SOCIAL MODULATION OF INDIVIDUAL DECISION-MAKING IN FORAGING BUMBLEBEES: MECHANISMS AND EVOLUTION

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ABSTRACT

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How and why animals choose to do what they do at any given moment is one of the fundamental questions in animal behavior. For social animals, influences on decision-making can come from both personal and social sources, and in eusocial insects like ants, bees, and wasps, the reliance on social information is taken to the extreme. Foraging bumblebees offer the perfect model in which to examine the social influences on individual decision-making because they are presented with extensive personal and social information, and when foraging they are solely focused on the task at hand. Chapter 1 reviews information use by foraging bumblebees, setting the stage for the subsequent data chapters. Chapter 2 examines how the motivation for bumblebees to feed from a known feeder is modified by the nutritive state of the colony, such that individuals in colonies with full food stores show lower motivation to feed. In addition to this behavioral result, a biochemical analysis reveals that lipid levels may be involved in the mechanism underlying this social effect. Eusocial insects are famous for collective behaviors, such as the swarming behavior of honeybees, the foraging trails of termites, and the bridge-building of ants. While the collective foraging strategy of other eusocial insects has been well-studied, it has not received attention in bumblebees. In Chapter 3 I use a behavioral experiment to reveal that bumblebees use a strategy of informed individual initiative to collectively ensure they are foraging from the best resources in the environment. In this strategy, individual bees adjust their reward expectations based on the quality of nectar stored in the nest. I followed up this experiment with a computational model to reveal that this strategy is adaptive, as it results in

higher fitness than does individual search alone. This strategy is markedly different from the spatial communication of the dance language used by honeybees, who are close relatives of bumblebees. This prompted me to extend the computational model to examine the selective pressures that shape foraging strategies in social insects, including the honeybee dance language and bumblebee strategy of informed individual initiative. In Chapter 4, I present the results of simulations of this extended model, demonstrating that, although resource density influences fitness for both the dance language and informed individual initiative, colony size only matters for the dance language. This suggests that the large colony sizes of honeybees may have been important for the dance language to evolve, whereas a similar spatial communication system would not be adaptive in bumblebees, which have smaller colony sizes. Taken all together, the results in this dissertation explore how individual decision-making is shaped by the social environment in bumblebees, and the potential selective pressures that led to these behavioral strategies over evolutionary time. Bumblebees are important pollinators in both agricultural and natural ecosystems, but many species are facing declines; a more thorough understanding of their behavior is imperative to help us conserve them as the planet continues to change due to climate change and other anthropogenic influences.

This dissertation is dedicated to all of the family and friends who have believed in me over the years, even when I didn’t believe in myself

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CHAPTER 1: A REVIEW OF INFORMATION USE BY FORAGING BUMBLEBEES

INTRODUCTION

Bumblebees are among the most important insects in the world, serving vital roles in both natural and managed ecosystems. With over 250 species distributed across the globe, they pollinate a diverse suite of both wild and domestic plant species and several species have been domesticated (Velthuis and Van Doorn 2006; Goulson 2010). Their experimental tractability and easy accessibility have made them valuable model organisms in studies of ecology, behavior, and evolution, contributing to advances in our understanding of social evolution (Amsalem et al. 2015), foraging theory (Pyke 1978), and plant-pollinator interactions (Real 1981; Dyer et al. 2007), among others. One area of research that has gained specific attention in bumblebees is decision-making; decades of work has revealed how bumblebees use various sources of information to inform their foraging decisions. Because bumblebees gather all of their resources from flowers, the decisions they make have serious consequences for the fitness of plant species in the landscape, as well as for the fitness of the bumblebee colonies themselves.

In a technical, theoretical sense, information can be thought of as any feature of the environment that reduces uncertainty about the state of the world for the purpose of making a decision (Shannon 1948; Floridi 2010). In the natural world, animals gain information about the environment by using sensory systems to detect signals (features that evolved for the purpose of transmitting information) and cues (features that can provide information, but did not evolve to do so; Laidre and Johnstone 2013). Signals and cues can be used in a variety of contexts, including mate choice (Candolin 2003), predator avoidance (e.g. Ings and Chittka 2009, Romero et al. 2011), and foraging (Raguso 2004). How animals use signals to make decisions is one of the key questions of animal behavior, and can be analyzed across all levels of Tinbergen's four levels of analysis (Tinbergen 1963).

Bumblebees are eusocial bees in the genus *Bombus*; they are members of the family Apidae along with their close relatives, the honeybees (*Apis*), the stingless bees (various genera in the subfamily Meliponinae), and the orchid bees (various genera in the subfamily Euglossinae). All *Bombus* species, with the potential exception of a few in the tropics, have annual lifecycles with maximum colony sizes in the low hundreds (Goulson 2010). Their ecological, economic, and evolutionary importance combined with their natural charisma has made them attractive model organisms for many decades. In addressing questions about bumblebees, comparative studies with honeybees are fruitful and often necessary, as the two genera, while related, have differing behavioral and cognitive traits that correspond to different ecologies (Thomson and Goodell 2001; Sherry and Strang 2015; Eeraerts et al 2020). Despite their ecological prominence and worldwide distribution, many bumblebee populations are in decline (Cameron et al. 2011; Soroye et al. 2020). A detailed understanding of how bumblebees make decisions, and what information they use from their environments to do so, can thus help answer fundamental questions in ecology, evolution, and behavior, while also informing conservation and recovery efforts for these important pollinators.

In this review, I will summarize the use of information by bumblebee foragers while also making reference to work on honeybees in order to draw contrasts or highlight generalities. I classify information as personal or social, with further subdivision of personal information into floral traits and body condition and social information into intranidal and extranidal categories. I will conclude by pointing out fruitful areas for future research. In the final section I discuss how the remaining chapters of this dissertation relate to ideas explored in this chapter.

PERSONAL INFORMATION

Bumblebees gain personal information through experience while foraging from sources including floral traits, traits of nectar and pollen rewards, location of rewards in space, plant-associated microbes, individual body condition, and pathogens, predators, and pesticides.

A. Floral Traits

Color is the classic floral trait known to be used by bumblebees, and many other pollinators, to discriminate among flowers. The first experiment on color vision in insects was performed by Charles Henry Turner, using honeybees (Turner 1910; Giurfa and de Brito Sanchez 2020). Turner made many other advancements in insect behavior, despite being denied a faculty position due to his being a Black man (Lee 2020). Karl von Frisch later addressed the same question with more definitive experiments, providing conclusive evidence that honeybees possess true color vision (an ability to discriminate hue independent of brightness; von Frisch 1914). This early research showed that honeybees can see ultraviolet (UV) as a distinct color, but not red.

Like honeybees, bumblebees have trichromatic color vision, with a general preference to search for food in association with violet-blue colors, though there are exceptions in certain species and populations (Briscoe and Chittka 2001; Spaethe et al. 2001). Bumblebees have been shown to be able to learn to discriminate flowers on the basis of color in both free-flying (Gumbert 2000) and restrained (Riveros and Gronenberg 2012) conditions. Interestingly, the bumblebee *Bombus impatiens* is capable of learning to associate visual stimuli with reward in the proboscis extension response (PER) assay, in which a restrained bee is trained to extend its tongue to get a sugar reward that has been paired with a stimulus (such as an odor or color).

Bumblebees can do this even though it is a difficult task for honeybees; the exact reasons for this are still unknown (Giurfa and Sandoz 2012; Avarguès-Weber and Mota 2016).

Many plant species have evolved floral nectar guides, visual patterns that exploit the visual capabilities of bumblebees and other pollinators. Many of these patterns fall into the UV range of the color spectrum and are thus not visible to the naked human eye (Chittka et al. 1994). The presence of these guides evokes an innate attraction from bumblebees and can also facilitate learning (Leonard and Papaj 2011). By easing the discovery of reward from the corolla of the flower, nectar guides may also promote pollination by discouraging bumblebees from robbing nectar by chewing through the flower base instead of interacting with the reproductive organs (Leonard et al. 2013).

In addition to color, bumblebees obtain other visual information from flowers. They can perceive and learn polarization patterns (Foster et al. 2014) and iridescence (Whitney et al. 2009a) from flowers, with the ordering of floral nanostructures being important for the production of visual signals that are salient to bees (Moyroud et al. 2017). They can also discriminate flowers based on shape (Muller and Chittka 2012), height (Wiegmann et al. 2000), and size (Blarer et al. 2002; Essenberg et al. 2015), and prefer bilaterally symmetrical over asymmetrical flowers (Møller 1995).

Flowers are also known to produce diverse odors, detectable by bumblebees (Kunze and Gumbert 2001; Raguso 2004). Bumblebees are capable of learning and discriminating odors (Riveros and Gronenberg 2009; Sommerlandt et al. 2014). The bumblebee *Bombus terrestris* has also been shown to preferentially learn odors that are honest signals of reward quality (Knauer and Schiestl 2015). Researchers are increasingly recognizing the role that microbes play in shaping floral odor profiles as well (Farré-Armengol et al. 2016; Vannette 2020).

Another floral trait that bumblebees respond to when making foraging decisions is flower complexity. Different bumblebee species respond differently to floral complexity (Stout et al. 1998), and bumblebees tend to be more constant to complex flowers once they've learned, through trial-and-error learning, to handle them (Laverty 1994). Recent work suggests that bumblebees prefer to forage from complex flowers, but the reasons for this are still unknown (Krishna and Keasar 2019).

There are also several less obvious floral traits that bumblebees can use to discriminate different flowers and make foraging decisions. These include overall floral temperature (Dyer et al. 2006; Whitney et al. 2008) and spatial patterns in temperature across individual flowers (Harrap et al. 2017), tactile cues from conical epidermal cells in petals (Whitney et al. 2009b), and the minute static electric fields detectable in close proximity to flowers (Clarke et al. 2013; Sutton et al. 2016). In sum, there are many floral traits that bumblebees detect and respond to beyond the traits of color and odor that are detectable by humans.

B. Reward Traits

Bumblebees, like most other bee species, collect both nectar and pollen from flowers. As such, it is adaptive for them to be able to detect the content of various nutrients within both rewards, so that suitable resources are collected and taken back to the nest. Bumblebees, like honeybees, are known to learn the quality of nectar rewards (Wiegmann et al. 2003; Gil et al. 2007), and respond with search behavior when their reward expectation isn't met (Townsend-Mehler et al. 2011; Incorvaia et al. 2021). This negative incentive contrast effect (Flaherty 1999)—the tendency to reject a reward simply because it is inferior to what has been experienced recently—how it is influenced by the social state of the colony, and its role in bumblebee collective foraging behavior, are addressed in Chapters 2 and 3 of this dissertation.

Reward quality can also be influenced by microbes, such as bacteria and yeast, that alter nectar chemistry (Vannette and Fukami 2018), impacting bumblebee behavior and fitness (Pozo et al. 2020). Foraging bumblebees also respond to reward variability (Pleasants 1981), and sample new resources more when they have experience with a variable reward (Keasar et al. 2013).

Bumblebees can also judge the quality of pollen on the basis of the relative composition of various macromolecules. For example, bees detect pollen chemistry through taste (Muth et al. 2016; Muth et al. 2018), and can detect certain amino acids using their antennae (Ruedenauer et al. 2019). Bumblebees also develop preferences for flowers that offer pollen as rewards, but not nectar, demonstrating the importance of pollen for determining bumblebee foraging decisions (Somme et al. 2015; Russell et al. 2016). They also detect and respond to toxic defensive chemicals in pollen, which has implications for decision-making and subsequent pollen transfer (Wang et al. 2019).

C. Spatial and Temporal Location

Bumblebees have robust spatial memories that enable them to remember the locations of rewarding flower patches (Burns and Thomson 2006; Church and Plowright 2006), and have been shown to even learn the location of specific rewarding inflorescences (Thomson 1988). They can also display traplining behavior, visiting the same resources in the same order on subsequent foraging trips and updating this order as new resources appear (Heinrich 1976; Saleh and Chittka 2007; Lihoreau et al. 2010; Woodgate et al. 2017), and showing variability between individuals in the traplines developed (Klein et al. 2017). Bumblebees can adaptively choose when to encode spatial information as a predictor of reward, based on whether this information impacts foraging speed. This phenomenon suggests that bumblebees have evolved to be sensitive to the speed-accuracy tradeoff, where rapid decision-making entails more errors (Chittka et al. 2003; Tsujimoto and Ishii 2017).

Honeybees have shown the capacity to learn the times of day at which resources are available in the environment, and to visit patches preferentially at those times (Moore et al. 2011; Wagner et al. 2013). Similar studies in bumblebees are currently lacking, though some studies of circadian rhythm in bumblebee foraging exist (e.g. Stelzer et al. 2010). Future work should endeavor to study temporal learning and memory in bumblebees, as their differences in behavior and cognition may allow a comparative approach to lead to general insights in how insects use time as an information source when foraging (Sherry and Strang 2015).

D. Microbes

As mentioned previously, floral microbes play a role in shaping flower odor profiles that are learned and recognized by bumblebees (Farré-Armengol et al. 2016; Vannette 2020). In addition to this indirect influence, microbes themselves are detectable by bumblebees through the production of chemical cues, and bees can learn to discriminate flowers based on the presence of certain microbes (Russell and Ashman 2019), and play a key role in microbial dispersal between flowers as well (Russell et al. 2019). The role microbes play in mediating plant-pollinator interactions has gained tremendous attention recently, and has been the subject of several review and opinion articles (e.g. Vannette 2020, Klaps et al. 2020, Adler et al. 2020, Francis et al. 2020).

E. Predators and Parasites

The most common predators encountered by bumblebees are those, such as crab spiders, that live on flowers. Personal experience with predators can impact the decisions made by foragers. Bees that experienced simulated predation events showed lowered foraging activity for hours after the attack if it occurred on a low-reward flower, and avoided the flower type where the attack occurred (Ings and Chittka 2009; Jones and Dornhaus 2011). Bumblebees learn to avoid crab spider predators by shape, independent of color (Ings et al. 2012). Predator avoidance can be overcome by the presence of conspecifics, suggesting that foragers can use social cues to determine that a given flower is safe even if they have previously encountered a predator on another flower of the same type (Dawson and Chittka 2014). The response of a foraging bee to predation risk is also influenced by the bee's own body size, with smaller bees perhaps counterintuitively changing their behavior less in response to attempted predation than larger bees (Gavini et al. 2020). The bumblebee *Bombus impatiens* also avoids both conspecific and heterospecific (honeybee) hemolymph on flowers, a reliable cue of bee predation (Goodale and Nieh 2012).

Bumblebees are hosts for various parasites, including the trypanosome *Crithidia bombi*, the microsporidians *Nosema bombi* and *N. cerane*, and the neogregarine *Apicystis bombi* (Carnell et al. 2020). Infection with parasites may itself influence foraging behavior through self-medication (e.g. Baracchi et al. 2015), but more extensive field studies are needed to determine the prevalence of this behavior under natural conditions (de Roode and Hunter 2019). Pathogen transmission is mediated by plant species and floral traits (Adler et al. 2018), and bumblebees have been shown to learn through experience to avoid flowers contaminated with *C. bombi* (Fouks and Lattorff 2011; Fouks et al. 2019).

F. Body Condition

Researchers often consider the nutritive and energetic state of bees at the colony level (discussed later in this review), rather than the individual level. However, in honeybees at least, a spate of research over the past decade has revealed that individual energetic state plays a role in mediating foraging decisions (Mayack and Naug 2013; Katz and Naug 2015; Mayack and Naug 2015). Given the differences between honeybee and bumblebee social organization, it would be interesting to see if a similar effect can be found in bumblebees. This topic should be a focus of research going forward.

Bumblebees are holometabolous insects, and body condition is thus heavily influenced by larval feeding that occurs before eclosion. Generally, larvae that are fed less develop into smaller workers, and smaller workers tend to forage less frequently than larger workers (Goulson et al. 2002; Couvillon and Dornhaus 2009). Although larger bumblebees tend to contain a lower proportion of lipids relative to their body mass than smaller bumblebees (Couvillon et al. 2011), prior studies have not found a correlation between lipid levels and foraging behavior in bumblebees, as there is in honeybees (Toth and Robinson 2005). In Chapter 2 of this dissertation I examine the relationship between lipid levels and foraging motivation in bumblebees. Further work is needed to determine how other aspects of body condition influence foraging behavior and decision-making in bumblebees.

Body condition can also be influenced by chemicals in the environment, especially pesticides. Studies of the influence of pesticides on bumblebees have focused on neonicotinoids, such as imidacloprid and clothianidin, and pyrethroids. These pesticides have been shown to reduce bumblebee colony growth and development (Whitehorn et al. 2012) through impairment of natural foraging behavior and activity (Gill et al. 2012; Arce et al. 2017; Muth and Leonard 2019), and contribute to the widespread decline of bumblebees and other wild bees (Goulson et al. 2015). Pesticide exposure reduces odor learning abilities (Muth et al. 2019) and the ability to learn to handle flowers (Phelps et al. 2020). Research on whether bumblebees have a preference for pesticide-tainted nectar have shown conflicting results depending on the species investigated, with evidence for a preference in *Bombus terrestris* (Kessler et al. 2015; Arce et al. 2018) and no such evidence for *Bombus impatiens* (Muth et al. 2020). This difference highlights the need for more comparative studies of the behavioral effects of pesticide exposure across bumblebee species.

SOCIAL INFORMATION

A. Extranidal

Bumblebees have increasingly become a model system for studies of social learning, with work both in the laboratory and in the field on how the presence of conspecifics or scent marks left by them influence learning and decision-making (Leadbeater and Chittka 2007a; Leadbeater and Chittka 2007b; Grüter and Leadbeater 2014).

1. Presence of Conspecifics

Outside of the nest, there are numerous social cues bumblebees use to make foraging decisions. A basic example is the presence of conspecifics, which is known to draw bumblebees to novel flower types but deter them from visiting known flowers (Worden and Papaj 2005; Kawaguchi et al. 2007). These early studies provide evidence of social learning, for which bumblebees have since become an insect model system. In addition to learning to approach or avoid certain flower types, bumblebees can also learn more complex tasks by observing conspecifics, such as string-pulling and ball-rolling in a laboratory setting (Alem et al. 2016; Loukola et al. 2017) and ecologically relevant foraging techniques such as nectar-robbing (Leadbeater and Chittka 2008; Goulson et al. 2013).

2. Scent Marks

In addition to visual social information, bumblebees also detect scent marks passively left on flowers by conspecifics (Wilms and Eltz 2008). Bumblebees learn through experience to avoid these tarsal “footprints” as they typically signal an empty inflorescence; inexperienced foragers show no innate response to them (Schmitt et al. 1991; Goulson et al. 2000; Leadbeater and Chittka 2011). Rather than treating all scent marks the same, foragers can differentiate between their own footprints, the footprints of nestmates, and the footprints of non-nestmates (Pearce et al. 2017). Foragers use these social cues flexibly: for example, they are more likely to reject a flower with scent marks if the flower is complex (has a longer handling time) relative to a simpler flower with a short handling time (Saleh et al. 2006), and they can also adjust how long they avoid marked flowers based on the plant’s nectar secretion rate (Stout and Goulson 2002).

B. Intranidal

Within the nest, bumblebees can gain social information from odors, pheromones, food stored in honeypots, and contact with returning foragers.

1. Odors

In addition to odors learned outside the nest at flowers, bumblebees can also learn to associate odors within the nest with reward (Dornhaus and Chittka 1999; Molet et al. 2009), an ability dependent on contacting scented nectar stored in honeypots (McAulay et al. 2015). This odor learning, paired with contact-based foraging activation (see below) and the flexible adjustment of internal reward expectations based on the quality of stored food (informed individual initiative, see Incorvaia et al. 2021) to form an adaptive system of information transfer.

2. Contact-Based Foraging Activation: The Bumblebee “Dance”

Bumblebees do not possess a spatial communication system like the dance language of the related honeybee, but they do exhibit an in-nest recruitment system that is possibly ancestral to the dance language (Dornhaus and Chittka 1999; Barron and Plath 2017). Foragers that have discovered food return to the nest and perform excited, irregular runs, during this time also fanning their wings and contacting other bees (Dornhaus and Chittka 2001; Dornhaus and Cameron 2003; Dornhaus and Chittka 2004). Bees contacted by an excited forager are significantly more likely to leave the nest to forage themselves than bees that are not contacted (Renner and Nieh 2008).

3. Pheromones

Returning foragers performing excited runs also release a recruitment, or “alert” pheromone from their tergal glands (located in the cuticle of the abdomen), spreading it through the nest with their wing fanning (Dornhaus et al. 2003). This alert pheromone consists predominately of two monoterpenes and one sesquiterpene, with the monoterpene eucalyptol showing the strongest recruitment effect (Granero et al. 2005). Another component of the pheromone, the sesquiterpenoid farnesol, has an innate and unique neural representation within bumblebee brains (Strube-Bloss et al. 2015); this indicates that bumblebee brains are hard-wired to recognize this chemical. Response to the pheromone is mediated by the amount of stored food in the nest (see below), with bumblebees being less likely to respond with increased foraging activity if food stores are already high (Molet et al. 2008).

4. Stored Food

Bumblebees, unlike honeybees, do not store food long-term as honey; rather colonies typically only store enough nectar and pollen to last several days at a time (Goulson 2010). Bumblebees also adjust their foraging behavior according to the amount of stored food, with colonies showing greater foraging activity (Cartar 1992) and responding more to an influx of food (Dornhaus and Chittka 2005) when nectar stores are low. Similar results are seen for pollen foraging when pollen stores are high, though this has received less study than nectar foraging

(Kitaoka and Nieh 2009). Bumblebees also adjust their pollen preferences when foraging based on the nutrient ratios of pollen they've collected (Vaudo et al. 2016), with big implications for colony health and development (Vaudo et al. 2018).

COLLECTIVE OUTCOMES

Bumblebees, like other eusocial insects, show complex collective behaviors that emerge as outcomes of individual behaviors (Sumpter 2006). A well-studied example is how bumblebees collectively thermoregulate their nests through fanning behavior (Weidenmüller et al. 2002; Weidenmüller 2004; Garrison et al. 2018). The study of how collective foraging strategies emerge from individual behavior in bumblebees is still in its infancy, especially when compared to its study in honeybees (e.g. Seeley et al. 1991; Cook et al 2020). Early studies identified how bumblebee colony activity levels change based on food stores and foraging activation (Cartar 1992; Dornhaus and Chittka 2005; Kitaoka and Nieh 2009). In a recent study, Incorvaia et al. (2021) identified how individual foragers adjust their choice to exploit a known resource or explore for a new one based on social cues in the nest, with the cue investigated being the presence of high-quality sucrose solution. These individual adjustments collectively lead to adaptive allocation of foragers to resources in the environment.

While the process of collective decision-making in foraging has been extensively documented in honeybees (Seeley et al. 1991; Camazine and Sneyd 1991; Sumpter and Pratt 2003; Becher et al. 2014; Bidari et al. 2019), more research is needed to determine the behavioral algorithms used by bumblebee foragers to make decisions. Future work should build on Incorvaia et al. (2021) to examine how other sources of information mentioned in this review interact with stored nectar to influence foraging decisions across bumblebee species.

OTHER FUTURE DIRECTIONS

In addition to the need for more research on collective foraging behavior, there are other gaps in our knowledge of bumblebee foraging decisions that deserve attention.

First, there are several floral traits demonstrated to be used as information sources in other pollinators that have not yet been tested in bumblebees. For example, respiratory carbon dioxide from flowers serves as an attractant to the hawkmoth *Manduca sexta* (Goyret et al. 2008). Although bumblebees detect and respond to carbon dioxide levels in the nest (Weidenmüller et al. 2002; Jones 2013), whether or not they respond to carbon dioxide emitted from flowers has not been tested. Hawkmoths also use floral humidity (the humidity in the immediate space around the floral display) as a cue to assess nectar profitability (Von Arx et al. 2012); a recent preprint claims that bumblebees can detect floral humidity as well, but has not yet finished the review process (Harrap et al. 2021). Other social insects, such as honeybees (Walker and Bitterman 1985; Kirschvink et al. 1997; Liang et al. 2016) and paper wasps (Pereira-Bomfim et al. 2015) respond to magnetic fields, but this also has not been tested in bumblebees. Honeybees have also been shown to prefer warmer and less viscous nectar (Nicolson et al. 2013; Tan et al. 2014; Shi et al. 2020) and can learn to associate temperature with reward (Hammer et al. 2009), but to my knowledge data on bumblebees in this area do not exist.

Future studies should also endeavor to explore what sources of information male bumblebees use to make foraging decisions. Male bumblebees do not forage for the colony, and show some differences in foraging behavior from female workers (Jennersten et al. 1991; Ostevik et al. 2010) but no apparent differences in learning and memory when compared to females (Church et al. 2001; Lichtenstein et al. 2015; Wolf and Chittka 2016; Muth et al. 2021).

Overall, however, studies on foraging and cognition in male bumblebees are scarce. Given the different evolutionary pressures faced by male bumblebees compared to those faced by workers and queens, and the fact that they do not collect pollen, we might expect males to use information differently. More work is needed to explain how sexual selection has influenced male bumblebee information use.

Another area future research should prioritize is multimodal signaling and its impact on decision-making. Many of the information sources mentioned in this review have only been studied in isolation, but in reality bumblebees are constantly gathering new information from all of these sources and integrating them into foraging decisions. Bumblebees learn rewarding flowers better and make more accurate choices when signals are multimodal than when they are unimodal (Kulahci et al. 2008), and the presence of signals in multiple sensory modalities reduces uncertainty in foragers (Leonard et al. 2011). Much of the multimodal and sensory integration research in bumblebees has focused on scent and vision (Leonard and Masek 2014). Additionally, prior work has explored how bumblebees weigh social learning and personal experience when making decisions (e.g. Leonard and Florent 2014, Dunlap et al. 2016). Future work should expand to include less well-understood sensory modalities and information sources in studies of sensory integration and decision-making.

CONTRIBUTIONS OF THIS DISSERTATION

The chapters of this dissertation address various gaps in knowledge highlighted by this introductory review. Chapter 2 examines how the motivation for bumblebees to feed from a known feeder is modified by the amount of food stored in the nest, which represents an important social cue. In addition, a biochemical analysis reveals that lipid levels may be involved in the mechanism underlying this behavior. This chapter thus begins to elucidate the physiological mechanisms by which social information modifies individual decision-making in bumblebees.

Chapter 3 addresses the collective foraging strategy of bumblebees that results in allocation of foragers to the best resources in the environment. Although the collective foraging strategy for forager allocation has been well-studied in other eusocial insects, especially honeybees (as mentioned in section III), it had not received attention in bumblebees. In this chapter, which has been published as Incorvaia et al. (2021), I use a behavioral experiment to explore the "informed individual initiative" strategy that bumblebees use. In this strategy, individual bumblebees adjust their propensity to explore for new resources or exploit known ones based on the quality of nectar stored in the nest. I followed up this experiment with a computational model to reveal that this strategy is adaptive, as it results in higher fitness than that accruing via individual search alone.

Chapter 4 extends the model developed in Chapter 3 to address collective foraging from an evolutionary standpoint. The collective strategy used by bumblebees is markedly different from the spatial communication of the dance language used by honeybees, which are close relatives of bumblebees. I used a computational model to examine the selective pressures that shape foraging strategies in these social bees. Specifically, I examine the role of colony size and resource density as selection pressures influencing the fitness of the honeybee dance language and bumblebee informed individual initiative. As both colony size and resource density have been previously studied using empirical and modeling approaches in honeybees, yielding inconclusive results, (Sherman and Visscher 2002; Dornhaus et al. 2006; Donaldson-Matasci et al. 2013; Schürch and Grüter 2014; I'Anson Price et al. 2019), this chapter sheds new light on their debated role while also providing a new line of inquiry into the selection pressures that have shaped the evolution of the bumblebee collective foraging strategy.

REFERENCES

REFERENCES

Adler, Lynn S., et al. "Disease where you dine: plant species and floral traits associated with pathogen transmission in bumble bees." *Ecology* 99.11 (2018): 2535-2545.

Adler, Lynn S., et al. "Floral traits affecting the transmission of beneficial and pathogenic pollinator-associated microbes." *Current Opinion in Insect Science* (2020).

Alem, Sylvain, et al. "Associative mechanisms allow for social learning and cultural transmission of string pulling in an insect." *PLoS Biology* 14.10 (2016): e1002564.

Amsalem, Etya, et al. "The physiological and genomic bases of bumble bee social behaviour." Advances in Insect Physiology. Vol. 48. Academic Press, 2015. 37-93.

Arce, Andres N., et al. "Foraging bumblebees acquire a preference for neonicotinoid-treated food with prolonged exposure." *Proceedings of the Royal Society B* 285.1885 (2018): 20180655.

Arce, Andres N., et al. "Impact of controlled neonicotinoid exposure on bumblebees in a realistic field setting." *Journal of Applied Ecology* 54.4 (2017): 1199-1208.

Avarguès-Weber, Aurore, and Theo Mota. "Advances and limitations of visual conditioning protocols in harnessed bees." *Journal of Physiology-Paris* 110.3 (2016): 107-118.

Baracchi, David, Mark JF Brown, and Lars Chittka. "Behavioural evidence for self-medication in bumblebees?." *F1000Research* 4 (2015).

Barron, Andrew B., and Jenny Aino Plath. "The evolution of honey bee dance communication: a mechanistic perspective." *Journal of Experimental Biology* 220.23 (2017): 4339-4346.

Becher, Matthias A., et al. "BEEHAVE: a systems model of honeybee colony dynamics and foraging to explore multifactorial causes of colony failure." *Journal of Applied Ecology* 51.2 (2014): 470-482.

Bidari, Subekshya, Orit Peleg, and Zachary *p*. Kilpatrick. "Social inhibition maintains adaptivity and consensus of honeybees foraging in dynamic environments." *Royal Society open science* 6.12 (2019): 191681.

Blarer, Albert, Tamar Keasar, and Avi Shmida. "Possible mechanisms for the formation of flower size preferences by foraging bumblebees." *Ethology* 108.4 (2002): 341-351.

Briscoe, Adriana D., and Lars Chittka. "The evolution of color vision in insects." *Annual review of entomology* 46.1 (2001): 471-510.

Burns, James G., and James D. Thomson. "A test of spatial memory and movement patterns of bumblebees at multiple spatial and temporal scales." *Behavioral Ecology* 17.1 (2006): 48-55.

Camazine, Scott, and James Sneyd. "A model of collective nectar source selection by honey bees: self-organization through simple rules." *Journal of theoretical Biology* 149.4 (1991): 547-571.

Cameron, Sydney A., et al. "Patterns of widespread decline in North American bumble bees." Proceedings of the National Academy of Sciences 108.2 (2011): 662-667.

Candolin, Ulrika. "The use of multiple cues in mate choice." *Biological reviews* 78.4 (2003): 575-595.

Carnell, Joanne D., et al. "A review of nutrition in bumblebees: The effect of caste, life-stage and life history traits." *Advances in Insect Physiology* 59 (2020): 71.

