DISSERTATION

LEARNING AND DECISION MAKING ALONG A NUTRITIONAL GRADIENT

Submitted by

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ABSTRACT

LEARNING AND DECISION MAKING ALONG A NUTRITIONAL GRADIENT

Nutrition is fundamental to the life history of all animals and the behavioral processes by which animals acquire nutrition are of central interest to students of animal behavior. How an animal learns about available food resources, and the strategies adopted to acquire food resources are therefore of central importance. While animal nutrition is quite complex, energy is a fundamental nutrient and is the focus of this work. In chapter 1, honeybees were fed or starved before they were given a choice assay to determine how individual energetic state altered their choice between gathering information about food resources and consuming known food resources. It was found that bees which were relatively satiated prioritized the collection of information over energy. This work was expanded in chapter 2, in which the energetic states of honeybee colonies were manipulated, in addition to the manipulation of individual energetic state. This experiment provided insights into how group members make decisions in the presence of conflicting individual and group level interests and found that honeybee behavioral phenotypes vary in how they prioritize group and individual needs. The first two chapters focus on how animals make decisions after they have acquired some information, but differences in learning also play a vital role in the acquisition of nutrition. In chapter 3, bees were weighed early and late in their lifetimes, and it was found that bees with more stable weight percentile ranks performed better in a learning assay than bees with unstable weight percentile ranks. As nutritional environment plays a significant role on the body weight of individuals, this may indicate that consistent nutritional conditions contribute to bee cognition. Along with nutrition, body weight is also correlated with the metabolic rate of

individuals. Metabolic rate is directly tied to the energy acquisition behavior of animals, as it determines how and at what rate energy is processed by an animal. In order to evaluate how metabolic rate alone influences nutrient acquisition, a model, presented in Chapter 4, was constructed that evaluated the performance of different metabolic rates in different nutritional environments. In general, high metabolic rates were more favorable in rich nutritional environments and low metabolic rates were more favorable in poor nutritional environments. It was also shown that diversity of metabolic rates within a group is advantageous in some environments. Taken together, this work indicates that nutrition, in the form of energy, plays a vital role in the how animals learn and make decisions. This is true for nutrition at both the individual and group level, over immediate and long-term timescales, and for physiological differences in the capacity of an animal to assimilate energy. These findings have broad implications in behavioral ecology and are discussed in terms of optimal foraging, group behavior, developmental plasticity, and gene-environment interactions.

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This dissertation could not have been completed without the help and guidance of many people. I'll begin by thanking my advisor Dhruba Naug for endless hours of discussing research methods, data interpretation, and manuscript editing. He was always willing to stop whatever he was working on to help me think through a problem and for that I am very grateful. I would also like to thank my committee members, Kim Hoke, Stephen Pratt, and Boris Kondratieff, for their comments on my manuscripts and their constant encouragement.

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Many members of the Bee Lab have come and gone during my dissertation project and they all helped me in different ways. They taught me how to teach bees and how to paint them; they helped me develop my own research methods; they collected valuable data for me, and they taught me how to have fun while remaining productive. For all of these things, I would like to thank Abbie Reade, Carrie Tait, Chris Mayack, Hannah Grace, Amanda Lark, Colton O'Brien, Aja Mattise-Lorenzen, Amanda Stammer, Robin Scudelari, Michael Prantis, and Tyler Smith.

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CHAPTER 1

ENERGETIC STATE REGULATES THE EXPLORATION–EXPLOITATION TRADE-OFF IN HONEYBEES[1]

SUMMARY

Foragers must divide their time between consuming known resources (exploitation) and learning about new resources (exploration). As opposed to classical optimal foraging theory, the information primacy hypothesis predicts that only starved animals will show higher levels of exploitation while more satiated animals will show higher levels of exploration. We tested these predictions in honeybee foragers using a conditioning assay to make them associate different odors with sucrose rewards that differed in energetic values and the certainty of these values (measured by the number of conditioning trials and recency of those trials). We then tested their choice between these rewards at different levels of hunger. Fed bees showed higher sampling and a lower consumptive effort compared to starved bees. Fed bees also showed a higher preference for rewards with completely uncertain values (novel rewards) but not for rewards with only partially uncertain values. These results show that switching between exploration and exploitation strategies during foraging is driven by the energetic state of an animal and therefore by an interaction

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[1] This is a pre-copyedited, author-produced version of an article accepted for publication in Behavioral Ecology following peer review. The version of record is available online at: http://beheco.oxfordjournals.org/content/26/4/1045.full.

Katz, K., & Naug, D. (2015). Energetic state regulates the exploration–exploitation trade-off in honeybees. *Behavioral Ecology* 26(4), 1045-1050. doi: 10.1093/beheco/arv045

between the value of food and the value of information. We discuss these results in the context of energetic shortfalls in animals.

INTRODUCTION

The fundamental process of acquiring energy and nutrition by foraging is inextricably tied with acquiring information (Dall et al. 2005). Classical optimal foraging theory generally assumes foragers have perfect information about their environment (Charnov 1976), but this is rarely true in nature. Foragers often have incomplete information about available resources and must spend time and energy sampling their environment to update their knowledge (Krebs et al. 1978, Lima 1984, Tamm 1987, Naug and Arathi 2007). More recently, foraging studies have used Bayesian approaches to explain some of the observed departures from the predictions of optimal foraging by showing that animals combine prior and current information about a patch when making foraging decisions (McNamara et al. 2006; Valone 2006; Trimmer et al. 2011). The value of gathering information, also known as environmental tracking, is not constant and is known to depend on a number of factors such as the frequency of environmental change, the relative values of different patches, and the cost of information gathering itself (Stephens 1987). However, what has been frequently overlooked is how an animal's nutritional state impacts its tendency to gather information.

