloom and semi-natural habitat on wild bee populations in southern Alberta

4.1 Introduction

Pollinator abundance is limited by two main factors: floral resources and nest site availability (Roulston and Goodell, 2011). Undisturbed semi-natural land (SNL) may satisfy both of these conditions, as it can provide nesting habitat for ground- and cavity-nesting bees (Potts et al., 2005), as well diverse set of floral resources compared to crop flowers (Sutter et al., 2017). SNL is a key factor in explaining pollinator diversity and abundance at the scale of the landscape (Steffan-Dewenter et al., 2002; Haenke et al., 2009; Bukovinszky et al., 2017), and the presence of SNL typically has a positive effect on both abundance and diversity of pollinators (but see Holzschuh et al., 2016; Fijen et al., 2019). Similarly, the loss of SNL has been implicated in loss of native pollinators (Winfree et al., 2009), or changes in pollinator community composition (Baldock et al., 2015; Theodorou et al., 2016; Harrison et al., 2017), depending on nesting habitats and disturbance types (Williams et al., 2010). Given that

wild pollinators benefit our agricultural and economic supply chains (Klein et al., 2007), the fitness of wild flowering plants (Motten, 1986; Chateil and Porcher, 2015), as well as the inherent value of biodiversity to humans (Silvertown, 2015; Coffey, 2016), there is a clear imperative to increase our understanding of this topic.

Because of constraints on nest site availability and competition for flowering resources, pollinating insect populations may experience density-dependent growth, but this effect is not universal. Insects exhibit a range of population dynamics (Turchin and Taylor, 1992), from stable to oscillating to chaotic, but studies on bee population dynamics are less common. Food availability (Crone, 2013; Scheper et al., 2015), weather (Wcislo et al., 1994), or their interaction (Forrest and Chisholm, 2017; Ogilvie et al., 2017) act as strong regulators of pollinator populations, but of these, only food availability acts in a density-dependent manner (Dainese et al., 2018). Nest site availability is also important in regulating bee population growth and abundance (Potts et al., 2005; Steffan-Dewenter and Schiele, 2008), but nest site availability is not likely to change strongly from year-to-year, except in the case of fires (Ponisio et al., 2017) or other disturbances. Finally, nest parasitism can also reduce local bee abundance, and can act either in a density-dependent (Steffan-Dewenter and Schiele, 2008), or density-independent manner (Bischoff, 2003; Dainese et al., 2018), but this is complicated by the fact that parasite abundance often vary widely between years (Wcislo et al., 1994). This suggests that bee populations can be influenced by density-dependent factors (forage, nest sites, parasites), but that other factors such as weather may play a larger role in regulating their numbers. Because of the small number of studies of population regulation of pollinators, it is unclear whether this applies more generally across all bees.

Mass-flowering crops (MFCs) have the potential to provide a large temporary food source for wild pollinators (Thom et al., 2017), but because of tillage and pesticide practices in agricultural areas, are unlikely to provide nest sites for ground or stem-nesting insects. The value of MFCs as a food resource is contingent on several factors: 1) the floral morphology must be suited to a variety of pollinators, 2) flowers of the crop must provide both nectar and

pollen, 3) the flowering crop must be relatively near nesting habitat, as well as necessary nesting materials (*e.g.* leaf material, floral oils) and 4) the flowering period of the crop must overlap the seasonal phenology of the pollinator. Canola (*Brassica napus* L.) may serve as an ideal MFC for wild pollinators, as it satisfies all of these conditions. Most plants are pollinated by generalist pollinators (Waser et al., 1996; Bascompte and Jordano, 2007), so generalist foragers should benefit the most from MFC bloom (but see Fijen et al., 2019). However, MFCs have a negative impact on bumble bees (*Bombus*), as successful colonies require resources that span longer periods of time than a MFC bloom (Williams et al., 2012; Riedinger et al., 2015). MFCs can have positive effects on shorter-lived solitary (or quasi-social) bees, such as *Osmia* or *Andrena* (Le Féon et al., 2013; Riedinger et al., 2015). If MFCs supply resources only in part (*e.g.* nectar but not pollen, pollen lacking necessary amino acids), they can still lower foraging competition by reducing foraging on flowers in SNL (Holzschuh et al., 2011). MFCs may complement existing floral resources from SNL (Diekötter et al., 2014; Stanley and Stout, 2014), but only *a*) if they lessen foraging competition, *b*) if they exist at an appropriate spatial scale and arrangement, and *c*) if the bloom period overlaps with the flight phenology of the pollinator. These effects are well-established for bumble bees (Diekötter et al., 2010; Kovács-Hostyánszki et al., 2013), but not for other types of wild bees (but see Riedinger et al., 2015).

MFCs can alter pollinator abundance by increasing reproduction in the year following a MFC bloom. In univoltine bees, emergence occurs in the following year, meaning that increased reproduction resulting from an MFC bloom is seen during the following year (Crone, 2013), causing a lagged “echo” of abundance through higher trophic levels (Ostfeld and Keesing, 2007; Yang et al., 2008, 2010). These lagged responses occur in pollinator populations in both wild grasslands and agro-ecosystems (Crone, 2013; Dainese et al., 2018), but have only been studied in a handful of bee genera (mainly *Bombus*, but also *Anthophora* and *Osmia*). MFCs can also potentially increase pollinator abundance in SNL during the bloom (“spillover effect”, Haenke et al., 2009; Kovács-Hostyánszki et al., 2013; Kremen et al.,

2019), or after the bloom ends (“mass effect”, Shmida and Wilson, 1985), but a dilution effect seems to be more common (Holzschuh et al., 2011; Riedinger et al., 2014; Holzschuh et al., 2016). In particular, Riedinger et al. (2015) found that the current year’s cover of MFCs had a negative effect on pollinator abundance, indicating a dilution effect, but also found that the previous year’s cover of MFCs had a negative effect on *Bombus* abundance, but not other pollinators. Their work showed that both past and present MFCs can influence pollinator abundance, and can do so differently for different groups of pollinators (*Bombus* and non-*Bombus* in this case). However, whether this effect is common across solitary and quasi-social bees is not known.

To examine the lagged and immediate effects of mass flowering crops on pollinator abundance, I studied the effects of blooming canola and semi-natural land on solitary and quasi-social (hereafter, “solitary”) wild bee abundance in southern Alberta, Canada. Specifically, I hypothesized that:

1. SNL provides both long-term food resources and/or nest sites, therefore, wild bees should be more abundant in areas where SNL is abundant.
2. Solitary bee populations are influenced by both density-dependent factors (forage, nest sites, parasites) and density-independent factors (weather). If density-independent factors dominate, abundance should be positively related to last year’s abundance, but if density-dependent factors dominate, they will be unrelated or negatively related last year’s abundance.
3. Canola flowers have a generalist morphology, making them attractive to a wide range of bee species. If canola flowers are abundant, foraging bees will be drawn to blooming canola fields, changing their abundance at sites with canola via dilution (Montero-Castaño et al., 2016) or spillover (Kovács-Hostyánszki et al., 2013).
4. Generalist foragers can take advantage of extra food provided by MFCs, whereas specialists cannot. Generalist species near blooming canola during year 1 will be more

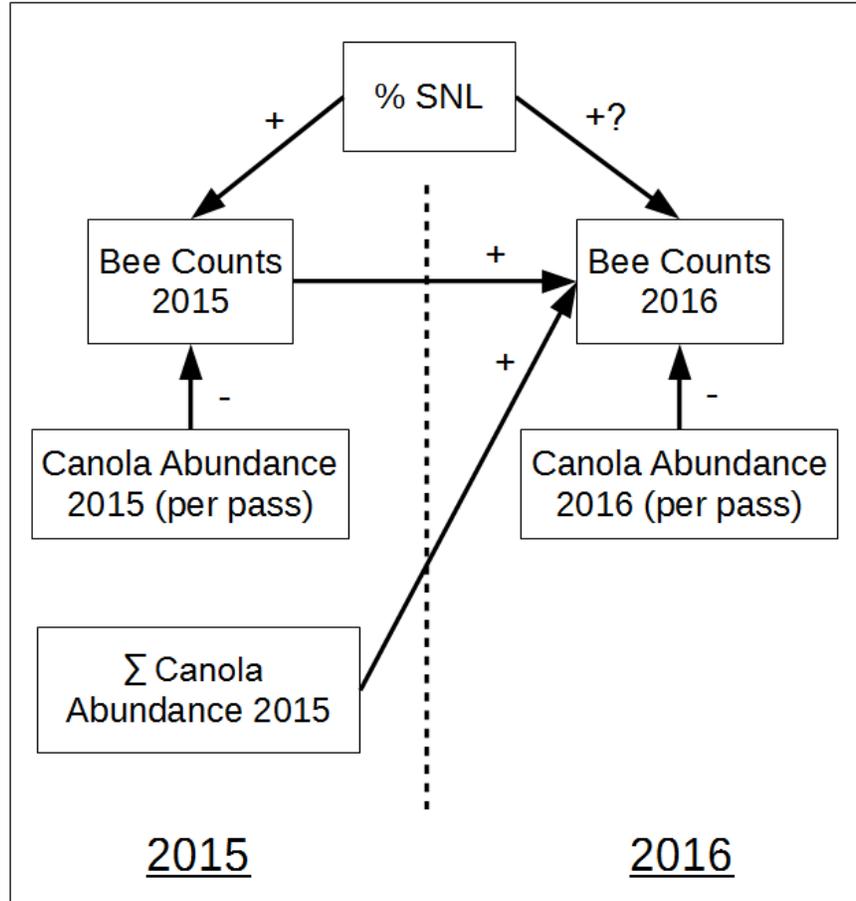


Figure 4.1: Hypothesized effects of canola and SNL. SNL refers to local abundance of semi-natural land. Canola abundance *per pass* refers to the abundance of canola flowers during a specific time of the season (trapping period). Σ canola abundance refers to the total amount of canola available during the previous year.

locally abundant in year 2, but specialist species will be unaffected (depending on the type of specialization).

Figure 4.1 summarizes these predictions, along with the expected direction of effects. I tested these predictions using a two-year dataset of solitary bee abundance gathered across a range of agricultural and natural landscapes in southern Alberta.

4.2 Methods

4.2.1 Data collection

I used wild bee specimens collected during 2015 and 2016 by Galpern et al. (2017) using blue vane traps, installed in ditches, road allowances, and field margins at 53 sites in southern Alberta, Canada (Figure 4.2). Sites were located across a landscape composition gradient of semi-natural to agricultural land, ranging from 0 to 96% SNL (non-SNL was mainly canola, wheat, or barley), and were placed at least 2 m from road margins. During placement and collection of each trap, observers visually estimated the amount of canola bloom occurring in neighbouring fields, ranging from 0% (no flowers present) to 100% (highest possible flower density). Trapping started near the beginning of the canola bloom in each year (late June) and lasted until after the end of the canola bloom (late July). Traps were filled with propylene glycol, placed at the field sites on June 23 in 2015, and June 28 in 2016, and were emptied at week-long intervals until the end of trapping. Each trapping interval (“pass”) lasted approximately one week, with five complete trapping passes per site per year, with trapping ending on August 7 in 2015, and August 22 in 2016. Blue vane traps attract some groups of bees more than others, especially small oligolectic bees, but have similar attractiveness to coloured pan traps, in terms of the range of species that they attract (Geroff et al., 2014; Joshi et al., 2015). All traps were assumed to be equally attractive to the same subset of species during each year, and equally attractive within species. Specimens were washed, pinned, and identified to species. Cryptic specimens were identified to sub-genus, and were then classified to morphospecies. All *Bombus*, managed species, and cleptoparasites were also identified; however, *Bombus* food requirements extend beyond the lifetime of an individual worker, and cleptoparasite taxonomy and host-specificities are poorly known in western Canada, so these taxa excluded from the rest of the analysis.

I used classified land cover data from Agriculture and Agri-Food Canada (2018) to estimate the amount of canola cover within a 250 m radius of each trapping location during

each year. Solitary bees have maximum foraging distances of less than 1500 m, but foraging typically occurs at distances of 100–300 m (Zurbuchen et al., 2010), justifying the use of a small landscape radius. In 2015 and 2016, 21 and 19 traps, respectively, were within 250 m of a canola field, and the median canola coverage surrounding those traps was 21.5% in 2015 (range: 0.5 – 100%) and 12.4% in 2016 (range: 0.5 – 95.3%). I used a 500 m radius to estimate the amount of SNL surrounding each trap location, considering all “forest”, “native grassland”, and “shrubland” cover classes as “semi-natural land”. Classification accuracy was high for cropland (2015: 88.9%, 2016: 90.8%), but was lower for non-agricultural land (2015: 68.6%, 2016: 68.5%), so I used a larger radius in order to provide a more consistent measure of SNL. Measurements of SNL were consistent between years at the 500m radius (correlation=0.97). 44 fields had SNL within a 500m radius, and the median cover in those fields was 32.1% (range: 0.1 – 96.3%). Tame pastures and hay fields were not included because I did not measure mowing or grazing intensity, and potentially beneficial flowers such as alfalfa (*Medicago sativa*) are usually cut before full flowering (Undersander et al., 2011).

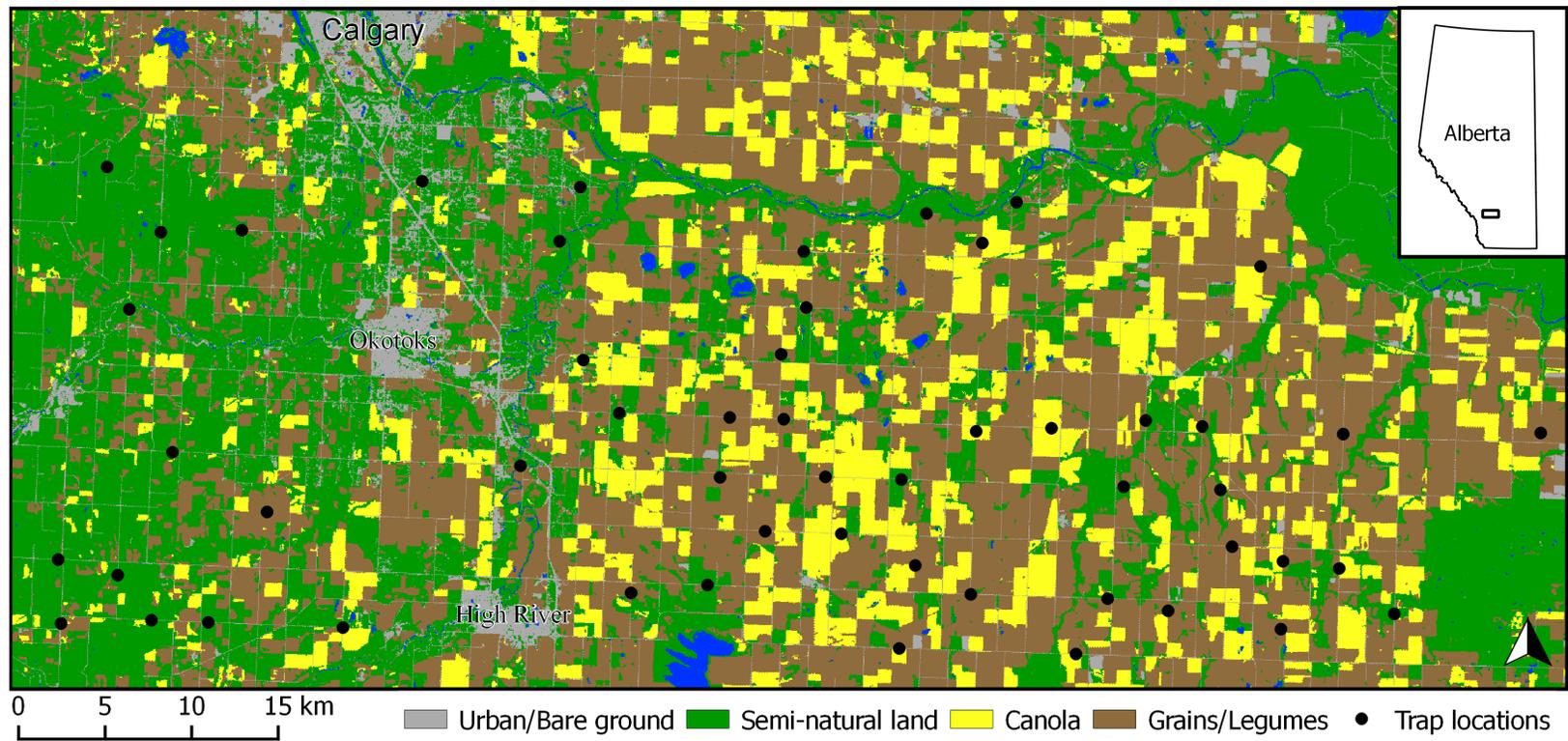


Figure 4.2: Map of blue-vane trapping locations in southern Alberta, showing trapping locations used in 2015 and 2016 (land cover from 2015 only). Inset map shows provincial boundary and outline of sampling area.

4.2.2 Model structure

I used a piecewise structural equation model (pSEM, see Chapter 3 Methods) to assess changes in bee numbers across the season, between sites, and how this is altered by canola and local abundance of SNL (Figure 4.1). In this model, abundance during the first year was a function of SNL cover and the surrounding canola bloom at the time of trapping (“current” canola), while abundance during the second year was a function of SNL, current canola, canola bloom from the previous year, and bee abundance from the previous year. Instead of using point measurements of canola bloom, I modelled the bloom using data from all sites by fitting a single gaussian curve with an amplitude of 100 for each year. Variation in planting times can cause variation in bloom times, but the timing of bloom was similar within each year, so this approach predicted bloom well (R^2 2015=0.72, 2016=0.93). I used predictions from the fitted model of canola bloom from each year to estimate whether canola flowers were present during each trap period; I defined flowers to be “present” if the bloom exceeded 10%.