Cartar, Ralph V. "Adjustment of foraging effort and task switching in energy-manipulated wild bumblebee colonies." *Animal Behaviour* 44.1 (1992): 75-87.

Chittka, Lars, et al. "Bees trade off foraging speed for accuracy." *Nature* 424.6947 (2003): 388-388.

Chittka, Lars, et al. "Ultraviolet as a component of flower reflections, and the colour perception of Hymenoptera." *Vision research* 34.11 (1994): 1489-1508.

Church, Dana L., and Catherine MS Plowright. "Spatial encoding by bumblebees (Bombus impatiens) of a reward within an artificial flower array." *Animal Cognition* 9.2 (2006): 131-140.

Church, Dana, Catherine Plowright, and Diana Loyer. "Discriminations of color and pattern on artificial flowers by male and female bumble bees, Bombus impatiens (Hymenoptera: Apidae)." *The Great Lakes Entomologist* 34.2 (2001): 11.

Clarke, Dominic, et al. "Detection and learning of floral electric fields by bumblebees." *Science* 340.6128 (2013): 66-69.

Cook, Chelsea N., et al. "Individual learning phenotypes drive collective behavior." *Proceedings of the National Academy of Sciences* 117.30 (2020): 17949-17956.

Couvillon, Margaret J., and Anna Dornhaus. "Location, location, location: larvae position inside the nest is correlated with adult body size in worker bumble-bees (Bombus impatiens)." *Proceedings of the Royal Society B: Biological Sciences* 276.1666 (2009): 2411-2418.

Couvillon, Margaret J., et al. "Percent lipid is associated with body size but not task in the bumble bee Bombus impatiens." *Journal of Comparative Physiology A* 197.11 (2011): 1097.

Dawson, Erika H., and Lars Chittka. "Bumblebees (Bombus terrestris) use social information as an indicator of safety in dangerous environments." *Proceedings of the Royal Society B: Biological Sciences* 281.1785 (2014): 20133174.

de Roode, Jacobus C., and Mark D. Hunter. "Self-medication in insects: when altered behaviors of infected insects are a defense instead of a parasite manipulation." *Current opinion in insect science* 33 (2019): 1-6.

Donaldson-Matasci, Matina C., Gloria DeGrandi-Hoffman, and Anna Dornhaus. "Bigger is better: honeybee colonies as distributed information-gathering systems." *Animal behaviour* 85.3 (2013): 585-592.

Dornhaus, A., A. Brockmann, and L. Chittka. "Bumble bees alert to food with pheromone from tergal gland." *Journal of Comparative Physiology A* 189.1 (2003): 47-51.

Dornhaus, Anna, and L. Chittka. "Evolutionary origins of bee dances." *Nature* 401.6748 (1999): 38-38.

Dornhaus, Anna, and Lars Chittka. "Bumble bees (Bombus terrestris) store both food and information in honeypots." *Behavioral Ecology* 16.3 (2005): 661-666.

Dornhaus, Anna, and Lars Chittka. "Food alert in bumblebees (Bombus terrestris): possible mechanisms and evolutionary implications." *Behavioral Ecology and Sociobiology* 50.6 (2001): 570-576.

Dornhaus, Anna, and Lars Chittka. "Information flow and regulation of foraging activity in bumble bees (Bombus spp.)." *Apidologie* 35.2 (2004): 183-192.

Dornhaus, Anna, and Sydney Cameron. "A scientific note on food alert in Bombus transversalis." *Apidologie* 34.1 (2003): 87-88.

Dornhaus, Anna, et al. "Benefits of recruitment in honey bees: effects of ecology and colony size in an individual-based model." *Behavioral Ecology* 17.3 (2006): 336-344.

Dunlap, Aimee S., et al. "Foraging bumble bees weigh the reliability of personal and social information." *Current Biology* 26.9 (2016): 1195-1199.

Dyer, Adrian G., et al. "Bees associate warmth with floral colour." *Nature* 442.7102 (2006): 525-525.

Dyer, Adrian G., et al. "Mutations perturbing petal cell shape and anthocyanin synthesis influence bumblebee perception of Antirrhinum majus flower colour." Arthropod-Plant Interactions 1.1 (2007): 45-55.

Eeraerts, Maxime, Guy Smagghe, and Ivan Meeus. "Bumble bee abundance and richness improves honey bee pollination behaviour in sweet cherry." *Basic and Applied Ecology* 43 (2020): 27-33.

Essenberg, Carla J., et al. "The value of information in floral cues: bumblebee learning of floral size cues." *Behavioral Ecology* 26.5 (2015): 1335-1344.

Farré-Armengol, Gerard, et al. "Bidirectional interaction between phyllospheric microbiotas and plant volatile emissions." *Trends in plant science* 21.10 (2016): 854-860.

Flaherty, Charles F. "Incentive relativity." (1999).

Floridi, Luciano. *Information: A very short introduction*. OUP Oxford, 2010.

Foster, James J., et al. "Bumblebees learn polarization patterns." *Current Biology* 24.12 (2014): 1415-1420.

Fouks, Bertrand, and H. Michael G. Lattorff. "Recognition and avoidance of contaminated flowers by foraging bumblebees (Bombus terrestris)." *PLoS One* 6.10 (2011): e26328.

Fouks, Bertrand, Emily G. Robb, and H. Michael G. Lattorff. "Role of conspecifics and personal experience on behavioral avoidance of contaminated flowers by bumblebees." *Current zoology* 65.4 (2019): 447-455.

Francis, Jacob S., et al. "Microbes and Pollinator Behavior in the Floral Marketplace." *Current Opinion in Insect Science* (2020).

Garrison, Linda Karen, Christoph Johannes Kleineidam, and Anja Weidenmüller. "Behavioral flexibility promotes collective consistency in a social insect." *Scientific reports* 8.1 (2018): 1-11.

Gavini, Sabrina S., Carolina Quintero, and Mariana Tadey. "Intraspecific variation in body size of bumblebee workers influences anti-predator behaviour." *Journal of Animal Ecology* 89.2 (2020): 658-669.

Gil, Mariana, Rodrigo J. De Marco, and Randolf Menzel. "Learning reward expectations in honeybees." *Learning & Memory* 14.7 (2007): 491-496.

Gill, Richard J., Oscar Ramos-Rodriguez, and Nigel E. Raine. "Combined pesticide exposure severely affects individual-and colony-level traits in bees." *Nature* 491.7422 (2012): 105-108.

Giurfa, Martin, and Jean-Christophe Sandoz. "Invertebrate learning and memory: fifty years of olfactory conditioning of the proboscis extension response in honeybees." *Learning & memory* 19.2 (2012): 54-66.

Giurfa, Martin, and Maria Gabriela de Brito Sanchez. "Black Lives Matter: Revisiting Charles Henry Turner’s experiments on honey bee color vision." *Current Biology* 30.20 (2020): R1235-R1239.

Goodale, Eben, and James C. Nieh. "Public use of olfactory information associated with predation in two species of social bees." *Animal Behaviour* 84.4 (2012): 919-924.

Goulson, Dave, et al. "Bee declines driven by combined stress from parasites, pesticides, and lack of flowers." *Science* 347.6229 (2015).

Goulson, Dave, et al. "Can alloethism in workers of the bumblebee, Bombus terrestris, be explained in terms of foraging efficiency?." *Animal Behaviour* 64.1 (2002): 123-130.

Goulson, Dave, et al. "Identity and function of scent marks deposited by foraging bumblebees." *Journal of Chemical Ecology* 26.12 (2000): 2897-2911.

Goulson, Dave, et al. "Social learning drives handedness in nectar-robbing bumblebees." *Behavioral Ecology and Sociobiology* 67.7 (2013): 1141-1150.

Goulson, Dave. *Bumblebees: behaviour, ecology, and conservation*. Oxford University Press on Demand, 2010.

Granero, Angeles Mena, et al. "Chemical compounds of the foraging recruitment pheromone in bumblebees." *Naturwissenschaften* 92.8 (2005): 371-374.

Grüter, Christoph, and Ellouise Leadbeater. "Insights from insects about adaptive social information use." *Trends in Ecology & Evolution* 29.3 (2014): 177-184.

Hammer, Tobin J., Curtis Hata, and James C. Nieh. "Thermal learning in the honeybee, Apis mellifera." *Journal of Experimental Biology* 212.23 (2009): 3928-3934.

Harrap, Michael JM, et al. "Bumblebees can detect floral humidity." *bioRxiv* (2021).

Harrap, Michael JM, et al. "The diversity of floral temperature patterns, and their use by pollinators." *Elife* 6 (2017): e31262.

Heinrich, Bernd. "The foraging specializations of individual bumblebees." *Ecological monographs* 46.2 (1976): 105-128.

I'Anson Price, R, et al. "Honeybees forage more successfully without the “dance language” in challenging environments." *Science advances* 5.2 (2019): eaat0450.

Incorvaia, Darren C., Arend Hintze, and Fred C. Dyer. "Spatial allocation without spatial recruitment in bumblebees." *Behavioral Ecology* 32.2 (2021): 265-276.

Ings, T. C., M-Y. Wang, and L. Chittka. "Colour-independent shape recognition of cryptic predators by bumblebees." *Behavioral Ecology and Sociobiology* 66.3 (2012): 487-496.

Ings, Thomas C., and Lars Chittka. "Predator crypsis enhances behaviourally mediated indirect effects on plants by altering bumblebee foraging preferences." Proceedings of the Royal Society B: Biological Sciences 276.1664 (2009): 2031-2036.

Ings, Thomas C., and Lars Chittka. "Predator crypsis enhances behaviourally mediated indirect effects on plants by altering bumblebee foraging preferences." *Proceedings of the Royal Society B: Biological Sciences* 276.1664 (2009): 2031-2036.

Jennersten, Ola, Douglass H. Morse, and Pamela O'Neil. "Movements of male and worker bumblebees on and between flowers." *Oikos* (1991): 319-324.

Jones, Emily I., and Anna Dornhaus. "Predation risk makes bees reject rewarding flowers and reduce foraging activity." *Behavioral Ecology and Sociobiology* 65.8 (2011): 1505-1511.

Jones, Walton. "Olfactory carbon dioxide detection by insects and other animals." *Molecules and cells* 35.2 (2013): 87-92.

Katz, Keziah, and Dhruba Naug. "Energetic state regulates the exploration–exploitation trade-off in honeybees." *Behavioral Ecology* 26.4 (2015): 1045-1050.

Kawaguchi, Lina G., Kazuharu Ohashi, and Yukihiko Toquenaga. "Contrasting responses of bumble bees to feeding conspecifics on their familiar and unfamiliar flowers." *Proceedings of the Royal Society B: Biological Sciences* 274.1626 (2007): 2661-2667.

Keasar, Tamar, Uzi Motro, and Avi Shmida. "Temporal reward variability promotes sampling of a new flower type by bumblebees." *Animal behaviour* 86.4 (2013): 747-753.

Kessler, Sébastien C., et al. "Bees prefer foods containing neonicotinoid pesticides." *Nature* 521.7550 (2015): 74-76.

Kirschvink, J., et al. "Measurement of the threshold sensitivity of honeybees to weak, extremely low-frequency magnetic fields." *Journal of Experimental Biology* 200.9 (1997): 1363-1368.

Kitaoka, T. K., and J. C. Nieh. "Bumble bee pollen foraging regulation: role of pollen quality, storage levels, and odor." *Behavioral Ecology and Sociobiology* 63.4 (2009): 501-510.

Klaps, Joon, Bart Lievens, and Sergio Álvarez-Pérez. "Towards a better understanding of the role of nectar-inhabiting yeasts in plant–animal interactions." *Fungal biology and biotechnology* 7.1 (2020): 1-7.

Klein, Simon, et al. "Inter-individual variability in the foraging behaviour of traplining bumblebees." *Scientific reports* 7.1 (2017): 1-12.

Knauer, Anina C., and Florian *p*. Schiestl. "Bees use honest floral signals as indicators of reward when visiting flowers." *Ecology letters* 18.2 (2015): 135-143.

Krishna, Shivani, and Tamar Keasar. "Bumblebees forage on flowers of increasingly complex morphologies despite low success." *Animal Behaviour* 155 (2019): 119-130.

Kulahci, Ipek G., Anna Dornhaus, and Daniel R. Papaj. "Multimodal signals enhance decision making in foraging bumble-bees." *Proceedings of the Royal Society B: Biological Sciences* 275.1636 (2008): 797-802.

Kunze, Jan, and Andreas Gumbert. "The combined effect of color and odor on flower choice behavior of bumble bees in flower mimicry systems." *Behavioral Ecology* 12.4 (2001): 447-456.

Laidre, Mark E., and Rufus A. Johnstone. "Animal signals." *Current Biology* 23.18 (2013): R829-R833.

Laverty, Terence M. "Costs to foraging bumble bees of switching plant species." *Canadian Journal of Zoology* 72.1 (1994): 43-47.

Leadbeater, Ellouise, and Claire Florent. "Foraging bumblebees do not rate social information above personal experience." *Behavioral ecology and sociobiology* 68.7 (2014): 1145-1150.

Leadbeater, Ellouise, and Lars Chittka. "Do inexperienced bumblebee foragers use scent marks as social information?." *Animal cognition* 14.6 (2011): 915.

Leadbeater, Ellouise, and Lars Chittka. "Social learning in insects—from miniature brains to consensus building." *Current biology* 17.16 (2007a): R703-R713.

Leadbeater, Ellouise, and Lars Chittka. "Social transmission of nectar-robbing behaviour in bumble-bees." *Proceedings of the Royal Society B: Biological Sciences* 275.1643 (2008): 1669-1674.

Leadbeater, Ellouise, and Lars Chittka. "The dynamics of social learning in an insect model, the bumblebee (Bombus terrestris)." *Behavioral Ecology and Sociobiology* 61.11 (2007b): 1789-1796.

Lee, Danielle N. "Diversity and inclusion activisms in animal behaviour and the ABS: a historical view from the USA." *Animal Behaviour* (2020).

Leonard, Anne S., and Daniel R. Papaj. "'X'marks the spot: The possible benefits of nectar guides to bees and plants." *Functional Ecology* 25.6 (2011): 1293-1301.

Leonard, Anne S., and Pavel Masek. "Multisensory integration of colors and scents: insights from bees and flowers." *Journal of Comparative Physiology A* 200.6 (2014): 463-474.

Leonard, Anne S., Anna Dornhaus, and Daniel R. Papaj. "Flowers help bees cope with uncertainty: signal detection and the function of floral complexity." *Journal of Experimental Biology* 214.1 (2011): 113-121.

Leonard, Anne S., et al. "Floral nectar guide patterns discourage nectar robbing by bumble bees." *PLoS One* 8.2 (2013): e55914.

Liang, Chao-Hung, et al. "Magnetic sensing through the abdomen of the honey bee." *Scientific reports* 6.1 (2016): 1-7.

Lichtenstein, Leonie, Frank MJ Sommerlandt, and Johannes Spaethe. "Dumb and lazy? A comparison of color learning and memory retrieval in drones and workers of the buff-tailed bumblebee, Bombus terrestris, by means of PER conditioning." *PloS one* 10.7 (2015): e0134248.

Lihoreau, Mathieu, Lars Chittka, and Nigel E. Raine. "Travel optimization by foraging bumblebees through readjustments of traplines after discovery of new feeding locations." *The American Naturalist* 176.6 (2010): 744-757.

Loukola, Olli J., et al. "Bumblebees show cognitive flexibility by improving on an observed complex behavior." *Science* 355.6327 (2017): 833-836.

Mayack, Christopher, and Dhruba Naug. "Individual energetic state can prevail over social regulation of foraging in honeybees." *Behavioral Ecology and Sociobiology* 67.6 (2013): 929-936.

Mayack, Christopher, and Dhruba Naug. "Starving honeybees lose self-control." *Biology letters* 11.1 (2015): 20140820.

McAulay, Megan K., Gard W. Otis, and Angela E. Gradish. "Honeypot visitation enables scent learning and heightens forager response in bumblebees (Bombus impatiens)." *Learning and Motivation* 50 (2015): 22-31.

Molet, Mathieu, et al. "Colony nutritional status modulates worker responses to foraging recruitment pheromone in the bumblebee Bombus terrestris." *Behavioral Ecology and Sociobiology* 62.12 (2008): 1919-1926.

Molet, Mathieu, Lars Chittka, and Nigel E. Raine. "How floral odours are learned inside the bumblebee (Bombus terrestris) nest." *Naturwissenschaften* 96.2 (2009): 213-219.

Møller, Anders Pape. "Bumblebee preference for symmetrical flowers." *Proceedings of the National Academy of Sciences* 92.6 (1995): 2288-2292.

Moore, Darrell, Byron N. Van Nest, and Edith Seier. "Diminishing returns: the influence of experience and environment on time-memory extinction in honey bee foragers." *Journal of Comparative Physiology A* 197.6 (2011): 641-651.

Moyroud, Edwige, et al. "Disorder in convergent floral nanostructures enhances signalling to bees." *Nature* 550.7677 (2017): 469-474.

Muller, Helene, and Lars Chittka. "Consistent interindividual differences in discrimination performance by bumblebees in colour, shape and odour learning tasks (Hymenoptera: Apidae: Bombus terrestris)." *Entomologia Generalis* 34.1 (2012): 1.

Muth, F., and A. S. Leonard. "A neonicotinoid pesticide impairs foraging, but not learning, in free-flying bumblebees." *Scientific reports* 9.1 (2019): 1-13.

Muth, Felicity, et al. "A pollen fatty acid enhances learning and survival in bumblebees." *Behavioral Ecology* 29.6 (2018): 1371-1379.

Muth, Felicity, et al. "No sex differences in learning in wild bumblebees." *Behavioral Ecology* (2021).

Muth, Felicity, Jacob S. Francis, and Anne S. Leonard. "Bees use the taste of pollen to determine which flowers to visit." *Biology Letters* 12.7 (2016): 20160356.

Muth, Felicity, Jacob S. Francis, and Anne S. Leonard. "Modality-specific impairment of learning by a neonicotinoid pesticide." *Biology letters* 15.7 (2019): 20190359.

Muth, Felicity, Rebekah L. Gaxiola, and Anne S. Leonard. "No evidence for neonicotinoid preferences in the bumblebee Bombus impatiens." *Royal Society open science* 7.5 (2020): 191883.

Nicolson, Susan W., et al. "Honeybees prefer warmer nectar and less viscous nectar, regardless of sugar concentration." *Proceedings of The Royal Society B: Biological Sciences* 280.1767 (2013): 20131597.

Ostevik, Katherine L., Jessamyn S. Manson, and James D. Thomson. "Pollination potential of male bumble bees (Bombus impatiens): movement patterns and pollen-transfer efficiency." *Journal of Pollination Ecology* 2.4 (2010): 21-26.

Pearce, Richard F., Luca Giuggioli, and Sean A. Rands. "Bumblebees can discriminate between scent-marks deposited by conspecifics." *Scientific reports* 7.1 (2017): 1-11.

Pereira-Bomfim, Maria da Graça Cardoso, William Fernando Antonialli-Junior, and Daniel Acosta-Avalos. "Effect of magnetic field on the foraging rhythm and behavior of the swarm-founding paper wasp Polybia paulista Ihering (Hymenoptera: Vespidae)." *Sociobiology* 62.1 (2015): 99-104.

Phelps, Jordan D., Caroline G. Strang, and David F. Sherry. "Imidacloprid impairs performance on a model flower handling task in bumblebees (Bombus impatiens)." *Ecotoxicology* 29.3 (2020): 359-374.

Pleasants, John M. "Bumblebee response to variation in nectar availability." *Ecology* 62.6 (1981): 1648-1661.

Pozo, María I., et al. "The impact of yeast presence in nectar on bumble bee behavior and fitness." *Ecological Monographs* 90.1 (2020): e01393.

Pyke, Graham H. "Optimal foraging: movement patterns of bumblebees between inflorescences." Theoretical population biology 13.1 (1978): 72-98.

Raguso, Robert A. "Flowers as sensory billboards: progress towards an integrated understanding of floral advertisement." Current opinion in plant biology 7.4 (2004): 434-440.

Real, Leslie A. "Uncertainty and pollinator-plant interactions: The foraging behavior of bees and wasps on artificial flowers." Ecology 62.1 (1981): 20-26.

Renner, M. A., and J. C. Nieh. "Bumble bee olfactory information flow and contact-based foraging activation." *Insectes sociaux* 55.4 (2008): 417-424.

Riveros, Andre J., and Wulfila Gronenberg. "Decision-making and associative color learning in harnessed bumblebees (Bombus impatiens)." *Animal cognition* 15.6 (2012): 1183-1193.

Riveros, Andre J., and Wulfila Gronenberg. "Olfactory learning and memory in the bumblebee Bombus occidentalis." *Naturwissenschaften* 96.7 (2009): 851-856.

Romero, Gustavo Q., Pablo AP Antiqueira, and Julia Koricheva. "A meta-analysis of predation risk effects on pollinator behaviour." PloS one 6.6 (2011): e20689.

Ruedenauer, Fabian A., et al. "Bumblebees are able to perceive amino acids via chemotactile antennal stimulation." *Journal of Comparative Physiology A* 205.3 (2019): 321-331.

Russell, Avery L., and Tia-Lynn Ashman. "Associative learning of flowers by generalist bumble bees can be mediated by microbes on the petals." *Behavioral Ecology* 30.3 (2019): 746-755.

Russell, Avery L., et al. "Bees learn preferences for plant species that offer only pollen as a reward." *Behavioral Ecology* 27.3 (2016): 731-740.

Russell, Avery L., et al. "Movers and shakers: Bumble bee foraging behavior shapes the dispersal of microbes among and within flowers." *Ecosphere* 10.5 (2019): e02714.

Saleh, Nehal, and Lars Chittka. "Traplining in bumblebees (Bombus impatiens): a foraging strategy's ontogeny and the importance of spatial reference memory in short-range foraging." *Oecologia* 151.4 (2007): 719-730.

Saleh, Nehal, et al. "Facultative use of the repellent scent mark in foraging bumblebees: complex versus simple flowers." Animal Behaviour 71.4 (2006): 847-854.

Schmitt, Ulrich, Gunther Lübke, and Wittko Francke. "Tarsal secretion marks food sources in bumblebees (Hymenoptera: Apidae)." *Chemoecology* 2.1 (1991): 35-40.

Schürch, Roger, and Christoph Grüter. "Dancing bees improve colony foraging success as long-term benefits outweigh short-term costs." *PLoS One* 9.8 (2014): e104660.

Seeley, Thomas D., Scott Camazine, and James Sneyd. "Collective decision-making in honey bees: how colonies choose among nectar sources." *Behavioral Ecology and Sociobiology* 28.4 (1991): 277-290.

Shannon, Claude E. "A mathematical theory of communication." *The Bell system technical journal* 27.3 (1948): 379-423.

Sherman, Gavin, and P. Kirk Visscher. "Honeybee colonies achieve fitness through dancing." *Nature* 419.6910 (2002): 920-922.

Sherry, David F., and Caroline G. Strang. "Contrasting styles in cognition and behaviour in bumblebees and honeybees." *Behavioural processes* 117 (2015): 59-69.

Shi, Lianhui, et al. "Drinking made easier: honey bee tongues dip faster into warmer and/or less viscous artificial nectar." *Journal of Experimental Biology* 223.18 (2020).

Somme, Laurent, et al. "Pollen and nectar quality drive the major and minor floral choices of bumble bees." *Apidologie* 46.1 (2015): 92-106.

Sommerlandt, Frank MJ, Wolfgang Rössler, and Johannes Spaethe. "Elemental and non-elemental olfactory learning using PER conditioning in the bumblebee, Bombus terrestris." *Apidologie* 45.1 (2014): 106-115.

Soroye, Peter, Tim Newbold, and Jeremy Kerr. "Climate change contributes to widespread declines among bumble bees across continents." Science 367.6478 (2020): 685-688.

Spaethe, J., et al. "Adaptation, constraint, and chance in the evolution of flower color and pollinator color vision." *Cognitive ecology of pollination: animal behavior and floral evolution*. Cambridge University Press., 2001.

Stelzer, Ralph Jürgen, Ralf Stanewsky, and Lars Chittka. "Circadian foraging rhythms of bumblebees monitored by radio-frequency identification." *Journal of Biological Rhythms* 25.4 (2010): 257-267.

Stout, Jane C., and Dave Goulson. "The influence of nectar secretion rates on the responses of bumblebees (Bombus spp.) to previously visited flowers." *Behavioral Ecology and Sociobiology* 52.3 (2002): 239-246.

Stout, Jane C., John A. Allen, and Dave Goulson. "The influence of relative plant density and floral morphological complexity on the behaviour of bumblebees." *Oecologia* 117.4 (1998): 543-550.

Strube-Bloss, Martin F., et al. "Extracting the behaviorally relevant stimulus: unique neural representation of farnesol, a component of the recruitment pheromone of Bombus terrestris." *PLoS One* 10.9 (2015): e0137413.

Sumpter, D., and Stephen Pratt. "A modelling framework for understanding social insect foraging." *Behavioral Ecology and Sociobiology* 53.3 (2003): 131-144.

Sumpter, David JT. "The principles of collective animal behaviour." *Philosophical transactions of the royal society B: Biological Sciences* 361.1465 (2006): 5-22.

Sutton, Gregory P., et al. "Mechanosensory hairs in bumblebees (Bombus terrestris) detect weak electric fields." *Proceedings of the National Academy of Sciences* 113.26 (2016): 7261-7265.

Tan, Ken, et al. "Preferences and tradeoffs in nectar temperature and nectar concentration in the Asian hive bee Apis cerana." *Behavioral Ecology and Sociobiology* 68.1 (2014): 13-20.

Thomson, James D. "Effects of variation in inflorescence size and floral rewards on the visitation rates of traplining pollinators of Aralia hispida." *Evolutionary Ecology* 2.1 (1988): 65-76.

Thomson, James D., and Karen Goodell. "Pollen removal and deposition by honeybee and bumblebee visitors to apple and almond flowers." *Journal of Applied ecology* (2001): 1032-1044.

Tinbergen, Niko. "On aims and methods of ethology." *Zeitschrift für tierpsychologie* 20.4 (1963): 410-433.

Toth, Amy L., and Gene E. Robinson. "Worker nutrition and division of labour in honeybees." *Animal behaviour* 69.2 (2005): 427-435.

Townsend-Mehler, John M., Fred C. Dyer, and Kim Maida. "Deciding when to explore and when to persist: a comparison of honeybees and bumblebees in their response to downshifts in reward." *Behavioral ecology and sociobiology* 65.2 (2011): 305-312.

Tsujimoto, Shohei G., and Hiroshi S. Ishii. "Effect of flower perceptibility on spatial-reward associative learning by bumble bees." *Behavioral Ecology and Sociobiology* 71.7 (2017): 1-11.

Turner, C. H. "Experiments on color-vision of the honey bee." *The Biological Bulletin* 19.5 (1910): 257-279.

Vannette, Rachel L. "The floral microbiome: Plant, pollinator, and microbial perspectives." *Annual Review of Ecology, Evolution, and Systematics* 51 (2020): 363-386.

Vannette, Rachel L., and Tadashi Fukami. "Contrasting effects of yeasts and bacteria on floral nectar traits." *Annals of botany* 121.7 (2018): 1343-1349.

Vaudo, Anthony D., et al. "Consistent pollen nutritional intake drives bumble bee (Bombus impatiens) colony growth and reproduction across different habitats." *Ecology and evolution* 8.11 (2018): 5765-5776.

Vaudo, Anthony D., et al. "Macronutrient ratios in pollen shape bumble bee (Bombus impatiens) foraging strategies and floral preferences." *Proceedings of the National Academy of Sciences* 113.28 (2016): E4035-E4042.

Velthuis, Hayo HW, and Adriaan Van Doorn. "A century of advances in bumblebee domestication and the economic and environmental aspects of its commercialization for pollination." *Apidologie* 37.4 (2006): 421-451.

Von Arx, Martin, et al. "Floral humidity as a reliable sensory cue for profitability assessment by nectar-foraging hawkmoths." *Proceedings of the National Academy of Sciences* 109.24 (2012): 9471-9476.

Von Frisch, Karl. "Der farbensinn und formensinn der biene." (1914).

Wagner, Ashley E., et al. "Persistence, reticence and the management of multiple time memories by forager honey bees." *Journal of Experimental Biology* 216.7 (2013): 1131-1141.

Walker, Michael M., and M. E. Bitterman. "Conditioned responding to magnetic fields by honeybees." *Journal of Comparative Physiology A* 157.1 (1985): 67-71.

Wang, Xiao-Yue, et al. "Bumblebee rejection of toxic pollen facilitates pollen transfer." *Current Biology* 29.8 (2019): 1401-1406.

Weidenmüller, Anja, Christoph Kleineidam, and Jürgen Tautz. "Collective control of nest climate parameters in bumblebee colonies." *Animal Behaviour* 63.6 (2002): 1065-1071.

Weidenmüller, Anja. "The control of nest climate in bumblebee (Bombus terrestris) colonies: interindividual variability and self reinforcement in fanning response." *Behavioral Ecology* 15.1 (2004): 120-128.

Whitehorn, Penelope R., et al. "Neonicotinoid pesticide reduces bumble bee colony growth and queen production." *Science* 336.6079 (2012): 351-352.

Whitney, Heather M., et al. "Conical epidermal cells allow bees to grip flowers and increase foraging efficiency." *Current Biology* 19.11 (2009b): 948-953.

Whitney, Heather M., et al. "Floral iridescence, produced by diffractive optics, acts as a cue for animal pollinators." *Science* 323.5910 (2009a): 130-133.

Whitney, Heather M., et al. "The interaction of temperature and sucrose concentration on foraging preferences in bumblebees." *Naturwissenschaften* 95.9 (2008): 845-850.

Wiegmann, Daniel D., Douglas A. Wiegmann, and Faith A. Waldron. "Effects of a reward downshift on the consummatory behavior and flower choices of bumblebee foragers." *Physiology & behavior* 79.4-5 (2003): 561-566.

Wiegmann, Daniel D., et al. "Transposition of flower height by bumble bee foragers (Bombus impatiens)." *Animal Cognition* 3.2 (2000): 85-89.

Wilms, Jessica, and Thomas Eltz. "Foraging scent marks of bumblebees: footprint cues rather than pheromone signals." *Naturwissenschaften* 95.2 (2008): 149-153.

Wolf, Stephan, and Lars Chittka. "Male bumblebees, Bombus terrestris, perform equally well as workers in a serial colour-learning task." *Animal behaviour* 111 (2016): 147-155.

Woodgate, Joseph L., et al. "Continuous radar tracking illustrates the development of multi-destination routes of bumblebees." *Scientific reports* 7.1 (2017): 1-15.

Worden, Bradley D., and Daniel R. Papaj. "Flower choice copying in bumblebees." *Biology Letters* 1.4 (2005): 504-507.