Since animals must adaptively divide their time between gathering information and using this information to gather food, they are subject to what is called the exploration-exploitation trade-off (Kramer and Weary 1991; Cohen et al. 2007; Eliassen et al. 2007), the scope of which extends well beyond behavioral ecology to many other disciplines in the context of search problems (Azoulay-Schwartz et al. 2004; Berger-Tal et al. 2014; Hills et al. 2015). In a foraging context, it refers to a trade-off between sampling or exploring food patches of uncertain values to gather information about their quality and exploiting known patches to reduce current nutritional needs (Forkman 1991). While it has been suggested that the extent of energetic deprivation may determine a switching point between exploration and exploitation strategies (Lea et al. 2012), the vast majority of studies on foraging behavior are conducted with hungry animals, simply because they are the most motivated to seek food. This has limited our understanding of foraging behavior to some degree as most studies primarily focus on how foraging is motivated by the need to meet the nutritional demands of an animal (Nonacs 2001).

The information primacy hypothesis provides an explicit framework regarding how the value of information and the resulting exploration-exploitation trade-off may depend on the energetic state of a forager and drive its foraging behavior (Inglis et al. 2001), an idea that has received relatively little attention in empirical studies. According to this hypothesis, animals are intrinsically motivated to reduce their uncertainty regarding the environment, but primary needs such as hunger or thirst can override the drive to seek information (Inglis 1983; 2000; Inglis et al. 2001). Therefore, information gathering is the primary motivator of behavior when hunger is low and optimal foraging in the traditional sense is expected only when animals are hungry. Information primacy has generally been used to explain contrafreeloading, animals preferring to work for food rather than consume identical free food (Bean et al. 1999; Inglis et al. 1997; Inglis and Shepherd 1994; Ogura 2011; Vasconcellos et al. 2012), but some studies outside this framework also provide support for this hypothesis (Shani et al. 2011; Barnett et al. 1978). However, none of these studies explicitly test the effect of an animal's nutritional state on the trade-off between exploration and exploitation.

If two patches vary independently with respect to their nutritional values and the uncertainty associated with them, one can have the following four patch types: 1) Low Value-Low Uncertainty, 2) High Value-High Uncertainty, 3) High Value-Low Uncertainty, and 4) Low Value-High Uncertainty. Both optimal foraging and information primacy models make the same predictions for the first two patch types - that all animals would prefer a High Value-High Uncertainty patch over a Low Value-Low Uncertainty patch, whether they are foraging for food (optimal foraging) or for information (information primacy). However, optimal foraging and information primacy make opposite predictions for the last two patch types. Optimal foraging predicts that animals would always prefer the High Value-Low Uncertainty patch, irrespective of their own energetic state, in order to maximize their energetic returns. In contrast, information primacy predicts that more satiated animals would prioritize information over energy and prefer the Low Value-High Uncertainty patch in order to gather information (despite the low value of the patch) and only hungry animals would choose the High Value-Low Uncertainty patch.

Since social information can play a large role in reducing uncertainty, social signals and cues have traditionally been considered to be the major force that regulate the foraging behavior of individuals in social insect colonies (Seeley 1995). However, there is increasing evidence that individual nutritional state plays a significant role in this regulation (Toth et al. 2005; Mayack and Naug 2013), which in turn suggests that the fundamental mechanisms related to food-seeking behavior have been conserved during the evolution of social foraging from solitary ancestors (Toth and Robinson 2007). This makes it important to understand the extent to which nutritional state can affect the foraging behavior of social insect individuals. We have recently shown that the energetic state of an individual has a significant influence on its sensitivity to uncertainty in terms of risk (determinate uncertainty, which refers to the true variability of an outcome) in honeybee foragers (Mayack and Naug 2011). In complement, the goal of this study was to use the information primacy framework to test if energetic state affects how bees deal with uncertainty in terms of ambiguity (indeterminate uncertainty, which refers to an individual's lack of information regarding the true variability of an outcome). We specifically tested if the energetic state of an individual influences: (1) the choice between a familiar patch and a novel patch, and (2) the choice between two familiar patches with different reward values and uncertainties associated with them. We consider novelty as a case of complete uncertainty as a novel patch is a patch for which the animal lacks any information. The choice for a novel or a Low Value-High Uncertainty patch can be considered exploration as sampling is the primary benefit of a visit to such a patch and the choice for a familiar or a High Value-Low Uncertainty patch can be regarded as exploitation since it allows the forager to reduce its nutritional needs.

METHODS

We collected returning foragers from 5-7 colonies of the honeybee *Apis mellifera*, by blocking the entrance to a hive with wire mesh. We chilled these bees on ice to immobilize them and harnessed them into plastic straws with tape. We fed each bee to satiation with 30% sucrose solution to equalize their energetic states and starved them for 24 hours in an incubator set at 25 °C and 60% RH in order to increase their motivation for learning in an appetitive conditioning assay. We used the Proboscis Extension Response (PER) assay to train bees to associate an odor with a sucrose reward. An unconditioned stimulus (US) of sucrose placed on the antenna was paired with the conditioned stimulus (CS) of an odor (eugenol and 1-octanol or 2-octanone and 1-hexanol) to elicit a conditioned response (CR) of proboscis extension (Bitterman et al. 1983). Each conditioning trial for a bee consisted of presenting the odor for 6 seconds with the sucrose reward being presented for the final 2 seconds of the odor pulse, with the inter trial interval (ITI) being 11 minutes.

Subsequent to the conditioning procedure, we fed half the bees with 30 µl of sucrose solution (Fed group) and did not feed the other half (Starved group) to create two groups of bees at different energetic states (Mayack and Naug 2010). We kept these bees in an incubator for three hours before testing their choice with the two-alternative forced choice assay, which consists of presenting a bee with two odors on opposite sides of her head and recording her head turning response (Shafir et al. 1999; Mayack and Naug 2011). Each odor was presented twice in two alternating 0.8 second non-overlapping pulses with 0.2 seconds of odorless air in between successive odor pulses. We made video recordings of the proboscis extension and head turning response of each bee as she sampled the two odors. Using this general protocol, we performed the following experiments.