To model bee between-year abundance in response to the surrounding landscape, I fit a zero-inflated negative binomial model with a single zero-inflation term for each year. I included SNL as a fixed effect for each year, with the effect in the first year representing the long-term influence of SNL on bee abundance, whereas the effect in the second year represents changes from the first year while controlling for previous abundance ($\% SNL$ in Figure 4.1). To measure the dilution effect from current bloom, I included a fixed effect for the availability of canola bloom during each pass (*Canola abundance per pass* in Figure 4.1), where the availability of canola was calculated as: proportion canola at 500m \times proportion of time during the pass where bloom was $>10\%$. I summed the availability of canola for each site, and used it as a fixed effect in year 2 ($\sum Canola Abundance 2015$ in Figure 4.1), as a way of calculating the lagged effect of canola on the next year’s bee population. *Log-number of days during which each trap was deployed* was included as an “offset” term (slope fixed at 1) to account for different levels of exposure at each site.

Bee abundances vary over the season, as well as from site-to-site (Kohler et al., 2008), meaning that measurements at each site-time combination are not necessarily independent. I used a gaussian process model (GPM) to account for variation among sites, and a second GPM to model variation over time. GPMs model the distribution of a set of measurements using a multivariate normal distribution with a mean of zero and a matrix of covariance values derived from the pairwise distance values between each point, using an exponentiated quadratic function to model decay in covariance with distance (Neal, 1997; Banerjee et al., 2008). In this case, the distances were the Euclidean distance (km) between each pair of sites, and the temporal distance (days) between passes. This allowed me to model a continuous process of bee flight phenology instead of using point measurements at each site, and account for spatial variation in abundance that was not captured by the SNL term. Finally, I modelled year-to-year changes in site abundance using a single term γ , representing the change in site intercepts between years (see Box 1).

To compare results between species, I fit the same model for each of the 20 most-abundant bee species at the sites, and compared parameter values between and across species. Unlike the pSEM from Chapter 3, there were no missing paths from endogenous variables (variables with a path leading into them, *bee counts 2015* and *bee counts 2016*), meaning that my model was saturated, and I could not perform tests of d-separation to verify the structure of the model as in Chapter 3 (Grace, 2006; Grace et al., 2012). I wrote the model using Stan 2.17 (Gelman et al., 2015) because it allowed coding of each GPM, estimation of all parameters simultaneously, and gives posterior distributions for inference (see Equation set S1 for the entire model likelihood statements). I used weakly informative normal priors ($\mu = 0, \sigma = 5$) for the fixed effects terms, gamma priors ($\alpha = 1, \beta = 1$) for the variance components, inverse-gamma priors for the length-scale components of the Gaussian process model ($\alpha = 7.5, \beta = 15$), and beta prior ($\alpha = 3, \beta = 7$) for the zero-inflation term (recommended by Neal, 1997 and Gelman et al., 2013). I ran three separate chains with an adaptive phase of 2000 iterations, and a sampling phase of 2000 iterations, then checked for convergence

of the chains (\hat{R} values close to 1) and low autocorrelation within chains (high N_{eff}), as recommended by (Gelman et al., 2013). p-values listed below are *posterior* p-values, equal to the amount of the posterior distribution that overlapped zero, and intervals shown are credible intervals (CIs), where 95% of the posterior distribution lies.

Box 1: Year-to-year spatial random effects

A mixed effects model with a “random” intercept *sensu* Laird and Ware (1982) can be written as:

$$y \sim Normal(\mu, \sigma_r)$$

$$\mu = X\beta + U\zeta$$

$$\zeta \sim Normal(0, \sigma_g)$$

where a set of observations y are normally distributed around their mean μ , with variance of σ_r . The “fixed” effects consist of a matrix X of “fixed” predictors and a vector of coefficients β , and the “random” effects consist of a matrix U of site or group identity, and a vector of intercepts ζ . The latent variable ζ is normally distributed with a mean of zero, and has its own variance parameter σ_g . Thus, variance in y can be partitioned into explained variance ($\text{var}(X\beta)$), between-group variance, σ_g , and residual variance, σ_r (Nakagawa et al., 2013).

Spatial random effects are similar to standard random effects, but use an exponential distance decay model to account for correlation between sites (McElreath, 2015):

$$\begin{aligned}
y &\sim \text{Normal}(\mu, \sigma_r) \\
\mu &= X\beta + U\zeta + e \\
\zeta &\sim \text{MVNormal}(0, \Sigma_g) \\
\Sigma_g &= \begin{pmatrix} \sigma_{1,1} & \sigma_{1,2} & \cdots & \sigma_{1,j} \\ \sigma_{2,1} & \sigma_{2,2} & \cdots & \sigma_{2,j} \\ \vdots & \vdots & \ddots & \vdots \\ \sigma_{i,1} & \sigma_{i,2} & \cdots & \sigma_{i,j} \end{pmatrix} \\
\sigma_{i,j} &= \alpha^2 \exp\left(-\frac{1}{2\rho^2} D_{i,j}^2\right)
\end{aligned}$$

where Σ_g is a symmetric covariance matrix, $D_{i,j}$ is the Euclidean distance between the i th and j th sites, α is the maximum amount of covariance as D approaches zero, and ρ is the slope of the decay in covariance with distance. This allows for modeling of underlying spatial variation that is unexplained by any of the fixed effects. The vector ζ can be estimated directly from a multivariate normal distribution, but a faster method is to decompose Σ_g into its Cholesky matrix L ($\Sigma_g = LL^{-1}$), and multiply L by a vector of unit normals η , creating a correlated vector of intercept values ζ .

The intercepts fit by this model may not be the same during every year. Instead of fitting a separate spatial random effect for each year, I fit a single vector of random effects ζ_1 during the first year and allowed the second year ζ_2 to vary as a function of a year-to-year slope term γ .

$$\begin{aligned}
y_1 &\sim \text{Normal}(\mu_1, \sigma_r^2) \\
\mu_1 &= X_1\beta_1 + U_1\zeta_1 \\
\zeta_1 &\sim \text{MVNormal}(0, \Sigma_g) \\
&\dots \\
y_2 &\sim \text{Normal}(\mu_2, \sigma_r^2) \\
\mu_2 &= X_2\beta_2 + U_2\zeta_2 \\
\zeta_2 &= \gamma\zeta_1
\end{aligned}$$

Since the vector of random intercepts ζ_1 is unexplained variation accounted for only by the site identity, γ represents how the random intercepts at each site change across a single time step. Negative values of γ imply density-dependent transitions, where sites with high values in year 1 have lower values in year 2. $\gamma = 0$ implies no relationship between years, $\gamma = 1$ implies stable ranking of sites, and $\gamma > 1$ indicates that site ranking becomes stronger and more extreme during the following year (Figure 4.3 below).

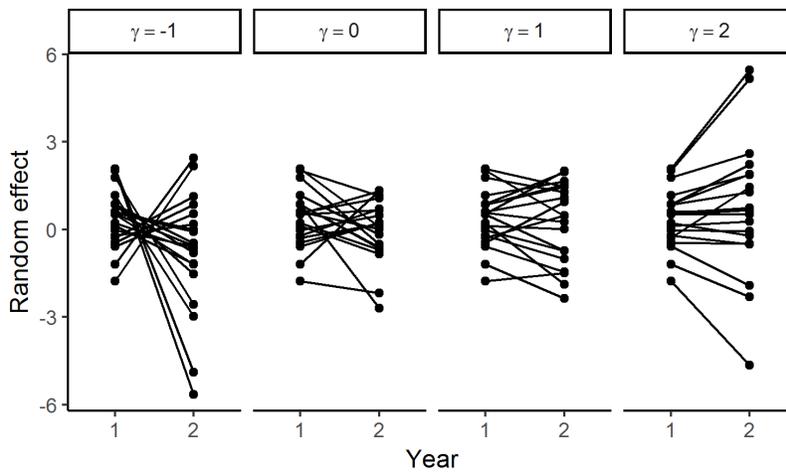


Figure 4.3: Example of effects of γ , the year-to-year slope term for the random intercepts.

In the context of a zero-inflated negative-binomial distribution (“mixture” model),
the model is written as:

$$y_1|y_1 > 0 \sim \text{NegativeBinomial}(\exp(\mu_1), \theta_1) \times \text{Bernoulli}(1 - \phi_1)$$

$$y_1|y_1 = 0 \sim \text{NegativeBinomial}(\exp(\mu_1), \theta_1) \times \text{Bernoulli}(\phi_1)$$

$$\mu_1 = X_1\beta_1 + U_1\zeta_1$$

$$\zeta_1 \sim \text{MVNormal}(0, \Sigma_g)$$

...

$$y_2|y_2 > 0 \sim \text{NegativeBinomial}(\exp(\mu_2), \theta_2) \times \text{Bernoulli}(1 - \phi_2)$$

$$y_2|y_2 = 0 \sim \text{NegativeBinomial}(\exp(\mu_2), \theta_2) \times \text{Bernoulli}(\phi_2)$$

$$\mu_2 = X_2\beta_2 + U_2\zeta_2$$

$$\zeta_2 = \gamma\zeta_1$$

where θ is the dispersion parameter of the Negative Binomial (“Polya”) distribution (Hilbe, 2011), and ϕ is the zero-inflation parameter, representing the chance of a zero being generated outside of the Negative Binomial distribution (Zuur et al., 2010;

McElreath, 2015).

Table 4.1: The most abundant 20 non-*Bombus* bee species captured in traps (6902 specimens total). Canola visitation information is from Zink (2013), and nest substrate and floral associations are from DiscoverLife and BeesOfCanada. Managed bees (*Apis mellifera*, *Megachile rotundata*), and cleptoparasites were not considered.

Species	Family	Overall abundance	Canola visiting?	Likely floral hosts	Likely nests
<i>Andrena amphibola</i>	Andrenidae	938	No	Generalist	Ground
<i>Andrena lupinorum</i>	Andrenidae	190	No	Fabaceae	Ground
<i>Andrena medionitens</i>	Andrenidae	73	No	Generalist	Ground
<i>Andrena thaspiae</i>	Andrenidae	489	Yes	Generalist	Ground
<i>Anthophora occidentalis</i>	Apidae	79	No	Generalist	Ground
<i>Anthophora terminalis</i>	Apidae	935	No	<i>Monarda</i> , <i>Phacelia</i>	Stems
<i>Melissodes confusus</i>	Apidae	684	No	<i>Helianthus</i> , Asteraceae	Ground
<i>Hylaeus</i> (<i>Hylaeus</i>) spp.9	Colletidae	98	No	-	Cavity
<i>Agapostemon texanus</i>	Halictidae	237	No	Generalist	Ground
<i>Dufourea maura</i>	Halictidae	192	No	<i>Campanula</i>	Ground
<i>Halictus rubicundus</i>	Halictidae	363	Yes	Generalist	Ground
<i>Lasioglossum colatum</i>	Halictidae	332	No	Generalist	Ground
<i>Lasioglossum leucozonium</i>	Halictidae	359	Yes	Asteraceae	Ground
<i>Lasioglossum zonulum</i>	Halictidae	724	Yes	Generalist	Ground
<i>Lasiglossum</i> (<i>Dialictus</i>) spp.1	Halictidae	113	No	-	Ground
<i>Lasiglossum</i> (<i>Dialictus</i>) spp.2	Halictidae	195	No	-	Ground
<i>Lasiglossum</i> (<i>Dialictus</i>) spp.5	Halictidae	174	No	-	Ground
<i>Lasiglossum</i> (<i>Dialictus</i>) spp.17	Halictidae	421	No	-	Ground
<i>Megachile perihirta</i>	Megachilidae	142	Yes	Generalist	Ground
<i>Osmia</i> (<i>Melanosmia</i>) spp.1	Megachilidae	91	No	-	Cavity

4.3 Results

4.3.1 Summary of wild bee community

The blue-vane traps caught 19009 specimens across the two years of study. Of these, 5434 *Bombus*, 5248 managed bees, and 208 cleptoparasitic specimens were excluded, leaving 8119 specimens of solitary bees (5887 in 2015, 2232 in 2016), comprising 22 genera, and 130 species (Figure S6). Overall trapping rates were lower during 2016 (paired t-test, $p < 0.0001$, bees per trap per week \pm SE, 2015: 14.7 ± 1.35 , 2016: 5.94 ± 0.62). Table 4.1 lists the 20 most abundant species caught in the traps. Most species were ground-nesting floral generalists, and five species were known to visit canola.

The canola bloom model explained a large amount of variance in bloom (R^2 2015: 0.72, 2016: 0.93), and showed that canola bloomed earlier in 2015 than 2016 (Figure 4.4). The amplitude of bloom varied between years, but this was likely due to differences in observer scoring between years, so I scaled the curves to equal 100%.

Overall abundance was higher in 2015 than 2016 (Intercept coefficients 2015: 1.65, 2016: 0.069), and this was largely consistent among species. The temporal GPM for each year captured a large amount of temporal variation among overall abundance in 2015, but not in 2016 (R^2 2015: 0.27, 2016: 0.05). Abundances largely declined going into July and August (Figure 4.5), indicating that the samples largely represented the latter portions of species' phenologies. Some species displayed a second peak of abundance later into the season (*Melissodes confusus*, *Lasioglossum leucozonium*), indicating possible bivoltinism.

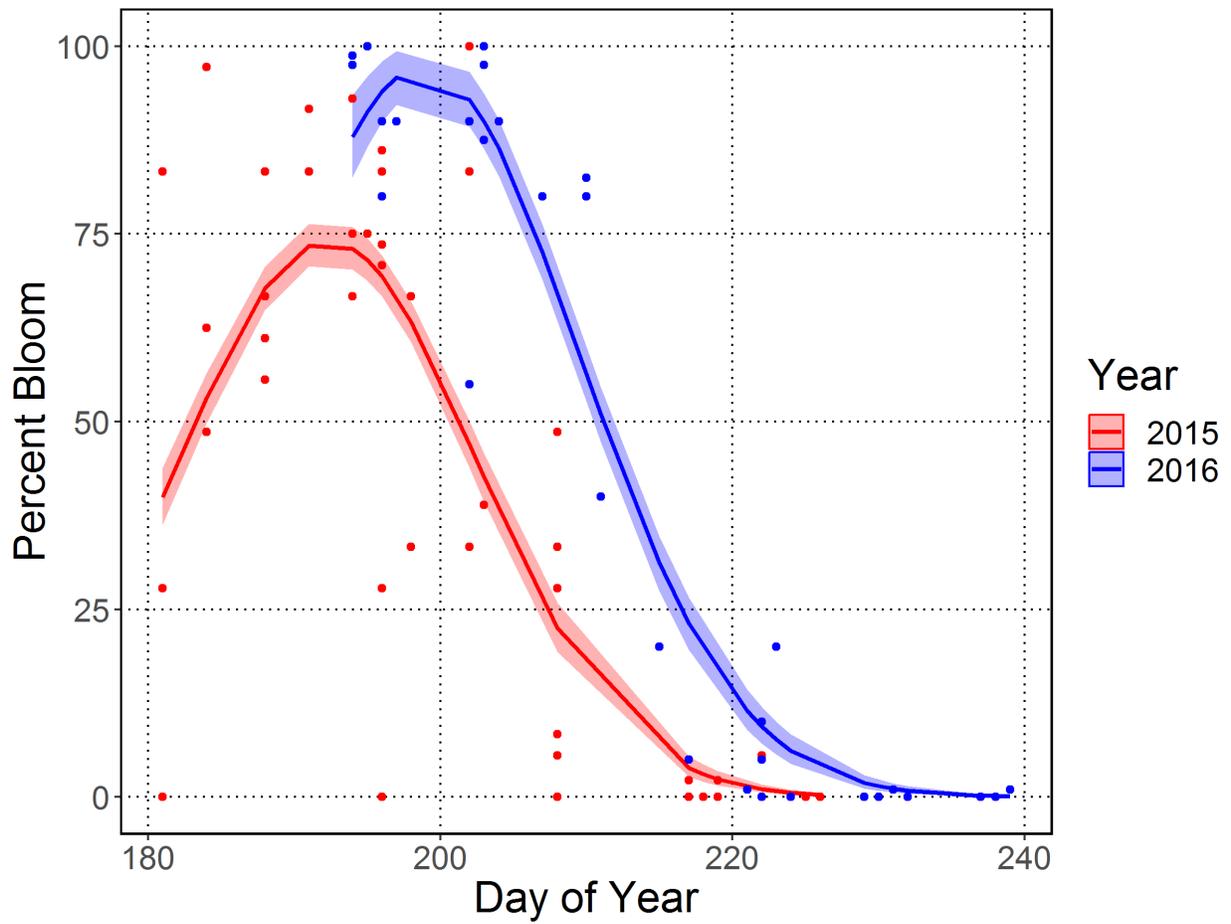


Figure 4.4: Variation in canola bloom during 2015 and 2016, with points representing measurements taken in the field, lines representing model predictions, and shaded areas representing 95% CIs in the mean.