CHAPTER 2: SHORT AND LONG-TERM MODULATION OF FORAGER MOTIVATION BY COLONY STATE IN BUMBLEBEES

The question of how animals make decisions has been intensely studied by ethologists, behavioral ecologists, psychologists, and neuroscientists alike. Foraging bumblebees are an excellent system in which to study decision-making because, as eusocial insects, foragers are solely focused on the task of collecting food for the colony. Bumblebees are generalist foragers of ephemeral resources who do not store food long-term, and are thus expected to show flexible adjustments in foraging motivation in response to stored food. However, their feeding behavior at resources as a function of stored food has not been explored. Here, we present results demonstrating that bumblebees show flexible adjustments in foraging motivation in response to colony food stores across different time scales. First, bumblebees show decreased foraging motivation as the colony accumulates food over the course of a day. Second, bees that develop in colonies with full food stores show persistently lower motivation than bees developing in colonies with impoverished food stores even days after those food stores are removed. We further demonstrate that this persistent low motivation may be explained by the total amount of abdominal lipids in well-nourished vs. nutrient-depleted colonies. Our results provide evidence for a mechanism that may mediate the social control of individual foraging motivation, an important step in the evolution of eusociality.

INTRODUCTION

Animals with complex behavioral repertoires may have the potential to perform an uncountable number of possible actions, yet at any given time an animal can only perform one. How does the animal decide what to do? The study of decision-making has long interested ethologists (McFarland 1977, Dukas 1998, Couzin et al. 2005), psychologists (Deci and Ryan 1985; Svenson 1996), and neuroscientists (Basten et al. 2010), and this research shows that the process of making decisions can be influenced by many factors. One important factor is the motivational state of the animal, which itself can be influenced by both physiological mechanisms, such as circulating lipid concentrations (Toprak et al. 2020) or an emotional response from a recent traumatic event (Bateson et al. 2011), and external stimuli, such as the presence of a predator (Ings and Chittka 2009). Motivational state can influence the threshold a stimulus must reach before an animal will respond to it (Pankiw et al. 2001, Scheiner et al. 2004), or the strength of the response itself (Crespi 1942).

One behavior that depends strongly upon motivational state is foraging. Animals are known to alter their foraging behavior (such as whether to forage at all, how long to forage, and what patches to forage from) depending on internal variables such as fat stores or nutrient levels (Witter and Cuthill 1993), as well as on the risk of predation (e.g. Dill 1983; Kohler and McPeek 1989; Relyea 2001) and previous foraging experience (Barker et al. 2018). Indeed, foraging animals have been assumed for decades to attempt to maximize the amount of energy they bring in (Pyke 1984) while minimizing costs associated with foraging (Caraco et al. 1980, McNamara and Houston 1992). Balancing such benefits and costs demands flexibility in behavior that is sensitive to the context: for example, an animal that is starving should be more willing to incur foraging costs, whereas an animal that is well-fed should not (e.g. Cartar 1991, Blecha et al. 2018).

Eusocial insects present a unique opportunity for the study of foraging and motivation because their colonies contain a work force devoted solely to the task of collecting food resources. Foraging social insects, therefore, must often respond to the need of the colony rather than their own personal nutritive needs, and while working as foragers they are singularly focused on that task. One of the most well-studied groups of these social insects are the bumblebees (Family: Apidae, Genus: *Bombus*). Bumblebee colonies consist of a single queen and a work force of her sterile daughters, some of which tend to forage and others that tend to perform in-nest tasks (Goulson et al. 2002, Goulson 2010). There are 250 species of bumblebee spread across the globe (Goulson 2010; Williams et al. 2014), and their charisma combined with their ecological importance has made them a favorite for researchers interested in foraging behavior.

For nectar-feeding social bees, a major factor that can potentially influence the costs and benefits of foraging, and hence the motivation of foraging workers, is the colony's need for more nectar. Bumblebees are closely related to honeybees (Danforth et al. 2019), but show many striking differences, among which is the tendency to store food only for a few days at a time (Goulson 2010). This is explained by their annual life cycle, which does not require massive stores of food as does the perennial lifestyle of honeybees. This leads to an interesting difference between the closely related bumblebees and honeybees; roughly speaking, whereas honeybees remain ravenous for nectar so long as there is empty comb in the nest in which to receive it, the foraging motivation of bumblebees seems more sensitive to the colony's current food stores, and to the quality of incoming food, even when the nest is not full of food (Dornhaus and Chittka

2005, Incorvaia et al. 2021). Bumblebee foraging activity increases when food stores are low or when a high-quality resource is brought back to the nest, but decreases when food stores are high (Cartar 1992, Dornhaus and Chittka 2004, Dornhaus and Chittka 2005) but before the nest is full (Cartar 1992).

Although much is known about how colony nutritive state affects the overall foraging activity of bumblebee colonies on the level of the group, the impacts of colony state on individual-level foraging behavior remains less explored, and is often limited to studies of resource choice (e.g. Cartar 1991) rather than consummatory behavior at a food source—specifically, whether a forager accepts a reward of a given quality. Understanding how colony state influences individual consummatory behavior is important, because consumption of resources is the ultimate marker of an individual's decision to feed. Therefore, if we wish to understand how colony state, as a component of the social environment, influences individual decision-making, it is imperative that we examine consummatory behavior and not just presence or absence of foragers at a food source.

In this study, we sought to determine the effects of colony nutritive state on individual-level foraging decisions in the bumblebee *Bombus impatiens*. Based on prior observations, we hypothesized that colony food stores would influence individual consummatory behavior at a sugar source in the environment. From this hypothesis we predicted, first, that forager bumblebees would show high motivation to feed outside the nest at the beginning of the day, and declining motivation as food is brought in; and second, that foraging activity and motivation to feed will be depressed (both initially and after foraging has begun) when the colony already contains a large amount of stored food. In addition to testing these predictions, we also investigated the long-term effects of stored food on foragers from colonies that had a history of being well provisioned with sugar; our prediction here, based upon preliminary observations, was that foragers would continue to show reduced foraging motivation for several days after the colony's food stores are removed. Finally, we explored why this delayed effect on motivation might occur by quantifying abdominal lipids in bumblebees that developed in colonies with either full or empty food stores. Based on prior work implicating lipids as a physiological mechanism underlying feeding motivation in bees and other insects (Toth and Robinson 2005; Konuma et al. 2016; Nagata 2019), we hypothesized that the lipid levels in individual workers would be higher if they had developed in well-provisioned rather than in empty nests. Taken together, our results reveal a prominent role for colony state in modulating individual motivation in foraging bumblebees, while also implicating a potential causal mechanism underlying this motivational control.

METHODS

We conducted experiments during the summers of 2017, 2018, and 2019. In each summer we placed 8 commercial *Bombus impatiens* colonies (Koppert Biological Systems, MI, USA) in individual small flight cages (Coleman 10 ft. by 10 ft. screen canopies). Colonies were housed in East Lansing, Michigan, USA, just south of Michigan State University's campus. In 2018 and 2019, four of these colonies came provisioned with an approximately 60% sugar solution that Koppert typically provides ("syrup," or "S," colonies), while the other four came without this provisioning ("no syrup," or "NS," colonies). In 2017, we had three colonies that were provisioned and five that were not, meaning in total we used 13 unprovisioned (NS) and 11 provisioned (S) colonies in our behavioral experiment. All colonies were queenright with between 50 and 75 workers at the beginning of the experiment. Because our experiments focused on nectar-foraging, we provided colonies with *ad lib* honeybee-collected pollen placed directly into the nest.

We placed a wooden platform inside each flight cage, on top of which we could place an artificial feeder with sucrose solution. Each feeder was constructed by turning a bottlecap upside-down and covering it with a piece of wire mesh on which bees could stand while drinking the sugar solution. We set up the artificial feeders each morning, typically leaving them up for two to three hours, before removing them. We did not conduct any experiments until we confirmed that bees from each colony had discovered the feeder.

After an initial period of behavioral observation (described in more detail below) of each colony, we closed off the in-nest sugar solution given to the provisioned bees. We visually confirmed this was successful by inspecting honeypots; while the in-nest food was available the colony had the majority of its honeypots full, even before the feeders had been set up for the day, but after the in-nest sugar was taken away we observed fewer full honeypots the following day and mostly empty honeypots by the day after. Observation of foraging then continued as before.

A. Foraging Observations

We began foraging observations once workers from all colonies had discovered the feeder in their enclosure. We recorded two-hour videos of the feeders immediately after filling them with 0.5M sucrose solution; from these videos we observed each contact of a bee with the sucrose solution, and measured how long the bee's proboscis was in contact with the sucrose solution (rounded to the nearest second); we called this measure "contact duration." A contact that took place in less than a second was rounded up to one second. To document changes in motivation as the colony accumulated food from the feeder, we extracted contact durations from video for two 15-minute time periods: one immediately following feeder set-up, and the other an hour after feeder set-up. During these same observation periods, we also extracted from the videos a measure of colony foraging activity, defined as the average maximum number of bees seen simultaneously at the feeder. For example, if during the first minute of recording a maximum of 5 unique bees were visible at once, then the next minute 4 were seen, and the next minute 5 again, the measure of foraging activity would be 4.67 bees/minute. We relied on this estimate rather than a direct count because we did not individually mark the bumblebees, due to the disruption it would have caused the colonies and the time it would have taken to mark all the bees from eight colonies each field season.

B. Data Analysis

We constructed general linear mixed models using the packages "lme4" (Bates et al. 2014) and "glmmTMB" (Brooks et al. 2017) in R version 4.0.3 to perform our analyses. In what follows, "feeding behavior" refers to our measure of contact duration, while "foraging activity" refers to our counts of the number of bees seen at the feeder.

Effect of Stored Food on Feeding Behavior

To test the effect of stored food on feeding behavior, we only used data collected before the supplemental sugar was removed from the treatment colonies. Because our contact duration data can only take integer values greater than zero, we constructed a truncated negative-binomial mixed model with contact duration as the response variable. We modeled colony state (S vs. NS), time period (immediately after feeder became available vs. one hour after), and temperature as fixed effects and colony identity and year as random effects. We allowed for an interaction between colony state and time period.

Effect of Stored Food on Foraging Activity

To test the effect of stored food on foraging activity, we again only used data collected before the supplemental sugar was removed from the treatment colonies. Because our foraging activity data includes decimals, a truncated negative-binomial distribution was not appropriate; instead, we constructed a general linear mixed model with foraging activity (in bees per minute) as the response variable. We modeled colony state (S vs. NS), time period (immediately after feeder became available or one hour after), and temperature as fixed effects and colony identity and year as random effects.

Effect of Removing Supplemental Sugar on Feeding Behavior

To test how feeding behavior changed after removing supplemental food from the S colonies, we used only data collected after the food was removed. We also chose to focus on data from the first daily observation period, as this reflects behavior at the beginning of a day of foraging, when the colonies should be maximally motivated. We again constructed a truncated negative-binomial mixed model with contact duration as the response variable. We modeled colony state (S vs. NS), days after removing food, and temperature as fixed effects, with colony identity and year serving as random effects. We allowed for an interaction between colony state and days after removing food.

Effect of Removing Supplemental Sugar on Foraging Activity

To test how foraging activity changed after removing supplemental food from the S colonies, we again used only data collected after the food was removed and from the first time period. We again constructed a general linear mixed model with foraging activity as the response variable. We modeled colony state (S vs. NS), days after removing food, and temperature as fixed effects, with colony identity and year as random effects. We again allowed for an interaction between colony state and days after removing food.

Lipid Analysis

To examine the relationship between abdominal lipids and foraging behavior we used eight colonies of *B. impatiens*, separate from the colonies used for behavioral analysis. We kept these colonies in a laboratory, and prevented bees from leaving the nest to forage or for any other purpose. We allowed four of the colonies to keep supplemental sugar provided by Koppert (corresponding to the S treatment in the behavioral study), while we removed this sugar source from the other four colonies (corresponding to the NS treatment). We fed all colonies a minimal quota of 5 mL of 0.5M sucrose solution every day (to prevent starvation), along with *ad lib* pollen. After one week under this feeding regime, we removed the supplemental sugar syrup from the S colonies. We discontinued all feeding for two days to allow the bees' crops to empty (Couvillon et al. 2011), and then flash froze all colonies at -80^{o} C (considered a humane way to euthanize bees, as their natural response to cold is to enter torpor and they thus die in a torpid state; see Heinrich 1993 and Jones et al. 2015). We then sampled 10 bees from each colony for the lipid analysis, for a total of 80 bees evenly split between treatment conditions.

We quantified abdominal lipids using a sulfo-phospho-vanillin colorimetric assay, modified from Toth and Robinson (2005), whose assay was based on work done by Amenta (1964). In short, we separated the abdomens from bee workers and removed the digestive tract (leaving the cuticle). We homogenized abdomen cuticles using a motorized pestle and placed them in 2:1 chloroform-methanol solution, leaving them overnight to extract. Following extraction, we dried samples completely in a Savant SS21 vacuum centrifuge (ThermoFisher, Waltham, MA, USA), added sulfuric acid, and then boiled for 15 minutes. Following boiling, we added vanillin reagent (vanillin and 85% phosphoric acid) to a 200 uL aliquot of each sample, vortexed, and left the samples in a dark area for 15 minutes to allow the reaction to occur. We then read absorbance of the samples at 525 nm using a Molecular Devices Softmax Pro5 Microplate Spectrophotometer. We compared the results to a cholesterol standard curve to calculate the amount of lipid. We adjusted lipid quantities by body mass, and used this adjusted lipid amount in our analyses. The samples used for lipid quantification were weighed “wet,” but we also wanted to estimate lipid quantity per unit dry mass. This is because wet mass could be influenced by bees having different amounts of water or nectar in their bodies at the time they died, which would alter mass in a way that isn’t biologically meaningful. To address this we weighed a separate sample of 80 bees before and after drying, then created a linear model (R^2 = 0.899) that we used to predict the dry mass of the original samples based on their wet mass.

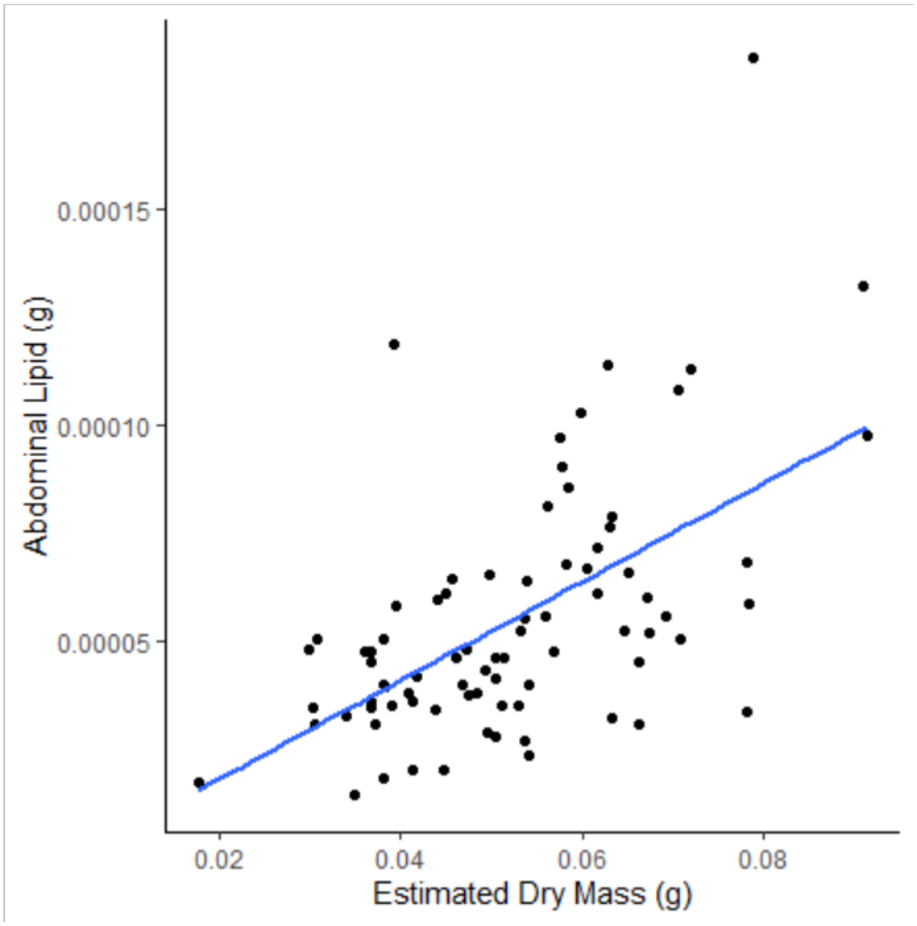

Figure 2.1. Relationship between abdominal lipids and estimated dry mass in 80 bumblebees sampled from 8 colonies (4 NS and 4 S). Dry mass for these bees was estimated from a linear model of wet mass vs. dry mass from 80 different bumblebees (see methods). There is a significant positive relationship between dry mass and abdominal lipids ($p = 0.02$).

We determined the effect of treatment (S vs. NS) on variables of interest by constructing mixed linear models in R, with treatment as a fixed effect and colony identity as a random variable.

RESULTS

Daily Pattern of Foraging Activity and Feeding Behavior

As hypothesized, we found a strong effect of time period on both contact duration and foraging activity, such that after bees had accumulated resources over an hour of foraging, they were less motivated to feed (as revealed by reduced contact duration), and showed reduced foraging activity (Figures 2.2 and 2.3). However, this reduced foraging activity in the second time period was only present for bees in the S condition; bees in the NS condition instead showed increased foraging activity in the second time period. The full model output, including effect sizes and p-values, can be found in Tables 2.1 and 2.2.

Treatment (NS vs. S) Effect

As we had hypothesized, we found a strong effect of treatment on contact duration, such that bees from S colonies fed for significantly shorter durations (implying lower motivation) than bees from NS colonies (Figure 2.2). We did not find a difference between treatments in foraging activity, though the trend, which approached statistical significance, was for S colonies to show less foraging activity than NS colonies. The full model output, including effect sizes and p-values, can be found in Tables 2.1 and 2.2.

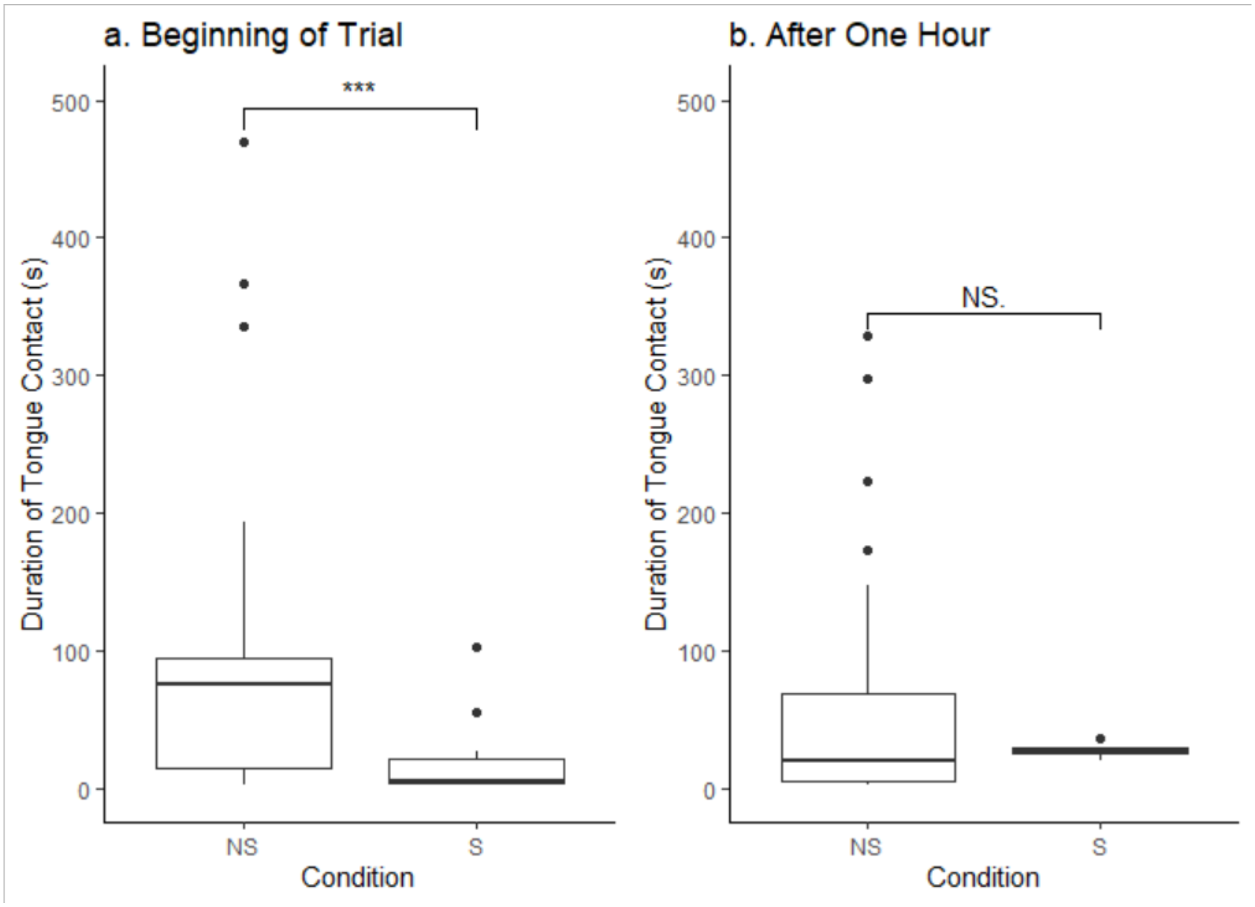

Figure 2.2. Effect of treatment condition (NS vs. S) and time period (beginning of trial vs. after one hour of foraging) on length of time bees contacted the sucrose feeder with their tongues. Bees in S colonies contacted the feeder significantly less than bees in NS colonies at the beginning of trials, but not after an hour had passed and NS colonies had accumulated sugar reserves.

Table 2.1: Effect of stored food on feeding behavior

Coefficient	**Estimate**	**Standard Error**	**z-value**	**p-value**
Condition (S vs. NS)	-1.62525	0.66568	-2.441	0.0146
Time Period (Second vs. First)	-0.66378	0.10071	-6.591	< 0.0001
Temperature (ºC)	0.01161	0.03313	0.35	0.726
Condition (S vs. NS) * Time Period (Second vs. First)	1.42510	0.8423	1.692	0.0907

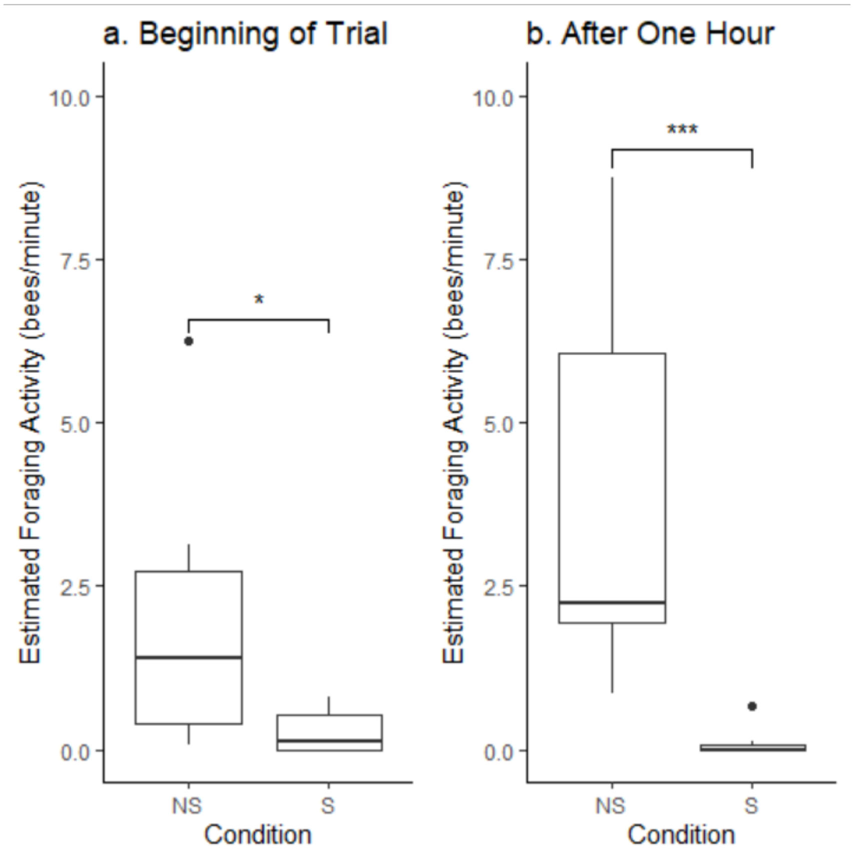

Figure 2.3. Effect of treatment condition (NS vs. S) and time period (beginning of trial vs. after one hour of foraging) on estimated foraging activity at the sucrose feeder. Bees in S colonies showed significantly less foraging activity than bees from NS colonies, and also showed less foraging activity after an hour had elapsed. Bee from NS colonies showed increased foraging activity after an hour had elapsed.

Table 2.2: Effect of stored food on foraging activity

Coefficient	**Estimate**	**Standard Error**	**t-value**	**p-value**
Condition (S vs. NS)	-1.61691894	0.8351975	-1.9359719	0.05287115
Time Period (Second vs. First)	1.95712408	0.3511851	5.5729131	< 0.0001
Temperature (°C)	0.05207896	0.1380581	0.3772251	0.7060063
Condition (S vs. NS) * Time Period (Second vs. First)	-2.07018341	0.5468221	-3.7858443	< 0.0001

Delayed Effect of Food Removal on Motivation

When we observed colonies for several days following the removal of food from S colonies, we again found that bees from S colonies continued to show significantly shorter contact durations than bees from NS colonies (Figures 2.4 and 2.5). We also found a marginally significant interaction between treatment condition and days after food removal, such that bees from S colonies slowly gained motivation to feed over time (Figure 2.4). We found no significant relationship between any of our predictors and foraging activity; most important, S and NS colonies did not differ in foraging activity on the days after food removal. The full model output, including effect sizes and p-values, can be found in Tables 2.3 and 2.4.

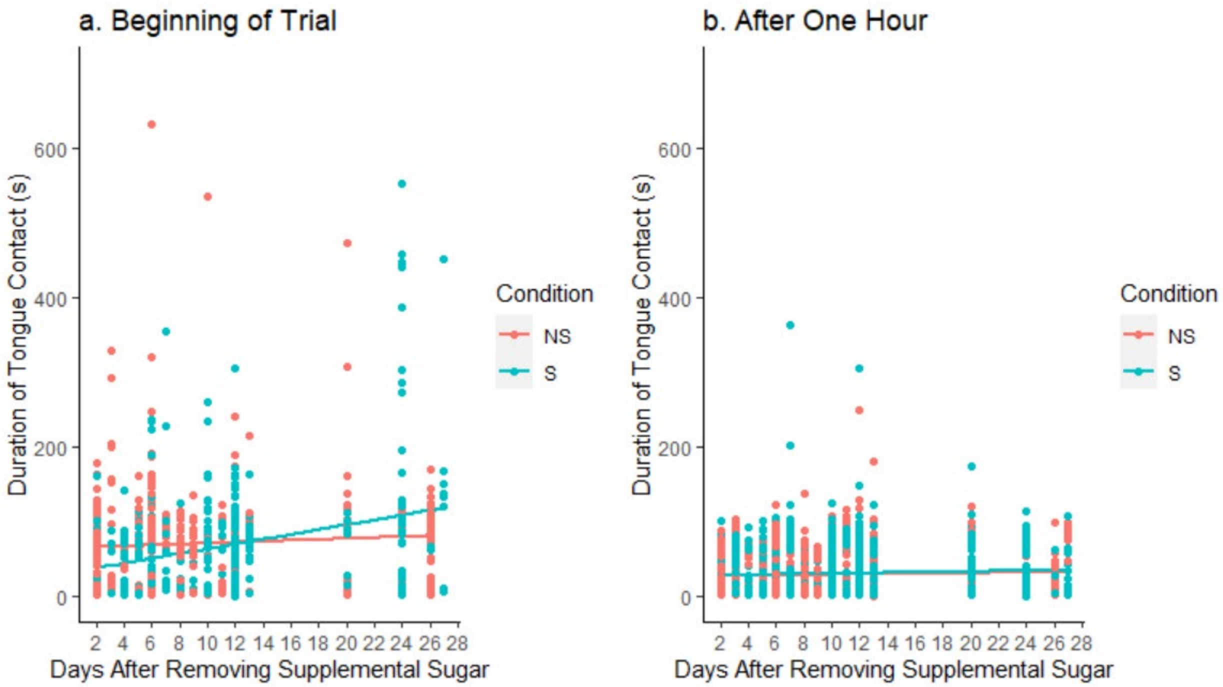

Figure 2.4. Effect of food removal on motivation to feed from sucrose feeders. Bees in S colonies contacted the feeder for significantly shorter durations than bees from NS colonies, and showed a steady increase in contact duration over time when looking at data from a) the beginning of trials, but there was no such evidence of a change across days when looking at the data b) after one hour of foraging time had passed.

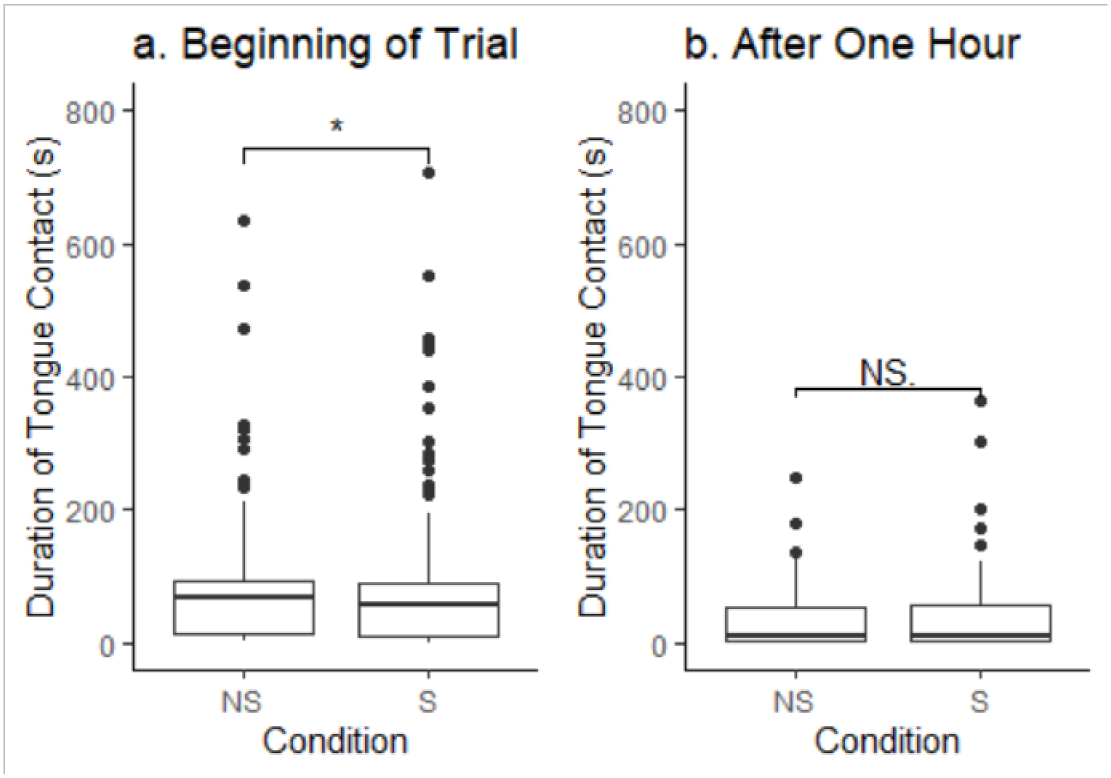

Figure 2.5. Effect of treatment condition (NS vs. S) and time period (beginning of trial vs. after one hour of foraging) on length of time bees contacted the sucrose feeder with their tongues, after food was removed from S colonies. Data were pooled across all days of observation following food removal from S colonies. Bees in S colonies contacted the feeder significantly less than bees in NS colonies at the beginning of trials, but not after an hour had passed and NS colonies had accumulated sugar reserves.