Novelty experiment

We performed six conditioning trials for each bee to associate an odor with a 0.2 µl reward of 30% sucrose and we refer to this odor as the familiar odor. The choice test involved presenting a bee with the familiar odor and a novel odor with which she had no prior association of a food reward.

Partial uncertainty experiment

We performed 12 conditioning trials for each bee to associate two different odors with two reward distributions of different values and different uncertainties associated with them. The Low

Value-High Uncertainty reward (Lv) was comprised of two trials with 10% sucrose and another two trials with 20% sucrose, resulting in a mean reward of 15% with a variance of 25. The High Value-Low Uncertainty reward (Hv) was comprised of four trials with 40% sucrose and another four trials with 50% sucrose, resulting in a mean reward of 45% with a variance of 25. The trials were organized in the pseudo random order Hv, Hv, Lv, Lv, Hv, Lv, Hv, Lv, Hv, Hv, Hv, Hv, such that both the higher number of total exposures and the more recent exposures to the High Value-Low Uncertainty reward pairing decreased the uncertainty associated with it compared to the Low Value-High Uncertainty reward.

Well-being assay

In order to ascertain that the starved bees in the behavioral experiments were as able as the fed bees to respond to the odor cues during the choice test, a parallel group of bees was set up during the Partial Uncertainty Experiment. This group was treated similarly to the bees in the conditioning assay, but was not subjected to the actual conditioning trials. These bees were fed or not fed similarly to the conditioned bees following the completion of the conditioning trials to create a Starved and a Fed group, and they were subjected to the same choice test along with the conditioned bees.

Data analysis

We analyzed the video recordings of the choice tests at half the normal speed and recorded the number of head turns, the final head position, and the duration of proboscis extension with the observer being blind to the direction of each odor and therefore the identity of the reward a bee chose. Bees that did not express the conditioned response to an odor at least once during the conditioning trials were not used in the analysis. The number of head turns made by each bee toward the two odors was defined as a measure of sampling or exploration, and the duration of proboscis extension during the presentation of the two odors was defined as a measure of exploitation. The final head position of the bee with respect to one of the two odors one second after the final odor was presented was defined as a choice for that odor. A choice for the odor associated with the familiar or High Value-Low Uncertainty reward was considered as exploitation and a choice for the odor associated with the novel or Low Value-High Uncertainty reward was considered as exploration.

Generalized Linear Models (GLM) were used to determine the effect of energetic state (amount of sucrose fed) on the number of head turns, total duration of proboscis extension and choice, modeled respectively as Poisson, Gaussian, and binomial distributions. Pearson's product-moment correlation was used to determine the relationship between the number of head turns and the total duration of proboscis extension. The effects of specific odors used during conditioning and the identity of the colony from which subject bees came from were analyzed for all the dependent variables in all the experiments (see Appendix I).

RESULTS

Novelty experiment

The number of head turns made by a bee significantly increased with her energetic state (GLM: Wald's $\chi^2 = 18.06$, d.f. = 1, $p < 0.001$, Fig. 1.1A). The total duration of proboscis extension significantly decreased with energetic state (Wald's $\chi^2 = 27.77$, d.f. = 1, $p < 0.0001$, Fig. 1.2A). The number of head turns showed a significant negative correlation with the duration of proboscis extension (Pearson's product-moment correlation: $r = -0.44 \pm 0.11$, $t = -4.12$, d.f. = 71, $p < 0.0001$).

The choice made by a bee was significantly affected by her energetic state (Wald's $\chi^2 = 4.73$, d.f. = 1, p = 0.02, Fig. 1.3A), with fed bees showing a higher preference for novelty.

Partial uncertainty experiment

The number of head turns made by a bee significantly increased with her energetic state (GLM: Wald's $\chi^2 = 6.08$, d.f. = 1, p = 0.01, Fig. 1.1B). The total duration of proboscis extension significantly decreased with energetic state (Wald's $\chi^2 = 33.46$, d.f. = 1, $p < 0.0001$, Fig. 1.2B). The number of head turns showed a significant negative correlation with the duration of proboscis extension (Pearson's product-moment correlation: r = - 0.23 ± 0.09, t = - 2.59, d.f. = 118, p = 0.01). The choice made by a bee was unaffected by her energetic state (Wald's $\chi^2 = 0.27$, d.f. = 1, p = 0.60, Fig. 1.3B).

Well-being assay

Energetic state did not have a significant effect on the number of head turns made by a bee (GLM: Wald's $\chi^2 = 0.62$, d.f. = 1, p = 0.43), or on the duration of proboscis extension (Wald's $\chi^2 = 0.30$, d.f. = 1, p = 0.57). The number of head turns was not correlated with the duration of proboscis extension (Pearson's product-moment correlation: t = 1.25, d.f. = 80, p = 0.21) and the choice made by a bee was unaffected by her energetic state (Wald's $\chi^2 = 2.86$, d.f. = 1, p = 0.09).

DISCUSSION

Manipulating the energetic state of individual bees followed by testing their choice for precisely defined rewards allowed us to test the predictions of the information primacy hypothesis in terms of how the exploration-exploitation trade-off is influenced by the energetic state of a forager. We used the well-established Proboscis Extension Response assay to measure not only choice, but also the sampling behavior that generally precedes a choice and the consumptive effort displayed by a subject. The lack of behavioral differences in terms of head turning and duration of proboscis extension between fed and starved bees in the well-being assay demonstrates that the observed differences in the same parameters in the novelty and the partial uncertainty experiments are not due to any simple differences in their well-being or in their response to the odors.