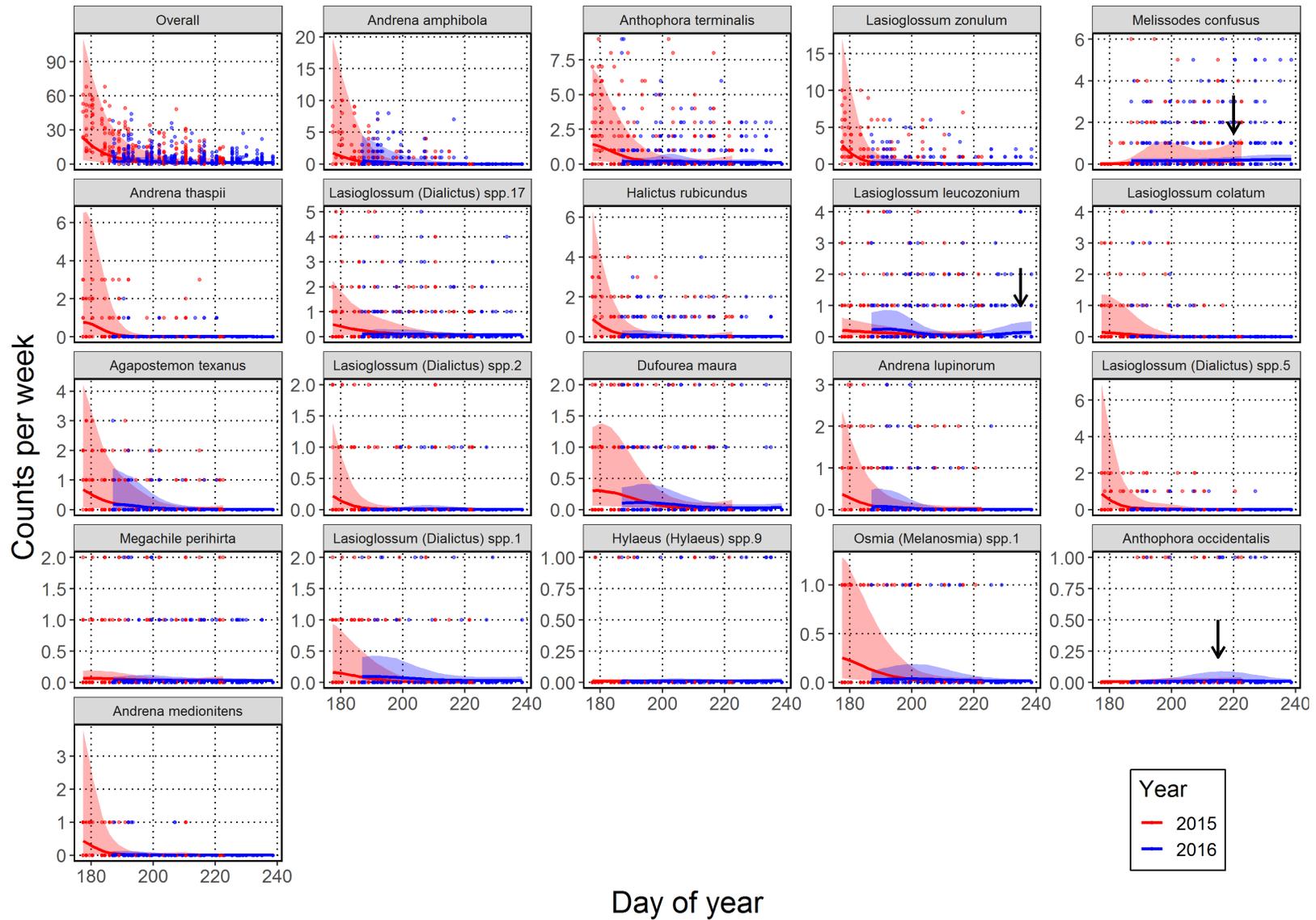


Figure 4.5: Partial effect of temporal trends (estimated by Gaussian process model) for 2015 and 2016, with shaded intervals representing 95% CIs of the mean. Black arrows indicate a mid-season peak in abundance for *Anthophora occidentalis*, and a potential second peak in *Lasioglossum leucozonium* and *Melissodes confusus*.

4.3.2 Effects of landscape and previous abundance

I found support for the predictions of the positive effect of SNL and that of inverse density-dependence between years, but I found no support for the predictions of current and lagged effects of canola on bee abundance. SNL had no effect on overall abundance in 2015 ($p=0.31$), but had a positive effect in 2016 ($p=0.002$). There was a large positive effect of abundance from 2015 on abundance in 2016 ($p<0.001$), indicating that sites with higher abundance in 2015 also had higher abundance in 2016 (inverse density-dependence). However, neither past nor present canola had any effect on overall solitary bee abundance (Figure 4.6, top row). There was no large effect of nearby canola abundance in either 2015 ($p=0.25$) or 2016 ($p=0.42$), indicating that sites with a large bloom of canola close to the field *during that year* did not experience a decrease in overall abundance of wild bees (21 and 19 traps in 2015 and 2016, respectively; see Methods above). Finally, there was no lagged effect of canola from 2015 on abundance in 2016 ($p=0.34$), indicating that a large bloom of canola close to the field *during the last year* did not affect the abundance of wild bees in the next year.

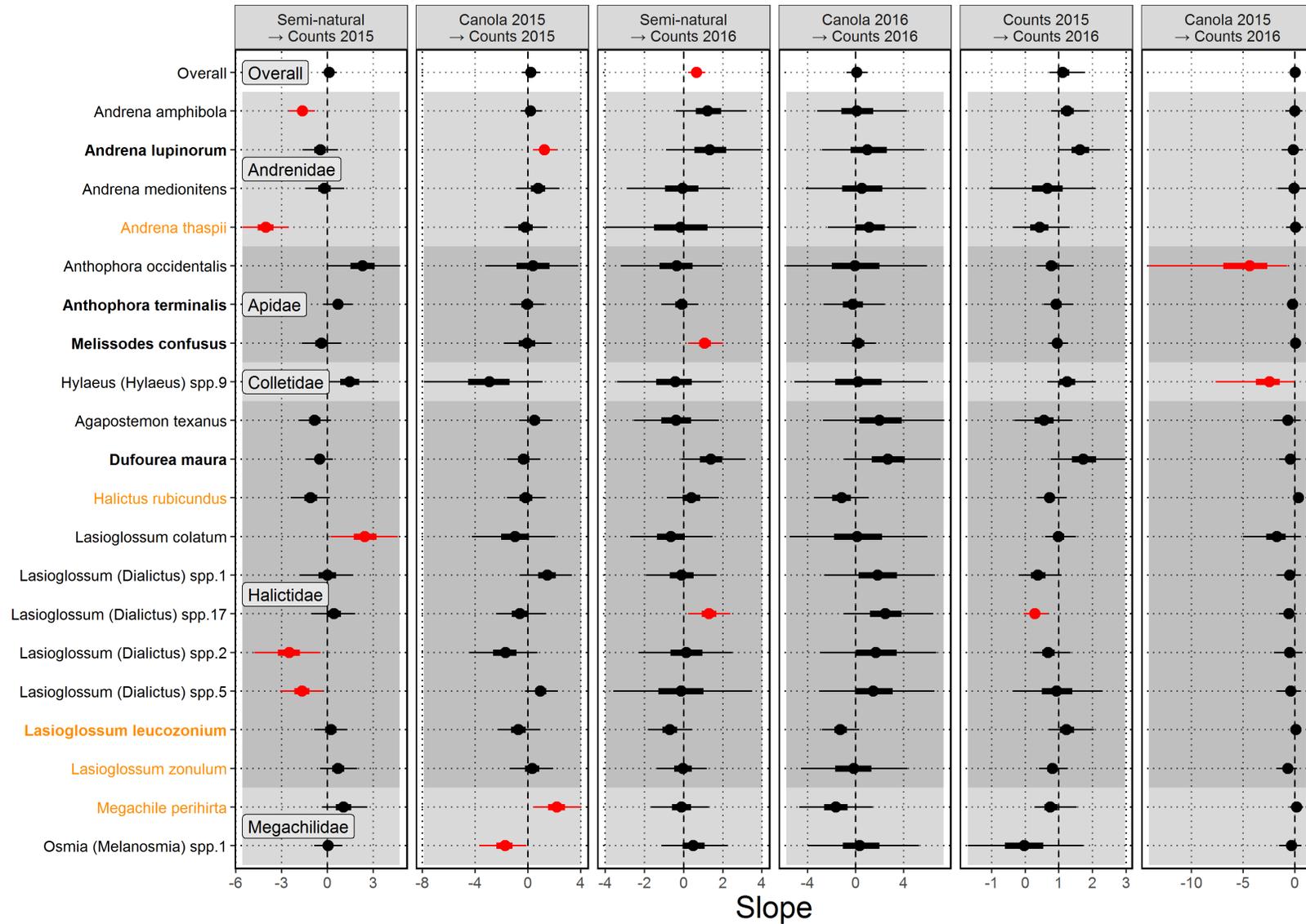


Figure 4.6: Slopes (\pm CIs) for SNL effects, canola effects, and abundance effects (see Figure 4.1) on the abundances of the 20 most abundant bee species from 2015 and 2016. Thin lines span 95% CIs, thick lines span 50% CIs, and dots represent the median. CIs of the values displayed in red do not overlap zero. Yellow labels indicate species known to visit canola, and bold labels identify specialist foragers.

The main effects for the model varied among the 20 species. SNL had a variety of effects, both positive and negative, on abundance in 2015 (Figure 4.6, column 1). For example, SNL had a positive effect on *Anthophora occidentalis* ($p=0.03$), but a negative effect on *Andrena thaspii* ($p<0.001$). In 2016, SNL had a positive effect on the abundance of only a few species, particularly *Melissodes confusus* ($p=0.006$, Figure 4.6, column 3). Only *Megachile perihirta* ($p=0.007$, column 2) and *Osmia* spp. ($p=0.02$, column 5) were affected by current canola abundance during 2015. There was little evidence of a lagged canola effect, as most species in 2016 were not influenced by canola abundance from 2015 (column 6), but for those that were, the effect of canola tended to be negative (*Anthophora occidentalis*, *Hylaeus* spp, both $p<0.02$). *Halictus rubicundus* experienced a weak increase from the the 2015 canola bloom ($p=0.074$), and is known to visit canola (Zink, 2013), but this species appeared to be the sole beneficiary. Finally, abundance in 2016 was positively influenced by abundance in 2015 for almost all species (Figure 4.6, column 5), indicating that sites with higher relative abundance in 2016 also had similar relative abundance during 2015. *Lasioglossum* spp. 17 had a median slope of 0.28 (CI: -0.05–0.67), indicating that abundance in 2016 was not strongly related to abundance in 2016, but all other species had slopes overlapping 1, indicating strong positive dependence on last year’s abundance. The effect of last year’s abundance was lower (*Osmia*, *Lasioglossum* spp. 1) or higher (*Andrena lupinorum*, *Andrena amphibola*) in a few species, but were not strongly different from 1 (95% of posterior overlapped 1).

4.4 Discussion

4.4.1 Prediction 1: SNL results in higher bee abundance

Overall, SNL had no effect on total wild bee abundances during 2015, but it had a positive effect in 2016, supporting the hypothesis that SNL enhances population increase between years. Increased amounts of SNL can increase overall wild bee abundance independently of the previous year’s abundance, but may do so via increases in a few dominant species only

(Cariveau et al., 2013; Fijen et al., 2019). However, the effect in both years varied among species, meaning that changes in total bee abundance were mediated by changes in a few dominant species. For example, the effect of SNL on abundance in 2016 was strongly positive only for *Melissodes confusus* and *Lasioglossum* spp. 17 (5th- and 6th-most abundant species, Figure S6).

The negative responses to SNL by *Andrena amphibola* and *A. thaspiae* were unexpected, as SNL should have provide greater amounts of nesting habitat and floral resources. This negative effect may have been caused by nesting site features that are more common in areas with low SNL, such as exposed soil from ditches and embankments in disturbed field margins (Potts and Willmer, 1997; Hopwood, 2008). It may have also been caused by higher abundance of weedy flowering plants (e.g. *Cirsium*, *Taraxacum*, *Trifolium*) in road allowances and field margins, causing an overall decrease in flowering resources in areas with high SNL. Disturbances can create bee habitat (Potts et al., 2003; Ponisio et al., 2016), and bee abundances can sometimes be higher in urban areas (Baldock et al., 2015; Samuelson et al., 2018), likely due to increased food and nest availability (Theodorou et al., 2016). However, the sets of traits selected for in bees in developed areas tend to be very different than those in undisturbed areas (Harrison et al., 2017). Therefore, bees with a negative response to SNL could represent “disturbance specialists” that thrive in areas with low SNL. The diversity of individual responses to SNL reveals a corresponding diversity of habitat requirements for the most common 20 species in the trapping environment, meaning that a homogeneous definition of “semi-natural land” may not be generally useful (Hall et al., 2019), and is likely related to specific nesting, foraging, and life-history traits of individual species.

4.4.2 Prediction 2: Bee abundances show inverse density-dependence

Bee abundances were positively related to last year’s abundance at each site, indicating that sites with a high abundance in 2015 also had a high abundance in 2016. The slope of the

effect of last year's abundance was less than 1 for *Osmia*, while others species had slopes greater than 1 (*Andrena lupinorum*, *Dufourea maura*), but these tended to be less-common species. However, an unnamed species of *Lasioglossum* (spp. 17) had relatively high numbers (421 individuals, Table 4.1), and had a median slope of 0.28 (CI: -0.05 – 0.66), suggesting that at least some species have populations that are closer to density-independent. This could have been caused by cleptoparasites causing a lagged drop in the population (Dainese et al., 2018), or could simply be a year-specific effect, given that these data were collected over a span of only two years (making lags of >2 years undetectable). However, these results support the prediction that pollinator populations are limited more by density-independent factors rather than density-dependent factors.

Few studies have examined both temporal and spatial variation in bee abundance, but most have found similar patterns (Bischoff, 2003; Steffan-Dewenter and Schiele, 2008; Riedinger et al., 2015; Dainese et al., 2018). Specifically, most of them found that parasites were capable of reducing bee populations, but that parasite abundance was highly variable. Steffan-Dewenter and Schiele (2008) found an inverse relationship between parasitism rates and population in *Osmia rufa*, indicating that inverse density-dependent parasitism may be common in wild bees (but see Rosenheim, 1990), but found no evidence of top-down population regulation. Similarly, Bischoff (2003) found that large declines in populations of *Andrena vaga* were likely caused by nest parasites (*Bombylius major*). This suggests that wild bee populations tend to be relatively stable year-to-year in the absence of parasites, suggesting that resource variation between years is relatively low compared to variation among sites (Roulston and Goodell, 2011), and that population growth is largely density-independent, at least at the levels that occur naturally. Species-specific cleptoparasite relationships should be identified in order to incorporate parasite abundance as a factor for future studies.

4.4.3 Prediction 3: Generalist foragers will be recruited to canola, reducing abundance in traps

The presence of nearby canola caused no change in total wild bees caught per trap, implying that canola does not dilute solitary bees via recruitment, or cause a spillover into adjacent SNL via mass effects. *Megachile perihirta* and *Osmia* abundances were positively and negatively (respectively), affected by nearby canola bloom, but only in 2015. Both *M. perihirta* and bees from the genus *Osmia* visit canola (Zink, 2013), but for *M. perihirta*, the effect was positive, meaning that nearby canola bloom would have been causing higher trapping rates. This implies a potential spillover of *M. perihirta* during canola bloom (similar to Kovács-Hostyánszki et al., 2013), but this pattern only occurred during 2015. Therefore, canola likely has little effect on the abundance of southern Albertan wild solitary bees, since both *M. perihirta* and *Osmia* were uncommon in both years (Table 4.1), and these species were the only ones affected by canola bloom.

Bombus abundance in SNL can be diluted by nearby MFCs (shown in Holzschuh et al., 2011, 2016), but this pattern does not seem to extend to solitary bee species. I expected to see this dilution effect in canola-visiting wild bees, and floral generalists (Table 4.1), but the bloom affected neither. It is possible that the low abundance of some species made any reduction in abundance outside of the crop difficult to detect (as in Fijen et al., 2019). Flowering plants in adjacent SNL may also be more attractive than canola flowers, either because they produce more nectar and pollen, match the morphology of floral specialists better (e.g. *Anthophora terminalis*, *Dufourea maura*), or because pesticides used in canola fields make the flowers less attractive to wild bees (Garbuzov et al. 2015, but see also Kessler et al. 2015). Bumble bee nests present in SNL could also potentially compete with solitary bees, but this would require very large numbers of foragers to do so, so this seems equally implausible. Therefore, I consider the “low-abundance” hypothesis to be the most likely, as many of the bees are known to visit canola (Table 4.1), canola produces large amounts of floral resources, and has a generalist floral morphology.

4.4.4 Prediction 4: Foraging generalists will increase their abundance in year following a canola bloom

Generalist foragers in areas with large amounts of canola should experience a demographic increase during the next year, but canola bloom seemed to cause no strong increases in overall abundance for any species, and was associated with *decreases* in the abundance of two species. *Halictus rubicundus*, a generalist known to visit canola, was the only species that gained a lagged benefit from canola, but this effect was weak. *Hylaeus* and *Anthophora occidentalis* had lower numbers during the year following a canola bloom, but neither of these species is known to visit canola, nor did either of them experience concurrent changes in abundance due to nearby canola bloom. It may be that canola bloom attracts foragers and creates a spillover of potential competitors (either wild or managed) into the foraging habitat of *Hylaeus* and *A. occidentalis*, resulting in lower abundances. Both species had low catch rates in 2015 and 2016 (Table 4.1), so this reduction may simply be an artifact of the low sample size. However, Galpern et al. (2017) found similar results for *Bombus* and *Halictus rubicundus*, and suggest that part of the reason that *Bombus* suffered declines close to blooming canola was that nest-searching queens aggregated to canola more easily, leading to establishment in areas with no forage aside from canola (mass effect, Shmida and Wilson, 1985).

These findings contrast with the work of Riedinger et al. (2015) and Dainese et al. (2018), who found that adjacent MFCs increased abundance of solitary wild bees during the next year. Riedinger et al. (2015) did not separate solitary bees by taxonomic identity, as they used a transect census method to assess wild bee visitation, and conducted observations in the flowering crop itself, rather than in the adjacent SNL. This points to the problem of ignoring species when making inferences about impacts of MFCs, as my overall model that treated all solitary bees as equal had different results than the models of individual species.