Table 2.3: Effect of food removal on feeding behavior

Coefficient	**Estimate**	**Standard Error**	**z-value**	**p-value**
Condition (S vs. NS)	-0.516052	0.174536	-2.957	0.00311
DaysAfterClosing	-0.010526	0.007311	-1.440	0.14995
Temperature (ºC)	-0.025455	0.015161	-1.679	0.09315
Condition (S vs. NS) * DaysAfterClosing	0.022420	0.011506	1.948	0.05136

Table 2.4: Effect of food removal on foraging activity

Coefficient	**Estimate**	**Standard Error**	**t-value**	**p-value**
Condition (S vs. NS)	-1.29166960	0.98425241	-1.3123357	0.18940688
DaysAfterClosing	-0.02950858	0.05265159	-0.5604498	0.57517264
Temperature (ºC)	-0.06015725	0.09851034	-0.6106694	0.54141845
Condition (S vs. NS) * DaysAfterClosing	0.04298461	0.06906611	0.6223691	0.53369920

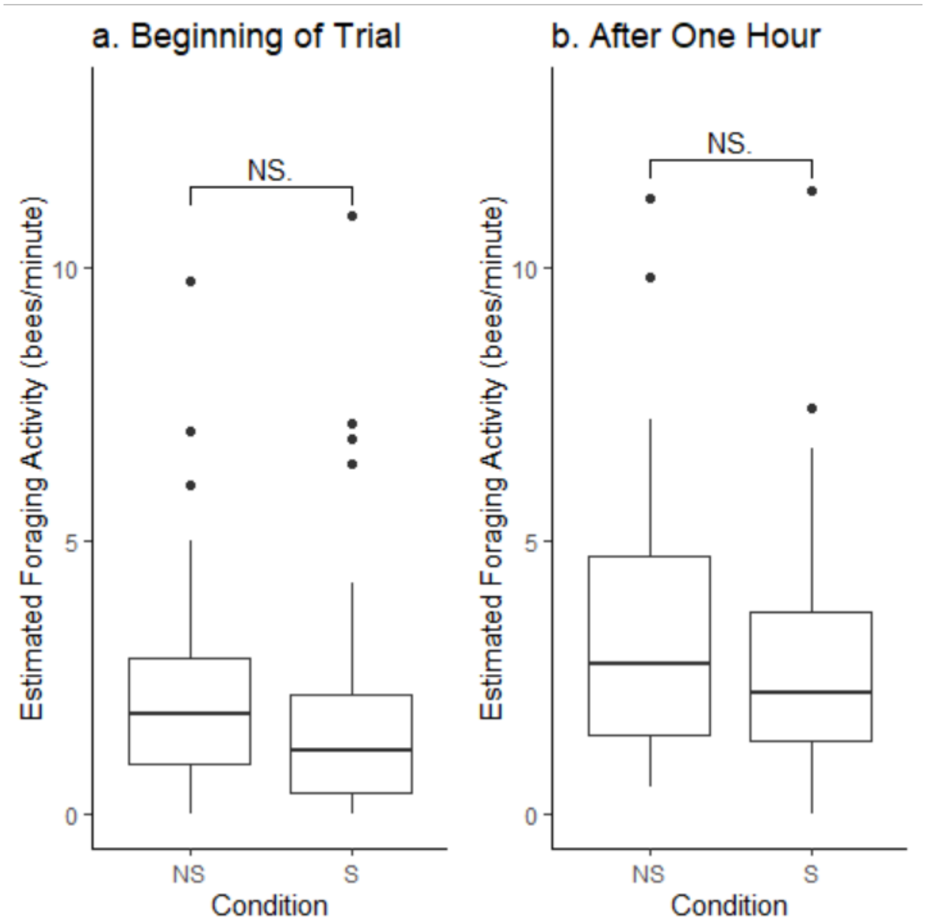

Figure 2.6. Effect of treatment condition (NS vs. S) and time period (beginning of trial vs. after one hour of foraging) on estimated foraging activity at the sucrose feeder, after food was removed from S colonies. Data were pooled across all days of observation following food removal. There was no significant difference between NS and S colonies, or between the first and second time period.

Lipid Analysis

Bees sampled from the S condition had significantly greater wet mass (Factor Treatment S = 0.0363075, t-value = 3.17, $p = 0.0015$) and estimated dry mass (predicted dry mass based on regression from a separate sample of 80 bees—see Methods and Figure 2.1) (Factor Treatment S = 0.01357901, t-value = 3.17, $p = 0.0015$) than bees from the NS condition. In the sample used for measuring the relationship between wet mass and dry mass, we found a significant positive relationship between dry body mass and thorax width (Factor Thorax Width = 0.0184, t-value = 4.423, $p < 0.00001$; Figure 2.7), but no difference in dry mass between treatments (Factor Treatment S = -0.0131, t-value = -0.5783, $p = 0.563$) and no interaction between treatment and thorax width (Thorax Width x Treatment Interaction = 0.0072, t-value = 1.465, $p = 0.1428$).

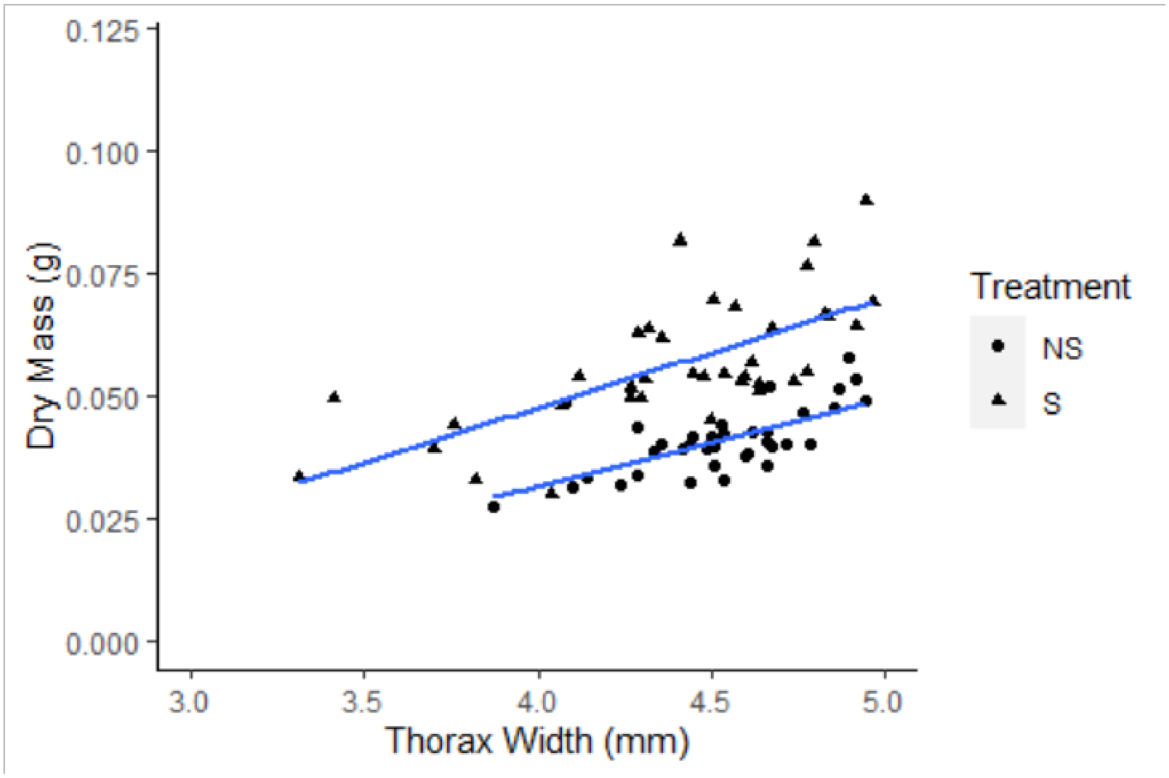

Figure 2.7. Relationship between dry mass and thorax width in 80 bumblebees sampled from 8 different colonies (4 NS and 4 S). These bees were not the ones used for the lipid quantification reaction. There is a significant positive correlation between dry mass and thorax width ($p < 0.00001$), but no effect of treatment on thorax width ($p = 0.1428$).

Bees from S colonies contained significantly greater absolute levels of abdominal lipid than bees from NS colonies, but this outcome seems largely to be explained by the greater average mass of bees from S colonies (Factor Estimated Dry Mass = 0.0006, t-value = 2.31, p = 0.02); there was no independent effect of treatment (Factor Treatment S = -0.0000005, t-value = -0.0212, p = 0.983). This means that bees from the S colonies contained more lipids, not because they had more lipids in proportion to worker body mass but because S colonies had heavier workers and heavier workers had more lipids (Figure 2.8).

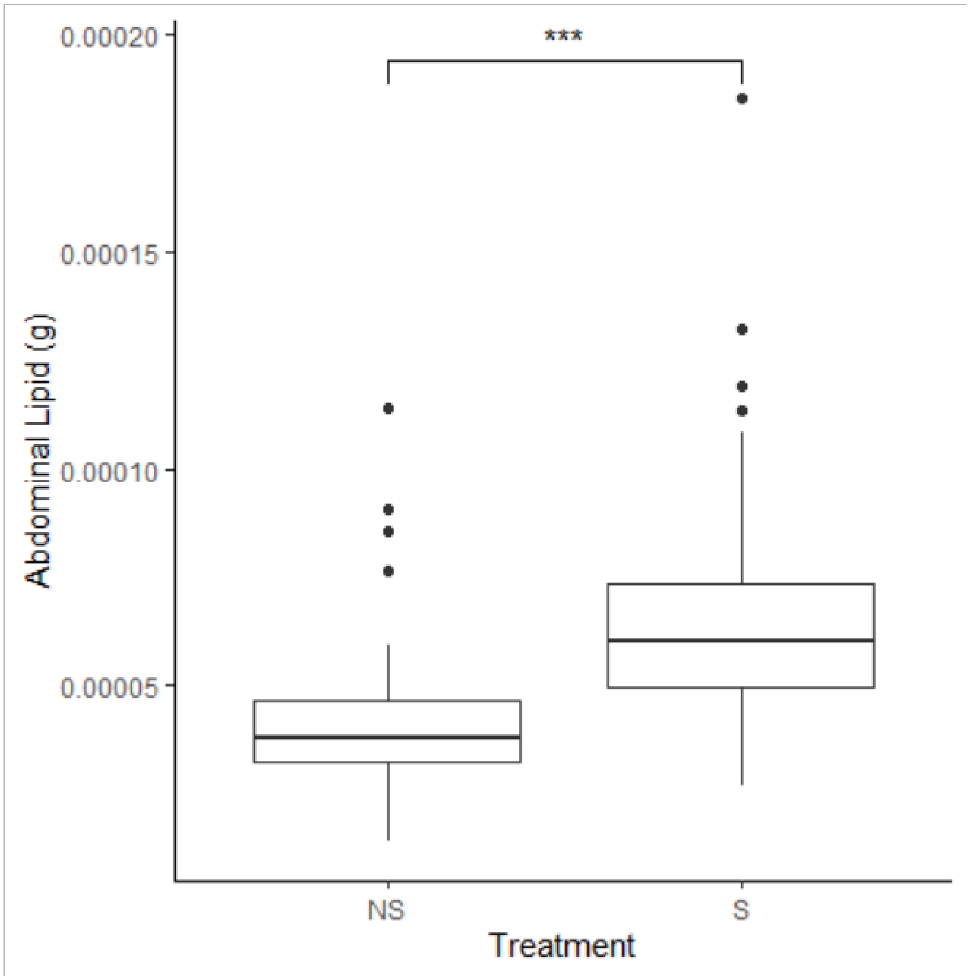

Figure 2.8. Effect of treatment on total abdominal lipid levels in 80 bumblebees sampled from 8 colonies (4 NS and 4 S). Bees from S colonies had significantly greater levels of abdominal lipids than bees from S colonies. However, this effect was explained by the greater mass of bees from S colonies rather than by an independent effect of treatment (p = 0.02 for effect of estimated dry mass, p = 0.983 for effect of treatment).

The NS and S colonies were not different in any other biologically meaningful manner, suggesting no systematic bias differentiating the two treatment groups. We found no difference between the two treatments in number of workers (F = 0.5387, p = 0.4907), and no evidence of differential mortality. Three colonies contained males (two S and one NS), and one S colony contained a virgin queen; there was no difference between treatments in probability of entering the reproductive phase ($\chi2 = 1.33$, p = 0.2482). Early onset of the reproductive phase is known to occur in commercially reared *B. impatiens* colonies.

DISCUSSION

We sought to examine how the foraging decisions made by individual foragers are influenced by the colony's nutritive state. Our results show that bumblebees respond to stored food in the nest with reduced feeding and foraging activity across both the time scales of a single day and several weeks. Our results also support the hypothesis that lipids play a role in mediating the long-term effect we observed, such that bees raised in colonies flush with food contain more abdominal lipids and have greater overall body mass than bees raised without these abundant food stores.

Bumblebee nests act as information centers, and foragers are known to sense and act on social cues such as the amount of stored food and odors (Dornhaus and Chittka 2004; Dornhaus and Chittka 2005; Molet et al. 2009; Incorvaia et al. 2021). Our study extends these insights by examining how a social cue, the colony's food stores, influences individual foraging decisions at a food source. This provides a launching point for future work on the ecological impacts of these modulated foraging decisions. Because the decisions made by bumblebees (and other pollinators) directly affects the pollination services they provide (Goulson 1999), understanding how the social environment modulates individual decisions will allow us to mechanistically link the bumblebee social environment with pollination and plant population dynamics.

We found clear evidence that the nutritive state of the colony influences foraging behavior at both the individual and the group level. When bees come from colonies with high food stores, they tend to contact a sugar source for shorter durations, even when highly motivated on their first foraging trips of the day (Figure 2.2, Table 2.1), as compared with bees from colonies with low food stores. Less contact with the sucrose solution represents weaker motivation to feed from the resource, best explained by a lack of need due to the colony already possessing enough food. This also explains the reduction in contact duration from initial to later time periods for NS colonies; after an hour of access to the feeder, the colony had accumulated enough resources such that individuals no longer needed to remain highly motivated to collect more. This effect is not as strong for S colonies, but is still present, indicating that some food had been collected from the resource and added to the supplemental supply already present in the nest.

The relationship between stored food and foraging activity is more difficult to interpret. Our analysis shows a marginally significant effect of condition (S vs NS) on foraging activity before supplemental food was removed, such that S colonies showed less activity than NS colonies (Figure 2.3, Table 2.2). However, we also found a significant effect of time period and a significant interaction between condition and time period: NS colonies showed an increase foraging activity after one hour had passed. How can we reconcile this with the evidence that bees from NS colonies showed shorter contact durations with the feeder during this same time period? One likely explanation is that this reflects a shift in the exploitation-exploration tradeoff; the bees showed higher activity, but were probing the feeder rather than exploiting the feeder, as evidenced by their shorter contact durations in the same time period (Townsend-Mehler et al. 2011; Mehlhorn et al. 2015; Young et al. 2021). This interpretation is consistent with other data from our lab, showing that bumblebees are more exploratory when they have full colony food stores (Dyer et al. in preparation).

We found evidence that the effect of stored food occurs across multiple time scales; bees from S colonies did not immediately become as highly motivated as NS colonies after their supplemental food source was removed, but instead regained motivation over several days (Figures 2.4-2.6, Table 2.3). This suggests that the experience of being raised in a colony with abundant resources has an enduring influence on the motivation of bumblebee foragers. These patterns are reminiscent of the phenomenon known as developmental priming, which is when molecular mechanisms respond to conditions during an organism's development in a manner that shapes later adult phenotype. Developmental priming has been identified in numerous animal taxa, including bees and humans (e.g. Caldji et al. 1998; Relyea 2004; Schulz 2010; Kapheim et al. 2011). More research is needed to determine exactly if and how development impacts behavior in this system, and whether lipids are part of the underlying mechanism.

Our behavioral results directly led to the question of what mechanisms underlie the difference in motivation between bees from NS and S colonies, especially when considering the delayed effect on motivation for days after food is removed. We found a significant effect of differential rearing environment on the total amount of abdominal lipids, which in turn seems most parsimoniously explained by a difference between groups in worker body mass. Bees from colonies with abundant food stores had greater body masses and total abdominal lipid levels, due to the positive correlation between the two (Figures 2.7 and 2.8). These results suggest a connection between body mass and total abdominal lipids and the lower foraging motivation we observed in our S field colonies. Lipid levels in hemolymph are known to influence feeding motivation in crickets (Konuma et al. 2016), and nurse honeybees have greater abdominal lipid levels than forager honeybees (Toth and Robinson 2005). Abdominal lipids serve as energy stores, and make up the fat body organ known to play important roles in various insect bodily functions such as metabolism, protein synthesis, hormone production, and detoxification (Arrese and Soulages 2010). Thus, even if lipids themselves are not influencing bumblebee foraging behavior, the fat body they comprise may play a role in behavioral regulation through another mechanism, such as through the production of hormones or an effect on carbohydrate or protein metabolism.

Our results suggest that lipids play a role in regulating bumblebee foraging motivation. The factors influencing feeding motivation in insects have received some study, but many open questions remain (Nagata 2019). In honeybees, lipid levels dramatically decrease as workers transition from nursing to foraging (Toth and Robinson 2005), and individual energetic state can influence foraging behavior separate from social regulation (Mayack and Naug 2013). To our knowledge, no study like Mayack and Naug's (2013) has been performed in bumblebees. Our results suggest such a study would be fruitful, as they clearly implicate lipids as a regulator of individual foraging motivation, which in turn are influenced by the developmental environment.

We found more variation in both mass and lipid levels in S colonies than in NS colonies. Body mass in bumblebees is determined by feeding levels, with variation produced due to differential feeding related to the spatial organization of the nest—larvae towards the center are fed more than larvae on the periphery (Couvillon and Dornhaus 2009; Shpigler et al. 2013). Body size variation is thought to be adaptive for colony performance in bumblebees, but the specific function it serves remains unresolved (Goulson et al. 2002; Couvillon and Dornhaus

2010; Chole et al. 2019; Kelemen et al. 2020). With our data, we cannot address whether the differences in variation we observed between NS and S colonies is adaptive or a product of the colony's spatial organization, which may have evolved under different selection pressures. The lower variation in NS colonies may be due to food stores not being high enough for substantial differences in feeding to occur.

Altogether, our study demonstrates that stored nectar reserves in bumblebee colonies mediates foraging motivation across time scales. On the time scale of a day or a few days, motivation may be affected by food stores due to foragers actively sampling honeypots to assess the colony's nutritive state (Dornhaus and Chittka 2005). On the longer time scale of many days to weeks, our results suggest that foraging motivation may instead be influenced by the body mass and total abdominal lipid levels of foragers, which are in turn determined by the rearing environment. In this way, reduced foraging motivation can persist even after food stores have been depleted and the colony would presumably benefit from an increase in foraging. This suggests that developing bumblebees may be primed by the social environment to behave adaptively as adults, such that they do not undertake unnecessary foraging risks when the colony is already well-stocked with food. The potential for developmental mismatches, as seen in other taxa, should be examined in bumblebees, especially given the propensity of agricultural monocultures where large amounts of single crops all fall in and out of availability at once (Schulz 2010; Bateson et al. 2014; Van Dyck et al. 2015).

REFERENCES

REFERENCES

Amenta, J. S. "A rapid chemical method for quantification of lipids separated by thin-layer chromatography." *Journal of lipid research* 5.2 (1964): 270-272.

Arrese, Estela L., and Jose L. Soulages. "Insect fat body: energy, metabolism, and regulation." *Annual review of entomology* 55 (2010): 207-225.

Barker, Jessica L., et al. "Learning about larceny: experience can bias bumble bees to rob nectar." *Behavioral ecology and sociobiology* 72.4 (2018): 68.

Basten, Ulrike, et al. "How the brain integrates costs and benefits during decision making." *Proceedings of the National Academy of Sciences* 107.50 (2010): 21767-21772.

Bates, Douglas, et al. "Fitting linear mixed-effects models using lme4." *arXiv preprint arXiv:1406.5823* (2014).

Bateson, Melissa, et al. "Agitated honeybees exhibit pessimistic cognitive biases." *Current Biology* 21.12 (2011): 1070-1073.

Bateson, Patrick, Peter Gluckman, and Mark Hanson. "The biology of developmental plasticity and the Predictive Adaptive Response hypothesis." *The Journal of physiology* 592.11 (2014): 2357-2368.

Blecha, Kevin A., Randall B. Boone, and Mathew W. Alldredge. "Hunger mediates apex predator's risk avoidance response in wildland–urban interface." *Journal of Animal Ecology* 87.3 (2018): 609-622.

Brooks, Mollie E., et al. "glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling." *The R journal* 9.2 (2017): 378-400.

Caldji, Christian, et al. "Maternal care during infancy regulates the development of neural systems mediating the expression of fearfulness in the rat." *Proceedings of the National Academy of Sciences* 95.9 (1998): 5335-5340.

Caraco, Thomas, Steven Martindale, and Thomas S. Whittam. "An empirical demonstration of risk-sensitive foraging preferences." *Animal Behaviour* 28.3 (1980): 820-830.

Cartar, Ralph V. "A test of risk-sensitive foraging in wild bumble bees." *Ecology* 72.3 (1991): 888-895.

Cartar, Ralph V. "Adjustment of foraging effort and task switching in energy-manipulated wild bumblebee colonies." *Animal Behaviour* 44.1 (1992): 75-87.

Chole, Hanna, Sarah Hollis Woodard, and Guy Bloch. "Body size variation in bees: regulation, mechanisms, and relationship to social organization." *Current opinion in insect science* 35 (2019): 77-87.

Couvillon, M. J., and Anna Dornhaus. "Small worker bumble bees (Bombus impatiens) are hardier against starvation than their larger sisters." *Insectes sociaux* 57.2 (2010): 193-197.

Couvillon, Margaret J., and Anna Dornhaus. "Location, location, location: larvae position inside the nest is correlated with adult body size in worker bumble-bees (Bombus impatiens)." *Proceedings of the Royal Society B: Biological Sciences* 276.1666 (2009): 2411-2418.

Couvillon, Margaret J., et al. "Percent lipid is associated with body size but not task in the bumble bee Bombus impatiens." *Journal of Comparative Physiology A* 197.11 (2011): 1097.

Couzin, Iain D., et al. "Effective leadership and decision-making in animal groups on the move." *Nature* 433.7025 (2005): 513.

Crespi, Leo P. "Quantitative variation of incentive and performance in the white rat." *The American Journal of Psychology* 55.4 (1942): 467-517.

Danforth, Bryan N., et al. *The solitary bees: biology, evolution, conservation*. Princeton University Press, 2019.

Deci, Edward, and Richard M. Ryan. *Intrinsic motivation and self-determination in human behavior*. Springer Science & Business Media, 1985.

Dill, Lawrence M. "Adaptive flexibility in the foraging behavior of fishes." *Canadian Journal of Fisheries and Aquatic Sciences* 40.4 (1983): 398-408.

Dornhaus, Anna, and Lars Chittka. "Bumble bees (Bombus terrestris) store both food and information in honeypots." *Behavioral Ecology* 16.3 (2005): 661-666.

Dornhaus, Anna, and Lars Chittka. "Information flow and regulation of foraging activity in bumble bees (Bombus spp.)." *Apidologie* 35.2 (2004): 183-192.

Dukas, Reuven, ed. *Cognitive ecology: the evolutionary ecology of information processing and decision making*. University of Chicago Press, 1998.

Goulson, Dave, et al. "Can alloethism in workers of the bumblebee, Bombus terrestris, be explained in terms of foraging efficiency?." *Animal Behaviour* 64.1 (2002): 123-130.
Goulson, Dave. "Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution." Perspectives in plant ecology, evolution and systematics 2.2 (1999): 185-209.

Goulson, Dave. *Bumblebees: behaviour, ecology, and conservation*. Oxford University Press on Demand, 2010.

Heinrich, Bernd. "Bumblebees out in the cold." *The Hot-Blooded Insects*. Springer, Berlin, Heidelberg, 1993. 227-276.

Incorvaia, Darren C., Arend Hintze, and Fred C. Dyer. "Spatial allocation without spatial recruitment in bumblebees." *Behavioral Ecology* 32.2 (2021): 265-276.

Ings, Thomas C., and Lars Chittka. "Predator crypsis enhances behaviourally mediated indirect effects on plants by altering bumblebee foraging preferences." *Proceedings of the Royal Society B: Biological Sciences* 276.1664 (2009): 2031-2036.

Jones, Patricia L., Michael J. Ryan, and Lars Chittka. "The influence of past experience with flower reward quality on social learning in bumblebees." *Animal Behaviour* 101 (2015): 11-18.

Kapheim, Karen M., et al. "Support for maternal manipulation of developmental nutrition in a facultatively eusocial bee, Megalopta genalis (Halictidae)." *Behavioral ecology and sociobiology* 65.6 (2011): 1179-1190.

Kelemen, Evan P., Goggy Davidowitz, and Anna Dornhaus. "Size variation does not act as insurance in bumble bees; instead, workers add weight in an unpredictable environment." *Animal Behaviour* 170 (2020): 99-109.

Kohler, Steven L., and Mark A. McPeek. "Predation risk and the foraging behavior of competing stream insects." *Ecology* 70.6 (1989): 1811-1825.

Konuma, Takahiro, et al. "Imbalanced Hemolymph Lipid Levels Affect Feeding Motivation in the Two-Spotted Cricket, Gryllus bimaculatus." *PloS one* 11.5 (2016): e0154841.

Mayack, Christopher, and Dhruba Naug. "Individual energetic state can prevail over social regulation of foraging in honeybees." *Behavioral Ecology and Sociobiology* 67.6 (2013): 929-936.

McFarland, D. J. "Decision making in animals." *Nature* 269.5623 (1977): 15.

McNamara, John M., and Alasdair I. Houston. "Risk-sensitive foraging: a review of the theory." *Bulletin of mathematical biology* 54.2-3 (1992): 355-378.

Mehlhorn, Katja, et al. "Unpacking the exploration–exploitation tradeoff: A synthesis of human and animal literatures." *Decision* 2.3 (2015): 191.

Molet, Mathieu, Lars Chittka, and Nigel E. Raine. "How floral odours are learned inside the bumblebee (Bombus terrestris) nest." *Naturwissenschaften* 96.2 (2009): 213-219.

Nagata, Shinji. "Feeding modulation in insects through factors in the hemolymph." *Bioscience, biotechnology, and biochemistry* 83.1 (2019): 33-38.

Pankiw, Tanya, Keith D. Waddington, and Robert E. Page. "Modulation of sucrose response thresholds in honey bees (Apis mellifera L.): influence of genotype, feeding, and foraging experience." *Journal of Comparative Physiology A* 187.4 (2001): 293-301.

Pyke, Graham H. "Optimal foraging theory: a critical review." *Annual review of ecology and systematics* 15.1 (1984): 523-575.

Relyea, Rick A. "Morphological and behavioral plasticity of larval anurans in response to different predators." *Ecology* 82.2 (2001): 523-540.

Relyea, Rick A. "Fine-tuned phenotypes: tadpole plasticity under 16 combinations of predators and competitors." *Ecology* 85.1 (2004): 172-179.

Scheiner, Ricarda, Robert E. Page, and Joachim Erber. "Sucrose responsiveness and behavioral plasticity in honey bees (Apis mellifera)." *Apidologie* 35.2 (2004): 133-142.

Schulz, Laura C. "The Dutch Hunger Winter and the developmental origins of health and disease." *Proceedings of the National Academy of Sciences* 107.39 (2010): 16757-16758.

Shpigler, Hagai, et al. "Social influences on body size and developmental time in the bumblebee Bombus terrestris." *Behavioral Ecology and Sociobiology* 67.10 (2013): 1601-1612.

Svenson, Ola. "Decision making and the search for fundamental psychological regularities: What can be learned from a process perspective?." *Organizational behavior and human decision processes* 65.3 (1996): 252-267.

Toprak, Umut, et al. "A journey into the world of insect lipid metabolism." *Archives of insect biochemistry and physiology* 104.2 (2020): e21682.

Toth, Amy L., and Gene E. Robinson. "Worker nutrition and division of labour in honeybees." *Animal behaviour* 69.2 (2005): 427-435.

Townsend-Mehler, John M., Fred C. Dyer, and Kim Maida. "Deciding when to explore and when to persist: a comparison of honeybees and bumblebees in their response to downshifts in reward." *Behavioral ecology and sociobiology* 65.2 (2011): 305-312.

Van Dyck, Hans, et al. "The lost generation hypothesis: could climate change drive ectotherms into a developmental trap?." *Oikos* 124.1 (2015): 54-61.

Williams, Paul H., et al. *Bumble bees of North America: an identification guide*. Princeton University Press, 2014.

Witter, Mark S., and Innes C. Cuthill. "The ecological costs of avian fat storage." *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 340.1291 (1993): 73-92.

Young, Allison M., Axel Brockmann, and Fred C. Dyer. "Adaptive tuning of the exploitation-exploration trade-off in four honey bee species." *Behavioral Ecology and Sociobiology* 75.1 (2021): 1-15.

CHAPTER 3: SPATIAL ALLOCATION WITHOUT SPATIAL RECRUITMENT IN BUMBLEBEES

This chapter is an edited version of:

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Any foraging animal is expected to allocate its efforts among resource patches that vary in quality across time and space. For social insects, this problem is shifted to the colony level: the task of allocating foraging workers to the best patches currently available. To deal with this task, honeybees rely upon differential recruitment via the dance language, while some ants use differential recruitment on odor trails. Bumblebees, close relatives of honeybees, should also benefit from optimizing spatial allocation but lack any targeted recruitment system. How bumblebees solve this problem is thus of immense interest to evolutionary biologists studying collective behavior. It has been thought that bumblebees could solve the spatial allocation problem by relying on the summed individual decisions of foragers, who occasionally sample and shift to alternative resources. We use field experiments to test the hypothesis that bumblebees augment individual exploration with social information. Specifically, we provide behavioral evidence that, when higher-concentration sucrose arrives at the nest, employed foragers abandon their patches to begin searching for the better option; they are more likely to accept novel resources if they match the quality of the sucrose solution experienced in the nest. We explored this strategy further by building an agent-based model of bumblebee foraging. This model supports the hypothesis that using social information to inform search decisions is advantageous over individual search alone. Our results show that bumblebees use a collective foraging strategy built on social modulation of individual decisions, providing further insight into the evolution of collective behavior.