Having different measures of exploration and exploitation allows a powerful evaluation of any trade-off between these two key components of foraging behavior. The significant negative correlation between the number of head turns and the duration of proboscis extension in both the novelty and partial uncertainty experiments suggests that there is indeed an exploration-exploitation trade-off that is related to the energetic state of an individual in a manner consistent with the predictions of the information primacy hypothesis. Fed bees sampled their environment more and extended their proboscis for a shorter duration than starved bees. As the severity of energetic needs declines, animals dedicate more time to gathering information about their environment and less time to consuming resources. However, the two behaviors may not always be mutually exclusive as information on patch quality can also be gained during resource exploitation.

Fed bees had an increased preference for the novel odor in the novelty experiment, which is consistent with the predictions of the information primacy hypothesis that animals at a higher energetic state would explore more. However, choice made by the bees was unaffected by their energetic state in the partial uncertainty experiment, with the bees consistently showing a preference for the High Value-Low Uncertainty reward over the Low Value-High Uncertainty reward. This seems to be inconsistent with the predictions of the information primacy hypothesis but instead supports standard optimal foraging models, which predict bees to choose the higher reward regardless of their energetic state. This contrast between the choice made by bees in the novelty and the partial uncertainty experiments suggests that foraging for information might be valuable only when uncertainty is above some threshold, such as in the novelty experiment where they lack any information about the novel option. These results are also consistent with the idea that foragers are likely to be "optimistic" and over-estimate the value of novel patches (Berger-Tal and Avgar 2012). When uncertainty is below some threshold, the drive to forage for food might trump the drive to forage for information. The switch between foraging for food and foraging for information therefore might be driven by an interaction between the value of food and the value of information for an animal at any given state.

Exploiting when more hungry and exploring when more satiated allows foragers to sample their environment and prioritize their energetic and information needs in an adaptive manner. Foraging bumblebees choosing among floral species that differ in food rewards are known to not always exclusively choose the highest rewarding option. This well-known phenomenon of "majoring" and "minoring" in bumblebees (Heinrich 1979), whereby individuals restrict most of their foraging to flowers of a single common and highly rewarding species (the 'major') while occasionally visiting flowers of one or a few additional species (the 'minors') at low frequency, can be interpreted in the light of an exploration-exploitation trade-off. While the proportion of time spent in these two behaviors has been shown to be influenced by the relative values and the stability of the rewards (Keasar et al. 2002, 2013), it is not known if it is also affected by the energetic state of the foragers. Similarly, the observed tendency of bumblebees to be both quicker in abandoning a past-profitable food source and in returning to a previously visited site, compared to honeybees (Townsend-Mehler et al. 2011), could be an outcome of the higher metabolic rate and energetic demand faced by a honeybee forager that compels it to exploit more than explore. Allocating more time or energy to exploitation could also result from the benefits associated with the ability to respond to social signals about the location of patches (Beekman and Lew 2008) and the ability to store large amounts of food in some social insects. Periods of colony starvation have been shown to cause an increase in foraging activity (Wallis 1964; Schulz et al. 1998; Toth et al. 2005; Mailleux et al. 2010) and this has sometimes been interpreted as an increase in exploration. However, these studies were not designed to explicitly discriminate between exploration and exploitation behaviors and the trade-off between the two as a function of hunger. In future studies, we plan to more specifically investigate the exploration-exploitation trade-off in honeybee foragers as a function of colony nutrition.

The relative amounts of time spent on exploration and exploitation and how these are influenced by the nutritional state of the animal have broad biological significance in terms of learning, decision making, and life history processes. Honeybees experiencing an energetic or nutritional stress due to a disease or habitat loss (Naug 2009; Mayack and Naug 2010) can lead foragers to dedicate less time in gathering information about their environment, which might be counterproductive in the longer run. The trade-off between exploration and exploitation may also be altered by the risk of mortality since foragers are expected to invest less in information acquisition as life expectancy decreases (Eliassen et al. 2007). While exploring could help a starving animal discover new food sources, such behavior might not be energetically favored (Graf and Sokolowski 1989) despite the potential benefits that can result from such exploration. Persistently poor nutrition could therefore make starved animals even more vulnerable to the effects of malnutrition. One could therefore speculate that access to supplemental food might allow animals to increase their exploratory behavior and assist them in better resource exploitation. The foraging behavior of animals has long been assumed to be driven nearly entirely by hunger, but the present study suggests that the motivation for foraging can change based on the energetic state of the forager. Naturally foraging animals experience a broad range of nutritional states and are therefore likely to use both hunger and information driven foraging strategies and it is important that foraging studies recognize the difference between hunger and information motivated animals and view the results in the proper context.