Another important point to consider is the overall timing of MFC bloom. Spring-planted canola bloom in southern Alberta commonly occurs from late June until late July, peaking

in early July, which misses a large number of earlier wild bee species that are present in May and June (Wonneck, 2014, this work). Riedinger et al. (2015) reported bloom times in late April to early May for winter-planted canola in southern Germany, which may overlap the flight period of wild pollinators more completely than the spring-planted canola planted in southern Alberta. While I considered canola cover within a 500m radius, smaller scales of analysis may have been more appropriate, as Zurbuchen et al. (2010) found that 50% of small wild bees did not forage at distances of more than 300m. It is also possible that the species attracted to blue-vane traps were not a representative sample of all the bee species that use canola, but 25% of the species I found were known to visit canola (Zink, 2013, Rader 2010), so blue-vane traps are at least somewhat representative of the canola-visiting bee community. *Osmia bicornis* was the main bee species that Dainese et al. (2018) and Holzschuh et al. (2012) found benefitted from canola, indicating that their results could represent a species-specific response of *O. bicornis* to canola. This could also be a more general pattern in stem- or cavity-nesting bees, whereas most of the common bee species were ground-nesting. My results suggest that canola has little positive effect on common ground-nesting bees in southern Alberta.

4.4.5 Summary

In my two-year study of wild bee abundance in southern Alberta, Canada, I found that SNL had a weak positive overall effect on solitary bee abundance, but that many individual species' abundances were neutrally or even negatively related to SNL abundance. Unexpectedly, I found that adjacent MFCs had little effect on abundance, either during the bloom, or the following year, and that this effect was no greater for floral generalists or species known to visit canola. Site-level abundance during 2016 was mainly related to site-level abundance in 2015, and the rank abundance at sites was fairly similar from year to year.

These results suggest two important directions for future research: First, pollinator conservation efforts should identify specific landscape elements (*e.g.* shrubland, bare ground,

grassland) that are important to wild pollinator abundance. Measures of habitat, such as percent cover of SNL at a given radius, are a coarse tool for understanding how pollinators use their environment, and we will gain a better understanding of how these communities are regulated using more precise measurements. Since many of these western North American species are taxonomically confusing, and little is known about their life-history and ecology, this also speaks to the ongoing value of natural history and taxonomy in general. Secondly, while I found that MFCs seem to have fairly little effect on wild pollinator abundance, it is important to identify why *Osmia bicornis* (or similar species) benefitted from MFCs in the studies of Riedinger et al. (2015) and Dainese et al. (2018). For example, it may be that the bloom period of winter-planted canola (which is common in Europe, but not in southern Alberta) overlaps more completely with the flight phenology of common pollinators. Alternatively, pollinator traits, such as body size, specific nesting habitat, or measures of sociality, could provide a better predictor of how well pollinators can use nearby MFCs (Hall et al., 2019). These details could help to inform future conservation effort and landscape design for ecosystem services, especially development of pollinator habitats in field margins.

Chapter 5

Conclusion

My thesis has dealt with three interrelated topics in ecology, comprising elements of behavioural, landscape, and population ecology, all operating within an agronomic framework. Chapter two deals with the general question of what energetic currency motivates central-place foragers, and more specifically, the implications of this foraging currency for the distributions of central-place foragers. Chapter three examines the connections between foraging behaviour in canola crops, and the resulting pollination and seed yield. Chapter four examines how canola fields influence the communities of wild flower-visiting bees surrounding them. Together, these systems interact with each other (Figure 1.1) in the context of agroecosystems of southern Alberta.

5.1 Summary

5.1.1 Chapter two: Extending the ideal free distribution to central-place foragers

Chapter two approaches the problem of how competing foragers distribute themselves over a landscape from the behavioural perspective of central-place foraging (CPF, Orians and Pearson, 1979) and the ideal-free distribution (IFD, Fretwell and Lucas, 1969). In the context

of bee foraging, neither model is linked to realistic competitive principles (Possingham, 1988). I created a hybrid IFD-CPF model using two types of energetic currencies and socialities, and tested the model using honey bee foraging data from commodity canola fields. Honey bee visitation most closely follows the predictions of efficiency maximization by solitary foragers who prioritize nearby patches much more than rate-maximizers or social efficiency maximizers.

This work builds on previous models of foraging behaviour, and makes testable predictions about how foragers should act in novel environments. Other hybrid models of CPF and IFD did not include a mechanistic model of competition, while my model uses a realistic model of nectar depletion (Possingham, 1988) to model competition within a patch. Solitary and social foraging have been examined before (Dukas and Edelman-Keshet, 1998; Ydenberg et al., 1994), but they have not been examined beyond two-patch scenarios (Ydenberg et al., 1986), and have never been tested in actual landscapes. These simulations replicate foraging behaviours (*e.g.* load size increases with distance), and provide realistic estimates of visitation. They also revealed the novel peaked relation of trip time to distance from the nest of efficiency maximizers, but not rate maximizers, with solitary efficiency maximizers having a more distinct hump than social efficiency maximizers. Visitation decreased quickly with distance from the central place: in a single quarter section of canola stocked with 40 honey bee hives (a typical stocking rate in Alberta), half of the visitation occurs within the first 200m. All visitation in this scenario occurred within a 1 km radius from the central place, meaning that pollen transfer between fields outside of this radius is unlikely (similar to Cresswell et al., 2000; Chifflet et al., 2011). These distances are conservative, because they do not include competition with other honey bee colonies, and the influence of competitors likely constrains foraging distances. Because the foraging radius of CPFs depends on the surrounding landscape, buffer distances that are used to limit gene flow in transgenic canola should also depend on the composition of the foraging landscape. This suggests that hybrid seed producers or organic canola producers may be able to reduce inter-field distances based

on local floral cover while still limiting gene flow between fields (Damgaard and Kjellsson, 2005; Hayter and Cresswell, 2006; Ronca et al., 2017).

5.1.2 Chapter three: Bee visitation, pollination services, and plant yield in commodity and hybrid seed canola

Chapter three examined the links between visitation and pollination, and pollination and yield, in seed canola and commodity canola. Agricultural pollination can be treated as a black box (Morandin and Winston, 2006; Ricketts et al., 2008; Bartomeus et al., 2015), without reference to the underlying ecological mechanisms that contribute to fruit production. I used a SEM of two systems of canola production to relate seed production based on bee foraging and plant size. As in chapter two, visitation by honey bees was strongly related to distance in both commodity and seed canola fields, with visitation decreasing with distance from their apiary, but there was no relation between visitation and pollen deposition. In seed fields, leafcutter bee visitation decreased with distance from their shelter, and unexpectedly, also decreased with distance from the edge of the field, meaning that foragers likely migrate to shelters at the edge or off-field nest sites. Leafcutter bees increased pollen deposition, but honey bee visitation had no direct impact on pollen deposition (but may increase pollen indirectly). Pod number in commodity canola fields was mainly influenced by plant size, and there was no underlying link between between pollen deposition and yield. In contrast, pod number in seed canola was affected by pollen deposition as well as plant size. Finally, seed size (per pod) is positively related to seed number in commodity canola, and negatively related in seed canola. I propose that this pattern is caused by resource limitations at different times of the season in commodity canola. Seed production in seed canola plants is limited by pollen, so resources vary among plants due to size, but are more readily available over the course of the season than they are in commodity plants. This approach to analysis serves as a step towards a mechanistic model of pollination services (Sáez et al., 2017), and points to the contextual importance of pollination services in seed canola production.

Studies of crop pollination generally use the following conceptual model:

Insect visitation \rightarrow Pollen deposition \rightarrow **Fruit production** \leftarrow Plant resources

Most studies of agricultural pollination examine part of the process of how insect visitation influences fruit production, but rarely examine the entire chain of production, and few examine the resource context of the plants in conjunction with pollination (Marini et al., 2015; Tamburini et al., 2019). Pollination experiments are typically performed in scenarios where both insect visitation and nutrient resources are abnormally high compared to conditions used in fields, but rarely measure levels of visitation or pollen deposition, treating both qualitatively (Sabbahi et al., 2005; Durán et al., 2010). Isolation treatments using net excluders are used to exclude insect pollinators from plots, but very few studies (Marini et al., 2015) account for reduction in yield as a result of a shading or microclimate effect (Kearns and Inouye, 1993), meaning that any bias from these treatments is unmeasured. Other studies exclude pollinators from individual parts of the plant (Bommarco et al., 2012; Perrot et al., 2018), ignoring any plastic responses of the plant to pollen deficit. Since the benefits of extra pollen are context-dependent (Melathopoulos et al., 2015; Tamburini et al., 2016), unless we understand the nutrient context that a plant exists in, inferences about about pollination are limited. My analysis approach quantifies the effect of the agricultural context (plant density and size) as well as the effect of pollen deposition itself, and found that the plant growth context is stronger than the pollination effect in explaining reproduction in both seed and commodity canola. This work supports the findings of Lindström et al. (2016) and Marini et al. (2015) by *a*) demonstrating that hybrid commodity canola has little dependence on insect pollination (at the stocking levels we observed), and depends almost entirely on the nutrient context (plant size), and that *b*) seed canola yield depends on both the nutrient and the pollination context.

My work also sheds light on multi-species pollination schemes in seed fields, since there

is very little literature on how pollinators behave in canola seed fields (but see Mohr and Jay, 1988; Soroka et al., 2001), and even less on how they interact with each other. In hybrid seed crops that use multiple species of insect pollinators, some studies indicate that *Apis mellifera* do not behave as efficient pollinators (Tepedino, 1997; Gaffney et al., 2019, but see Currie et al., 1990), which my study confirmed. Honey bees tend to use the centre of the female bays in seed canola fields far more than the edge plots, and there appears to be minimal movement of individuals between male and female bays (see also Greenleaf and Kremen, 2006b; Waytes, 2017). In contrast, leafcutter bees tend to visit the edge of the bays more than the centre, making movement of pollen between bays more likely. I also found that leafcutter bees are strongly constrained by the distance from their shelter, as most visitation occurs within the first 20 m, and that this has a direct feedback on seed production surrounding the shelters (Currie, 1997). Finally, leafcutter bees visit more frequently at the edge of the seed field, which has not previously been reported in hybrid canola (see Goerzen et al., 1995 for data from alfalfa fields). These results suggests that to optimize yield in seed canola crops, growers should consider the following future lines of research. First, thinner female bays may help to reduce the edge effects in hybrid seed fields, but come at the cost of reducing the total harvestable area within the field (since plants in male bays are removed). Secondly, “leaf-material” crops planted within the male bays to provide leafcutter bees at the centre of the field with material for cocoons (Robert Currie, *pers. comm.*) may help to avoid drifting of leafcutter bees, keeping them at the shelters in the centre of the field.

5.1.3 Chapter four: Effects of canola bloom and semi-natural habitat on wild bee populations in southern Alberta

Chapter four examined the effect of canola crops on wild bee abundance in the context of the agricultural landscape, SNL, and changes in populations. Population dynamics of wild insects can be varied (Turchin and Taylor, 1992), and pollinating insects require both nearby flowering plants and nesting sites to reproduce. The matrix of SNL surrounding cultivated

crops can provide both of these resources, supporting an increased abundance and richness of pollinating insects (Ricketts et al., 2008). Flowering crops offer a large temporary boost in floral resources that can increase pollinator populations during the following year, but this may depend on the diet breadth of foragers, with floral generalists being more able to take advantage of these flowering resources than specialists. I tested *a*) the year-to-year stability of wild bee populations, *b*) the current and lagged effect of SNL, and *c*) the current and lagged effect of nearby canola crops on wild bee populations. I found that the most important predictor of bee abundance was abundance during the previous year, and that populations showed positive density-dependence. SNL increased abundance during the second year, but not during the first year, indicating that SNL did not control long-term bee abundances at our sites. However, the effects of SNL were highly species-dependent, with SNL having positive, negative, or neutral effects on the populations of individual species. Finally, there was no effect of the current or the previous year's canola bloom on wild bee abundance, but this may have been due to a low overlap between canola bloom and wild bee flight phenology. Most of the species were ground-nesting generalist foragers, but these findings were not largely different for floral specialists, suggesting that neither generalists nor specialists derive large benefits from nearby canola crops, and are likely more dependent on forage conditions within the SNL (Rollin et al., 2013). My results suggest that bee populations are largely stable year-to-year, and canola bloom does not affect solitary bee abundance, at least in the summer-flying species that we examined. They also suggest that the relation between SNL and bee abundance is highly species-specific, with some species thriving in areas with more abundance SNL, while others responded neutrally or even negatively to SNL. Given that these results are derived from only two years of data, more data should be collected to support these findings, as differences in population dynamics between years are very common in bee populations (Steffan-Dewenter and Schiele, 2008).

5.2 Synthesis

Chapters two and three are both linked by the common theme of distance-based foraging. However, chapter three extends this theme further by examining how visitation links to pollen deposition and yield, and examines interactions between multiple species of foragers using multiple aggregations, which are not covered by my model from chapter two. In chapter three, I used a log-linear regression model of visitation rates with distance, for both honey bees and leafcutter bees, and showed that honey bee visitation increased with distance away from leafcutter shelters. As expected from foragers with unequal distance costs (Ydenberg et al., 1986; Currie, 1997), the increase was not simply the inverse of the leafcutter bee decrease. Leafcutter bees are highly constrained by travel distance (Peterson and Roitberg, 2005), with their visitation rates decreasing quickly with distance away from their shelter, and I found anecdotal evidence that they also interfere directly with honey bees, meaning that they may compensate for higher distance costs by using direct interference to defend nearby patches (Ydenberg et al., 1986). Honey bee visitation decreased with distance from their hives, and I expected that leafcutter visitation would be lower closer to the bee hives due to greater competition (as implied by chapter two). However, I found the opposite result: leafcutter bee visitation rates were higher at the edge of the field, and they visited there almost twice as frequently as they did at 100m into the field. This result was *not* predicted by the model from chapter two because it only deals with costs for foragers who maximize their fitness by foraging alone and use one type of foraging resource (represented in energetic terms, as nectar). Since leafcutter bees require pollen, nectar, and leaf material to provision their larvae, and only two of those are readily available in the seed canola field. Therefore, I suggest that a proportion of the foraging leafcutter bees migrated from tents in the centre of the field to tents at the edge of the field to gain better access to leaf material (since cocoons are initially evenly distributed in shelters throughout the field).

Chapter two and chapter four are linked by their use of distance, as chapter two explicitly deals with the impact of canola on honey bee foraging, while chapter four implicitly involves

foraging on canola by wild bees, but doesn't involve honey bees. In this way chapter four can be thought of as an extension of chapter two using the wild bee community in the context of a given foraging landscape (Figure 1.1). While chapter two showed that canola was far more attractive than forage from SNL for honey bees, I found no evidence to suggest that it is as attractive to wild bees. Almost no species showed declines in trapping rates next to canola bloom, implying that canola does not change the attractiveness of the blue-vane traps, and there was no evidence of canola crops causing an increase in abundance during the next year. My analysis in chapter four deals with foraging distance more crudely than the simulation in chapter two, as we have little idea about the foraging habits or nesting requirements of most wild solitary bees, other than that they tend to have smaller flight ranges than social bees (Greenleaf et al., 2007; Zurbuchen et al., 2010). Modelling the foraging behaviour of solitary wild bees presents a similar challenge to modelling leafcutter foraging, in that the fitness-maximizing behaviour for a solitary bee involves a mixture of nest defence, pollen foraging, and nectar foraging, which likely changes with size of the nesting aggregation (Michener, 1969). However, it would be relatively simple to parameterize a model using honey bees in SNL to gauge how they might compete with wild bees for nectar, that is, by how much they reduce the nectar standing crop. This could be used to create some kind of distance threshold for placing apiaries in relation to conservation targets, for example, to set a minimum distance for apiaries of a certain size, since honey bees have been implicated as competitors of wild bees (Steffan-Dewenter and Tscharntke, 2000; Thomson, 2004, 2016).

While wild pollinators are important components of some canola systems (Bommarco et al., 2012; Perrot et al., 2018), but I was unable to consider their influence in chapter three due to very low abundances, while the visiting flies that I considered as potential pollinators had no effect on pollen deposition (see Chapter 3). Much of the work linking canola pollination to SNL typically makes a 1-way link between the presence of SNL and visitation by wild foragers, framing this relationship as the provision of ecosystem services (Stanley et al., 2013). This relationship does not operate in only one direction, as canola crops

feed back into populations of wild insects surrounding the field, with most work indicating that canola causes a lagged increase in bee abundance during the next year, at least for non-*Bombus* species (Westphal et al., 2009; Holzschuh et al., 2016; Dainese et al., 2018). MFCs also have the potential to lure pollinators away from neighbouring SNL, diluting pollinator abundance (Holzschuh et al., 2011; Diekötter et al., 2010). However, I found that this influence was far less strong, as canola had almost no effect on abundance of individual wild bee species present in our traps, nor on overall wild bee abundance as a whole. This suggests that any relation between canola and the wild bee community appears to be largely one-way (at least in our study area, which plants exclusively spring canola), with no apparent pollinator dilution for solitary bees. However, blue-vane traps are known to attract certain subsets of the total pollinator population (Joshi et al., 2015), so it may be that eusocial bees, which I did not consider in my study, are more affected by canola bloom than solitary bees (Galpern et al., 2017).