INTRODUCTION

A classic problem animals face is how to best allocate their time and energy to acquiring resources from various patches in the environment in order to maximize benefits while minimizing costs (Schoener 1971; Stephens and Krebs 1986). This problem is especially challenging in natural environments where profitable patches can change in quality and patches of higher value can appear in novel locations. Solving this problem requires balancing the exploitation of known resources with the exploration for new, potentially more profitable resources, a phenomenon known as the exploration–exploitation trade-off (Mehlhorn et al. 2015).

Social insects face the problem of spatial allocation to resources on the group level. Given intense energetic demands and heterogeneous distribution of resources in the environment—for example, floral resources that vary in quality, quantity, density, and time and duration of availability (Heinrich 1975; Gross and Werner 1983; Hegland and Totland 2005)—we would expect social insect colonies to have evolved mechanisms that allocate foragers efficiently across currently available patches. Indeed, such allocation processes have evolved in honeybees and in several species of ants. The honeybee system, which relies upon the dance language (von Frisch and Lindauer 1956; Seeley 1995; Dyer 2002), is particularly well understood. The waggle dance enables the communication of spatial locations to nestmates. In a foraging context, the dance is first and foremost an efficient system for communicating the location of food sources, but it is modulated by social mechanisms in a way that enables the efficient reallocation of foragers when resource conditions change (Seeley et al. 1991; Seeley 1995; Thom et al. 2007; Gilley 2014; Kietzman and Visscher 2015; Chatterjee et al. 2019; George and Brockmann 2019). In an analogous fashion, some ant colonies are capable of reallocating their recruitment to resources as profitability changes by using odor trails and tandem runs (Beckers et al. 1992; Gordon 2012; Shaffer et al. 2013; Gordon 2019).

Bumblebee colonies would presumably benefit by solving the allocation problem, but bumblebees have neither a dance language that can communicate spatial information nor the ability to lay odor trails (Goulson 2010). Classic work by Bernd Heinrich (1979a) proposed that bumblebee colonies find and exploit the best resources by primarily relying on the accumulated success of independently searching foragers. According to this idea of "foraging optimization by individual initiative" (Heinrich 1979a), naive bumblebee foragers begin their careers by sampling many different types of floral resources before finally settling on one primary type (the "major"), which makes up a majority of future flower visits, and one or more secondary types (the "minors"), which are visited much less frequently (Heinrich 1979b). Once these preferences are established, bumblebee foragers are remarkably constant, typically visiting the same sequence of flowers on each successive foraging trip, a phenomenon known as traplining (Comba 1999; Ohashi et al. 2006; Saleh and Chittka 2007; Woodgate et al. 2017), while retaining a slight tendency to sample novel resources. This can enable foragers to shift to better resources that are discovered.

This low-level propensity for individuals to spontaneously seek out and sample novel resources, and switch preferences according to the value of those resources, would enable individual foragers and, eventually, the colony as a whole to reallocate effort to better resource patches as conditions change. Such a process would be slow, however, in adjusting to the dynamic and heterogeneous landscape of floral rewards that bumblebees and other pollinators encounter (Heinrich 1979c; Pleasants and Zimmerman 1979; Vaudo et al. 2015) and ignores the potential for social exchange of information useful for speeding up reallocation of workers.

Bumblebees are known to use social information gathered outside the nest while foraging. They can recognize odor marks on flowers left by conspecifics and learn to associate them with rewards (Renner and Nieh 2008; Pearce et al. 2017) and weigh the presence of conspecifics as cues for reward as an adjunct to what is learned through personal experience (Dunlap et al. 2016). This use of social information can even lead bees to make suboptimal foraging choices (Avarguès-Weber et al. 2018).

In addition to social information from the external environment, bumblebee foragers also use the nest as an information center, similar to colonial vertebrates, such as the common raven (Marzluff et al. 1996) and female Bechstein's bats (Kerth and Reckardt 2003). The nest serves as a place where returning bees can—and do—sample honeypots and thereby assess what their nestmates are bringing back (Dornhaus and Chittka 2005; Molet et al. 2008), paying attention to odors as well (McAulay et al. 2015). In addition, foragers returning from a good resource run excitedly throughout the nest and release pheromones to communicate that they have found a rewarding food source (Dornhaus and Chittka 2004, 2005; Renner and Nieh 2008). This combination of honeypot sampling and the behavior of returning foragers serves to increase overall colony foraging activity in a manner that is dependent on colony nutritive state (Cartar 1992; Pelletier and McNeil 2004; Dornhaus and Chittka 2005; Martin et al. 2019). What has not been tested, however, is the possibility that an informed forager could pass information to other currently occupied foragers about the existence of better resources in the environment, hence indicating to those foragers the value of increasing their tendency to explore. This kind of information sharing, whether direct or indirect, could cause currently employed foragers to disengage from known resources and to search for the source of better food in the field, thereby speeding up the reallocation of foragers as resources change.

We propose that currently employed bumblebee foragers will respond to an influx of high-quality food into the nest by adjusting their behavior in the environment in a way that resembles the negative incentive contrast effect (NICE). The NICE phenomenon occurs when an animal has an expectation for a certain outcome (e.g., a certain quality of reward) that is not met, which leads to disrupted behavior that has historically been compared to frustration (Crespi 1942; Couvillon and Bitterman 1984; Pecoraro et al. 1999; Wendt et al. 2019). In foraging bumblebees, this is seen when foragers arrive at a familiar resource that is suddenly downgraded in quality; what ensues is the exploration for novel food sources (Wiegmann et al. 2003; Waldron et al. 2005; Townsend-Mehler et al. 2011). We propose that, in the social context, an influx of higher-quality food into the nest could act as a social cue via the same NICE mechanism, causing experienced foragers to reject previously acceptable food on subsequent foraging trips and to search for something better. If so, then the NICE mechanism could mediate the social triggering of exploration and the reallocation of foragers to the best-known resources.

This study employs a combination of experiments and an agent-based computer model. The bee experiments, with the bumblebee *Bombus impatiens*, address three specific hypotheses about the role of the NICE mechanism in the reallocation of foraging effort: 1) an influx of high-quality food into the nest disrupts the foraging of bees that are exploiting a known resource of lower quality; 2) following this disruption at a known resource, bees are spurred to search for a novel resource; and 3) bees that find the novel resource feed from it only if it matches the high-quality food introduced into the nest.

The agent-based model builds on the results from the field experiments to examine the circumstances under which the use of social information in the nest provides a fitness advantage to the colony over the individual initiative of foragers. Such questions are often addressed through comparisons of species that differ in whether they possess a given trait; however, species typically differ in many traits, and so it is hard to isolate the adaptive significance of any one trait while holding others constant. For example, honeybees are thought to rely more heavily upon social information in foraging than bumblebees, but they also differ in having a spatial recruitment system (Seeley 1995; Dyer 2002), much larger colonies (Goulson 2010), and different search strategies in the field (Townsend-Mehler et al. 2011; Townsend-Mehler and Dyer 2012) to name just a few key differences. Additionally, in field experiments, it is impossible to control the likelihood that an individual bumblebee will respond to social information, while this can be explored by manipulating parameters in a model. We developed a model in which a colony of foragers has to search for and collect resources in a spatial grid. Resource patches differ in quality, and the individual and collective problem is to shift foraging effort to the best available patches. We varied the degree to which social information from nestmates triggers foragers to search for better resources rather than exploit what they have already found and then examined how socially triggered search can lead to an improvement in the allocation of foraging effort to better resources.

METHODS

A. Field Experiments

We carried out experiments during the summers of 2017, 2018, and 2019. Commercially reared *Bombus impatiens* colonies (Koppert Biological Systems, MI) were established in a large outdoor flight cage measuring 22 (l) × 5.6 (w) × 2.3 m (h). This allowed the bees to fly freely, while food resources in the environment could be controlled and manipulated. Four colonies were used in total: one in 2017, one in 2018, and two in 2019. All colonies were healthy with approximately 75 workers at the time they were obtained and were provided ad lib honeybee pollen throughout the duration of the field season.

During this project, only one colony was ever present in the flight cage at a time. Once the colony had adjusted to the flight cage environment (a period of about 2 days), we trained individual bees to a "constant feeder" containing sucrose solution. Feeders are made of plexiglass and consist of a base platform and an inverted jar; the platform contains multiple grooves that enable numerous bees to feed from the feeder simultaneously. Individuals were trained by coaxing them onto a plastic pipette coated with sugar water (matching the constant feeder's concentration)—once a bee was clinging to the pipette, we carried her to the constant feeder and gently placed her onto the platform so she could feed. Bees quickly learn to return to use the feeder as their foraging resource. We used 0.5 M sucrose solution in the constant feeder for most colonies, but we used 0.25 M sucrose solution for one colony because of that colony's unusually low motivation to search for alternatives to the constant feeder. The constant feeder was only available to the bees when they were actively being trained or during an experimental trial. Food quality at this constant feeder never changed, and the feeder was set up in the same location around the same time each day, typically between 9 and 11 AM EST. Once a bee was observed coming to the constant feeder on her own (i.e., observed making two or three unaided trips from the nest to the feeder), we labeled her either with a unique paint mark or an individual numbered plastic tag (Opalithplättchen, Germany).

Following initial training, we allowed bees to visit the constant feeder for one or more reinforcement days. During reinforcement days, we labeled new unmarked arrivals as described. While we did not explicitly keep track of experience with the feeder, all bees had their first test within 3 days of being initially trained.

All three hypotheses were tested using the same basic experimental paradigm. On the day of a trial, we first visually confirmed that the colony was low on nectar reserves by observing the number of filled honeypots in the nest. An experiment only took place if the colony had no observable nectar stored in honeypots; we used hungry colonies because we wanted to exclude colony or individual energetic state as possible influences on decision-making within the exploitation–exploration trade-off (see Seeley 1995; Schulz et al. 2002; Katz and Naug 2015). We then set up the constant feeder simultaneously with a different feeder in a different location (the “novel feeder”). The novel feeder had sucrose solution of either the same quality as the constant feeder (0.5 or 0.25 M) or better quality (2 M), depending on the condition being tested that day. After setting up the feeders, we used video cameras to record activity at each feeder. Each feeder was initially recorded for either 10 or 20 min; after this initial recording, we injected 2.5 mL of sucrose solution directly into the nest through the nest entrance, mimicking an influx of nectar. The concentration of this solution was either the same as the constant feeder (the control condition) or better than the constant feeder (2 M, to mimic the discovery by a forager of a better resource; the treatment condition). An injection of 2.5 mL is about 25 times as much as a single forager brings back in one trip (see Dornhaus and Chittka 2005), but we chose this amount to ensure that currently employed foragers returning to the nest would have a high chance of detecting the influx of food. After the injection of sucrose solution, we again recorded both feeders for 10 min or longer. The longest recording period after injection was 50 min, as we felt this was a sufficient amount of time to observe an effect on behavior given the small size of the foraging environment the bees had access to and the scarcity of resources it contained. If the after-injection recording went longer than 20 min, then a second injection of sucrose solution occurred at the 20-min mark.

We used different recording periods to test each of the hypotheses as each had different potential confounding variables. Because hypothesis 1 focused on disruption at a known food source based on the injection of better food, we used 10-min recording periods to ensure that satiety did not influence the decision to reject food, which we observed when using 20-min recording periods. This satiety effect is interesting and the subject of other projects in our research group but is outside the scope of this study. Because hypothesis 2 focused on the discovery of the novel feeder following the abandonment of the constant feeder, we used the longer 20-min recording periods to avoid false negatives. Here, satiety is less of an issue because each condition involved the injection of the same amount of food and the same time periods before injection—we can thus reasonably assume that satiety was the same between treatments, and any difference between them is due to the differences in injected food quality. Hypothesis 3 was tested using the same bees that discovered the novel feeder during the testing of hypothesis 2.

The primary unit of our analyses are observations of bees, with a few bees being tested multiple times. All presented results come from models with colony identity and individual identity as random effects. We also performed analyses with only colony identity as a random effect—these results were qualitatively the same and are included in the Supplementary Material. All statistical analyses were performed using R version 3.6.1. We constructed all survival curves using the function “survdiff” in R package “survival” and compared them using the log-rank Mantel–Haenszel test (Therneau and Lumley 2014). For more information about each experiment, including sample sizes and number of trials, see Table 3.1.

Table 3.1:

Summary of experiments performed for this study, including sample sizes and number of trials[1]

Hypothesis	# Colonies Used	Sample Size	# Bees Used	# of Trials	Description of Data Used
1	3	61 focal bee observations	50	5 control trials; 9 treatment trials	Latency to resume feeding
2[2]	4	81 focal bee observations	68	6 control trials; 10 treatment trials	Latency to discover novel feeder
3	4	14 focal bee observations	13	1 trial with better quality feeder; 5 trials with same quality feeder	Latency to feed, behavior upon discovering novel feeder (either "Feed" or "Not Feed")

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[1] There are many more observations for H2 than for H3 because H3 could only be tested using bees that discovered the novel feeder. Fourteen out of the 68 bees used in H2 discovered the novel feeder, so these are the bees that were used.

[2] Values represent combined data (see text).

Hypothesis 1: disruption at a known food source

To test whether the injection of better food into the nest disrupts feeding at a known resource, we used video recordings to measure the latency to resume feeding after bees returned to the constant feeder following the injection of food into the nest. Latency to feed has been used in earlier studies with bumblebees as a measure of disruption and exploration (Townsend-Mehler et al. 2011). We used only individually marked bees and removed any unmarked bees for the duration of the trial. In analyzing the video recordings, we identified a feeding event as when a bee's proboscis had unbroken contact with the feeder for at least 30 s (Townsend-Mehler et al. 2011; Townsend-Mehler and Dyer 2012). We then measured how much time elapsed between the first contact with the feeder (following the injection of food into the nest) and the initiation of feeding according to our criterion. A long latency to feed indicates disrupted feeding behavior (the bee is willing to tolerate the opportunity cost of not feeding), while a bee motivated to feed will have a short latency or, if she feeds right away, a latency of zero.

The hypothesis that social information produces a NICE in employed foragers predicts that foragers should be disrupted upon returning to the constant feeder when the injected food is of better quality, but not when it is the same quality, as the constant feeder. This disruption entails rejecting the constant feeder, with some foragers potentially deciding to accept the constant feeder after some time spent probing or searching for alternative resources (see Townsend-Mehler et al. 2011; Townsend-Mehler and Dyer 2012). To test this hypothesis, we constructed and compared survival curves for each condition.

Hypothesis 2: search for a novel food source

Here, we focus on the search behavior of foragers that had been observed at the constant feeder during the initial recording period (before the injection of food into the nest). Our question was whether these focal bees respond to the injection by seeking out a novel food source. We predicted that foragers trained to the constant feeder would seek out and discover the novel feeder when the injected food is better in quality, but not when it is the same quality, as the constant feeder. From the video, we recorded the number and identity of marked bees appearing at the novel feeder after the injection of sucrose solution into the colony. Unmarked bees (whose past foraging history was unknown) that appeared at the novel feeder were captured and removed. To determine if there is a difference in the rate of novel feeder discovery based on the quality of the injected sucrose solution, we constructed and compared survival curves (with the timer starting at the point of sucrose injection into the nest) for each condition.

Hypothesis 3: feeding behavior at novel food sources

To determine if bees that find the novel feeder are seeking out sucrose solution that is better in quality than the constant feeder, or simply any novel resource, we compared the latency to feed from the low-quality novel feeder after discovering it to the latency to resume feeding at the constant feeder after the injection of better food into the nest (the same survival curve used to address hypothesis 1). Because there is the potential for bees that discover the 2 M novel feeder to transmit new social information within the nest, we excluded bees that arrived at the novel feeder after the first discoverer had returned to the nest from this analysis, which left us with nine subjects for this survival curve. We also compared the proportion of bees that fed immediately from the novel feeder upon its discovery when it was better quality (2 M) to when it was the same quality (0.5 or 0.25 M) as the constant feeder. We defined “feeding immediately” as initiating a feeding bout (30 s continuous contact as before) within 10 s of landing on the novel feeder. These data were analyzed using Fisher’s exact test of independence as detailed by McDonald (2009).

B. Agent-Based Model

To further explore the hypothesis that using social information to allocate foraging effort in bumblebees provides an advantage over personal information alone, we built an agent-based model in Python. The model consists of 100 agents (representing bees) foraging on a 2D 100 × 100 bounded grid meant to mimic a foraging landscape. In the grid, there are 10 resource patches (grid cells) of different qualities: 2 patches each of quality 1, 2, 3, 4, and 5, with 5 being the highest quality (i.e., most rewarding to the agents). This resulted in 0.1% of the grid cells containing resources. We simulated a situation in which a group of foragers that is naive to all resources in the environment must discover the best resources and allocate foragers efficiently to them. The simulation time represents the natural system over a period of a few hours or days.

Agents are modeled as finite state machines, which can be in three modes: "exploring," "exploiting," and "in the nest" (before or after a foraging bout); additionally, each agent has an internal state encoding the quality of the resource it last exploited. Each agent's experiences in the environment determine transition probabilities and, in turn, influence behavioral state transitions. An agent's current internal state (value of the resource they are exploiting) is the value they return to the nest at the end of each update (step) of the trial. At the beginning of a foraging trial, all agents are naive and, hence, have internal state 0, but the internal state is expected to increase for each agent across the trial as they discover higher-value rewards. Each trial consists of 200 updates. At the beginning of a trial, none of the agents have found a resource, so all must spend each update searching until they have done so. Search is implemented by moving the agent instantaneously to a random space on the landscape and having them do a 100-step random walk, with each step being preceded by a random turn in any direction, including diagonal. If an agent finds a resource during this search, its internal state changes to the value of that resource, which it continues to exploit on subsequent trials until another search is triggered. So, for example, if an agent with state 0 finds a resource of value 2, the agent's internal state changes to 2 and it returns to the nest. On this and on each subsequent update (until a better resource is found through a search or the update is wasted in an unsuccessful search), the agent will add 2 to the colony's resource total.

Once an agent has found a resource, it may either continue to exploit that patch or search for a new resource in subsequent updates. For our main experiment, we assigned a probability ($p = 0.01$) that an agent will search for a new resource instead of exploiting (foraging from) a known resource. This is analogous to the underlying propensity for a bumblebee to randomly seek out novel resources instead of exploiting a known one (Heinrich 1979b). This low probability was chosen so that the effect of the underlying search would be minimal compared to the effect of socially triggered search (discussed below). If the search leads the agent to encounter a resource that is higher in quality than its current state, the internal state updates to the new value. If, for example, an agent with a state of 2 discovers a resource of value 3 while searching, that agent's internal state changes from 2 to 3. If the agent finds nothing better while searching, its state stays the same and it does not collect any resources that update, hence wasting that update. The effect of this is to impose a considerable opportunity cost for exploration. The best resource found by any agent becomes the current "social state" of the colony, which is perceivable by all foragers.

Search can also be triggered through the use of social information: with an experimentally controlled probability (q), an agent will search if another agent from the colony has discovered a higher-value resource (in other words, social state > internal state). Search triggered this way operates the same as search described previously.

Whether a search is triggered spontaneously or via social encounters, each agent should have a chance to progress toward higher-value rewards. Our goal was to see whether social triggering of search would provide an advantage over a purely individual initiative. In different conditions of the experiment, we varied the probability (q) of social state triggering search from 0 to 1 in increments of 0.1 (i.e., if social state > internal state, there is a probability q that an agent will search). For each level of q, we ran 1000 replicates with 200 updates each. To compare performance, we measured the total resources collected by the colony, as well as the distribution of resources discovered by agents at the end of the trial.

Because this main experiment did reveal an advantage of socially triggered search over spontaneous search through individual initiative, we considered whether this advantage was simply the result of having exploration be more likely and, if so, whether a higher probability of spontaneous search by itself would be advantageous. To explore this question, we did a separate experiment where we systematically varied p (probability of spontaneous search), as well as q (probability of socially triggered search).

RESULTS

A. Behavioral Experiments

Hypothesis 1: disruption at a known food source

Our initial goal was to study whether the injection of higher-quality food into the nest would disrupt the feeding of foragers when they return to a familiar feeding place. As we predicted, foragers took longer to resume feeding from the constant feeder after the injection of better-quality sucrose solution into the nest compared to when the same quality of sucrose solution was injected (log-rank statistic = 103, $p < 0.0001$; Figure 3.1).

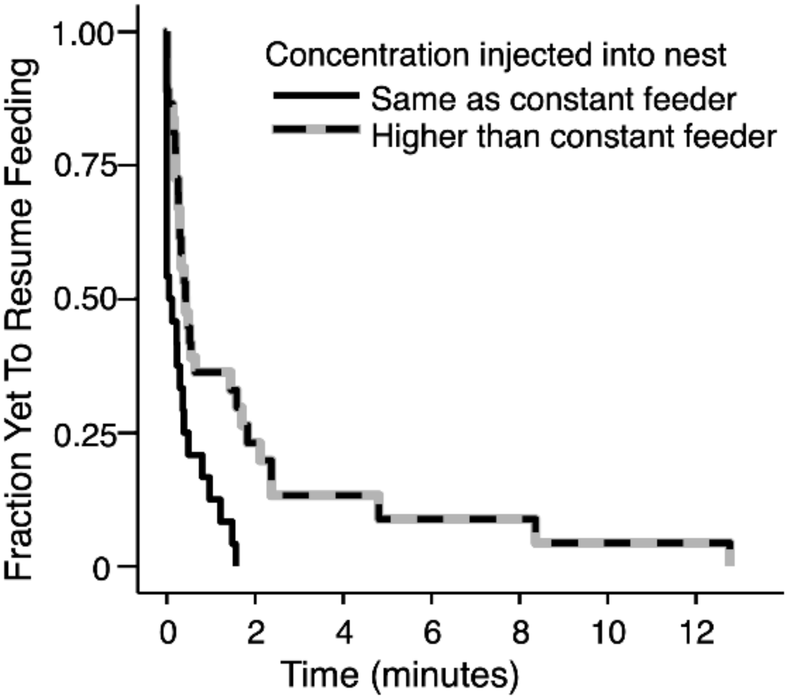

Figure 3.1. Disruption of feeding at constant feeder. Survival curves represent latency to resume feeding at the constant feeder after experiencing an injection of sucrose solution into the nest. Survival curves are significantly different from each other (log-rank Mantel–Haenszel test, $p < 0.0001$). The longest it took a bee to feed when the injected sucrose matched the constant feeder was 94 s; when the injected sucrose was better than the constant feeder, the longest it took a bee to feed was 766 s, with some bees (10.8%) not feeding at all during the observation period. n = 37 observations, across nine trials, for the dashed curve; n = 24 observations, across five trials, for the solid black curve.

Hypothesis 2: search for a novel food source

Next, we asked whether the disruption of feeding at a familiar resource was associated with the search for, and discovery of, a novel food source in the environment. As predicted, bees discovered the novel feeder at a faster rate when the injected sucrose solution was of better quality than the constant feeder than they did when the sucrose solution was the same quality (log-rank statistic = 105, $p < 0.0001$; Figure 3.2). This significant relationship holds true if data from 20-min initial recording videos are combined with 10-min initial recording videos, which were shorter overall and thus offered less time to observe the discovery of the novel feeder (log-rank statistic = 255, $p < 0.0001$).

In addition, the proportion of bees that discovered the novel feeder was higher when better quality food was injected compared to the control condition. Forty-five percent of focal bees discovered the novel feeder when the injected food was of higher quality compared to 5.2% for when the injection was the same quality as the constant feeder, and these proportions are significantly different from each other (Fisher's exact test, odds ratio = 13.79, $p = 0.008$). In the combined data (which includes trials where only 10 min were allowed for the discovery of the novel feeder), these proportions are not significantly different from each other (Fisher's exact test, odds ratio = 2.86, $p = 0.10$) but follow the same pattern: 30% in the treatment versus 13% in the control.

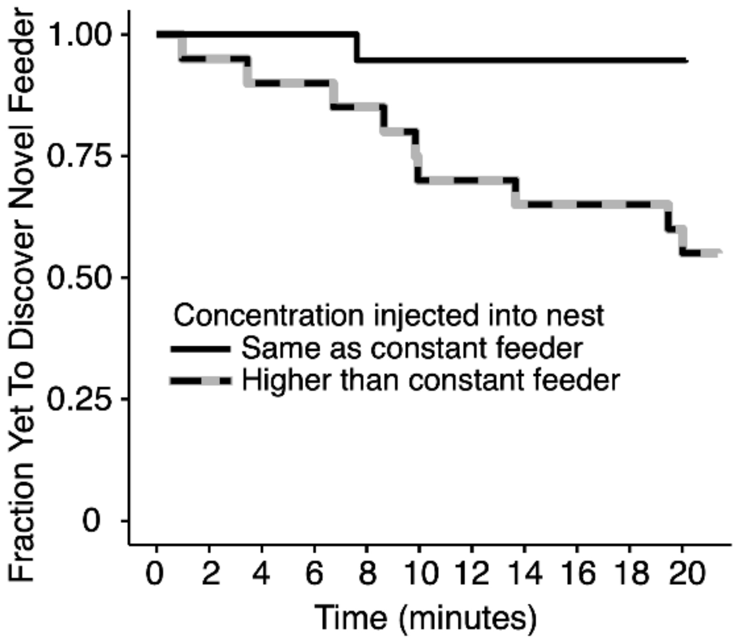

Figure 3.2. Discovery of novel feeder after disruption at constant feeder. Bees discovered the novel feeder at a significantly faster rate when injected sucrose was of better quality than the constant feeder than when it was of the same quality (log-rank Mantel–Haenszel test, $p < 0.0001$). $n = 19$ observations across two trials for the dashed curve; $n = 20$ observations across two trials for the solid black curve. Data in this figure come from the trials with 20-min initial recording periods (see text and Table 3.1).

Hypothesis 3: feeding behavior at novel food resources

Results presented so far suggest that experiencing better food in the nest causes foragers to disrupt their feeding at a lower-quality resource and to search for and discover a novel resource, but does this social experience also influence the acceptance of the novel resource? Here, we focus only on those bees that found the novel feeder after better-quality food (2 M sucrose solution) was injected into the nest. As we predicted, foragers fed from the novel feeder immediately only if it also contained 2 M sucrose (100%, five out of five bees) compared to when it contained the same sucrose concentration as the constant feeder (33.3%, three out of nine bees). The difference between these proportions is marginally significant (Fisher's exact test, odds ratio = 0, $p = 0.03097$).

The latency to resume feeding on low-quality food (after the injection of better food into the nest) is significantly longer after the same low-quality food is discovered in the novel feeder than after bees return to find that food in the constant feeder (log-rank statistic = 76.7, $p < 0.001$; Figure 3.3). This implies that bees that are spurred to search by the injection of better food are not seeking out just any novel resource but are being guided by an expectation of finding a better resource. If they were not guided by such an internal expectation, we would expect the curves to be significantly different in the opposite direction.

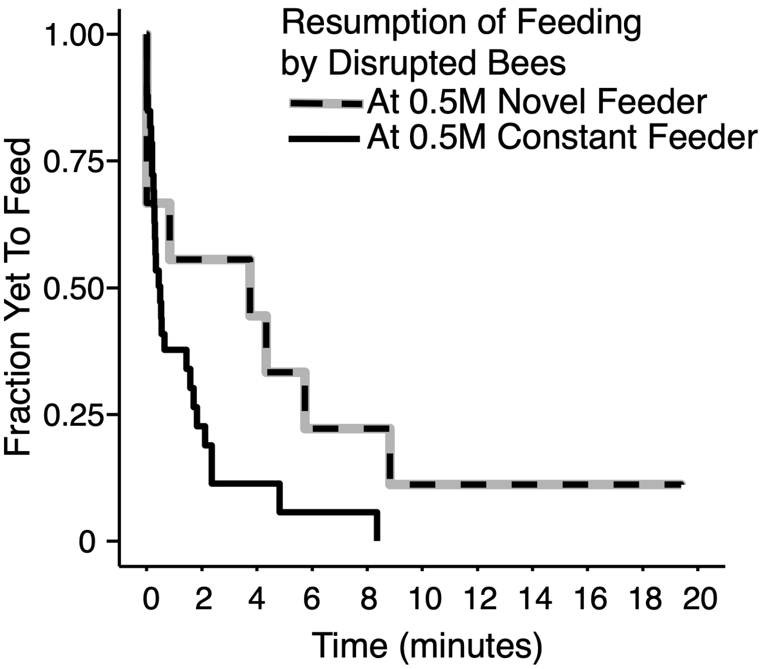

Figure 3.3. Acceptance of novel feeder. Comparison of the time it took foragers to resume feeding at the constant feeder after being initially disrupted (through injection of better-quality food into the nest) versus the time it took foragers to feed from the novel feeder after discovering it was of the same quality as the constant feeder (log-rank Mantel–Haenszel test, $p < 0.001$). Bees that would have appeared in both curves were removed from the data to ensure independence.

B. Agent-Based Model

Given our behavioral evidence that bumblebees can use social information to trigger an individual search for better alternatives, we assume that doing so provides a fitness benefit to the colony. We built the model to test this hypothesis and to explore the circumstances under which socially triggered search is advantageous.

A flowchart of the agent decision-making process in the model can be found in Figure 3.4. For a full description of the assumptions underlying the model, see the Supplementary Material in the published paper, available at:

academic.oup.com/beheco/article/32/2/265/6122599?casa_token=l6_vNQK6Vp8AAAAA:-C1jqA0_z0G4fIQQekLraJPKjyOaZLEiSPd4MHnle9IsPIB7ieDGpmpBqT5Tt0t1inM9i17O_kaiLg#supplementary-data

The model code is available at: https://github.com/dcincorvaia/ Spatial-Allocation.