FIGURES

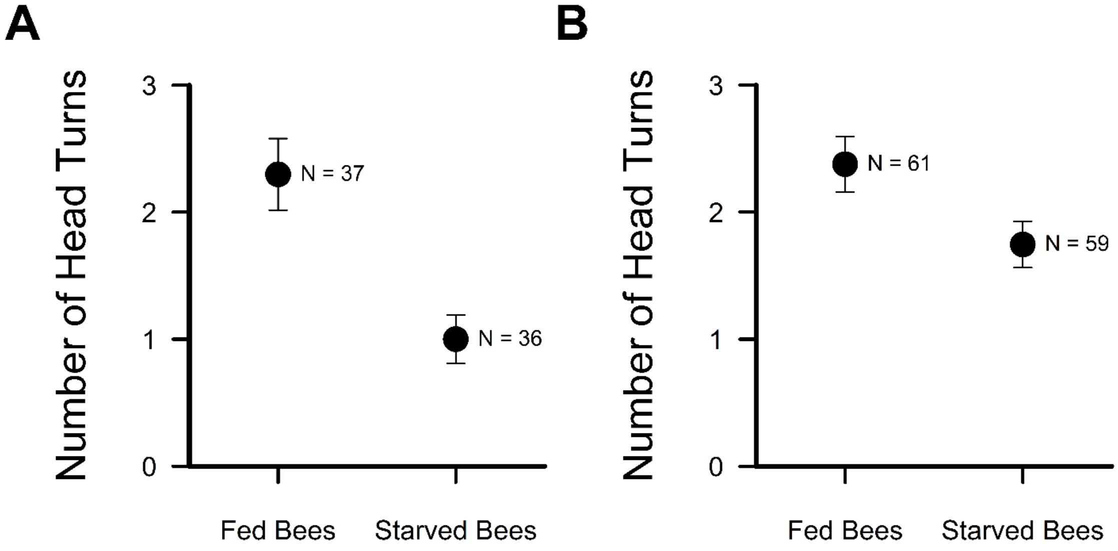

Figure 1.1: Exploration behavior of bees as a function of their energetic state in the (A) novelty experiment and the (B) partial uncertainty experiment. Data consist of means with standard error bars. Exploration decreased with increased hunger in both experiments.

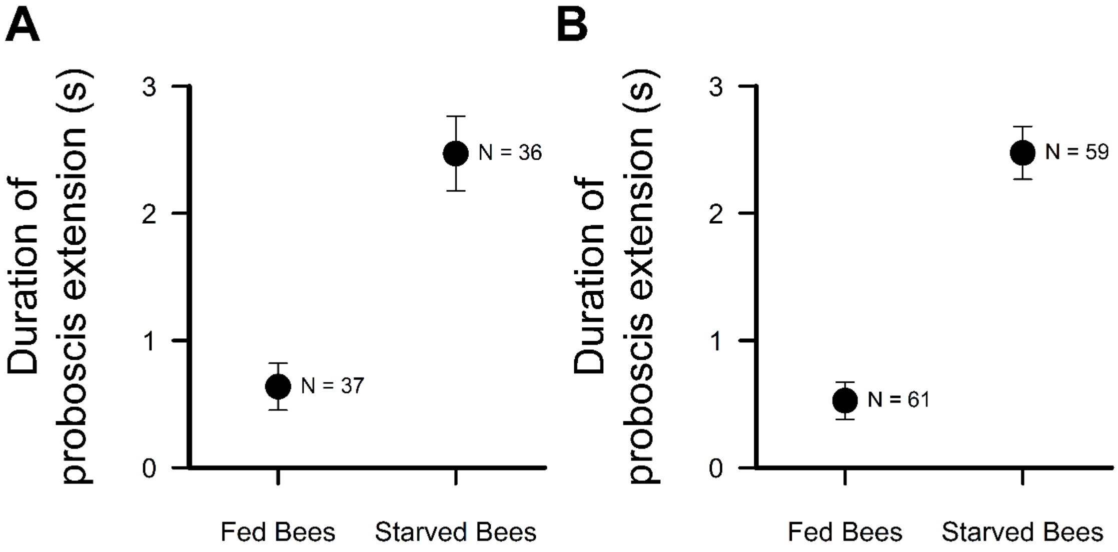

Figure 1.2: Exploitation behavior of bees as a function of their energetic state in the (A) novelty experiment and the (B) partial uncertainty experiment. Data consist of means with standard error bars. Exploitation increased with increased hunger in both experiments.

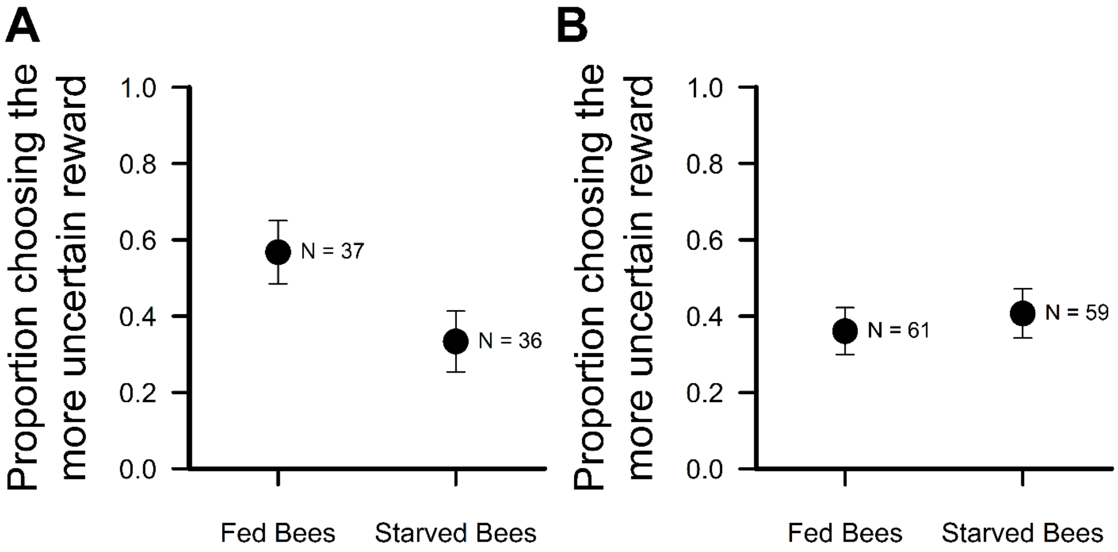

Figure 1.3: Choice behavior of bees as a function of their energetic state in the (A) novelty experiment and the (B) partial uncertainty experiment. Data consist of means with standard error bars. Fed bees had a higher preference for novelty than starved bees, but energetic state had no effect on choice in the partial uncertainty experiment.