The effect of landscape composition on pollinator abundances is usually dealt with at the scale of community abundance or diversity (Weiner et al., 2014; Sutter et al., 2017) or focuses on a single species (Dainese et al., 2018). This can be useful, but obscures responses of species *within* the community, as there are often large differences in the effect of landscape composition based on species' traits, such as body-size or nesting habitat (Westphal et al., 2006; Retzlaff, 2018; Diekötter et al., 2014; Hall et al., 2019). For example, I found that SNL caused no overall changes in total wild bee abundance in 2015, but for some species it had strongly positive (*Anthophora occidentalis*, *Lasioglossum colatum*) or negative effects (*Andrena thaspii*, *Halictus rubicundus*). However, this effect of SNL did not seem to be based on nesting or feeding traits, since most of the abundant species were ground nesting, and the direction of effects of SNL did not seem to be related to floral specialization. This points to the category of “semi-natural land” being too coarse of a measure of habitat and forage availability, and that other landscape features (soil type, slope, aspect, bare ground) may be more important. Secondly, pollinator populations appear to be largely stable, as the

best predictor of abundance (random effect intercept) in 2016 was abundance in 2015, and the relationship was roughly 1:1 (Turchin and Taylor, 1992), at least for these two years' of data. Since this inference was accomplished using a comparison of the random effects terms, this stability could be described more as “rank stability” rather than absolute stability, as I used yearly intercept terms to account for *overall* changes in abundance for each year. Finally, canola bloom had no overall effect on wild bee abundance, and had negative effects on only a few species (*Anthophora occidentalis*, *Hylaeus* spp), neither of which have been recorded visiting canola, indicating that canola availability does not seem to increase wild bee populations in solitary bees (similar to Galpern et al., 2017). This lack of influence of canola could be related to the emergence phenology of the pollinators not overlapping with the canola, but it is more likely that the regulation of bee populations is not primarily limited by food, but by nest site availability or parasitism (Michener, 1969; Soucy, 2002; Dainese et al., 2018), contrary to the findings of Roulston and Goodell (2011).

5.3 Future work

Chapter two built and tested a simulation model of central-place foraging that is more complete than other foraging models, but several additions are possible given the framework that I laid out. First, I used the random-visitation model of Possingham (1988) to describe how visitation related to nectar standing crop, and briefly explored how nearest-neighbour foraging would change its predictions (see Chapter two, Appendix), but several other avenues are possible. In particular, foragers performing area-restricted search (Pyke, 1978a; Keasar et al., 1996) or traplining (Thomson et al., 1982, 1987) in flower patches would experience different levels of costs and rewards. Visitation rates could also be tied to an arrival model, making it possible to infer likelihoods of visitation given other parameters, rather than dealing in average visits per hour. However, the most important addition to my model would be incorporating game theory predictions from the IFD (Křivan et al., 2008) to model how

multiple aggregations should compete with each other, as well as incorporating interference competition. This will be able to offer a more complete model of how aggregations value patches at distance (Ydenberg et al., 1986), and how the location of one aggregation can alter the performance of another. Finally, it would be relatively simple to test how well my visitation model relates to honey production in a given foraging landscape, and would provide bee keepers with a direct estimate of potential benefits in a given landscape.

Chapter three models visitation, pollination, and seed yield in commodity and seed canola, and the same SEM could be used to simulate novel arrangement of leafcutter shelters in a field, and how this relates to yield. It would also be interesting to use the game theory model described above to test how leafcutters and honey bees compete with each other in seed fields, with the aim of optimizing seed yield given a fixed set of costs. Finally, while honey bee foragers allowed several simplifying assumptions, a more complete model of leafcutter foraging behaviour, using distance-based foraging with nectar, pollen, and leaf material would have both material and theoretical benefits.

Chapter four investigated how canola and SNL influenced wild solitary bee abundance, but one of the main results was that SNL appears to be too coarse a measure of forage and nest site availability. Future work should investigate SNL at a finer scale, breaking down landscape composition into finer categories (grassland, wetland, forest, etc), and could also use a functional data analysis approach to landscape composition, rather than simply picking a single landscape radius (Yen et al., 2014; Kremen et al., 2019). This would yield information about relevant landscape components, as well as information about the spatial grain at which a given bee species responds to its environment. It would also be beneficial to locate aggregations in the field, and relate smaller measures of nest site and floral availability, as well as competitors, directly at the source of the wild bees, rather than using trapping data. Finally, the multi-aggregation model described above could test how wild bees compete with honey bees that use the same foraging plants. I suspect that solitary bees have similar levels of aggressive behaviour towards honey bees foraging near their aggregation that leafcutter

bees do, but this has not been tested.

The similarities between agriculture and ecology (agro-ecology) have been recognized since the 1930s (Wezel and Soldat, 2009), as they are both interested in very similar problems. Agriculture can be thought of as a type of applied ecology, as farmers manage nutrient flows in and out of plant and animal systems, mitigate pest populations, and regulate plant and herbivore densities in order to sell their produce within the context of fluctuating global markets. Similarly, ecology can be thought of as a variety of “natural agriculture”, where researchers study flows of energy and nutrients between trophic levels, behavioural strategies of organisms, and interactions within groups or communities of organisms, all within the context of their biogeography and evolutionary history. Historically, many of the research methods used in ecology are derived from methods used in agriculture or silviculture (split-plot methods, analysis of variance). However, they are often treated as separate disciplines, as divisions between “fundamental” and “applied” science have historically plagued the fields (Levins, 1973).

This continued (somewhat artificial) division between fundamental and applied science still exists between ecology and agronomy, to the detriment to both fields. Ecology has many conceptual tools to offer to agriculture, from the individual level (foraging theory, plant competition, natural selection) to the community level (population dynamics, productivity-diversity relationships, island biogeography). Similarly, agronomy has much to offer to the field of ecology. Agricultural land can be considered the world’s largest biome, as it occupies one-third of the global ice-free area (Ramankutty et al., 2018), and accounts for roughly one-third of the global gross domestic product (World Bank, 2018). Given the huge amount of interest in improving production, and the relative simplicity of agricultural landscapes (in North America and Europe), this presents a wealth of opportunities for testing fundamental ecological theories that usually require simulation or microcosm experiments.

This partnership will require cooperation from both parties (Loucks, 1977). Agronomists must realize that as systems get more and more complex, or novel climates appear, historical

practices or “rules of thumb” may no longer work, meaning that they will have to increasingly adopt methods from ecology to predict how their systems will operate under novel conditions. Ecologists must also realize that these methods must ultimately be predictive in nature, not simply descriptive, as Harper (1974) noted in the first editorial of *Agro-Ecosystems*: “A strong science is a predictive science, and the strength of a science of agro-ecosystems must be proved by its development to a stage at which it becomes possible to predict interactions between and within ecosystems”. Farmers and agronomists require working solutions to problems, as their livelihood and cultural systems depend on these solutions (Altieri, 1996). Human populations will reach 10 billion by 2050 (Ramankutty et al., 2018), and will be faced with climate-driven yield declines of 17% during the same period of time (Nelson et al., 2014); this will require us to simultaneously increase agricultural productivity, while managing increased intensities of droughts and storms (Stocker et al., 2013). It will require a cooperative effort between agronomists, ecologists, and policy makers in order to help preserve biodiversity and decrease human inequality and suffering in the face of the effects of global climate change, and agro-ecologists are uniquely positioned to help in this effort.

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Appendix A: Supplementary materials for Chapter 2

Visitation and nectar standing crop within a patch

For visitation within a patch, the model of Possingham (1988) assumes independent, random visitation of flowers within a patch, which is different from area-restricted foraging that bees use while moving between inflorescences (Pyke, 1978a; Heinrich, 1979). To test this assumption, I modeled nearest-neighbour foraging, with the following assumptions: 1) Upon arriving at a patch, a forager randomly selects a flower to visit, 2) after visiting the flower, the forager chooses the nearest flower for the next visit, and 3) that the forager remembers and avoids flowers that it has visited within a foraging trip. While actual bee foraging behaviour is different (Reynolds and Rhodes, 2009), this local movement model is likely closer to their actual foraging behaviour than completely random visitation, where each flower in a patch is equally likely to be chosen next. I ran a simulation of randomly and nearest-neighbour foraging across a range of flower visitation rates, each using 500 randomly-generated patches of flowers. Nearest-neighbour foraging yielded nectar standing crops were similar to those of the random foraging model of Possingham (1988), except with high visitation rates (>10% of all flowers visited per hour), and few visits per forager (Figure S1). Since these differences caused small qualitative differences in my model, and further complicates the mathematics behind calculating S , I used random foraging for the remainder of the model.

Equation 6 in Possingham (1988) gives the equation for mean standing crop (μL) as a function of maximum nectar volume, visitation rate, and secretion rate:

$$\frac{\text{Maximum nectar}}{D_\lambda \times \text{Maximum nectar} + 1}, \text{ where } D_\lambda = \frac{\text{Visitation rate per flower}}{\text{Secretion rate}} \quad (\text{S1})$$

Using my terminology:

$$Sl = \frac{l}{D_\lambda l + 1} \quad (\text{S2})$$

However, visitation rate per flower is dependent on S , since it influences the amount of nectar gathered from each flower:

$$\begin{aligned}
\text{Visitation rate per flower} &= \frac{\text{Number of foragers} \times \text{Visits per forager}}{\text{Number of flowers} \times \text{Time per foraging bout}} \\
&= \frac{LN_{Frgr}}{N_{Flws}Sl\left(\frac{d(2L_{max}-L\beta)}{v(L_{max}-L\beta)} + \frac{L(Slp+h)}{Sl} + \frac{Lf}{Sl} + H\right)}, \\
D_\lambda &= \frac{LN_{Frgr}}{\mu N_{Flws}Sl\left(\frac{d(2L_{max}-L\beta)}{v(L_{max}-L\beta)} + \frac{L(Slp+h)}{Sl} + \frac{Lf}{Sl} + H\right)} \tag{S3}
\end{aligned}$$

Therefore, from Equation S2:

$$Sl = \frac{l}{\frac{LN_{Frgr}}{\mu N_{Flws}Sl\left(\frac{d(2L_{max}-L\beta)}{v(L_{max}-L\beta)} + \frac{L(Slp+h)}{Sl} + \frac{Lf}{Sl} + H\right)} + 1} \tag{S4}$$

Solving for S yields the following equation. This equation provides nectar standing crop

values close to those of random-foraging simulations (see Figure S1).

$$\begin{aligned}
S = & -(\text{sqrt}(((\mu^2 L^4 N_{Flws}^2 l^2 p^2 + (-2\mu L^4 N_{Flws} l^2 N_{Frgr} + 2\mu^2 H L^3 N_{Flws}^2 l^2 + \\
& (2\mu^2 L^4 N_{Flws}^2 h + 2\mu^2 L^4 N_{Flws}^2 f)l)p + L^4 l^2 N_{Frgr}^2 + \\
& ((2\mu L^4 N_{Flws} h + 2\mu L^4 N_{Flws} f)l - 2\mu H L^3 N_{Flws} l^2)N_{Frgr} + \mu^2 H^2 L^2 N_{Flws}^2 l^2 + \\
& (2\mu^2 H L^3 N_{Flws}^2 h + 2\mu^2 H L^3 N_{Flws}^2 f)l + \mu^2 L^4 N_{Flws}^2 h^2 + 2\mu^2 L^4 N_{Flws}^2 f h + \\
& \mu^2 L^4 N_{Flws}^2 f^2)v^2 + (2\mu^2 L^3 N_{Flws}^2 dl^2 p - 2\mu L^3 N_{Flws} dl^2 N_{Frgr} + \\
& 2\mu^2 H L^2 N_{Flws}^2 dl^2 + (2\mu^2 L^3 N_{Flws}^2 dh + 2\mu^2 L^3 N_{Flws}^2 df)l)v + \mu^2 L^2 N_{Flws}^2 d^2 l^2)\beta^2 + \\
& ((-2\mu^2 L^3 L_{max} N_{Flws}^2 l^2 p^2 + (4\mu L^3 L_{max} N_{Flws} l^2 N_{Frgr} - 4\mu^2 H L^2 L_{max} N_{Flws}^2 l^2 + \\
& (-4\mu^2 L^3 L_{max} N_{Flws}^2 h - 4\mu^2 L^3 L_{max} N_{Flws}^2 f)l)p - 2L^3 L_{max} l^2 N_{Frgr}^2 + \\
& (4\mu H L^2 L_{max} N_{Flws} l^2 + (-4\mu L^3 L_{max} N_{Flws} h - 4\mu L^3 L_{max} N_{Flws} f)l)N_{Frgr} - \\
& 2\mu^2 H^2 L L_{max} N_{Flws}^2 l^2 + (-4\mu^2 H L^2 L_{max} N_{Flws}^2 h - 4\mu^2 H L^2 L_{max} N_{Flws}^2 f)l - \\
& 2\mu^2 L^3 L_{max} N_{Flws}^2 h^2 - 4\mu^2 L^3 L_{max} N_{Flws}^2 f h - 2\mu^2 L^3 L_{max} N_{Flws}^2 f^2)v^2 + (-6\mu^2 L^2 L_{max} N_{Flws}^2 dl^2 p + \\
& 6\mu L^2 L_{max} N_{Flws} dl^2 N_{Frgr} - 6\mu^2 H L L_{max} N_{Flws}^2 dl^2 + (-6\mu^2 L^2 L_{max} N_{Flws}^2 dh - \\
& 6\mu^2 L^2 L_{max} N_{Flws}^2 df)l)v - 4\mu^2 L L_{max} N_{Flws}^2 d^2 l^2)\beta + (\mu^2 L^2 L_{max} N_{Flws}^2 l^2 p^2 + \\
& (-2\mu L^2 L_{max} N_{Flws} l^2 N_{Frgr} + 2\mu^2 H L L_{max}^2 N_{Flws}^2 l^2 + (2\mu^2 L^2 L_{max}^2 N_{Flws}^2 h + \\
& 2\mu^2 L^2 L_{max}^2 N_{Flws}^2 f)l)p + L^2 L_{max}^2 l^2 N_{Frgr}^2 + ((2\mu L^2 L_{max}^2 N_{Flws} h + 2\mu L^2 L_{max}^2 N_{Flws} f)l - \\
& 2\mu H L L_{max}^2 N_{Flws} l^2)N_{Frgr} + \mu^2 H^2 L_{max}^2 N_{Flws}^2 l^2 + (2\mu^2 H L L_{max}^2 N_{Flws}^2 h + \\
& 2\mu^2 H L L_{max}^2 N_{Flws}^2 f)l + \mu^2 L^2 L_{max}^2 N_{Flws}^2 h^2 + 2\mu^2 L^2 L_{max}^2 N_{Flws}^2 f h + \mu^2 L^2 L_{max}^2 N_{Flws}^2 f^2)v^2 + \\
& (4\mu^2 L L_{max}^2 N_{Flws}^2 dl^2 p - 4\mu L L_{max}^2 N_{Flws} dl^2 N_{Frgr} + 4\mu^2 H L_{max}^2 N_{Flws}^2 dl^2 + (4\mu^2 L L_{max}^2 N_{Flws}^2 dh + \\
& 4\mu^2 L L_{max}^2 N_{Flws}^2 df)l)v + 4\mu^2 L_{max}^2 N_{Flws}^2 d^2 l^2) + ((-\mu L^2 N_{Flws} l p + L^2 l N_{Frgr} - \mu H L N_{Flws} l + \\
& \mu L^2 N_{Flws} h + \mu L^2 N_{Flws} f)v - \mu L N_{Flws} dl)\beta + (\mu L L_{max} N_{Flws} l p - L L_{max} l N_{Frgr} + \\
& \mu H L_{max} N_{Flws} l - \mu L L_{max} N_{Flws} h - \mu L L_{max} N_{Flws} f)v + 2\mu L_{max} N_{Flws} dl)/ \\
& (((2\mu L^2 N_{Flws} l p + 2\mu H L N_{Flws} l)v + 2\mu L N_{Flws} dl)\beta + (-2\mu L L_{max} N_{Flws} l p - \\
& 2\mu H L_{max} N_{Flws} l)v - 4\mu L_{max} N_{Flws} dl)
\end{aligned} \tag{S5}$$

Figures and Tables

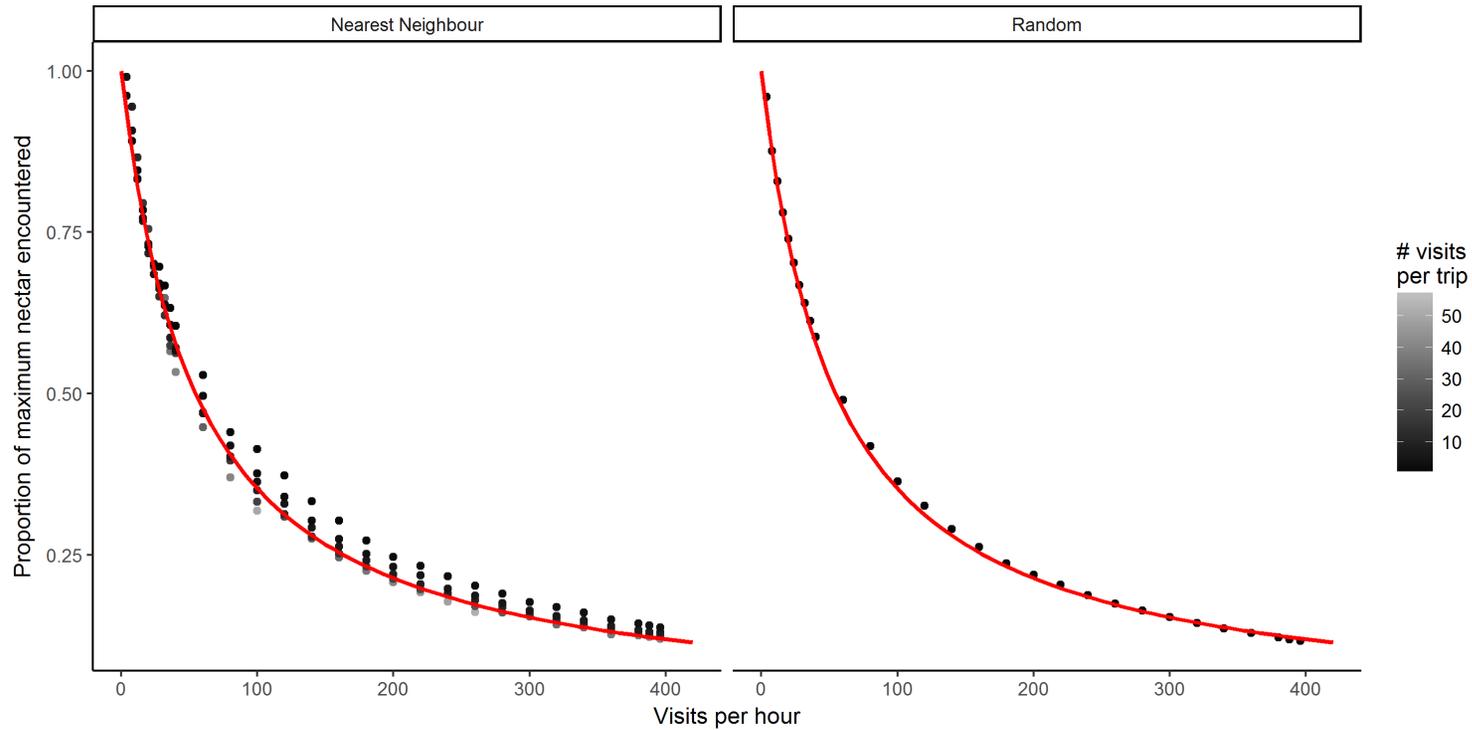


Figure S1: Results from foraging simulation using nearest-neighbour foraging principles, as well as random foraging. Red line shows results from equilibrium nectar concentration from Possingham (1988). Random foraging was closest to predictions from Possingham (1988), while nearest-neighbour foraging approached random foraging behaviour, but only at high numbers of visits per bout. Each point is the mean realized nectar from 500 randomly-generated patches of 400 flowers, after letting the simulation run 400 times for each generated patch.