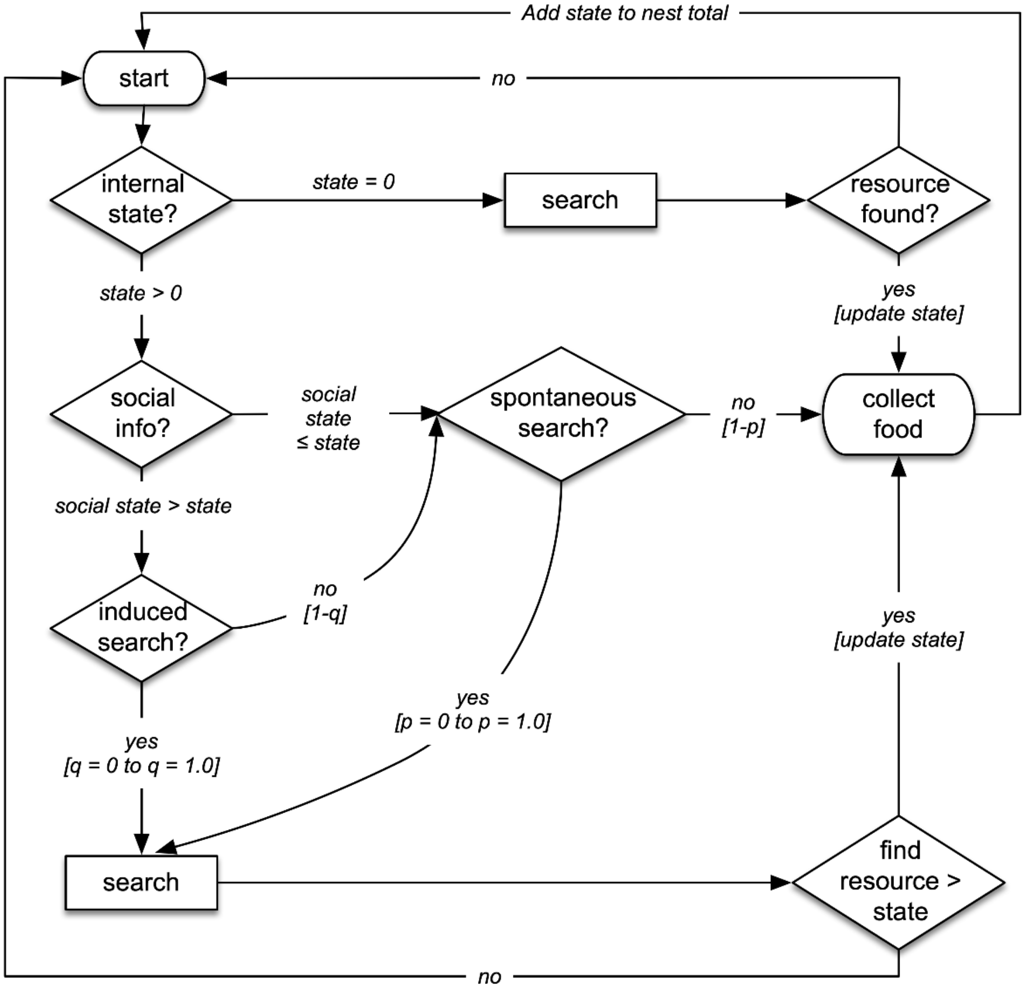

Figure 3.4. Flowchart of agent decision-making process. This process occurs for every agent (out of a colony of 100 agents) in each update. If the agent has not yet discovered a resource (e.g., at the beginning of a run), its internal state is 0 and it automatically searches. If an agent's internal state is greater than 0, search may be triggered through two independent processes. If the best resource found by a member of the colony (i.e., the social state) is greater than the agent's internal state, the agent will be triggered to search with probability q (which is varied experimentally). If search is not triggered through this social mechanism, the agent may be spontaneously spurred to search with probability *p*. If an agent does not search, it exploits (feeds from) the resource defined by its current internal state and adds that state value to the colony's resource total. If an agent searches and successfully finds a better resource (i.e., new resource > internal state), the agent's internal state changes to match the new resource and the new resource is exploited and added to the colony total. If an agent searches and does not find a better resource, the agent's turn ends with nothing being added to the colony's resource total.

If our hypothesis is correct, we should find that colonies are able to collectively accumulate more resources when foragers can use social information than when they rely only upon individual initiative. As seen in Figure 3.5, there was indeed a considerable benefit to the colony of using social information to trigger a search, even if there is only a low probability (*q* = 0.1) of using social information.

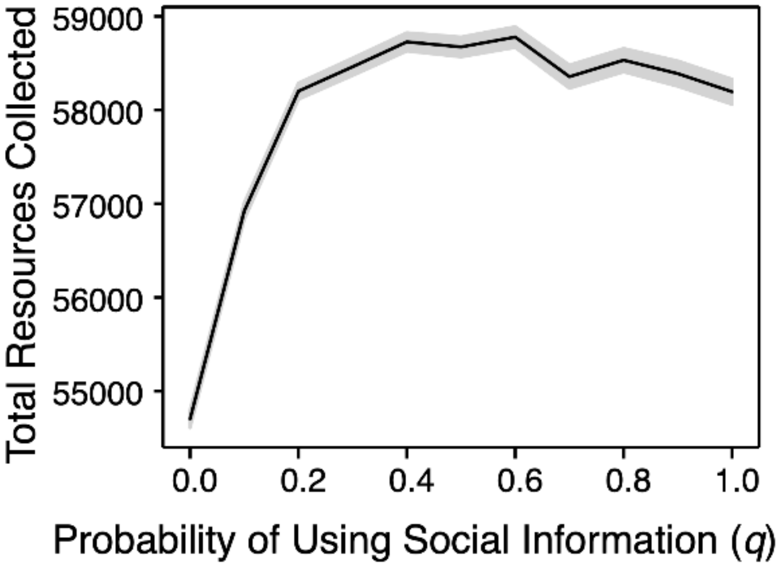

Figure 3.5. Effect of social information use on colony foraging success. Total resources collected by a colony of agents across different probabilities of using social information (*q*), when = 0.01. Values represent the total resources accumulated by a colony of agents after 200 updates. Each data point is an average of 1000 replicates. Shading corresponds to standard error of the mean.

Interestingly, the benefits of social information reached a plateau (and may even decline slightly) as the probability of using social information increases. If social information is advantageous compared to personal information alone, we would also expect to find that the average quality of resources that individual foragers can find and exploit should be higher when a search is triggered by social information than when they search via individual initiative alone. Two analyses support this expectation (Figure 3.6): first, the average total amount of resources accumulated over a trial is higher for colonies with social information use than for colonies without it (Figure 3.6a); second, agents end up concentrated on higher-valued rewards when social information is used to trigger search than when it is not (Figure 3.6b,c).

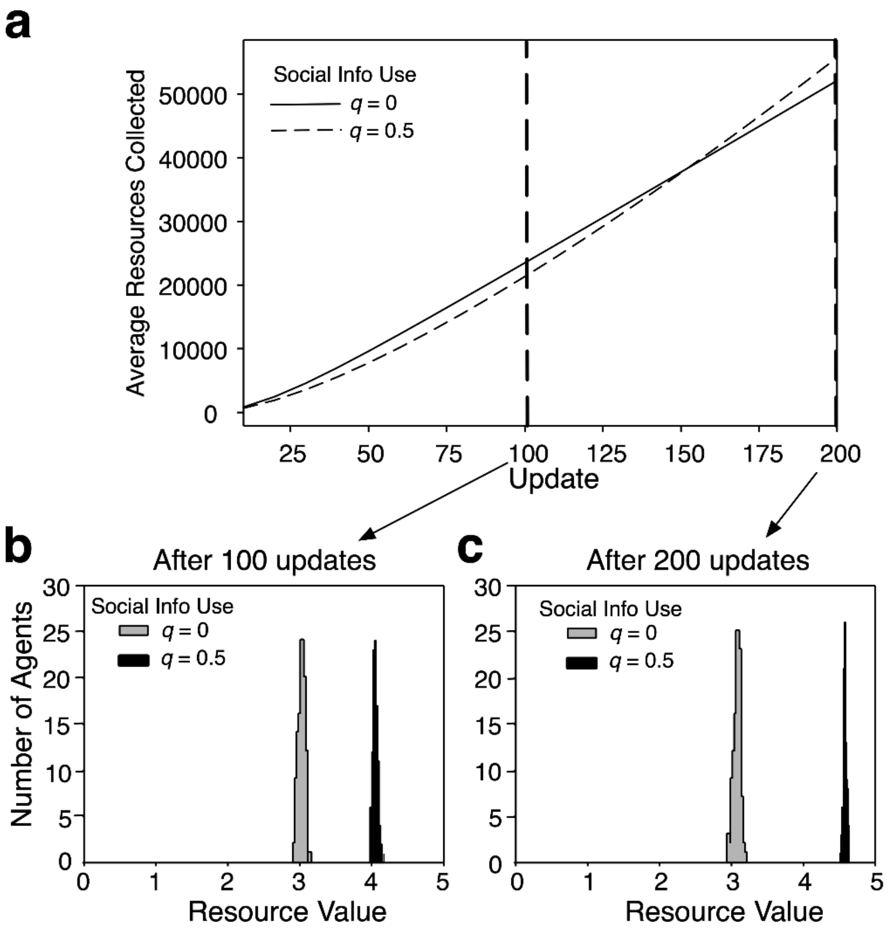

Figure 3.6. Change in performance over time within model run. (a) Average performance of colonies at every tenth update across a model run, with the probability of social information use set at q = 0 or q = 0.5 and the probability of spontaneous search set at $p = 0.01$. Early in the run, colonies without social information use (q = 0) do better but, by the end of the run, colonies with social information use (q = 0.5) do better. (b, c) Distribution of resources being exploited by agents ("Internal State" in the model; see Figure 3.4) at the middle of the model run (b, 100 updates) and at the end of the model run (c, 200 updates). The average resource quality was higher in the social information use condition at 100 updates, even though the colony at that point had not accumulated as many total resources as in the no-social information condition (see a). The figure represents the average distribution for 1000 replicates.

A closer look at the results reveals a potential trade-off between the opportunity cost of search and the benefit of using social information to inform when to search. Looking at total resources accumulated, we found that it takes a substantial fraction of the trial before colonies using social information ($q = 0.5$) outperform colonies using only individual search ($q = 0$; Figure 3.6a). In fact, the trend is for individual search to outperform socially triggered search early on, especially for high values of q. This occurs even though the agents are exploiting better resources by update 100 when using social information than when not. This implies that the benefits of social information are expressed only when enough foragers have found high-value resources that outweigh the total combined costs of individually triggered and socially triggered search.

Although the results of this main experiment are consistent with there being an advantage of socially triggered search over the individual initiative, perhaps the effects are merely the result of search being more likely overall. If so, then we would also expect to see an advantage of increasing p (as increasing p directly causes more searches to occur). However, when q is held at 0 and p instead varies, there is a negative relationship between p and fitness. For simplicity, only results from $q = 0.5$ are shown in the main manuscript as the general trend for the other probabilities is similar.

DISCUSSION

Here we have shown, using field experiments, that bumblebee foragers use social information from the nest to inform individual foraging decisions, specifically the decision to engage in exploration rather than to continue exploiting a known resource. We also provide evidence, from the computational model, that this social foraging indeed provides a benefit over purely individual solutions of the exploration versus exploitation decision. The effect of this socially triggered search is to enable the colony to concentrate foragers more quickly on the best available resources. The ability of a social insect colony to allocate foragers to profitable sites has been well studied in honeybees, which rely upon a dance language (Seeley et al. 1991; Dyer 2002), and in some ants that use odor trails (Beckers et al. 1992; Gordon 2012; Gordon 2019). Bumblebees, lacking a system for accurate spatial communication, have been known to rely upon "individual initiative" of foragers that engage in a low level of exploration and shift to better resources when they find them (Heinrich 1979a, 1979b), with in-nest cues regulating foraging activity and what type of resource is collected (Cartar 1992; Dornhaus and Chittka 2005; Kraus et al. 2019). We find that individual search behavior is also modulated by social information, specifically the arrival of higher-quality food into the nest. Bumblebee foragers that experience high-quality food in the nest show disruption in consummatory behavior at a known resource of lower quality (Figure 3.1), are spurred to search for a novel resource (Figure 3.2), and pay attention to the quality of discovered resources (do not accept novelty for novelty's sake; Figure 3.3). On the basis of this evidence, we propose that bumblebees solve the spatial allocation problem via a process of "informed individual initiative." The critical role of social information is to modulate internal expectations of foragers, and the summed effect of these influences allows the colony as a whole to exploit the best resources in the environment without a direct spatial communication system.

The disrupted feeding behavior that we observed at the constant feeder is similar to the disruption seen when bees arrive at a familiar food source and discover that it has been downgraded in quality (Townsend-Mehler et al. 2011). We interpret this as an example of a negative incentive contrast effect (Flaherty 1999), a phenomenon well studied in the psychology literature. When this effect has been observed in bumblebees (when individuals encounter a decreased reward value at a known site in the field), it is associated with an increased propensity to explore, as if the bees are looking for a reward matching the one they expected based on prior experience (Wiegmann et al. 2003; Townsend-Mehler et al. 2011). We suggest that the same underlying mechanism—disruption of feeding followed by the search for food matching an internal expectation—is triggered by social cues about higher rewards experienced in the nest. Since it is known that bumblebees are able to learn specific reward values (Wiegmann et al. 2003; Waldron et al. 2005), similar to the related European honeybee (Gil et al. 2007; Gil 2010), these results signify that knowledge about better rewards in the environment need not come only from personal experience in the field but can also be obtained socially from the nest environment.

Because our conclusions rest on comparing responses to food over time, we considered whether the disruption in feeding after injection of high-quality food in the nest could be explained by satiety as the colony accumulates sugar reserves. Satiety seems to lead to habituation at known resources and a loss of motivation to feed in bumblebees (personal observation), which could tip the scales in the exploration–exploitation trade-off toward exploration independently of our experimental treatment. Because the same quantity of food was injected into the nest during each trial, and this amount is much greater than what the bees would have brought back on their own by that point, it is safe to assume that the colony state (in terms of volume of stored sugar) was the same in each trial. We thus conclude that the differences observed between sucrose solution qualities in our experiment cannot be explained by satiety. Bumblebees showed some propensity to search for novel food sources before any new food was injected into the nest at all (personal observation); however, the rate of discovery was significantly faster when the injected food was of better quality than it was when the injected food matched what the bees were bringing back from the constant feeder (Figure 3.2). Thus, satiety does not seem to be sufficient to cause the degree of disrupted feeding that we observed or the subsequent increase in search behavior. Another way of stating this conclusion is to suggest that social information is a stronger trigger of search compared to individually initiated search, at least over the timescale used in this study. This makes sense given that seeking out novel food sources is an inherently risky process that is best undertaken when the animal has some information that novel food sources exist in the first place. Foraging is risky for bumblebees (Cartar and Dill 1990; Dukas and Morse 2003; Abbott 2006), and they should, therefore, not be expected to risk mortality or lost time by searching extensively for novel resources unless they have information that better food exists in the environment.

The bumblebee foragers that were triggered to search in our experiments were not just searching for any novel resource; rather, they behaved as if their search was guided by an internal representation of the reward value that they would accept. Bees that found the novel food source after being spurred to search by 2 M sucrose solution in the nest would accept the novel feeder readily only if it matched that high-quality stimulus, while a majority did not immediately feed upon discovering the novel feeder of the same quality as the constant feeder. In addition, it actually took foragers longer to feed from the novel feeder after discovering that it contained the same quality food as the constant feeder than it took them to resume feeding after initial disruption at the constant feeder (Figure 3.3). Though these two survival curves were formed using data from different time periods in the experiment, it is striking evidence that the bees were not searching for novel locations just for the sake of their novelty but, instead, pay attention to the quality of resources they discover. This supports our hypothesis that social information from the nest is used not just to spur search behavior, as has been previously demonstrated (Dornhaus and Chittka 2005; Renner and Nieh 2008), but is also used to form an expectation of improved foraging opportunities in the environment. In other words, the social information tells a foraging bumblebee not just that she should search for a novel resource for novelty's sake, but what quality of food she should be searching for.

Our results add to recent work showing the importance of social information in bumblebee behavior and ecology (Dornhaus and Chittka 2005; Dunlap et al. 2016; Avarguès-Weber et al. 2018; Pasquaretta et al. 2019). Future work should continue to examine how the benefits of access to social information, including in-nest social cues, contribute to the ecological success of social insects, as well as how social information affects plant–pollinator dynamics (e.g., Baude et al. 2008; Avarguès-Weber and Chittka 2014). One potential covariate not explored in this study is the effect of conspecific presence, which is known to influence bee decision-making (Kawaguchi et al. 2006; Kawaguchi et al. 2007; Baude et al. 2011; Dunlap et al. 2016). Further work is needed to determine how the presence of nestmates, conspecifics, and heterospecifics impact the decision to explore or exploit when presented with new social information in the nest.

This study considered allocation to resources based on one measure of reward quality: nectar sugar concentration. However, in nature, the nectar reward quality of a flower will also be determined by the nectar volume and the handling time, both of which vary across and within flower species (Krishna and Keasar 2018; Parachnowitsch et al. 2018). Bumblebees also respond to and learn odors encountered in the nest (Renner and Nieh 2008; McAulay et al. 2015), which this study did not consider. Recent work has also demonstrated that learning of flowers by bumblebees can be mediated by microbes (Russell and Ashman 2019), which may influence the floral scent or nectar quality depending on where on the flower the microbes are present (Vannette et al. 2013). Additionally, bumblebees do not forage solely for nectar but for protein and micronutrients from pollen as well (Vaudo et al. 2016; Nicholls and Hempel de Ibarra 2017). Given the many different axes of floral reward that inform bumblebee foraging behavior, this study should be seen as a first step toward understanding how one component of floral reward (nectar sugar concentration) influences the colony-level allocation of foragers to resources.

The agent-based model provided further support for the hypothesis that using social information to inform individual decisions is advantageous in bumblebees. Even when there is only a 10% chance of initiating a search in response to a nestmate having discovered better food, a colony of agents collects considerably more total resources than does a colony that relies upon individual initiative alone (Figures 3.5 and 3.6a). Social information use also enables agents to converge upon higher-quality resources quicker than when there is no social information use (Figure 3.6b,c). All these simulations were done with the same underlying probability of spontaneous search (p), which raises the possibility that our results are due to an effect of increased search alone rather than an effect of search being socially triggered. However, when we hold the probability of using social information (q) at 0 and vary p, we see that increasing the number of searches done by agents actually has a negative effect on fitness. This is because q, unlike p, is conditional on the presence of better food having been discovered by another agent. So, for example, if $p = 1$, then all bees would search every turn no matter what, whereas when $q = 1$, all bees search only if the best resource discovered by any agent is greater than their current internal state. This increased search when p is high would lead to agents discovering better resources, but it would also lead to a high proportion of failed searches, especially after agents have already converged on the best resource and thus have no chance of finding anything better. We have used the model to explore the effects of varying p and q in multiple combinations and find that increasing p never improves colony fitness.

The model also provided unexpected insights into the tradeoffs between the benefits and costs associated with social information. For example, the benefit of social information was not apparent early in a foraging trial. During early updates, the agents in social information conditions collected fewer resources than when no social information was used; the advantage of social information appeared only toward the end of the run (Figure 3.6a). We think this is the result of the way search costs arise in the model: when already engaged agents are to search by evidence of better food in the environment, they have a risk of wasting an update rather than exploiting a reward that they already know about. Those search costs are eventually outweighed, however, when repeatedly triggered searches enable the foragers to more quickly discover higher-value rewards (Figure 3.6b,c) and exploit them.

Another result that illustrates the interplay of costs and benefits in search is the apparent plateau effect in the benefit of social information use seen in Figure 3.5. This may be a consequence of foragers quickly discovering the highest-value rewards, which would limit the capacity of socially triggered search to increase the benefit while still entailing a cost in the form of risking a wasted update. In fact, the colony performance seemed to drop off when social information use was the highest, presumably because, in a colony where one individual has discovered the best resource, every other forager would be forced to search on every update until also discovering it. Thus, even this fairly simple model has captured a rich set of interactions of costs and benefits associated with search.

Trade-offs between exploitation and exploration have been extensively studied in many systems, including humans and other vertebrates, invertebrates, and genetic algorithms (Krebs et al. 1978; Alba and Dorronsoro 2005; Townsend-Mehler et al. 2011; Mehlhorn et al. 2015). In our model, the importance of the relative costs and benefits of search is readily apparent when parameters of the model are changed to reflect a greater cost of search. When the model is run with search constituting 50 steps instead of 100 (lowering the probability of resource discovery and, hence, elevating the cost of exploring rather than exploiting) and for 100 updates instead of 200 (limiting the time available for the colony to converge on the best resources), the relationship between total resources collected and the probability of using social information (q) becomes negative. Our results suggest that this model may be useful in future studies of this trade-off, especially in the relative importance of parameters such as search effort and the time at which fitness is assessed.

In building our model, we made several assumptions about the dynamics of search on the individual and social level (see Supplementary Material in published paper). While these assumptions generally reflect the problems faced by bumblebee individuals and colonies, modifying the assumptions, and hence the structure of the model, could enable one to explore the costs and benefits of exploration and exploitation under a wider range of circumstances. For example, adding additional ecological complexity would enable us to explore questions about the impact of predation risks or about how the presence or absence of heterospecific flowers either facilitates or interferes with foraging (and pollination) efficiency (Ghazoul 2006; Thomson et al. 2018).

This complementary blend of empirical and computational study could also be extended to examine patterns of exploration and exploitation in other social insect groups that differ in their foraging ecology. For example, while bees exploit patchy, relatively stable resources (Roubik 1989; Steffan-Dewenter and Kuhn 2003; Goulson 2010), other social insects, such as vespid wasps and desert ants, exploit resources that are ephemeral, dispersed, or highly mobile (Schmid-Hempel 1984; Richter 2000; Buehlmann et al. 2014). These ecological differences presumably have selected for different requirements for memory and information use, and it would be interesting to investigate whether there are associated differences in the benefits of socially versus individually initiated exploration behavior. All social insect foragers must respond to the energetic demands of the group to some degree, but what information they use to do so may differ. This study provides a framework for understanding how one group of social insects uses social information to effectively satisfy the energetic needs of the colony, which is a necessary prerequisite for their large, complex social structure to evolve. Extending this work to other social insect groups would be fruitful as a comparative analysis would help identify the ecological factors that led to the evolution of eusociality in the social insects.

This study contributes to a broader understanding of spatial allocation in cooperative foraging groups, a problem that has the potential for application outside of social insect behavioral biology. In the case of the study of spatial allocation in social insects, results from work with honeybees (Seeley et al. 1991) have been applied to the issue of Internet server allocation to great success (Nakrani and Tovey 2004)—indeed, multiple so-called "honeybee algorithms" currently exist and are used in different applications (Karaboga and Basturk 2007; Afshar et al. 2007). Regardless, the central role of colony state and the in-nest social environment in changing the motivation and search behavior of individual bumblebee foragers has the potential to guide management strategies for these important pollinators, many species of which are currently experiencing declines (Goulson et al. 2008; Cameron et al. 2011) in part due to changes in floral resource availability (Potts et al. 2010; Goulson et al. 2015).

REFERENCES

REFERENCES

Abbott, K. R. "Bumblebees avoid flowers containing evidence of past predation events." *Canadian Journal of Zoology* 84.9 (2006): 1240-1247.

Afshar, Abbas, et al. "Honey-bee mating optimization (HBMO) algorithm for optimal reservoir operation." *Journal of the Franklin Institute* 344.5 (2007): 452-462.

Alba, Enrique, and Bernabé Dorronsoro. "The exploration/exploitation tradeoff in dynamic cellular genetic algorithms." *IEEE transactions on evolutionary computation* 9.2 (2005): 126-142.

Avargués-Weber, Aurore, and Lars Chittka. "Observational conditioning in flower choice copying by bumblebees (Bombus terrestris): influence of observer distance and demonstrator movement." *PLoS One* 9.2 (2014): e88415.

Avargués-Weber, Aurore, Robert Lachlan, and Lars Chittka. "Bumblebee social learning can lead to suboptimal foraging choices." *Animal behaviour* 135 (2018): 209-214.

Baude, Mathilde, et al. "Conspecifics as informers and competitors: an experimental study in foraging bumble-bees." *Proceedings of the Royal Society B: Biological Sciences* 278.1719 (2011): 2806-2813.

Baude, Mathilde, Isabelle Dajoz, and Etienne Danchin. "Inadvertent social information in foraging bumblebees: effects of flower distribution and implications for pollination." *Animal Behaviour* 76.6 (2008): 1863-1873.

Beckers, Ralph, Jean-Louis Deneubourg, and Simon Goss. "Trails and U-turns in the selection of a path by the ant Lasius niger." *Journal of theoretical biology* 159.4 (1992): 397-415.

Buehlmann, Cornelia, et al. "Desert ants locate food by combining high sensitivity to food odors with extensive crosswind runs." *Current Biology* 24.9 (2014): 960-964.

Cameron, Sydney A., et al. "Patterns of widespread decline in North American bumble bees." *Proceedings of the National Academy of Sciences* 108.2 (2011): 662-667.

Cartar, Ralph V. "Adjustment of foraging effort and task switching in energy-manipulated wild bumblebee colonies." *Animal Behaviour* 44.1 (1992): 75-87.

Cartar, Ralph V., and Lawrence M. Dill. "Why are bumble bees risk-sensitive foragers?." *Behavioral Ecology and Sociobiology* 26.2 (1990): 121-127.

Chatterjee, Arumoy, et al. "Honey bees flexibly use two navigational memories when updating dance distance information." *Journal of Experimental Biology* 222.11 (2019).

Comba, Livio. "Patch use by bumblebees (Hymenoptera Apidae): temperature, wind, flower density and traplining." *Ethology Ecology & Evolution* 11.3 (1999): 243-264.

Couvillon, P. A., and M. E. Bitterman. "The overlearning-extinction effect and successive negative contrast in honeybees (Apis mellifera)." *Journal of Comparative Psychology* 98.1 (1984): 100.

Crespi, Leo P. "Quantitative variation of incentive and performance in the white rat." *The American Journal of Psychology* 55.4 (1942): 467-517.

Dornhaus, Anna, and Lars Chittka. "Information flow and regulation of foraging activity in bumble bees (Bombus spp.)." *Apidologie* 35.2 (2004): 183-192.

Dornhaus, Anna, and Lars Chittka. "Bumble bees (Bombus terrestris) store both food and information in honeypots." *Behavioral Ecology* 16.3 (2005): 661-666.

Dukas, Reuven, and Douglass H. Morse. "Crab spiders affect flower visitation by bees." *Oikos* 101.1 (2003): 157-163.

Dunlap, Aimee S., et al. "Foraging bumble bees weigh the reliability of personal and social information." *Current Biology* 26.9 (2016): 1195-1199.

Dyer, Fred C. "The biology of the dance language." *Annual review of entomology* 47.1 (2002): 917-949.

Flaherty, Charles F. *Incentive relativity*. Vol. 15. Cambridge University Press, 1999.

George, Ebi Antony, and Axel Brockmann. "Social modulation of individual differences in dance communication in honey bees." *Behavioral Ecology and Sociobiology* 73.4 (2019): 1-14.

Ghazoul, Jaboury. "Floral diversity and the facilitation of pollination." *Journal of ecology* 94.2 (2006): 295-304.

Gil, Mariana, Rodrigo J. De Marco, and Randolf Menzel. "Learning reward expectations in honeybees." *Learning & Memory* 14.7 (2007): 491-496.

Gil, Mariana. "Reward expectations in honeybees." *Communicative & integrative biology* 3.2 (2010): 95-100.

Gilley, David C. "Hydrocarbons emitted by waggle-dancing honey bees increase forager recruitment by stimulating dancing." *PLoS One* 9.8 (2014): e105671.

Gordon, Deborah M. "The dynamics of foraging trails in the tropical arboreal ant Cephalotes goniodontus." *PLoS One* 7.11 (2012): e50472.

Gordon, Deborah M. "The ecology of collective behavior in ants." *Annual review of entomology* (2019).

Goulson, Dave. *Bumblebees: behaviour, ecology, and conservation*. Oxford University Press on Demand, 2010.

Goulson, Dave, Gillian C. Lye, and Ben Darvill. "Decline and conservation of bumble bees." *Annu. Rev. Entomol.* 53 (2008): 191-208.

Goulson, Dave, et al. "Bee declines driven by combined stress from parasites, pesticides, and lack of flowers." *Science* 347.6229 (2015).

Gross, Ronald S., and Patricia A. Werner. "Relationships among flowering phenology, insect visitors, and seed-set of individuals: experimental studies on four co-occurring species of goldenrod (Solidago: Compositae)." *Ecological monographs* 53.1 (1983): 95-117.

Hegland, Stein Joar, and Ørjan Totland. "Relationships between species' floral traits and pollinator visitation in a temperate grassland." *Oecologia* 145.4 (2005): 586-594.

Heinrich, Bernd. "Bee flowers: a hypothesis on flower variety and blooming times." *Evolution* (1975): 325-334.

Heinrich, Bernd. *Bumblebee economics*. Harvard University Press, 1979a.

Heinrich, Bernd. "" Majoring" and" minoring" by foraging bumblebees, Bombus vagans: an experimental analysis." *Ecology* 60.2 (1979b): 245-255.

Heinrich, Bernd. "Resource heterogeneity and patterns of movement in foraging bumblebees." *Oecologia* 40.3 (1979c): 235-245.

Karaboga, Dervis, and Bahriye Basturk. "A powerful and efficient algorithm for numerical function optimization: artificial bee colony (ABC) algorithm." *Journal of global optimization* 39.3 (2007): 459-471.

Katz, Keziah, and Dhruba Naug. "Energetic state regulates the exploration–exploitation trade-off in honeybees." *Behavioral Ecology* 26.4 (2015): 1045-1050.

Kawaguchi, L. G., K. Ohashi, and Y. Toquenaga. "Do bumble bees save time when choosing novel flowers by following conspecifics?." *Functional Ecology* 20.2 (2006): 239-244.

Kawaguchi, Lina G., Kazuharu Ohashi, and Yukihiko Toquenaga. "Contrasting responses of bumble bees to feeding conspecifics on their familiar and unfamiliar flowers." *Proceedings of the Royal Society B: Biological Sciences* 274.1626 (2007): 2661-2667.

Kerth, Gerald, and Karsten Reckardt. "Information transfer about roosts in female Bechstein's bats: an experimental field study." *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270.1514 (2003): 511-515.

Kietzman, Parry M., and P. Kirk Visscher. "The anti-waggle dance: use of the stop signal as negative feedback." *Frontiers in Ecology and Evolution* 3 (2015): 14.

Kraus, Stéphane, et al. "Bumblebees adjust protein and lipid collection rules to the presence of brood." *Current zoology* 65.4 (2019): 437-446.

Krebs, John R., Alejandro Kacelnik, and Peter Taylor. "Test of optimal sampling by foraging great tits." *Nature* 275.5675 (1978): 27-31.

Krishna, Shivani, and Tamar Keasar. "Morphological complexity as a floral signal: from perception by insect pollinators to co-evolutionary implications." *International journal of molecular sciences* 19.6 (2018): 1681.

Martin, Callum D., et al. "Busier bees: Increasing nest traffic in commercial bumblebee colonies." *Journal of Pollination Ecology* 25 (2019).

Marzluff, John M., Bernd Heinrich, and Colleen S. Marzluff. "Raven roosts are mobile information centres." *Animal Behaviour* 51.1 (1996): 89-103.