CHAPTER 2

DANCERS AND FOLLOWERS IN A HONEYBEE COLONY DIFFERENTLY PRIORITIZE INDIVIDUAL AND COLONY NUTRITIONAL NEEDS[2]

SUMMARY

The evolution of sociality is often accompanied by nutritional conflicts and the evolution of mechanisms to resolve them. The foraging behavior of eusocial animals such as the honeybee, *Apis mellifera*, is generally considered to be largely regulated by the colony nutritional state, with a subset of individuals foraging for the entire group. Previous work based on the information primacy hypothesis has however found that satiated honeybee foragers explore (sample resources) more and exploit (consume resources) less in response to their individual nutritional state. We therefore hypothesized that individual and colony nutritional states differ in their influence on individuals of different behavioral phenotypes such as Dancers and Followers, who are akin to producers and scroungers, respectively. This leads to the prediction that these two behavioral groups will differ with respect to their exploration–exploitation trade-off and in terms of how they prioritize individual and colony nutritional states. We tested our predictions by creating a mismatch between individual and colony nutritional states. Our results show that Dancers and Followers do not differ in their levels of exploration and exploitation, but Dancers are more

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[2] This is a pre-copyedited, author-produced version of an article accepted for publication in Animal Behaviour following peer review. The version of record is available online at: http://www.sciencedirect.com/science/article/pii/S0003347216300999.

Katz, K., & Naug, D. (2016). Dancers and followers in a honeybee colony differently prioritize individual and colony nutritional needs. *Animal Behaviour* 119, 69-74. doi: 10.1016/j.anbehav.2016.06.011

responsive to colony nutritional state than Followers with regard to managing their exploration-exploitation trade-off. We discuss these results in the context of how these two behavioral phenotypes may differ in their sensitivity to the different nutritional pathways regulating worker behavior in a eusocial colony and the evolution of sociality in general.

INTRODUCTION

Social groups are typically characterized by not only cooperation, but also conflict among group members. While such within-group conflict has been mostly studied in the context of reproductive allocation (Keller & Reeve, 1994; Ratnieks et al., 2006), the basic principle behind such conflicts also applies in the context of altruistic foraging. Members of a group may differ in terms of their nutritional requirements and an individual's own requirements might not necessarily match those of the group as a whole. Integration of nutritional needs and metabolic complementation have been considered key prerequisites to the evolution of group living, and are regarded as critical drivers in the evolution of eukaryotes through endosymbiosis and the evolution of multicellularity (Blackstone, 2013). Mechanisms that mediate any nutritional conflicts among the lower-level components are therefore critical in order for higher-level units to evolve through cooperation.

Nutritional conflicts are likely to be especially strong when a subset of group members must obtain nutrition for the entire group. This is most obvious in the case of eusocial insects, where a subset of individuals – the foragers – meet the nutritional demands of the entire colony. It has been well established that the foraging behavior of honeybee workers is regulated to a large part by the nutritional state of the colony (Seeley, 1995), but recent work suggests that the nutritional state of an individual also plays a strong regulatory role in determining the foraging behavior of individual bees (Toth et al., 2005). While colony and individual nutritional states are normally tied to each other, uncoupling the two shows that fed bees in starved colonies behaved more similarly to bees in fed colonies than bees in starved colonies (Schulz et al., 1998), and that honeybee foragers at a higher nutritional state forage less often than bees at a lower nutritional state in a shared colony environment (Mayack & Naug, 2013). These studies suggest that honeybee foragers use information about both individual and colony nutritional states to make their foraging decisions.

The nutritional state of an animal has been predicted to be the primary driver of a key foraging decision – whether to explore or exploit. Foragers must divide their time between gathering information about available resources (exploration) and applying that information to utilize the best available resource (exploitation; Hill et al., 2015); these activities cannot be performed simultaneously and must trade-off with one another. The information primacy hypothesis predicts that animals will give precedence to information gathering (exploration) when they have a nutritional surplus and will prioritize food gathering (exploitation) when they are at a nutritional deficit (Inglis et al., 2001), thus allowing them to adaptively manage their own nutritional budget over time. A manipulation of the individual nutritional state in honeybees showed that those at a higher nutritional state explored more and exploited less compared to bees at a lower nutritional state, in support of this hypothesis (Chapter 1). However, since the foraging decisions of honeybees are known to be subject to the nutritional state of the colony, it is important to evaluate if colony nutrition has a similar influence on the exploration–exploitation trade-off.

Within a colony, some bees use the waggle dance to transmit foraging information to other bees which follow the dance. This allows us to divide the foragers into two behavioral phenotypes, information gatherers (the Dancers) and information consumers (the Followers) – colony-level units of exploration and exploitation. This Dancer–Follower framework thus allows an evaluation of the exploration–exploitation trade-off at the group level and helps us to determine if the colony nutritional state drives an adaptive allocation of individuals into these two behavioral phenotypes. The behavior of Dancers and Followers can also be interpreted in light of the producer–scrounger framework, according to which foraging groups consist of producers, which locate new food patches, and scroungers, which take advantage of the producer's find and feed at the same patch (Barnard & Sibly, 1981). As Followers forage at patches originally located by Dancers, it can be argued that these Followers are similar to scroungers while Dancers are similar to producers.

In this study, we manipulated colony nutritional state to study how it dictates the colony level distribution of behavioral phenotypes and their behavior, as per the information primacy hypothesis. Our 1st prediction is that colonies at a higher nutritional state will have a higher proportion of Dancers than colonies at a lower nutritional state and that Dancers will show an overall higher level of exploratory behavior. By creating either a match or a mismatch between individual and colony nutritional states, we also examined how Dancers and Followers prioritize individual and colony needs with respect to their exploration and exploitation behavior. Our 2nd prediction is that when colony and individual nutritional states are similar and therefore 'matched', all bees will respond to an overall high nutritional state by exploring more and respond to an overall low nutritional state by exploiting more. However, when the two states are 'mismatched' and the individual state differs from that of the colony, it presents a nutritional conflict to the bees. Our 3rd prediction is that under such a mismatch, Dancers would be more sensitive to colony nutritional state, as per the producer–scrounger framework. The test of these three predictions addresses if the two behavioral phenotypes, Dancers and Followers, differ in their predispositions to show exploration and exploitation behaviors, differ in their response to nutritional conflict, and if the information primacy hypothesis scales to the colony level.