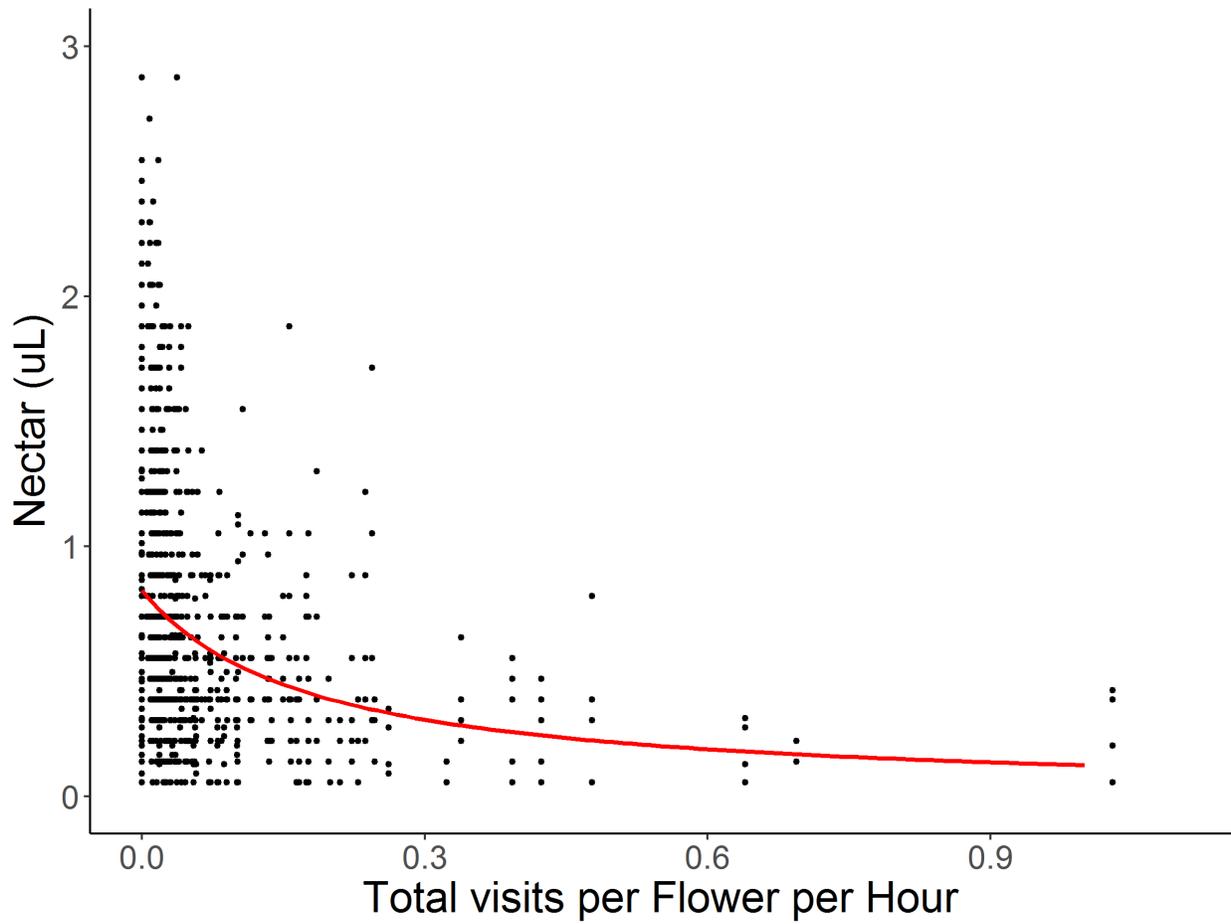


Figure S2: Observed nectar standing crop as a function of total visits per hour per flower. The red line is the nonlinear best fit using Equation 6 from Possingham (1988). Maximum nectar standing crop was $0.82 \mu L$ and production rate was $0.14 \mu L/hr$.

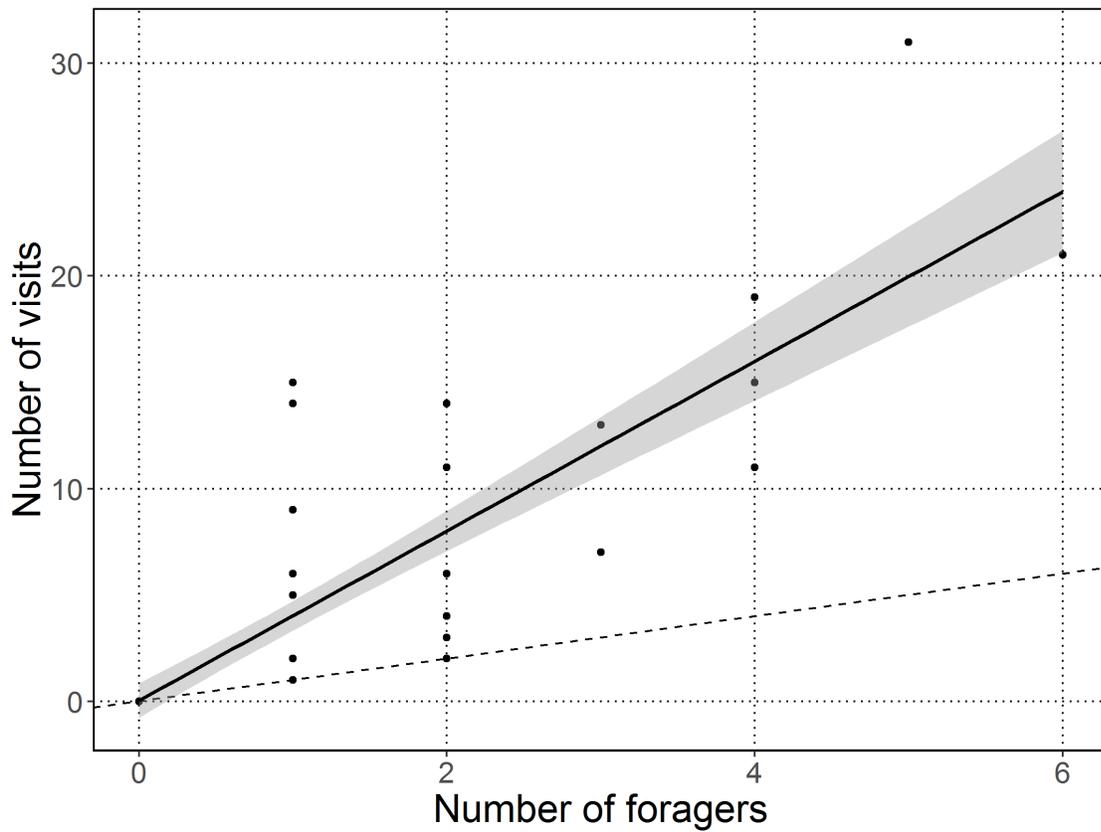


Figure S3: Visits per forager to 1 m² patches of canola observed in 2015. Dashed line represents each forager making a single visit (1:1 line). Slope of fitted line is 4.0 (SE: ± 0.37), indicating 4 visits per forager.

Table S1: Nectar production values for 20 most-abundant species from Galpern et al. (unpublished, <http://ecologics.ucalgary.ca/>), accounting for 71.6% of floral community. Proportion indicates the proportion of the floral community that made up of that species. Values recorded in literature were used for the same species, but where no records existed, closely related taxa were used.

Species	Proportion (%)	Nectar capacity (μL)	Production rate ($\mu\text{L/hr}$)	Energy value ($\text{J}/\mu\text{L}$)	Reference
<i>Cirsium arvense</i>	9.4	0.35	0.18	10.33	Hicks et al 2016, Somme et al. 2015 (<i>C. palustre</i>)
<i>Medicago sativa</i>	6.9	0.34	0.11	7.44	Nye and Pedersen 1962, Palmer-Jones and Forster 1965, Teuber et al 1980
<i>Tragopogon dubius</i>	5.9	7.4	3.7	11.62	Used <i>Taraxacum</i>
<i>Taraxacum officinale</i>	4.9	7.4	0.31	11.62	Hicks et al 2016, Tzabo 1984
<i>Solidago canadensis</i>	4.7	0	0	0	Heinrich 1971
<i>Crepis tectorum</i>	4.4	0	0	0	Hicks et al 2016 (<i>C. capillaris</i>)
<i>Eurybia conspicua</i>	4.3	0.041	0.020	10.33	Used <i>Aster</i>
<i>Achillea millefolium</i>	4.2	0.051	0.025	10.33	Hicks et al 2016
<i>Trifolium hybridum</i>	3.3	9.6	4.8	5.68	Somme et al 2015 (<i>T. pratense</i>), Rusterholz and Erhardt 1998
<i>Symphoricarpos albus</i>	2.8	2.7	1.35	6.55	Southwick et al 1981 (<i>Lonicera maackii</i>)
<i>Campanula rotundifolia</i>	2.6	0.03	0.015	7.91	Cresswell and Robertson 1994
<i>Melilotus</i> sp.	2.3	4	8	5.68	Stout and Goulson 2001 (<i>Melilotus officinalis</i>), Hirsch et al. 2002
<i>Thlaspi arvense</i>	2.2	0.08	0.014	12.42	Used 10% of value of <i>B. napus</i>
<i>Hieracium umbellatum</i>	2.2	7.4	3.7	11.62	Hicks et al 2016 (<i>Taraxacum</i>)
<i>Geranium viscosissimum</i>	2.1	0.057	0.029	5.68	Hicks et al 2016 (<i>G. molle</i>)
<i>Brassica</i> sp.	2.1	0.8	0.14	12.42	Used <i>Brassica napus</i>
<i>Symphyotrichum ericoides</i>	2.1	0.04	0.02	10.33	Heinrich 1976 (<i>Aster</i>)
<i>Brassica napus</i>	2.0	0.8	0.14	12.42	This data
<i>Rosa acicularis</i>	1.8	0.5	0.25	9.38	Southwick et al 1981 (<i>R. spinosissima</i>)
<i>Trifolium pratense</i>	1.3	9.6	4.8	5.68	Szabo and Najda 1985

Table S2: Nectar production values used for land cover classes surrounding sites. Flight time refers to time required to fly between flowers (inferred from canola visitation). Ditch values were substituted for the urban cover class, and grassland values for the shrubland cover class.

Cover class	Nectar capacity (μL)	Production rate ($\mu\text{L}/\text{hr}$)	Energy value ($\text{J}/\mu\text{L}$)	Flowers per m^2	Flight time (s)
Bare	0.00	0.00	0.00	0	Inf
Canola	0.87	0.15	12.42	480	0.86
Cereals	0.00	0.00	0.00	0	Inf
Forest	3.55	1.81	7.6	1	18.89
Grassland	1.62	0.849	7.78	2.48	11.99
Other agriculture	0.00	0.00	0.00	0	Inf
Pasture	2.12	0.889	8.09	7.15	7.06
Pulses	0.00	0.00	0.00	0	Inf
Shrubland	1.62	0.849	7.78	2.48	11.99
Urban	2.02	0.00	8.03	8	6.67
Water	0.00	0.00	0.00	0	Inf
Wetland	2.52	1.16	8.38	5.16	8.31
Ditch	1.92	1.21	8.11	6.23	7.56

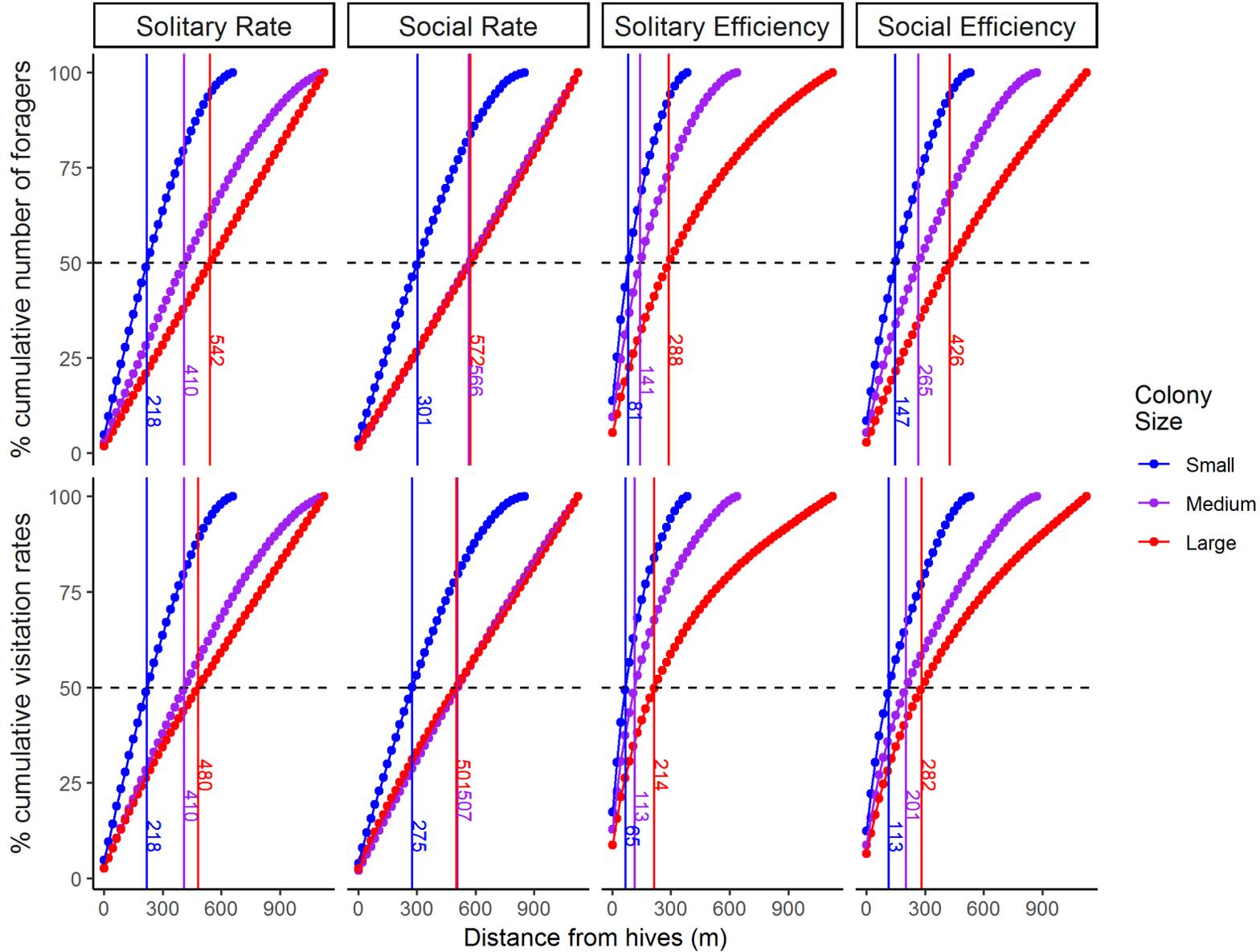


Figure S4: Cumulative distribution of forager numbers (upper) and visits per hour (lower) from the simple model. Dashed black line indicates 50% of distribution. Coloured lines show the distance at which 50% of forager numbers or visitation occurred before.

Table S3: Number of nectar foragers using non-canola resources within each full model simulation. Upper and Lower represent the 95% quantiles across all 28 sites.

Sociality	Currency	Size	Median	Upper	Lower
Social	Efficiency	Large	0.71	7.27	0.08
Social	Efficiency	Medium	0.21	4.82	0.03
Social	Efficiency	Small	0.10	2.51	0.00
Social	Net Rate	Large	0.00	4.50	0.00
Social	Net Rate	Medium	0.00	0.00	0.00
Social	Net Rate	Small	0.00	0.00	0.00
Solitary	Efficiency	Large	0.30	4.36	0.05
Solitary	Efficiency	Medium	0.10	2.76	0.00
Solitary	Efficiency	Small	0.00	1.49	0.00
Solitary	Net Rate	Large	0.00	0.00	0.00
Solitary	Net Rate	Medium	0.00	0.00	0.00
Solitary	Net Rate	Small	0.00	0.00	0.00

Table S4: Number of visiting insects observed for both years and locations, arranged by abundance, and total hours spent during observation.