McAulay, Megan K., Gard W. Otis, and Angela E. Gradish. "Honeypot visitation enables scent learning and heightens forager response in bumblebees (Bombus impatiens)." *Learning and Motivation* 50 (2015): 22-31.

McDonald, John H. *Handbook of biological statistics*. Vol. 2. Baltimore, MD: sparky house publishing, 2009.

Mehlhorn, Katja, et al. "Unpacking the exploration–exploitation tradeoff: A synthesis of human and animal literatures." *Decision* 2.3 (2015): 191.

Molet, Mathieu, et al. "Colony nutritional status modulates worker responses to foraging recruitment pheromone in the bumblebee Bombus terrestris." *Behavioral Ecology and Sociobiology* 62.12 (2008): 1919-1926.

Nakrani, Sunil, and Craig Tovey. "On honey bees and dynamic server allocation in internet hosting centers." *Adaptive behavior* 12.3-4 (2004): 223-240.

Nicholls, Elizabeth, and Natalie Hempel de Ibarra. "Assessment of pollen rewards by foraging bees." *Functional Ecology* 31.1 (2017): 76-87.

Ohashi, Kazuharu, James D. Thomson, and Daniel D'souza. "Trapline foraging by bumble bees: IV. Optimization of route geometry in the absence of competition." *Behavioral Ecology* 18.1 (2007): 1-11.

Parachnowitsch, Amy L., Jessamyn S. Manson, and Nina Sletvold. "Evolutionary ecology of nectar." *Annals of Botany* 123.2 (2019): 247-261.

Pasquaretta, Cristian, et al. "A spatial network analysis of resource partitioning between bumblebees foraging on artificial flowers in a flight cage." *Movement ecology* 7.1 (2019): 1-10.

Pearce, Richard F., Luca Giuggioli, and Sean A. Rands. "Bumblebees can discriminate between scent-marks deposited by conspecifics." *Scientific reports* 7.1 (2017): 1-11.

Pecoraro, Norman C., William D. Timberlake, and Matthew Tinsley. "Incentive downshifts evoke search repertoires in rats." *Journal of Experimental Psychology: Animal Behavior Processes* 25.2 (1999): 153.

Pelletier, Luc, and Jeremy N. McNeil. "Do bumblebees always forage as much as they could?." *Insectes Sociaux* 51.3 (2004): 271-274.

Pleasants, John M., and Michael Zimmerman. "Patchiness in the dispersion of nectar resources: evidence for hot and cold spots." *Oecologia* 41.3 (1979): 283-288.

Potts, Simon G., et al. "Global pollinator declines: trends, impacts and drivers." *Trends in ecology & evolution* 25.6 (2010): 345-353.

Renner, M. A., and J. C. Nieh. "Bumble bee olfactory information flow and contact-based foraging activation." *Insectes sociaux* 55.4 (2008): 417-424.

Richter, M. Raveret. "Social wasp (Hymenoptera: Vespidae) foraging behavior." *Annual review of entomology* 45.1 (2000): 121-150.

Roubik, David W. *Ecology and natural history of tropical bees*. Cambridge University Press, 1992.

Russell, Avery L., and Tia-Lynn Ashman. "Associative learning of flowers by generalist bumble bees can be mediated by microbes on the petals." *Behavioral Ecology* 30.3 (2019): 746-755.

Saleh, Nehal, and Lars Chittka. "Traplining in bumblebees (Bombus impatiens): a foraging strategy's ontogeny and the importance of spatial reference memory in short-range foraging." *Oecologia* 151.4 (2007): 719-730.

Schmid-Hempel, Paul. "Individually different foraging methods in the desert ant Cataglyphis bicolor (Hymenoptera, Formicidae)." *Behavioral Ecology and Sociobiology* 14.4 (1984): 263-271.

Schoener, Thomas W. "Theory of feeding strategies." *Annual review of ecology and systematics* 2.1 (1971): 369-404.

Schulz, D. J., et al. "Effects of colony food shortage on social interactions in honey bee colonies." *Insectes Sociaux* 49.1 (2002): 50-55.

Seeley, Thomas D., Scott Camazine, and James Sneyd. "Collective decision-making in honey bees: how colonies choose among nectar sources." *Behavioral Ecology and Sociobiology* 28.4 (1991): 277-290.

Seeley, Thomas D. *The wisdom of the hive: the social physiology of honey bee colonies*. Harvard University Press, 2009.

Shaffer, Zachary, Takao Sasaki, and Stephen C. Pratt. "Linear recruitment leads to allocation and flexibility in collective foraging by ants." *Animal Behaviour* 86.5 (2013): 967-975.

Steffan-Dewenter, Ingolf, and Arno Kuhn. "Honeybee foraging in differentially structured landscapes." *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270.1515 (2003): 569-575.

Stephens, David W., and John R. Krebs. *Foraging theory*. Vol. 1. Princeton University Press, 1986.

Therneau, Terry M., and Thomas Lumley. "Package 'survival'. Survival analysis" Published on CRAN. (2014).

Thom, Corinna, et al. "The scent of the waggle dance." *PLoS Biol* 5.9 (2007): e228.

Thomson, James D., Hannah F. Fung, and Jane E. Ogilvie. "Effects of spatial patterning of co-flowering plant species on pollination quantity and purity." *Annals of Botany* 123.2 (2019): 303-310.

Townsend-Mehler, John M., and Fred C. Dyer. "An integrated look at decision-making in bees as they abandon a depleted food source." *Behavioral Ecology and Sociobiology* 66.2 (2012): 275-286.

Townsend-Mehler, John M., Fred C. Dyer, and Kim Maida. "Deciding when to explore and when to persist: a comparison of honeybees and bumblebees in their response to downshifts in reward." *Behavioral ecology and sociobiology* 65.2 (2011): 305-312.

Vannette, Rachel L., Marie-Pierre L. Gauthier, and Tadashi Fukami. "Nectar bacteria, but not yeast, weaken a plant–pollinator mutualism." *Proceedings of the Royal Society B: Biological Sciences* 280.1752 (2013): 20122601.

Vaudo, Anthony D., et al. "Macronutrient ratios in pollen shape bumble bee (Bombus impatiens) foraging strategies and floral preferences." *Proceedings of the National Academy of Sciences* 113.28 (2016): E4035-E4042.

Vaudo, Anthony D., et al. "Bee nutrition and floral resource restoration." *Current opinion in insect science* 10 (2015): 133-141.

von Frisch, Karl, and Martin Lindauer. "The" language" and orientation of the honey bee." *Annual review of entomology* 1.1 (1956): 45-58.

Waldron, Faith A., Daniel D. Wiegmann, and Douglas A. Wiegmann. "Negative incentive contrast induces economic choice behavior by bumble bees." *International Journal of Comparative Psychology* 18.4 (2005).

Wendt, Stephanie, et al. "Positive and negative incentive contrasts lead to relative value perception in ants." *Elife* 8 (2019): e45450.

Wiegmann, Daniel D., Douglas A. Wiegmann, and Faith A. Waldron. "Effects of a reward downshift on the consummatory behavior and flower choices of bumblebee foragers." *Physiology & behavior* 79.4-5 (2003): 561-566.

Woodgate, Joseph L., et al. "Continuous radar tracking illustrates the development of multi-destination routes of bumblebees." *Scientific reports* 7.1 (2017): 1-15.

CHAPTER 4: EXPLORING THE SELECTION PRESSURES THAT SHAPE SOCIAL INSECT FORAGING STRATEGIES

Eusocial insects (especially the ants, bees, wasps, and termites) are some of the most ecologically dominant and economically important organisms on the planet. Living as a colony comes with intense energetic demands, and many social insect species have evolved collective foraging strategies to enable efficient and flexible exploitation of resources in the environment. Some of the best understood of these strategies, such as the dance language of honeybees and the pheromone trails of some ants, involve spatial communication that allows recruits to be led to specific resource locations. This feature, which intuitively seems advantageous, is not ubiquitous across social insects. Here, we use an agent-based model to test the hypothesis that colony size is important for the evolution of spatial recruitment in collective foraging strategies, such that it is advantageous only when the colony is large enough. In addition, we explore the same question with the bumblebee strategy of informed individual initiative, which does not use spatial communication. Because previous studies have reported mixed results, we also investigated the effect of resource density on the fitness of the dance language, and we address this question with the bumblebee strategy as well. Our results support the hypothesis that colony size is an important factor, with the opportunity cost of recruitment not being effectively counteracted by recruitment in small colonies. We also found that more dense resources lead to greater fitness for the dance language, but not for the bumblebee strategy of informed individual initiative. This study thus provides novel insights into the evolution of communication and foraging strategies in this important animal group.

INTRODUCTION

Eusocial insects are among the most ecologically dominant animals on Earth (Wilson 1990; Schultz 2000), thanks in large part to their having evolved complex social mechanisms that enable them to maintain and reproduce large colonies, and to exploit resources on a large scale (Wilson 1971; Beshers and Fewell 2001; Seeley 2009). Across the eusocial insects there is great diversity in phenotype and in ecology; amidst all this diversity, a consistent theme is that all eusocial insects face intense resource needs. Accordingly, we should expect natural selection to lead to the evolution of behavioral strategies that enable social insect colonies to allocate foraging effort efficiently, especially when resources are unevenly distributed in space and time. Foraging strategies used by social insect colonies range from completely individual foraging (Wehner et al. 1983) to complex social strategies, such as the trunk trail networks of some ants (Beckers et al. 1989; Czaczkes et al. 2015) or the dance language of honeybees (Dyer 2002). In such cases, an accumulation of individual actions leads to an emergent collective phenotype (Sumpter 2006). Within the study of social insect foraging, many researchers have studied the individual behaviors and ecological correlates of collective behavioral strategies (Beckers et al. 1989; Deneubourg et al. 1990; Seeley et al. 1991; Couzin and Franks 2003; Sumpter 2006; Couzin 2009; Perna et al. 2012; Gordon 2014; Lanan 2014; Gordon 2019). However, much remains unknown about the specific selective pressures that shape the evolutionary trajectory of foraging strategies employed by social insects.

Studies of the selection pressures that shape behavior can pursue either or both of two approaches: comparative studies in which trait differences between species are correlated with differences in ecology and presumed selection pressures (e.g. Tinbergen 1960; Young et al. 2021), or experimental studies in which one manipulates a phenotype of interest and observes subsequent fitness consequences (e.g. Hoogland et al. 1956; Andersson 1982; Starkey et al. 2019). Both approaches have limitations when applied to highly specialized and complex traits. A comparative approach is of limited utility if the trait in question—a trait like the honeybee dance language, for example—is qualitatively distinct from traits in potential comparison groups. Experimental manipulations are complicated by the fact that a complex phenotype is typically composed of a cluster of coadapted traits; manipulating any component trait may degrade fitness, making it hard to isolate specific fitness effects that occurred during the evolution of the complex phenotype as a whole. In this study of social foraging traits, we adopt a computational modeling approach that enables us to experimentally control aspects of a simulated ecology and thereby probe the effects on the performance of modeled traits. We pursued this approach by implementing a model that can incorporate either a honeybee-like spatial communication system or a less sophisticated system similar to what bumblebees have been shown to use (Incorvaia et al. 2021).

The dance language of honeybees has often been singled out as one of the most advanced communication systems of any non-human animal, as it involves symbolic communication of spatial information—a feat otherwise seen only in humans. Since the discovery of the dance language by Karl von Frisch, studies of its evolution have made use of comparisons among *Apis* species, but these have revealed more about how the dance language may have been adaptively tuned once its major elements had evolved than about how and why it evolved in the first place (reviewed in von Frisch 1967; Dyer 2002; Dornhaus and Chittka 2004). Meanwhile, experimental "lesioning" of spatial information from the dance (e.g. Sherman and Visscher 2002) has demonstrated a potent impact of this information on colony foraging performance, but otherwise does not isolate selection pressures that may have shaped the dance during its evolutionary origin.

The bumblebee collective foraging strategy, termed "informed individual initiative" (Incorvaia et al. 2021), has received limited attention, especially concerning the question of what has shaped its evolution. Several studies have manipulated colonies to probe how information about resources influences a social foraging response (Cartar 1992; Dornhaus and Chittka 2005), but how individual behaviors scale up to a collective strategy has only been addressed in one species, *Bombus impatiens* (Incorvaia et al. 2021). The strategy used by this species involves individual search by foragers, combined with the use of social information to trigger search again when a forager detects that the colony has discovered something better than the forager already knows about. Comparative studies of this strategy would be useful, but little is known about other species except that the food alert behaviors that comprise part of this strategy have been detected in multiple species (Dornhaus and Chittka 2001; Dornhaus and Cameron 2003; Renner and Nieh 2008). Thus we are again in the position of being limited in our ability to use comparative approaches to understand the selection pressures shaping a trait as it evolves.

The present study uses a computational model to investigate how ecological variables affect the fitness of social foraging strategies. Our model adapts a previously published spatially-explicit, agent-based computational model. This model, which was originally used to investigate the fitness consequences of social information use within the collective foraging strategy of bumblebees (Incorvaia et al. 2021), features a colony of agents that forage on a landscape with resources of various qualities. Agents can either exploit known resources or explore for new ones, with the dynamics of this trade-off strongly influencing fitness returns to the colony. We developed two new versions of this model: one where agents use a dance language strategy like honeybees where foragers can signal the rough location of resources they have found, and another where agents use an informed individual initiative strategy like bumblebees (for a fuller description of the important differences between the new model and the original, see Methods). Previous studies have focused on colony size and resource availability as potential selection pressures influencing the fitness of the honeybee dance language, but have produced inconsistent results (e.g. Dornhaus et al. 2006, Schürch and Grüter 2014). These previous models do not include a spatially-explicit nest environment, as our model does (see Methods); because of this research history and the potential for our model to reveal new insights, we chose to focus on these same two potential selection pressures, colony size and resource availability. Our hypothesis is that colonies with the dance language will have higher fitness returns at larger colony sizes, because the benefits of dance recruitment should outweigh the opportunity cost (i.e. wasted time spent not foraging) of in-nest communication only when there are enough individuals in the colony. We hypothesize no relationship between colony size and fitness when colonies use informed individual initiative, because there is no opportunity cost of social information under this strategy, as the relevant social cue is stored food that is equally detectable by all active foragers (Incorvaia et al. 2021). We also hypothesize that both strategies will show greater fitness returns when resources are more abundant, except at the low and high ends of resource availability for the dance language, where empirical data have shown greater benefit and less benefit respectively (Sherman and Visscher 2002). We leave open the possibility that colony size and resource availability may interact to influence fitness for both strategies. Our results will help address the debated importance of colony size and resource ecology for shaping the evolution of the dance language. They will also elucidate for the first time how these selection pressures shape the collective foraging strategy of the closely-related bumblebee.

METHODS

To test the effect of colony size and resources in the environment, as well as possible interactions between them, on the fitness benefits of collective foraging strategies, we built an agent-based model in Python. We examined the accumulation of resources by foraging agents in colonies that varied in size (number of agents) and strategy used (spatial communication or informed individual initiative), in an environment that varied in resource density. This model is an extension of a previously published model, which we originally developed to explore the use of social information in collective foraging by bumblebees (Incorvaia et al. 2021). We describe the model below using the "Overview, Design Concepts, and Details" protocol (Grimm et al. 2006; Grimm et al. 2010).

A. Overview of Computational Model

i. Purpose

We examined the effects of two hypothesized selection pressures—colony size and resource density—on the fitness returns of two social foraging strategies, the honeybee dance language and bumblebee informed individual initiative, in independent modeling simulations. This model is derived from a previously published model (Incorvaia et al. 2021), which was designed to explore the benefits of social information use in foraging bumblebees. The current model differs in several important respects from the original model: 1) it has been redone in an object-oriented programming framework, 2) it now contains a 3-D nest environment, where agents are located between foraging bouts, 3) agents no longer forage at each time step, but instead spend some time steps between foraging trips in the nest, and 4) code has been added that allows for agents to communicate in the nest in a manner similar to the honeybee dance language.

ii. Entities, state variables, and scales

Agents foraged on a 100x100 two-dimensional grid. When not foraging, agents were located in a three-dimensional 10x10x10 nest. The large size of the nest relative to the environment accounts for the fact that bees fly in the environment but walk in the nest, so we assume it would take about as long for a bee to walk across the nest as to fly across the environment. Food patches (single cells on the environment grid) could be either empty or contain resources of various qualities. All agents in the colony acted as foragers, and can thus be thought of as representing a subset of a colony's total workforce. Agents could occupy any of seven states: searching for resources, collecting food from resource, returning to nest after collecting food, returning to nest after failed search, idle in the nest, communicating via dance in the nest, and recruited by dancer. At each time step an agent could either remain in the same state or transition to a new state. All foragers were capable of being triggered to search either individually (with probability p) or socially (with probability q); this social trigger was either the presence of better food in the nest (the bumblebee strategy) or a dancing nestmate (the honeybee strategy). The influence of q on fitness therefore represents the overall fitness of the social strategy versus individual search, with $q = 0$ representing cases similar to when the dance language has been experimentally "lesioned" from honeybee colonies (e.g. Sherman and Visscher 2002). Previous models have shown equivocal evidence for the adaptive benefit of colony size in honeybee dance language communication (Dornhaus et al. 2006; Donaldson-Matasci et al. 2013; Schürch and Grüter 2014). We therefore chose a wide range of colony sizes to investigate, ranging from below to above naturalistic numbers of foragers.

Once the parameters for the model were set, they were consistent throughout the entire model run. The model included other simplifying assumptions. Resources did not degenerate or disappear, and new resources did not appear after initialization. Resources and agents could occupy any point in space on the grid at any point in time, but the colony itself did not occupy a space on the grid (hence this did not explicitly model a central-place foraging problem).

Table 4.1: Description of model parameters

	Variable	Description	Values Tested
N_{Agents}	Colony Size	Number of agents in colony	10, 50, 100, 1000, 2000, 5000, 10000
p	Probability of Spontaneous Search	Probability that an agent will search instead of exploiting a known resource, provided search has not already been triggered socially	0 to 1, in increments of 0.1
q	Probability of Socially Triggered Search	Probability that an agent will search instead of exploiting a known resource, provided that certain social conditions have been met	0 to 1, in increments of 0.1

Table 4.1 (cont'd).

T_{Search}	Search Time	Number of steps taken during search (equivalent to search duration)	100
T_{Nest}	Time in Nest	Number of timesteps an agent spends in the nest between foraging bouts	Random number between 1 and 5, set individually for each agent
D_{Error}	Dance Error	Limits of uniform distribution used to add noise to dance information, reflecting real-world imperfection in recruits' ability to interpret spatial information from dances	±5
$D_{Duration}$	Dance Duration	Number of timesteps a dancer spends communicating resource location information	5

Table 4.1 (cont'd).

$N_{Patches}$	Resource Density	Number of resource patches available in the landscape	5, 10, 100, 500, 2500, 5000

iii. Process overview and scheduling

We ran 1,000 replicates for each simulation, with each replicate consisting of 1,000 timesteps, except for simulations when colony size was 10,000, where, due to computational limitations, we were only able to run 529 replicates for the informed individual initiative (bumblebee) strategy and 778 replicates for the spatial communication (honeybee) strategy. This represents an increase from the 200 timesteps used in the original model (Incorvaia et al. 2021); we chose to increase the number of timesteps due to agents now spending time in the nest between foraging trips, in order to keep the number of foraging trips performed by agents similar to the previous model. Each simulation began with each agent naïve to all resources in the environment. Upon initiation, agents were assigned a random value between 1 and 5, which represents the number of timesteps they spent in the nest between foraging trips. This is meant to reflect the real-world observations that individuals may vary in how frequently and intensively they interact with nestmates. During a foraging trip, agents could either search for a new resource or continue exploiting a known resource. At the beginning of the simulation, all agents must search for a resource until they find one independent of p and q—after discovery of their first resource, future foraging trips could be either exploratory or exploitative, with search triggered by p or q. The probability of an agent exploring or exploiting was influenced by parameters shown in Table 4.1.

Between foraging trips, agents returned to the nest and moved throughout the nest environment. If the simulation used the dance communication (honeybee) strategy, an agent may have danced upon returning to the nest after successful discovery of a novel resource—if so, the agent was stationary in the nest while dancing. Another agent may have picked up the location of the resource being communicated via dance if they moved onto the same cell as the dancer. This is how socially triggered search, q, is implemented in the model when agents use the honeybee strategy.

If the simulation used the informed individual initiative (bumblebee) strategy rather than dance communication, q instead represented the probability that an agent was spurred to search by the presence of better food in the nest (see Incorvaia et al. 2021). Regardless of which strategy was used, q represented the probability of social information being used.

B. Design Concepts

This model is meant to simulate a foraging situation where workers from a colony leave the nest to find and forage from resources of varying quality before returning to the nest. The problem for the colony is to find and exploit the best possible resources in the environment. Our model implements two different behavioral strategies used by central place foragers, with both strategies employing sensing of the environment (both in the nest and in the environment) and only one involving the communication of spatial information among agents. The total resources collected by the colony (i.e. colony fitness) thus represent an emergent property of the actions of individual agents and the communication between them. Individual agents discover and exploit resources, but do not learn about them per se; rather, the quality and location of the resource are stored as state variables, which the agent does not need to actively recall to exploit the resource in future time steps. When agents are searching for a new resource, they check each patch they occupy for a resource and, if there is a resource on the patch, sense its quality (1-5) as well. When moving in the nest, agents analogously sense whether the space they occupy contains another agent and, if so, whether or not that agent is dancing.

C. Initialization

At initialization, a colony of size N_{Agents} is created and $N_{Patches}$ were randomly placed in the environment. Agents began naïve to all resources, and all agents acted as foragers. All agents were randomly assigned a length of time to spend in the nest between foraging bouts, T_{Nest}, again reflecting the individual variation observed in nature.

D. Statistical Methods

To examine the effects of colony size and the resource environment on colony fitness when different collective foraging strategies are used, we fit linear models in the statistical program R (version 4.0.3) using the "lm" base function and chose best-fitting models using the backward selection "step" function (R Core Team 2020). We then looked within each strategy to determine whether resource density influences fitness in the same way across colony sizes. Because our model varies colony size, we used per capita resources collected by the colony as our measure of fitness instead of absolute resources collected.

RESULTS

Fitness of Different Foraging Strategies Across Colony Sizes

To test the relationship between fitness, colony size, and foraging strategy, we focused on simulations when $p = 0$ (no individual tendency to explore once a resource is found) and analyzed q, colony size, and foraging strategy (either spatial communication or informed individual initiative) as fixed effects, with per capita resources collected as the response variable. The initial model allowed for interactions among all fixed effects. We found that the spatial communication strategy had significantly lower fitness than the informed individual initiative strategy (Factor Strategy [Spatial Communication]: -141.8 ± 10.86, $p < 0.0001$), a result that we will explore in the Discussion. As for the effect of colony size, we found that fitness was significantly higher at larger colony sizes for the spatial communication strategy, but not for the informed individual initiative strategy (Interaction Between q, Strategy [Spatial Communication], and Colony Size: 0.01427 ± 0.00431, $p = 0.0011$; Figures 4.1 and 4.2).

To examine the cause of the positive relationship with colony size and fitness under the spatial communication strategy (and at high values of q, meaning social information is used often), we examined the average number of dances detected by agents in the nest at different colony sizes. Here, we focus only on the spatial communication strategy and the fixed effects are q and colony size. We found that agents detected more dances at larger colony sizes (0.0004837 ± 0.000004436, $p < 0.0001$; Figure 4.3).

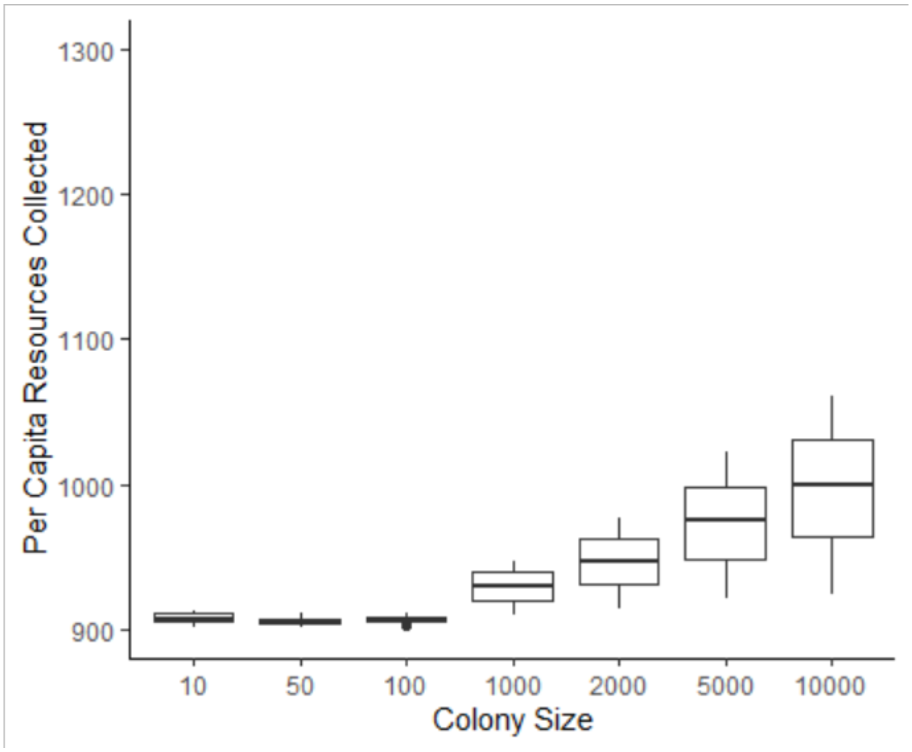

Figure 4.1. Per capita resources collected by agents when using the spatial communication, dance language strategy. Boxplots represent data collected across different values of *q*, while *p* = 0 and the resource density = 10. Black lines in boxplots represent the median, while the whiskers represent the upper and lower quartiles. Colony size, on the x-axis, is the number of agents used in the simulation, while the total resources collected per capita is on the y-axis. There is a significant positive effect of colony size on per capita resources collected when agents use spatial communication.

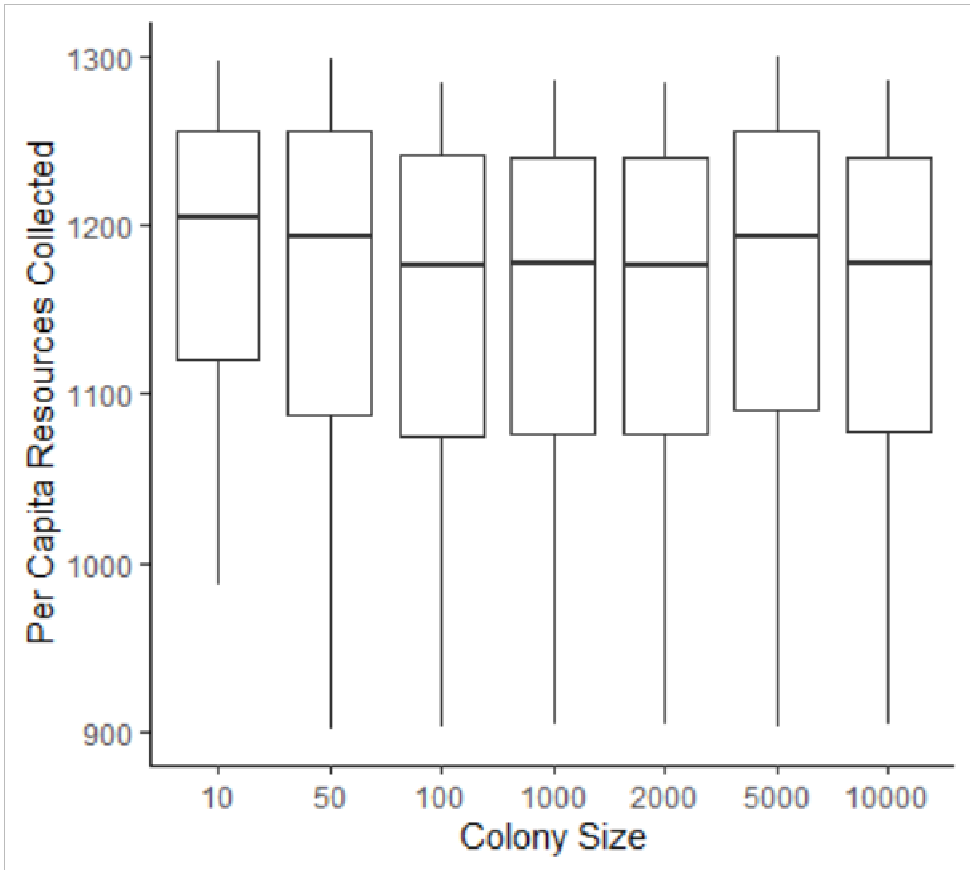

Figure 4.2. Per capita resources collected by agents when using the informed individual initiative strategy. Boxplots represent data collected across different values of *q*, while *p* = 0 and the resource density = 10. Black lines in boxplots represent the median, while the whiskers represent the upper and lower quartiles. Colony size, on the x-axis, is the number of agents used in the simulation, while the total resources collected per capita is on the y-axis. There is no effect of colony size on per capita resources collected when agents use informed individual initiative.

Table 4.2: Effects of colony size and foraging strategy on fitness

Coefficient	**Estimate**	**Standard Error**	**t-value**	**p-value**
q	405.4	13.13	30.871	< 0.0001
ColonySize	0.0003291	0.001781	0.185	0.85357
Strategy (Spatial Communication)	-141.8	10.86	-13.066	< 0.0001
q * ColonySize	-0.0003215	0.003047	-0.106	0.91604
q * Strategy (Spatial Communication)	-393.6	18.57	-21.194	< 0.0001
ColonySize * Strategy (Spatial Communication)	0.002074	0.002519	0.823	0.41095
q * ColonySize * Strategy (Spatial Communication)	0.01427	0.00431	3.312	0.00105

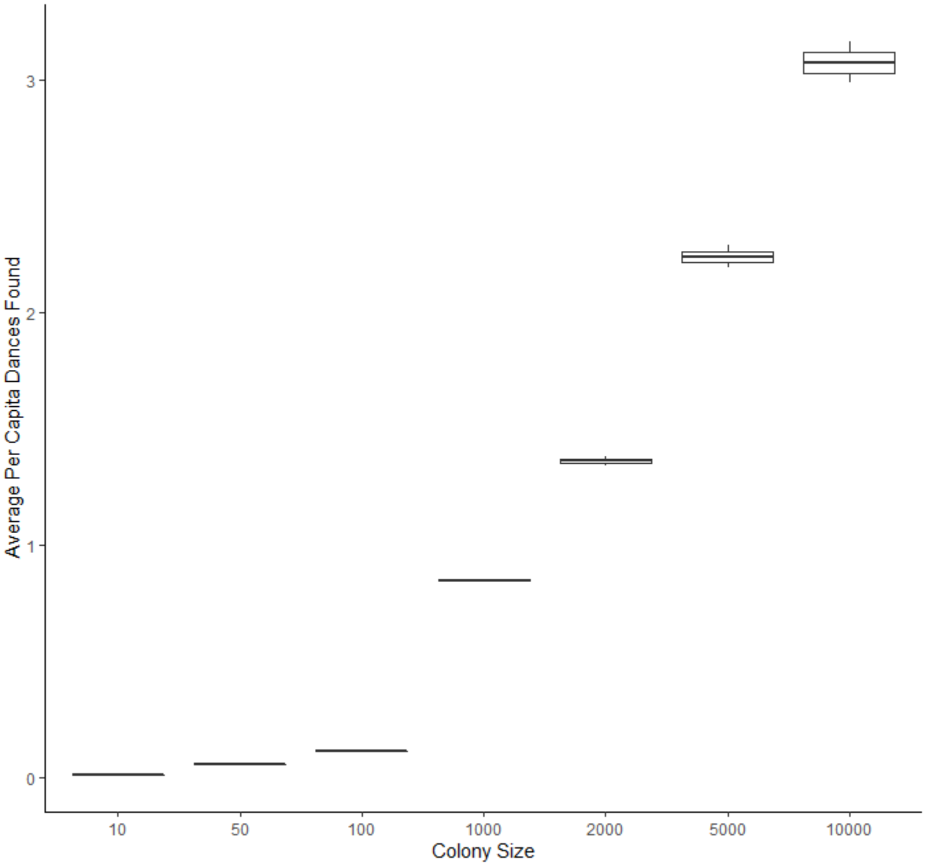

Figure 4.3. Per capita dances detected by agents at different colony sizes, when using the spatial communication strategy. Boxplots represent data collected across different values of *q*, while *p* = 0 and the resource density = 10. Black lines in boxplots represent the median, while the whiskers represent the upper and lower quartiles. Colony size had a significant positive effect on the per capita number of dances found by agents.