METHODS

Observation of In-hive Behavior

We set up two observation hives, each with one brood frame and about 3,000 bees, and created two nutritional treatments at the colony level. A colony with higher nutrition ('Full colony') was created by providing it with a frame that had at least 75% honey and a colony with lower nutrition ('Empty colony') was created by providing it with a frame that contained no more than 10% honey. These two nutritional treatments were rotated between the two colonies on a weekly basis to control for any confounding effects of colony identity for a total of 9 weeks of data collection. About 500 individually tagged newly emerged bees were added to each colony after the nutritional rotation each week. Allowing 2.5 days for the nutritional treatment to have an effect, we then observed the dance floor of each colony for 2 hours each week, using scan sampling to identify the bees performing a waggle dance or following a waggle dance. The scan sampling consisted of dividing the dance floor into squares that were 1/6th of the entire frame in size, sampling these squares sequentially for a duration of 1 minute each and recording the identities of all tagged bees found performing a waggle dance or following a waggle dance within the square during this period. Based on which of these two activities a bee was observed to perform during this entire observation period, we categorized each bee as either a 'Dancer' or a 'Follower', ignoring bees observed both dancing and following (3.5% of observed bees).

Two-alternative Proboscis Extension Response Assay

We captured a subset of these Dancers and Followers and harnessed them in plastic straws. The bees were starved for 3 hours inside a dark incubator maintained at 25°C and 60% relative humidity to increase their motivation for learning an appetitive stimulus. We trained these bees to associate an odor with a sucrose reward using an appetitive conditioning procedure involving the proboscis extension response (PER) assay (Bitterman et al., 1983). Sucrose placed on the antenna (the unconditioned stimulus, US) was paired with an odor (eugenol or 1-octanol; the conditioned stimulus, CS) to elicit a proboscis extension (a conditioned response, CR) in 6 conditioning trials. Each trial consisted of presenting the odor for 6 seconds with the final 2 seconds of the odor pulse coinciding with the presentation of the sucrose reward, with an 11 minute inter trial interval (ITI).

Subsequent to the conditioning procedure, we created a high and a low nutritional treatment at the individual level, by feeding half the bees with 30 µl of 30% sucrose solution ('Fed bees') and not feeding the other half ('Starved bees'), thus giving us a 2 x 2 nutritional treatment consisting of Fed and Starved bees from Full and Empty colonies. We kept these bees in an incubator, under the same conditions as described above, for 3 hours to allow the individual nutritional treatment to have an effect before subjecting them to a two-alternative assay (Shafir et al., 1999) designed to test for exploration and exploitation behavior (Chapter 1). The assay consisted of presenting each bee with the odor they were previously conditioned to and a novel odor on opposite sides of her head. Each odor was presented twice for 0.8 seconds with 0.2 seconds of odorless air in between successive odor pulses in the pattern ABAB. The number of head turns made by a bee as she sampled the two odors was interpreted as a measure of exploration and the duration of its proboscis extension was interpreted as a measure of exploitation (Chapter 1).

Statistical Analysis

All data were analyzed using ANOVAs chosen through step-wise AIC model selection. AIC selection for predicting colony proportion of Dancers started from a model including a three-way interaction between colony nutrition, day, and colony identity. AIC selection for predicting individual behavior started from a model including the three-way interactions between the two nutritional states and behavioral phenotype, and the main effects of colony identify and conditioning odor. Head turning (count data) was square root transformed to allow for parametric analysis. In order to control for any differences among individuals in overall activity level, a measure of relative exploration was calculated by converting head turns to a duration and calculating the proportion of time that each bee spent head turning out of total time spent active (head turning or extending her proboscis). Bees that did not extend their proboscis at least once during the conditioning procedure, or failed to perform either of the measured behaviors during the two-alternative assay were excluded from all analyses, resulting in a final sample size of 178 bees. The effects of colony and conditioning odor were dropped from all ANOVAs due to minimal contribution to explanatory power during model selection. A single combined plot for each behavioral response variable is presented to emphasize the similarity of trends found among them. The parameter eta squared (η2) is presented as a measure of effect size; 0.01 is considered a small effect size, 0.06 is considered a moderate effect size, and 0.14 is considered a large effect size (Maher et al., 2013).

RESULTS

In-hive Behavior

The proportion of Dancers within a colony (Number of Dancers / Number of Dancers + Followers) was not influenced by colony nutritional state (ANOVA: $F_{1,\,19} = 2.03$, P = 0.16, η2 =

0.07). This does not support our 1st prediction that the proportion of Dancers within a colony would be higher in colonies at a higher nutritional state. The proportion of Dancers was, however, affected by the day in the season a colony was observed with the proportion increasing as the summer progressed over the nine weeks of observation ($F_{1, 19} = 8.67$, $P = 0.008$, $\eta 2 = 0.30$). The interaction between day and colony nutritional state was not included in the AIC selected model.