Group	Lethbridge		Grande Prairie		Total
	2014	2015	2014	2015	
Honey bee (<i>Apis mellifera</i>)	150	42	61	217	470
Muscid fly (Muscidae, Anthomyiidae)	144	36	20	22	222
Hover fly (Syrphidae)	60	6	17	11	94
Other bee (<i>Andrena</i> , <i>Halictus</i> spp.)	32	4	0	11	47
Butterfly	4	0	12	0	16
Bumble bee (<i>Bombus</i> spp.)	0	0	12	13	25
Leafcutter bee (<i>Megachile</i> spp.)	2	2	0	0	4
Total Visits	17	60	11	6	878
<i>Total Time (hrs)</i>	<i>15.8</i>	<i>9.3</i>	<i>11.7</i>	<i>10.0</i>	<i>46.8</i>

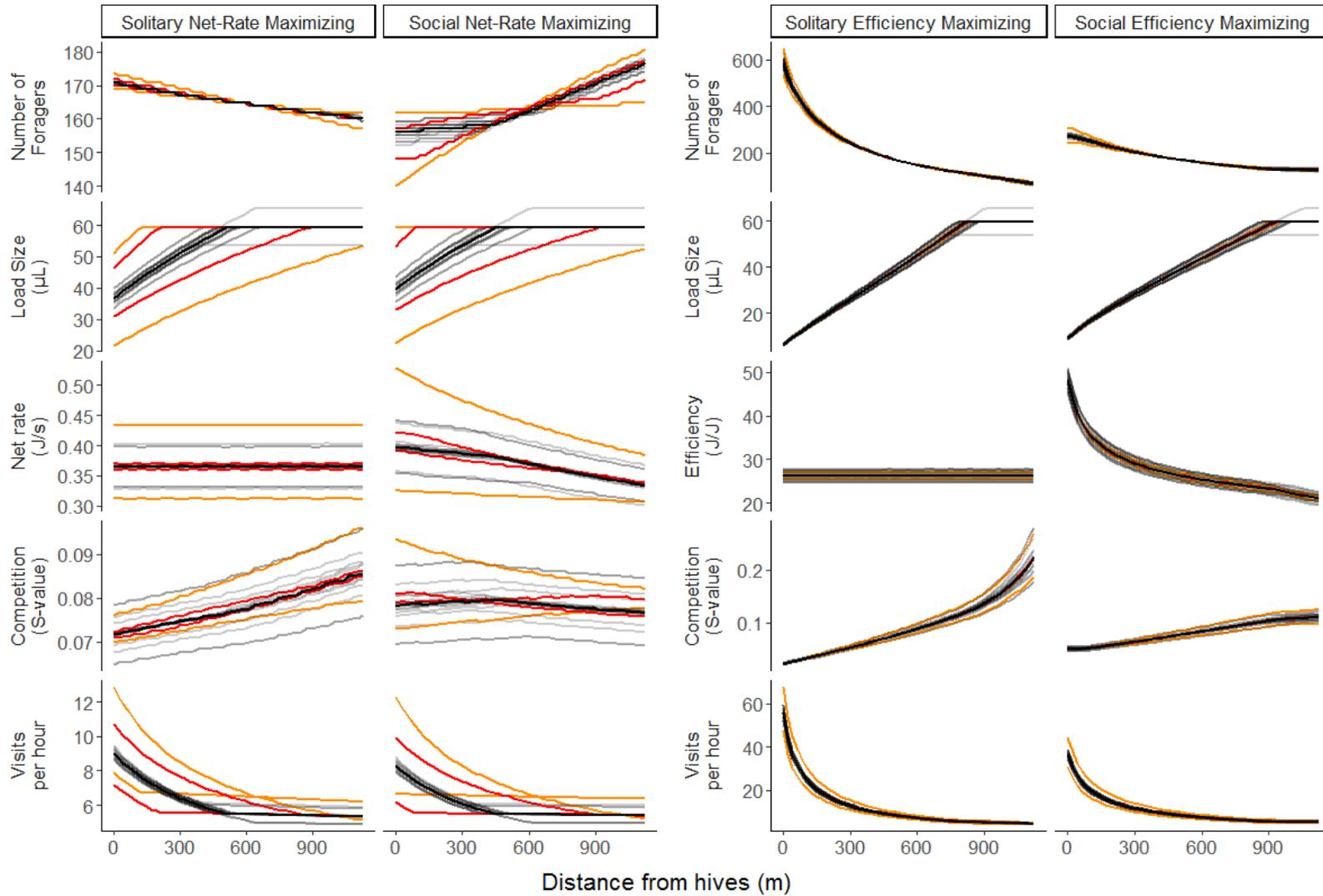


Figure S5: Variation in simulation output values from sensitivity analysis, using both candidate currencies and socialities. Only large-sized colonies were used for the simulations, and all parameters were varied by $\pm 10\%$ from original values. Black line indicates results from original simulation, while coloured lines indicate most influential parameters (red: Loaded flight speed (v_l), orange: Maximum nectar standing crop (l). Less-influential parameters are shown in grey (see Table 2.3).

Appendix B: Supplementary materials for Chapter 3

Taxon	Commodity fields		Seed fields	
	Visits	%	Visits	%
Honey bee	470	53.5	4850	77.1
Fly	222	25.3	74	0.878
Hover fly	94	10.7	151	1.79
Other bee	47	5.35	30	0.356
Bumble bee	25	2.85	0	0
Butterfly	16	1.82	0	0
Leafcutter bee	4	0.456	1675	19.9

Table S5: Number of flower visitors recorded over a total of 44.8 hours of observation in commodity fields (2014 and 2015), and 46.9 hours of observation in the seed fields (2015 and 2016). “Fly” refers to larger calyptrate muscoid flies (families Muscidae, Anthomyiidae, Caliphoridae), while “Hover fly” refers to Syrphid flies. “Other bee” included Halictid and Andrenid bees, while “Bumble bee” was *Bombus* spp. “Butterfly” refers to all visiting Lepidopterans, mostly Pierids.

Plant Density \sim Year * Irrigation + Distance + Site + (1|Field), distribution = log-normal

Plant Size \sim Plant Density + Distance + Site + Irrigation + Year + (1|Field/Plot),
distribution = log-normal

Flower Density \sim Plant Size + Distance + (1|Field), distribution = square root-normal

Honey bee visits \sim offset(log(Time)) + Year * Site + Irrigation + Distance +
Hive Stocking + Flower Density + (1|Field), family = negative binomial

Pollen per Stigma \sim Honey bee visits + Distance + (1|Field/Plot), distribution = negative binomial

Fruit Set \sim Honey bee visits + Pollen + Plant Size + Plant Density + Irrigation +
Year + (1|Field), distribution = beta-binomial

Flowers per Plant \sim Plant Size + Fruit Set + Year + (1|Field), distribution = negative binomial

Seeds per Pod \sim Honey bee visits + Pollen + Plant Size + Year + (1|Field/Plant),
distribution = negative binomial

Weight per Seed \sim Honey bee visits + Pollen + Seeds per Pod + Plant Size + Irrigation +
Year + (1|Field/Plant), distribution = exponential-normal

Equation set S1: Formulas for commodity canola model using `lmer`-style R formulas.

Terms on right side of \sim indicate fixed effects, while terms in brackets indicate random effects (hierarchical intercepts), with Field/Plot indicating *Plot* is nested below *Field*. * indicates an interaction between fixed effects. *distribution* indicates the type of probability distribution function used to model each variable.

Plant Density \sim Edge Distance + (1|Field), distribution = log-normal

Plant Size \sim Edge Distance + Plant Density + (1|Field), distribution = log-normal

Flower Density \sim Plant Size + Bay Centre + Year + Edge Distance + (1|Field),
distribution = square root-normal

Leafcutter bee visits \sim offset(log(Time)) + Tent Distance + Bay Centre + Male Bay +
Tent Stocking * Edge Distance + Year + Bay Centre : Edge Distance +
(1|Field), family = negative binomial

Honey bee visits \sim offset(log(Time)) + Edge Distance + Tent Distance + Leafcutter bee visits +
Bay Centre + Flower Density + Male Bay + (1|Field),
family = zero-inflated negative binomial

Pollen per Stigma \sim Honey bee visits + Leafcutter bee visits + Bay Centre + Edge Distance +
Flower Density + (1|Field/Plot), family = negative binomial

Fruit Set \sim Pollen + Plant Size + Bay Centre + Edge Distance + Tent Distance +
Flower Density + (1|Field/Plot), family = beta-binomial

Flowers per Plant \sim Plant Size + Bay Centre + Fruit Set + (1|Field),
family = negative binomial

Seeds per Pod \sim Pollen + Plant Size + Bay Centre + Edge Distance + Flower Density +
Fruit Set + (1|Field/Plant), family = negative binomial

Weight per Seed \sim Pollen + Seeds per Pod + Plant Size + Year + Tent Distance +
Plant Density + Tent Stocking + (1|Field/Plot), family = exponential-normal

Equation set S2: Formulas for seed canola model using lmer-style R formulas. Terms on

right side of \sim indicate fixed effects, while terms in brackets indicate random effects (hierarchical intercepts), with Field/Plot indicating *Plot* is nested below *Field*. * indicates an interaction between fixed effects. *distribution* indicates the type of probability distribution function used to model each variable.

Dependent	Independent	Median	Lwr	Upr	mean	sd	z	overlap	pvalue
Plant density	Intercept	0.060	-0.081	0.197	0.058	0.071	0.822	TRUE	0.4108
Plant density	Year	0.059	-0.144	0.260	0.056	0.103	0.542	TRUE	0.5878
Plant density	Irrigation	0.255	-0.028	0.522	0.255	0.140	1.826	TRUE	0.0679
Plant density	Year:Irrigation	-0.491	-0.918	-0.077	-0.496	0.214	-2.322	FALSE	0.0202
Plant density	Distance	0.016	-0.003	0.034	0.016	0.009	1.681	TRUE	0.0927
Plant density	Site	-0.237	-0.429	-0.042	-0.237	0.099	-2.395	FALSE	0.0166
Plant density	Residual σ	0.309	0.281	0.341	0.309	0.016	19.872	-	-
Plant density	Field-level σ	0.327	0.260	0.413	0.331	0.039	8.543	-	-
Plant size	Intercept	-0.112	-0.308	0.099	-0.111	0.104	-1.075	TRUE	0.2823
Plant size	Plant density	-0.139	-0.315	0.020	-0.141	0.087	-1.617	TRUE	0.1059
Plant size	Distance	-0.006	-0.033	0.023	-0.006	0.015	-0.382	TRUE	0.7026
Plant size	Site	-0.021	-0.270	0.215	-0.021	0.123	-0.170	TRUE	0.8648
Plant size	Irrigation	0.102	-0.164	0.356	0.100	0.131	0.761	TRUE	0.4468
Plant size	Year	0.266	0.066	0.472	0.268	0.106	2.533	FALSE	0.0113
Plant size	Field-level σ	0.295	0.208	0.399	0.297	0.047	6.297	-	-
Plant size	Plot-level σ	0.347	0.276	0.419	0.347	0.036	9.595	-	-
Plant size	Residual σ	0.603	0.570	0.641	0.603	0.018	33.607	-	-
Flower density	Intercept	-0.077	-0.963	0.831	-0.079	0.457	-0.173	TRUE	0.8624

Flower density	Plant size	0.385	-0.843	1.678	0.399	0.645	0.618	TRUE	0.5364
Flower density	Distance	0.705	0.497	0.917	0.706	0.107	6.571	FALSE	<0.0001
Flower density	Residual σ	3.515	3.198	3.883	3.522	0.175	20.078	-	-
Flower density	Field-level σ	3.665	2.991	4.567	3.692	0.399	9.246	-	-
Hbee visitation	Intercept	-1.849	-2.893	-0.968	-1.878	0.493	-3.812	FALSE	0.0001
Hbee visitation	Year	-0.243	-1.274	0.758	-0.239	0.517	-0.462	TRUE	0.6438
Hbee visitation	Site	-0.618	-1.593	0.495	-0.605	0.533	-1.135	TRUE	0.2565
Hbee visitation	Year:Site	1.478	0.215	2.672	1.470	0.629	2.339	FALSE	0.0194
Hbee visitation	Irrigation	-1.619	-3.065	-0.402	-1.654	0.679	-2.434	FALSE	0.0149
Hbee visitation	Distance	-0.333	-0.517	-0.159	-0.335	0.091	-3.685	FALSE	0.0002
Hbee visitation	Hives	0.677	0.432	0.933	0.679	0.128	5.323	FALSE	<0.0001
Hbee visitation	Flower density	0.055	-0.031	0.139	0.055	0.043	1.269	TRUE	0.2044
Hbee visitation	Field-level σ	0.982	0.418	1.605	0.990	0.303	3.269	-	-
Hbee visitation	Field-level λ (skew)	2.208	1.050	4.703	2.374	0.969	2.450	-	-
Hbee visitation	Dispersion (NB ϕ)	0.342	0.231	0.508	0.350	0.073	4.818	-	-
Pollen count	Intercept	5.581	5.448	5.720	5.582	0.070	80.271	FALSE	<0.0001
Pollen count	Hbee visitation	-0.007	-0.079	0.068	-0.006	0.038	-0.147	TRUE	0.8828
Pollen count	Distance	-0.030	-0.063	0.002	-0.030	0.017	-1.824	TRUE	0.0681
Pollen count	Field-level σ	0.451	0.349	0.577	0.455	0.058	7.876	-	-

Pollen count	Plot-level σ	0.227	0.089	0.570	0.257	0.129	1.990	-	-
Pollen count	Dispersion (NB ϕ)	0.674	0.628	0.721	0.674	0.024	28.271	-	-
Flowers per plant	Intercept	5.070	5.025	5.116	5.070	0.023	220.033	FALSE	<0.0001
Flowers per plant	Plant size	0.945	0.924	0.964	0.945	0.010	92.436	FALSE	<0.0001
Flowers per plant	Fruit set	-0.162	-0.188	-0.137	-0.162	0.013	-12.512	FALSE	<0.0001
Flowers per plant	Year	-0.116	-0.175	-0.059	-0.117	0.030	-3.874	FALSE	0.0001
Flowers per plant	Field-level σ	0.561	0.366	0.794	0.567	0.109	5.180	-	-
Flowers per plant (dispersion)	Intercept	3.661	3.456	3.874	3.662	0.106	34.543	FALSE	<0.0001
Flowers per plant (dispersion)	Plant size	0.663	0.484	0.826	0.662	0.088	7.518	FALSE	<0.0001
Flowers per plant (dispersion)	Field-level σ	0.129	0.104	0.163	0.130	0.015	8.865	-	-
Fruit set	Intercept	1.038	0.928	1.149	1.038	0.056	18.518	FALSE	<0.0001
Fruit set	Hbee visitation	0.017	-0.022	0.056	0.017	0.020	0.875	TRUE	0.3815
Fruit set	Pollen	-0.155	-0.348	0.044	-0.154	0.098	-1.575	TRUE	0.1152
Fruit set	Plant Size	0.124	0.079	0.168	0.124	0.023	5.488	FALSE	<0.0001
Fruit set	Plant Density	-0.079	-0.182	0.023	-0.079	0.051	-1.534	TRUE	0.1250
Fruit set	Irrigation	0.031	-0.142	0.207	0.031	0.088	0.352	TRUE	0.7249
Fruit set	Year	-0.075	-0.228	0.079	-0.075	0.077	-0.976	TRUE	0.3292
Fruit set	Field-level σ	0.245	0.187	0.315	0.247	0.032	7.604	-	-
Fruit set (dispersion)	Intercept	3.450	3.240	3.672	3.449	0.109	31.586	FALSE	<0.0001

Fruit set (dispersion)	Plant size	0.303	0.099	0.502	0.303	0.103	2.956	FALSE	0.0031
Fruit set (dispersion)	Field-level σ	0.593	0.428	0.804	0.598	0.096	6.230	-	-
Seeds per pod	Intercept	3.073	3.038	3.108	3.073	0.018	174.969	FALSE	<0.0001
Seeds per pod	Hbee visitation	-0.006	-0.025	0.014	-0.006	0.010	-0.595	TRUE	0.5521
Seeds per pod	Pollen	-0.004	-0.074	0.069	-0.003	0.036	-0.075	TRUE	0.9404
Seeds per pod	Plant size	0.011	-0.010	0.031	0.010	0.010	1.004	TRUE	0.3153
Seeds per pod	Year	0.130	0.074	0.184	0.129	0.027	4.714	FALSE	<0.0001
Seeds per pod	Field-level σ	0.075	0.052	0.102	0.076	0.013	5.904	-	-
Seeds per pod	Plant-level σ	0.150	0.134	0.167	0.150	0.008	17.918	-	-
Seeds per pod	Dispersion (NB ϕ)	22.246	20.784	23.812	22.248	0.778	28.587	-	-
Weight per seed	Intercept	1.865	1.681	2.064	1.865	0.099	18.791	FALSE	<0.0001
Weight per seed	Hbee visitation	-0.036	-0.105	0.036	-0.034	0.036	-0.961	TRUE	0.3364
Weight per seed	Pollen	-0.080	-0.370	0.190	-0.082	0.144	-0.569	TRUE	0.5695
Weight per seed	Seeds per pod	0.013	0.009	0.017	0.013	0.002	6.061	FALSE	<0.0001
Weight per seed	Plant size	-0.015	-0.090	0.056	-0.015	0.037	-0.400	TRUE	0.6889
Weight per seed	Irrigation	-0.345	-0.645	-0.034	-0.341	0.155	-2.205	FALSE	0.0274
Weight per seed	Year	0.270	0.022	0.513	0.271	0.125	2.162	FALSE	0.0306
Weight per seed	Field-level σ	0.321	0.239	0.423	0.323	0.047	6.837	-	-
Weight per seed	Plant-level σ	0.551	0.508	0.600	0.552	0.023	23.600	-	-

Weight per seed	Residual σ	0.468	0.428	0.507	0.468	0.020	23.146	-	-
Weight per seed	Residual λ (skew)	1.709	1.572	1.867	1.712	0.076	22.411	-	-

Table S6: Coefficients from commodity model. Terms with a colon between them indicate interactions.