Fitness of the Spatial Communication Strategy Across Colony Sizes and Resource Densities

To test for an effect of resource density on fitness when agents use spatial communication, we ran simulations at colony sizes of 10, 100, and 1000 where the landscape contained 100 resources instead of 10. We chose to restrict the colony sizes used because results with more colony sizes showed that an effect on fitness begins to appear when the number of agents reaches 1000. We focused on simulations when $p = 0$ (no individual search after the first resource is found), and use q, colony size, and resource density as fixed effects, allowing for all interactions. After this simulation, we chose to focus in on a colony size of 1000 and run further simulations at resource densities of 5, 500, 2500, and 5000, in order to capture the space of this parameter more fully. We again used per capita resources collected as the response variable. When all data from these simulations are taken together, we see that fitness is higher when colony size is larger (0.006222 ± 0.002111, p = 0.00347; Figure 4.1) and when resources are more dense (0.4532 ± 0.1247, p = 0.0003; Figures 4.4 and 4.5). We also see a negative interaction between colony size and resource density that seems to suggest that the dance becomes less beneficial when both colonies are large and resources are dense (-0.0004412 ± 0.0001242, p = 0.0004; Figure 4.4). This result is in line with empirical data from prior studies (Sherman and Visscher 2002).

In our focused series of simulations using a colony size of 1000 and resource densities of 5, 10, 100, 500, 2500, and 5000, we again focused on when $p = 0$, but use only q and resource density as fixed effects with per capita resources collected as the response variable. Here we again see that fitness is higher when resources are more abundant (0.01019 ± 0.003934, p = 0.0107), however fitness begins to plateau when resource density reaches 500 (Figure 4.5). This indicates that per capita fitness does not increase linearly with resource density, but rather that at a certain point the environment becomes oversaturated with resources to the point that per capita fitness is maximal.

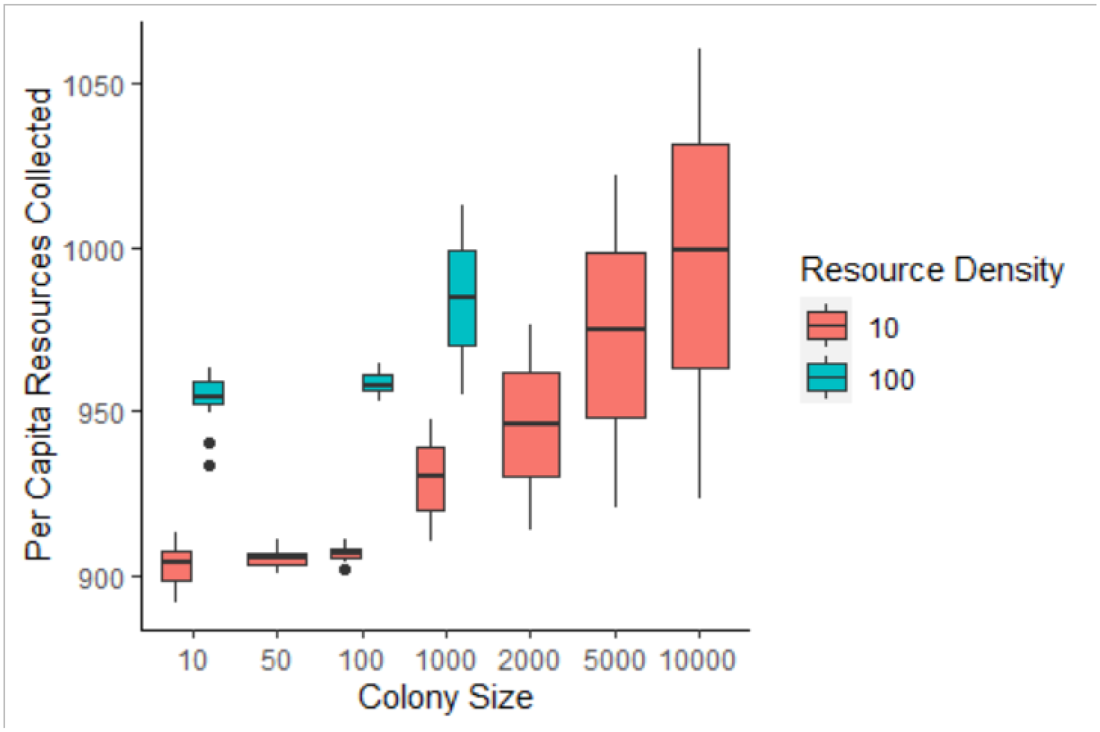

Figure 4.4. Per capita resources collected across colony sizes and at different resource densities when agents use the spatial communication strategy. Boxplots represent data collected across different values of q, while $p = 0$ and the resource density = 10. Black lines in boxplots represent the median, while the whiskers represent the upper and lower quartiles. Both colony size and resource density had significant positive effects on per capita resources collected, but have a significant negative interaction. For a given colony size, agents collected more resources per capita when resources were more abundant in the environment, but this increase becomes smaller at larger colony sizes. For a visualization of the targeted simulations at a colony size of 1000, see Figure 4.5.

Table 4.3: Effects of resource density and colony size on fitness when agents use spatial communication

Coefficient	**Estimate**	**Standard Error**	**t-value**	**p-value**
q	27.37	9.983	2.742	0.006489
ColonySize	0.006222	0.002111	2.947	0.003470
ResourceDensity	0.4532	0.1247	3.635	0.000329
q * ColonySize	0.01043	0.003612	2.889	0.004163
q * ResourceDensity	-0.1962	0.2133	-0.920	0.358414
ColonySize * ResourceDensity	-0.0004412	0.0001242	-3.554	0.000444
q * ColonySize * ResourceDensity	0.0002158	0.0002124	1.016	0.310543

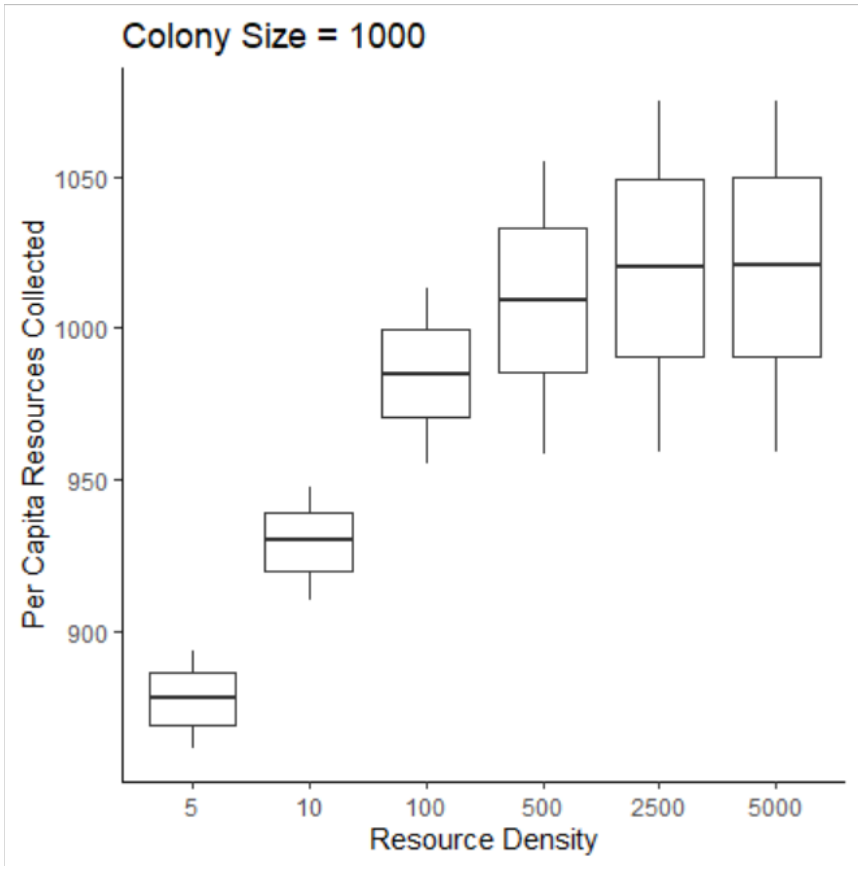

Figure 4.5. Per capita resources collected by agents across resource densities when colonies consist of 1000 agents. Boxplots represent data collected across different values of q, while p = 0. Black lines in boxplots represent the median, while the whiskers represent the upper and lower quartiles.

Fitness of the Informed Individual Initiative Strategy Across Colony Sizes and Resource Densities

To test for an effect of resource density on fitness when agents use informed individual initiative, we again ran simulations at colony sizes of 10, 100, and 1000 where the landscape contained 100 resources instead of 10. We focus on simulations when $p = 0$ (i.e. no individually triggered search), and analyze q (probability of using social information), colony size, and resource density as fixed effects, allowing for all interactions. We focused on when $p = 0$ because prior results revealed that the effects of social information are most easily captured when individual search occurs at a low frequency (Incorvaia et al. 2021). We again used per capita resources collected as the response variable. Colony size and all of its interactions were not included in the best-fitting model. We found that fitness was significantly higher at greater resource densities (3.6957 ± 0.2407, $p < 0.0001$), as visualized by Figure 4.6.

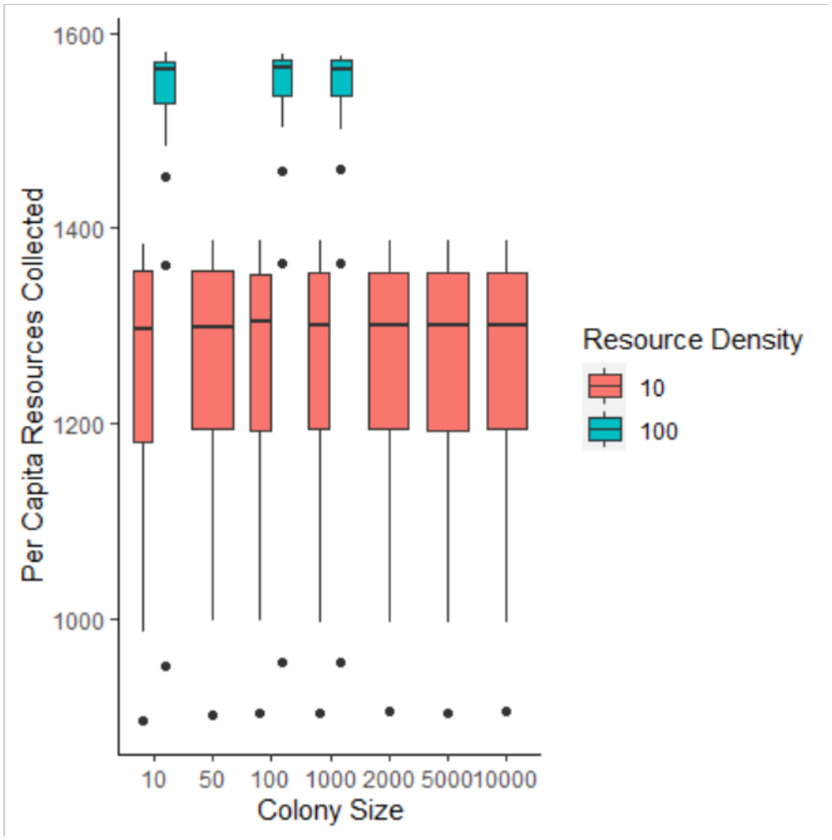

Figure 4.6. Per capita resources collected across colony sizes and at different resource densities when agents use the informed individual initiative strategy. Boxplots represent data collected across different values of *q*, while *p* = 0 and the resource density = 10. Black lines in boxplots represent the median, while the whiskers represent the upper and lower quartiles. Resource density had a significant positive effect on per capita resources collected, but colony size dropped out of the top model.

Table 4.4: Effect of resource density on fitness when agents use informed individual initiative

Coefficient	Estimate	Standard Error	t-value	p-value
q	419.82	22.8184	18.398	< 0.0001
ResourceDensity	3.6957	0.2407	15.353	< 0.0001
q * ResourceDensity	-1.5216	0.4118	-3.695	0.000282

DISCUSSION

We sought to use a modeling approach to explore how two hypothesized selection pressures, colony size and resource density, shape the fitness returns of two adaptive social foraging strategies used by social bees: the dance language of honeybees, and informed individual initiative of bumblebees. Our results demonstrate that when using the dance language, agents bring in more resources (our measure of fitness) at greater colony sizes (Figure 4.1) and resource densities (Figures 4.4 and 4.5). By contrast, colonies using informed individual initiative (the bumblebee strategy) had improved performance at greater resource densities (Figure 4.6), but there was no effect of colony size (Figure 4.2). For colonies using the dance language, we also found a negative interaction between colony size and resource density, suggesting that the dance becomes less beneficial when both colonies are large and resources are dense (Figure 4.4)—this is in line with previous empirical results (Sherman and Visscher 2002; Dornhaus and Chittka 2004). We also find that the effect of colony size on dance language fitness may be caused by agents finding more dances at larger colony sizes (Figure 4.3).

The relationship between colony size and foraging strategy in social insects has long been of interest. In ants, empirical and modeling results together support the hypothesis that colony size is related to foraging strategy. Beckers et al. (1989) reported a relationship between colony size and foraging strategy in ants, with smaller colonies more likely to use individual search and larger colonies more likely to use group strategies and spatial recruitment. However, this analysis did not control for phylogenetic relationships. A more recent phylogenetic analysis with 402 species of ant found that the spatiotemporal characteristics of resources are associated with the foraging strategy used, but did not examine colony size (Lanan 2014). Beekman et al. (2001) experimentally manipulated colony size in the pharaoh ant *Monomorium pharaonic* and found that at a threshold number of individuals (about 600), the colony switched from individual foraging to pheromone recruitment. Planqué et al. (2010) used a mathematical model, based on data from Beekman et al. (2001), to demonstrate that differences in foraging strategy can also be explained by differences in recruitment caused by colony size, with pheromone trails associated with larger colonies and individual foraging associated with smaller colonies; this is also in line with the results of Beckers et al. (1989). Warburg et al. (2017) recently found a similar correlation between colony size and foraging strategy in desert seed harvesting ants specifically.

In honeybees, results have been more variable. The dance has been shown experimentally to be more beneficial in larger honeybee colonies (Donaldson-Matasci et al. 2013), though this result disagrees with other modeling studies, which found no effect of colony size on the fitness benefits of dance communication (Dornhaus et al. 2006). Additionally, the dance has been shown to be most beneficial in environments with high floral species richness and abundant resources (Donaldson-Matasci and Dornhaus 2012; I'Anson Price et al. 2019), though another modeling study found that dance communication is most beneficial in environments where finding resources is more difficult (Beekman and Lew 2008). Many empirical studies have found no benefits of dance communication at all in some habitats (Dornhaus and Chittka 2004; Donaldson-Matasci and Dornhaus 2012; Nürnberger et al. 2017), while others have (Sherman and Visscher 2002). Despite these and other complications (Schürch and Grüter 2014; I'Anson Price et al. 2019), results suggest that both resources in the environment and colony size can influence the fitness benefits of dance communication.

For bumblebees, to our knowledge this is the first modeling study that has examined how potential selection pressures like colony size and resource density influence the fitness of collective foraging. Many past studies have examined how social information influences foraging decisions, including both intranidal (e.g. Dornhaus and Chittka 2005, Renner and Nieh 2008) and extranidal (e.g. Leadbeater and Chittka 2007, Dunlap et al. 2016, Pearce et al. 2017) sources. The study of collective foraging dynamics in bumblebees is still in its infancy (Incorvaia et al. 2021). Our results here are the first to demonstrate that this strategy's evolution may have been favored by greater resource availability (Figure 4.6), but most likely not by colony size (Figure 4.2). This makes sense, as informed individual initiative does not explicitly require foragers to contact one another in the nest; rather, the important social cue is stored food. However, while stored food is the primary social cue that has been explored so far in regard to informed individual initiative (in both this study and Incorvaia et al. 2021), future studies should endeavor to explicitly examine how other social information sources, such as contact-based foraging activation (Dornhaus and Chittka 2001; Renner and Nieh 2008) and tergal pheromones (Dornhaus et al. 2003; Granero et al. 2005), influence this collective strategy and its fitness relative to selective pressures.

While the purpose of our study was to examine how the spatial communication and individual initiative strategies perform under different selective pressures, and not to directly compare them, the result that informed individual initiative outperformed spatial communication prompted us to explore why the model produced this stark difference. One possible explanation for this difference comes from the lack of an in-nest spatial component in the informed individual initiative strategy; rather than agents needing to encounter a better resource in the nest, they can detect that a better resource exists (hence initiate search for something better) no matter where they are. In order to test whether this is the cause of the observed fitness differences between the strategies, we ran simulations of a modified version of the model where agents in the informed individual initiative condition now store resources they forage from in the nest. In order for an agent to respond (with probability q) to a better resource, it must now first encounter it in the nest during its regular nest movements. The results of these simulations showed that adding this constraint only slightly reduced fitness for the informed individual initiative strategy, suggesting that some other aspect of the model explains the large fitness discrepancy. Notably, the dance language's fitness may be hampered by the lack of a spatial location for the nest in the environment. This eliminates a key characteristic of the central place foraging problem—namely that foraging and exploration costs would increase with the distance of a resource from the nest. This may be the key to the importance of the dance in nature, a hypothesis that can be examined in future elaborations of this modeling approach.

Our results suggest that dance communication is more beneficial when colonies are large and resources are abundant. The bumblebee strategy of informed individual initiative, however, does not become more beneficial as colony size increases, but is instead only influenced by resource density. This result suggests that colony size at least partially explains why bumblebees have not evolved in-nest spatial communication strategies while honeybees, and potentially some stingless bees (Peng et al. 2021), have evolved them. The smaller colony size of bumblebees may be a necessary consequence of their annual lifecycle, which involves new colonies being started by queens every spring and then completely dying out in the fall (Goulson 2010); the evolution of in-nest spatial communication may therefore be limited to species with large colonies (like honeybees and stingless bees), which can grow to include many more individuals.

Other aspects of bee recruitment that could be explored in the model include the use by foragers of other information sources within the nest (such as odors), the chosen search time (T_{Search}, see Table 4.1), and changes in resource patches over time (Sherman and Visscher 2002). Search time in particular represents foraging costs in the model, as a longer search time duration would increase the probability of finding a resource without concomitant costs in terms of energy or actual wasted solar time; running simulations with lower search times would therefore enable us to examine the fitness of social foraging strategies when search is more costly. The modeling approach we took here gave us a chance to identify key parameters involved in nature that would be impossible to explore using conventional field-based approaches. Our model has succeeded in revealing the relationship between colony size, resource density, and fitness in social insects; it can be modified and expanded to study other related taxa (such as stingless bees) or other questions in honeybees and bumblebees; and, perhaps most importantly, the results apply to all organisms that behave according to the model, not just bees.

The honeybee dance language represents one of the most remarkable examples of communication in the animal kingdom, adaptively tuned to allow colonies to effectively find food sources and new nest sites (Seeley and Buhrman 1999; Dyer 2002; George et al. 2020; Kohl et al. 2020). Despite its centuries-long study, the natural history and ecology that led to its evolution has remained elusive and controversial. In this study, we have used a modeling approach to demonstrate that the honeybee strategy of spatially explicit communication via the dance language is favored when resources are abundant and the colony size is large; by contrast, the more individual strategy of bumblebees is not affected at all by colony size. Our results shed new light on the debated importance of colony size and resource ecology for the evolution of the dance language, and also begin a new line of inquiry into how these selection pressures shape the collective foraging strategy of the related bumblebee. Our results thus provide a starting point for further modeling studies of the selective pressures that shape foraging strategies in the social insects. An improved understanding of the evolution of social foraging strategies can help us understand how collective behaviors more broadly are influenced by ecology, as well as how honeybees and bumblebees, both important pollinators, are likely to respond under changing land use paradigms and global climate change (Cameron et al. 2011; I'Anson Price et al. 2019; Soroye et al. 2020).

REFERENCES

REFERENCES

Andersson, Malte. "Female choice selects for extreme tail length in a widowbird." *Nature* 299.5886 (1982): 818-820.

Beckers, Ralph, et al. "Colony size, communication and ant foraging strategy." *Psyche: A Journal of Entomology* 96.3-4 (1989): 239-256.

Beekman, Madeleine, and Jie Bin Lew. "Foraging in honeybees—when does it pay to dance?." *Behavioral Ecology* 19.2 (2008): 255-261.

Beekman, Madeleine, David JT Sumpter, and Francis LW Ratnieks. "Phase transition between disordered and ordered foraging in Pharaoh's ants." *Proceedings of the National Academy of Sciences* 98.17 (2001): 9703-9706.

Beshers, Samuel N., and Jennifer H. Fewell. "Models of division of labor in social insects." *Annual review of entomology* 46.1 (2001): 413-440.

Cameron, Sydney A., et al. "Patterns of widespread decline in North American bumble bees." *Proceedings of the National Academy of Sciences* 108.2 (2011): 662-667.

Cartar, Ralph V. "Adjustment of foraging effort and task switching in energy-manipulated wild bumblebee colonies." *Animal Behaviour* 44.1 (1992): 75-87.

Couzin, Iain D. "Collective cognition in animal groups." *Trends in cognitive sciences* 13.1 (2009): 36-43.

Couzin, Iain D., and Nigel R. Franks. "Self-organized lane formation and optimized traffic flow in army ants." *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270.1511 (2003): 139-146.

Czaczkes, Tomer J., Christoph Grüter, and Francis LW Ratnieks. "Trail pheromones: an integrative view of their role in social insect colony organization." *Annual review of entomology* 60 (2015): 581-599.

Deneubourg, J-L., et al. "The self-organizing exploratory pattern of the argentine ant." *Journal of insect behavior* 3.2 (1990): 159-168.

Donaldson-Matasci, Matina C., and Anna Dornhaus. "How habitat affects the benefits of communication in collectively foraging honey bees." *Behavioral ecology and sociobiology* 66.4 (2012): 583-592.

Donaldson-Matasci, Matina C., Gloria DeGrandi-Hoffman, and Anna Dornhaus. "Bigger is better: honeybee colonies as distributed information-gathering systems." *Animal behaviour* 85.3 (2013): 585-592.

Dornhaus, A., A. Brockmann, and L. Chittka. "Bumble bees alert to food with pheromone from tergal gland." *Journal of Comparative Physiology A* 189.1 (2003): 47-51.

Dornhaus, Anna, and Lars Chittka. "Bumble bees (Bombus terrestris) store both food and information in honeypots." *Behavioral Ecology* 16.3 (2005): 661-666.

Dornhaus, Anna, and Lars Chittka. "Food alert in bumblebees (Bombus terrestris): possible mechanisms and evolutionary implications." *Behavioral Ecology and Sociobiology* 50.6 (2001): 570-576.

Dornhaus, Anna, and Lars Chittka. "Why do honey bees dance?." *Behavioral Ecology and Sociobiology* 55.4 (2004): 395-401.

Dornhaus, Anna, and Sydney Cameron. "A scientific note on food alert in Bombus transversalis." *Apidologie* 34.1 (2003): 87-88.

Dornhaus, Anna, et al. "Benefits of recruitment in honey bees: effects of ecology and colony size in an individual-based model." *Behavioral Ecology* 17.3 (2006): 336-344.

Dunlap, Aimee S., et al. "Foraging bumble bees weigh the reliability of personal and social information." *Current Biology* 26.9 (2016): 1195-1199.

Dyer, Fred C. "The biology of the dance language." *Annual review of entomology* 47.1 (2002): 917-949.

George, Ebi Antony, et al. "Similarities in dance follower behaviour across honey bee species suggest a conserved mechanism of dance communication." *Animal Behaviour* 169 (2020): 139-155.

Gordon, Deborah M. "The ecology of collective behavior in ants." *Annual review of entomology* (2019).

Gordon, Deborah M. "The ecology of collective behavior." *PLoS Biol* 12.3 (2014): e1001805.

Goulson, Dave. *Bumblebees: behaviour, ecology, and conservation*. Oxford University Press on Demand, 2010.

Granero, Angeles Mena, et al. "Chemical compounds of the foraging recruitment pheromone in bumblebees." *Naturwissenschaften* 92.8 (2005): 371-374.

Grimm, Volker, et al. "A standard protocol for describing individual-based and agent-based models." *Ecological modelling* 198.1-2 (2006): 115-126.

Grimm, Volker, et al. "The ODD protocol: a review and first update." *Ecological modelling* 221.23 (2010): 2760-2768.

Hoogland, R., D. Morris, and N. Tinbergen. "The spines of sticklebacks (Gasterosteus and Pygosteus) as means of defence against predators (Perca and Esox)." *Behaviour* (1956): 205-236.

I'Anson Price, Robbie, et al. "Honeybees forage more successfully without the "dance language" in challenging environments." *Science advances* 5.2 (2019): eaat0450.

Incorvaia, Darren C., Arend Hintze, and Fred C. Dyer. "Spatial allocation without spatial recruitment in bumblebees." *Behavioral Ecology* 32.2 (2021): 265-276.

Kohl, Patrick L., et al. "Adaptive evolution of honeybee dance dialects." *Proceedings of the Royal Society B* 287.1922 (2020): 20200190.

Lanan, Michele. "Spatiotemporal resource distribution and foraging strategies of ants (Hymenoptera: Formicidae)." *Myrmecological news/Osterreichische Gesellschaft fur Entomofaunistik* 20 (2014): 53.

Leadbeater, Ellouise, and Lars Chittka. "The dynamics of social learning in an insect model, the bumblebee (Bombus terrestris)." *Behavioral Ecology and Sociobiology* 61.11 (2007): 1789-1796.

Nürnberger, Fabian, Ingolf Steffan-Dewenter, and Stephan Härtel. "Combined effects of waggle dance communication and landscape heterogeneity on nectar and pollen uptake in honey bee colonies." *PeerJ* 5 (2017): e3441.

Pearce, Richard F., Luca Giuggioli, and Sean A. Rands. "Bumblebees can discriminate between scent-marks deposited by conspecifics." *Scientific reports* 7.1 (2017): 1-11.

Peng, Tianfei, et al. "Foragers of the stingless bee Plebeia droryana inform nestmates about the direction, but not the distance to food sources." *Ecological Entomology* 46.1 (2021): 33-40.

Perna, Andrea, et al. "Individual rules for trail pattern formation in Argentine ants (Linepithema humile)." *PLoS Comput Biol* 8.7 (2012): e1002592.

Planqué, Robert, Jan Bouwe Van Den Berg, and Nigel R. Franks. "Recruitment strategies and colony size in ants." *PLoS One* 5.8 (2010).

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Renner, M. A., and J. C. Nieh. "Bumble bee olfactory information flow and contact-based foraging activation." *Insectes sociaux* 55.4 (2008): 417-424.

Schultz, Ted R. "In search of ant ancestors." *Proceedings of the National Academy of Sciences* 97.26 (2000): 14028-14029.

Schürch, Roger, and Christoph Grüter. "Dancing bees improve colony foraging success as long-term benefits outweigh short-term costs." *PLoS One* 9.8 (2014): e104660.

Seeley, Thomas D. *The wisdom of the hive: the social physiology of honey bee colonies*. Harvard University Press, 2009.

Seeley, Thomas D., and Susannah C. Buhrman. "Group decision making in swarms of honey bees." *Behavioral Ecology and Sociobiology* 45.1 (1999): 19-31.

Seeley, Thomas D., Scott Camazine, and James Sneyd. "Collective decision-making in honey bees: how colonies choose among nectar sources." *Behavioral Ecology and Sociobiology* 28.4 (1991): 277-290.

Sherman, Gavin, and P. Kirk Visscher. "Honeybee colonies achieve fitness through dancing." *Nature* 419.6910 (2002): 920-922.

Soroye, Peter, Tim Newbold, and Jeremy Kerr. "Climate change contributes to widespread declines among bumble bees across continents." *Science* 367.6478 (2020): 685-688.

Starkey, Jesse, Ahja Brown, and Etya Amsalem. "The road to sociality: brood regulation of worker reproduction in the simple eusocial bee Bombus impatiens." *Animal Behaviour* 154 (2019): 57-65.

Sumpter, David JT. "The principles of collective animal behaviour." *Philosophical transactions of the royal society B: Biological Sciences* 361.1465 (2006): 5-22.

Tinbergen, Niko. "Comparative studies of the behaviour of gulls (Laridae): a progress report." *Behaviour* 15.1-2 (1960): 1-69.

Von Frisch, Karl. "The dance language and orientation of bees." (1967).

Warburg, Ittai, Walter G. Whitford, and Yosef Steinberger. "Colony size and foraging strategies in desert seed harvester ants." *Journal of Arid Environments* 145 (2017): 18-23.

Wehner, Rudiger, Robert D. Harkness, and Paul Schmid-Hempel. *Foraging strategies in individually searching ants*. Fischer, 1983.

Wilson, Edward O. "The insect societies." *The insect societies.* (1971).

Wilson, Edward O. *Success and dominance in ecosystems: the case of the social insects*. Vol. 2. Oldendorf/Luhe: Ecology Institute, 1990.

Young, Allison M., Axel Brockmann, and Fred C. Dyer. "Adaptive tuning of the exploitation-exploration trade-off in four honey bee species." *Behavioral Ecology and Sociobiology* 75.1 (2021): 1-15.