Dependent	Independent	Median	Lwr	Upr	mean	sd	z	overlap	pvalue
Plant density	Intercept	0.033	-0.095	0.160	0.033	0.064	0.518	TRUE	0.6046
Plant density	Hbee distance	0.055	0.033	0.074	0.054	0.010	5.234	FALSE	<0.0001
Plant density	Residual σ	0.274	0.247	0.306	0.275	0.015	18.358	-	-
Plant density	Field-level σ	0.360	0.283	0.475	0.366	0.050	7.291	-	-
Plant size	Intercept	0.032	-0.015	0.081	0.032	0.025	1.281	TRUE	0.2003
Plant size	Plant density	-0.780	-0.902	-0.667	-0.781	0.059	-13.198	FALSE	<0.0001
Plant size	Hbee distance	0.076	0.050	0.104	0.076	0.014	5.373	FALSE	<0.0001
Plant size	Residual σ	0.614	0.580	0.649	0.614	0.017	35.245	-	-
Flower density	Intercept	0.430	-0.661	1.609	0.441	0.577	0.766	TRUE	0.4440
Flower density	Plant size	0.901	-1.891	3.621	0.863	1.421	0.608	TRUE	0.5434
Flower density	Bay position	0.904	0.118	1.728	0.899	0.411	2.188	FALSE	0.0287
Flower density	Year	-2.696	-4.402	-0.888	-2.686	0.914	-2.939	FALSE	0.0033
Flower density	Hbee distance	1.228	0.941	1.495	1.224	0.141	8.666	FALSE	<0.0001
Flower density	Residual σ	5.067	4.785	5.376	5.071	0.154	32.992	-	-
Flower density	Field-level σ	3.334	2.647	4.286	3.375	0.415	8.131	-	-
Lbee visitation	Intercept	2.242	1.787	2.686	2.242	0.234	9.598	FALSE	<0.0001
Lbee visitation	Hbee distance	-0.282	-0.413	-0.156	-0.282	0.065	-4.362	FALSE	<0.0001
Lbee visitation	Lbee distance	-0.839	-0.980	-0.696	-0.838	0.074	-11.353	FALSE	<0.0001

Lbee visitation	Bay position	-0.547	-1.065	-0.024	-0.549	0.265	-2.072	FALSE	0.0383
Lbee visitation	Male bay	-0.052	-0.332	0.237	-0.051	0.142	-0.357	TRUE	0.7211
Lbee visitation	Stocking	0.044	-0.584	0.678	0.044	0.329	0.134	TRUE	0.8936
Lbee visitation	Year	-0.575	-1.213	0.045	-0.574	0.317	-1.810	TRUE	0.0703
Lbee visitation	Bay position:Hbee distance	-0.192	-0.410	0.030	-0.191	0.113	-1.696	TRUE	0.0900
Lbee visitation	Stocking:Hbee distance	0.225	0.029	0.435	0.225	0.102	2.191	FALSE	0.0284
Lbee visitation	Flower density	0.051	0.023	0.080	0.051	0.014	3.572	FALSE	0.0004
Lbee visitation	Field-level σ	0.973	0.721	1.305	0.987	0.152	6.508	-	-
Lbee visitation	Dispersion (NB ϕ)	0.406	0.352	0.467	0.407	0.029	13.953	-	-
Hbee visitation	Intercept	2.992	2.724	3.279	2.995	0.139	21.612	FALSE	<0.0001
Hbee visitation	Hbee distance	-0.130	-0.234	-0.031	-0.130	0.053	-2.469	FALSE	0.0136
Hbee visitation	Lbee distance	0.350	0.176	0.523	0.349	0.089	3.934	FALSE	0.0001
Hbee visitation	Lbee:Hbee distance	0.071	-0.047	0.195	0.072	0.064	1.131	TRUE	0.2581
Hbee visitation	Lbee visitation	-0.061	-0.165	0.042	-0.062	0.052	-1.184	TRUE	0.2365
Hbee visitation	Bay position	0.564	0.149	0.974	0.564	0.213	2.647	FALSE	0.0081
Hbee visitation	Flower density	0.001	-0.021	0.024	0.001	0.012	0.110	TRUE	0.9121
Hbee visitation	Male bay	0.139	-0.147	0.418	0.139	0.141	0.987	TRUE	0.3238
Hbee visitation	Dispersion (NB ϕ)	0.608	0.473	0.763	0.611	0.074	8.225	-	-
Hbee visitation	Dispersion (ZI θ)	0.331	0.266	0.388	0.330	0.031	10.820	-	-

Pollen deposition	Intercept	2.389	2.045	2.747	2.390	0.180	13.248	FALSE	<0.0001
Pollen deposition	Hbee visitation	0.034	-0.034	0.102	0.034	0.035	0.979	TRUE	0.3275
Pollen deposition	Lbee visitation	0.172	0.064	0.277	0.172	0.054	3.171	FALSE	0.0015
Pollen deposition	Bay position	-0.548	-0.782	-0.309	-0.547	0.121	-4.510	FALSE	<0.0001
Pollen deposition	Hbee distance	-0.157	-0.226	-0.086	-0.157	0.036	-4.403	FALSE	<0.0001
Pollen deposition	Flower density	-0.017	-0.055	0.024	-0.017	0.020	-0.830	TRUE	0.4067
Pollen deposition	Field-level σ	0.839	0.629	1.131	0.850	0.126	6.733	-	-
Pollen deposition	Plot-level σ	0.644	0.525	0.772	0.646	0.064	10.117	-	-
Pollen deposition	Dispersion (NB ϕ)	0.816	0.737	0.897	0.817	0.041	19.724	-	-
Flowers per plant	Intercept	5.912	5.880	5.943	5.912	0.016	371.493	FALSE	<0.0001
Flowers per plant	Plant size	0.930	0.910	0.952	0.930	0.011	82.693	FALSE	<0.0001
Flowers per plant	Bay center	0.086	0.055	0.122	0.085	0.018	4.636	FALSE	<0.0001
Flowers per plant	Fruit set	-0.149	-0.172	-0.126	-0.149	0.012	-12.148	FALSE	<0.0001
Flowers per plant	Field-level σ	0.068	0.043	0.100	0.069	0.015	4.750	-	-
Flowers per plant (dispersion)	Intercept	4.044	3.630	4.401	4.035	0.197	20.500	FALSE	<0.0001
Flowers per plant (dispersion)	Plant size	0.294	0.018	0.576	0.289	0.137	2.114	FALSE	0.0345
Flowers per plant (dispersion)	Field-level σ	0.759	0.524	1.140	0.774	0.154	5.013	-	-
Fruit set	Intercept	0.747	0.587	0.910	0.747	0.081	9.259	FALSE	<0.0001
Fruit set	Pollen	0.148	0.057	0.245	0.148	0.048	3.095	FALSE	0.0020

Fruit set	Plant size	0.198	0.179	0.217	0.198	0.010	19.887	FALSE	<0.0001
Fruit set	Bay position	-0.236	-0.349	-0.120	-0.235	0.059	-3.961	FALSE	0.0001
Fruit set	Hbee distance	-0.107	-0.145	-0.066	-0.107	0.020	-5.344	FALSE	<0.0001
Fruit set	Lbee distance	-0.201	-0.328	-0.080	-0.202	0.064	-3.159	FALSE	0.0016
Fruit set	Flower density	-0.009	-0.026	0.008	-0.009	0.009	-1.065	TRUE	0.2870
Fruit set	Field-level σ	0.367	0.276	0.485	0.371	0.054	6.913	-	-
Fruit set	Plot-level σ	0.348	0.309	0.393	0.349	0.021	16.274	-	-
Seeds per pod	Intercept	2.834	2.736	2.930	2.835	0.049	57.527	FALSE	<0.0001
Seeds per pod	Pollen	0.061	0.010	0.117	0.062	0.027	2.279	FALSE	0.0226
Seeds per pod	Plant size	0.189	0.123	0.253	0.188	0.033	5.648	FALSE	<0.0001
Seeds per pod	Bay center	-0.135	-0.190	-0.075	-0.134	0.029	-4.597	FALSE	<0.0001
Seeds per pod	Hbee distance	-0.008	-0.025	0.010	-0.008	0.009	-0.897	TRUE	0.3696
Seeds per pod	Flower density	-0.005	-0.013	0.002	-0.005	0.004	-1.370	TRUE	0.1708
Seeds per pod	Fruit set	0.136	0.091	0.180	0.136	0.023	6.030	FALSE	<0.0001
Seeds per pod	Field-level σ	0.117	0.083	0.162	0.118	0.020	5.831	-	-
Seeds per pod	Plant-level σ	0.089	0.019	0.141	0.088	0.029	2.997	-	-
Seeds per pod	Dispersion (NB ϕ)	3.459	3.214	3.723	3.462	0.129	26.757	-	-
Weight per seed	Intercept	3.556	3.321	3.813	3.564	0.127	28.130	FALSE	<0.0001
Weight per seed	Pollen	0.069	-0.021	0.168	0.072	0.050	1.452	TRUE	0.1464

Weight per seed	Seeds per pod	-0.036	-0.041	-0.031	-0.036	0.002	-15.019	FALSE	<0.0001
Weight per seed	Plant size	0.260	0.150	0.362	0.260	0.056	4.640	FALSE	<0.0001
Weight per seed	Year	0.463	0.230	0.723	0.471	0.121	3.906	FALSE	0.0001
Weight per seed	Lbee distance	0.090	-0.046	0.223	0.090	0.067	1.347	TRUE	0.1779
Weight per seed	Plant density	0.475	0.258	0.658	0.472	0.103	4.583	FALSE	<0.0001
Weight per seed	Lbee stocking	0.231	0.003	0.458	0.235	0.121	1.948	FALSE	0.0514
Weight per seed	Plant density: Plant size	-0.204	-0.421	0.010	-0.203	0.109	-1.866	TRUE	0.0620
Weight per seed	Field-level σ	0.303	0.214	0.425	0.309	0.054	5.684	-	-
Weight per seed	Plot-level σ	0.645	0.593	0.716	0.648	0.032	20.510	-	-
Weight per seed	Residual σ	1.032	0.977	1.069	1.031	0.023	45.490	-	-
Weight per seed	Dispersion (Exp λ)	4.927	2.852	9.739	5.364	1.869	2.869	-	-

Table S7: Coefficients from seed field model. Terms with a colon between them indicate interactions. Shorthand terms: “Lbee” = “Leafcutter bee”, “Hbee” = “Honey bee”.

Appendix C: Supplementary materials for Chapter 4

Model for canola bloom in year y at site i at pass j

$$\mu Bloom_{y,j} = 100 \times \exp\left(-\frac{(\mathbf{end}_{y,i,j} - \mu Date_y)^2}{2\sigma Date_y^2}\right)$$

$$Bloom_{y,j} \sim \text{Normal}(\mu Bloom_y, \sigma Bloom_y)$$

$$bloomStart_y = \mu Date_y - (\sqrt{2} \times \sigma Date_y \times \log(\frac{100}{10}))$$

$$bloomEnd_y = \mu Date_y + (\sqrt{2} \times \sigma Date_y \times \log(\frac{100}{10}))$$

$$\begin{aligned} overlap_{y,i,j} &= \mathbf{percCanola}_{y,i} \times \\ &\frac{\max(\min(bloomEnd_y, \mathbf{end}_{y,i,j}) - \max(bloomStart_y, \mathbf{start}_{y,i,j}), 0)}{\mathbf{end}_{y,i,j} - \mathbf{start}_{y,i,j}} \\ center_{y,i,j} &= \frac{\mathbf{end}_{y,i,j} + \mathbf{start}_{y,i,j}}{2} \end{aligned}$$

Model for bee counts in year 1 at site i at time j

$$\mu_{1,i,j} = \mathbf{Intercept}_1 + \mathbf{SNL} \times \beta_{SNL1} + Bloom_{1,j} \times \beta_{Bloom1} +$$

$$\text{GP}(center_{1,i,j}, \alpha_1, \rho_1) + \mathbf{SiteIntercept}_{1,i}$$

$$\mathbf{counts}_{1,i,j} \sim \text{Zero-Inflated Negative Binomial}(\mu_{1,i,j}, \theta_1, \phi_1)$$

$$\mathbf{SiteIntercept}_i \sim \text{MVNormal}(0, \Sigma_{i,i'})$$

$$\Sigma_{i,i'} = \alpha_d \exp\left(-\frac{1}{2\rho_d^2} \mathbf{D}_{i,i'}^2\right)$$

Model for bee counts in year 2 at site i at time j

$$\mathbf{SiteIntercept}_{2,i} = \mathbf{SiteIntercept}_{1,i} \times \beta_{\mathbf{Site}}$$

$$\mu_{2,i,j} = \mathbf{Intercept}_2 + \mathbf{SNL} \times \beta_{SNL2} + Bloom_{2,j} \times \beta_{Bloom2} +$$

$$\text{GP}(center_{2,i,j}, \alpha_2, \rho_2) + \sum_{j=1}^{J_i} overlap_{1,j,i} \times \beta_{\mathbf{overlap}} + \mathbf{SiteIntercept}_{2,i}$$

$$\mathbf{counts}_{2,i,j} \sim \text{Zero-Inflated Negative Binomial}(\mu_{2,i,j}, \theta_2, \phi_2)$$

Equation set S1: Model structure used to estimate between-year effects of canola bloom. Terms in **red** are parameters that were estimated. Terms in **bold** are observed parameters from the data (dependent or independent, on the left or right-hand side of equations, respectively). Terms in *italics* are calculated from a combination of coefficients and variables. *Zero-Inflated Negative Binomial* refers to the Negative Binomial 2 (Pólya distribution) with a zero-inflation component, where e^μ is the mean, θ the dispersion, and ϕ the proportion of zeros not from the Negative Binomial distribution. GP is a gaussian process model with correlation α and length scale ρ , using a squared-exponential decay function (see Ch. 11 of Stan Development Team (2018) for more details).

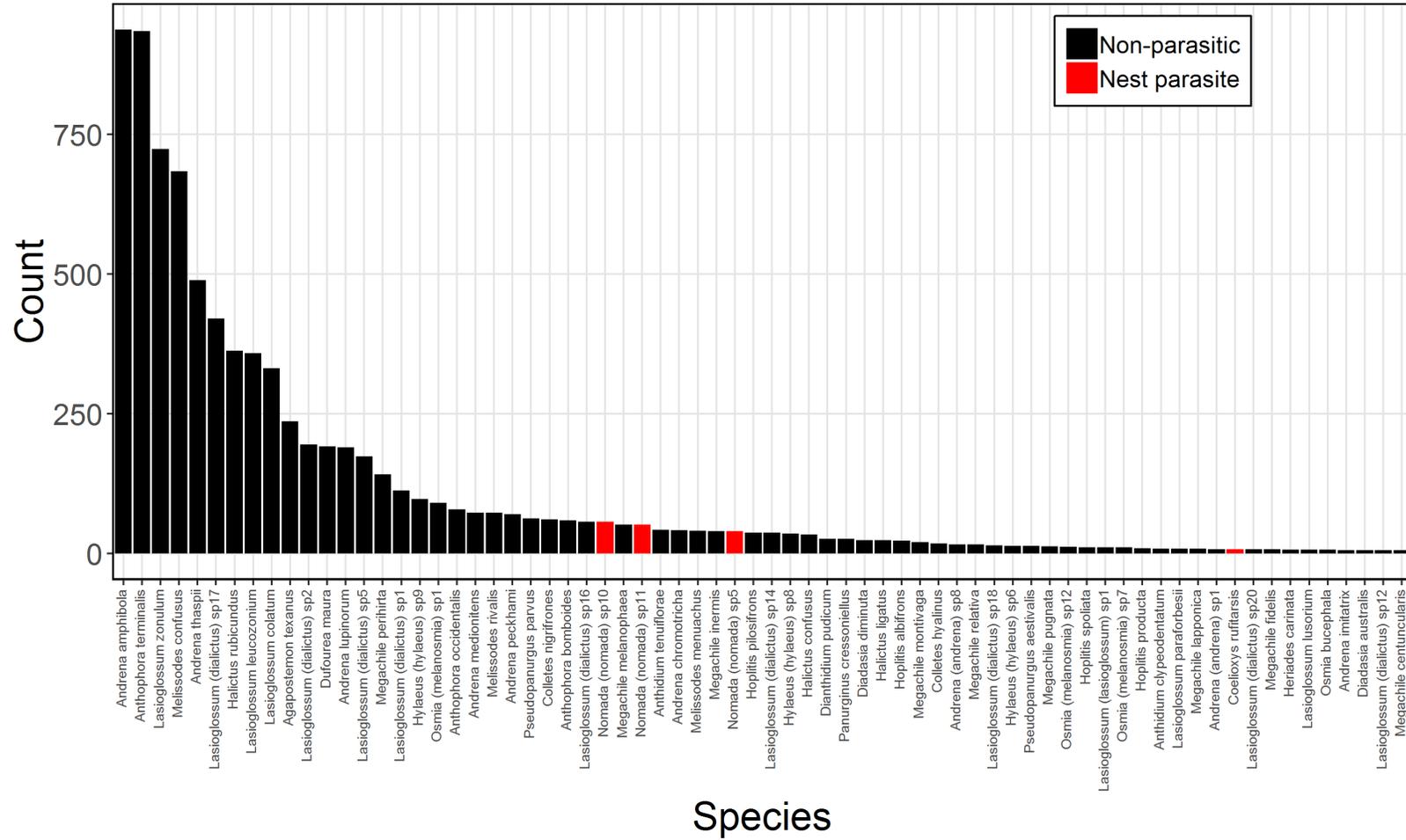


Figure S6: Counts of specimens collected during 2015 and 2015, excluding non-native managed species (*Apis mellifera* and *Megachile rotundata*).