Proboscis Extension Duration

The duration for which a bee extended her proboscis (exploitation) was significantly influenced by a three-way interaction between her individual nutritional state, colony nutritional state, and behavioral phenotype (Fig. 2.1A, Table 2.1), as well as by each of these factors alone. This indicates that Dancers and Followers did not respond identically to colony and individual nutrition. Under mismatched nutrition, Fed Followers extended their proboscis very briefly, as would be predicted for a bee prioritizing individual nutrition, while Fed Dancers extended their proboscis for an intermediate duration, as would be predicted for be a bee responding to both individual and colony nutrition. This supports our 3rd prediction that Followers would be less sensitive to the colony nutritional state than Dancers. This prediction is also supported by the significant two-way interactions between behavioral phenotype and colony nutritional state (Fig. 2.1B), which indicates that Dancers and Followers respond differently to the effects of colony nutritional state. The significant interaction between behavioral phenotype and individual nutritional state (Fig. 2.1C) indicates that Dancers and Followers also respond differently to the effects of individual nutrition, Dancers being slightly less sensitive to individual nutrition than Followers. The non-significant two-way interaction between individual and colony nutritional states (Fig. 2.1D) indicates that the effect of individual nutrition on exploitation is similar in Full and Empty colonies. In general, a Follower extended her proboscis for a significantly shorter duration than a Dancer, which is contrary to our 1st prediction that Followers would be less exploitative than Dancers. However, a Fed bee extended her proboscis for a significantly shorter duration than a Starved bee and a bee from a Full colony extended her proboscis for a significantly shorter duration than a bee from an Empty colony, supporting our 2nd prediction that bees would increase their exploitation behavior when both colony and individual nutritional states are low.

Head Turning

The number of head turns made by a bee (exploration) was not significantly influenced by a three-way interaction between her individual nutritional state, colony nutritional state, and behavioral phenotype (Fig. 2.1E, Table 2.2). There was a significant two-way interaction between behavioral phenotype and colony nutritional state (Fig. 2.1F), which indicates that a Dancer and a Follower responded differently to colony nutritional state. A Dancer turned her head more when she was from a Full colony than when she was from an Empty colony, but a Follower turned her head similarly, irrespective of colony nutrition, supporting our 3rd prediction that Followers would be less sensitive to colony nutritional state than Dancers. There was no significant interaction between behavioral phenotype and individual nutritional state (Fig. 2.1G), indicating that Dancers and Followers were similarly influenced by individual nutrition. There was a significant two-way interaction between individual and colony nutritional states (Fig. 2.1H), indicating that bees responded differently to the combined effects of individual and colony nutritional states. Fed bees turned their heads more than Starved bees in Empty colonies, but not in Full colonies, which partially supports our 2nd prediction that bees would increase their exploration in response to a higher level of nutrition at the individual and the colony level. The lack of a significant main effect of behavioral phenotype on head turning behavior is contrary to our 1st prediction that Dancers would be more exploratory than Followers. However, individual nutritional state had a significant main effect on head turning, and a Fed bee performed significantly more head turns than a Starved bee, supporting our 2nd prediction that bees would increase their exploration behavior when their individual nutritional state is high.

Relative Exploration

The number of head turns (exploration) and the duration of proboscis extension (exploitation) were negatively correlated (Pearson's correlation: N = 178, r = - 0.60, $P < 0.001$), indicating that these behaviors trade-off with one another. However, since a Dancer both extended her proboscis for a longer duration and turned her head more frequently than a Follower, this higher overall activity level of Dancers hinders a direct comparison between the two behavioral phenotypes in terms of their exploration and exploitation. We therefore converted the head turning data from count to duration (based on the duration of a single head turn, measured as 0.58 ± 0.16 seconds from a subset of randomly selected trials) and calculated a measure of relative exploration – the proportion of time spent by a bee turning her head out of the total time spent active in head turning and proboscis extension. Dancers were indeed significantly more active overall than Followers (ANOVA: $F_{1,174} = 9.3$, $P = 0.002$, $\eta 2 = 0.032$). In addition, Starved bees were significantly more active overall than Fed bees ($F_{1,174} = 74.8$, $P < 0.0001$, $\eta 2 = 0.281$), and bees from Empty colonies were significantly more active overall than bees from Full colonies ($F_{1,174} = 4.2$, $P = 0.04$, $\eta 2 = 0.016$). No interactions were included in the AIC selected model.

The relative exploration of a bee was found to be significantly influenced by the three-way interaction between her individual nutritional state, colony nutritional state, and behavioral phenotype (Fig. 2.1I, Table 2.3). This indicates that Dancers and Followers did not respond identically to the effects of colony and individual nutrition. Under mismatched nutrition, Fed Followers showed high relative exploration, as would be predicted for a bee prioritizing individual nutrition, and Dancers showed intermediate relative exploration, as would be predicted for be a bee responding to both individual and colony nutrition. This supports our 3rd prediction that Followers would be less sensitive to colony nutrition than Dancers. The two-way interactions between behavioral phenotype and colony nutritional state (Fig. 2.1J) and between behavioral phenotype and individual nutritional state (Fig. 2.1K) were significant, suggesting that that Dancers and Followers respond differently to the effects of colony and individual nutritional states. The two-way interaction between individual and colony nutrition was not significant (Fig. 2.1L), indicating that the effect of individual nutrition on relative exploration is similar in Full and Empty colonies. Relative exploration was also significantly affected by each of these factors alone. The relative exploration of a Fed bee was significantly higher than a Starved bee, and the relative exploration of a bee from a Full colony was significantly higher than a bee from an Empty colony. These findings support our 2nd prediction that bees would increase their exploration behavior when colony and individual nutritional states are high, and increase their exploitation behavior when colony and individual nutritional states are low. However, the finding that the relative exploration of a Follower was significantly higher than a Dancer is once again contrary to our 1st prediction that Dancers would be more exploratory and be less exploitative than Followers.

DISCUSSION

Bees consistently explored more and exploited less when their individual nutritional states were high. Colony nutritional state had a similar effect, such that bees from Full colonies explored more and exploited less than bees from Empty colonies. Both these results are consistent with our prediction and the previous findings regarding the effect of individual nutritional state on the exploration–exploitation trade-off (Chapter 1) according to the information primacy hypothesis (Inglis et al., 2001). It initially appears that colony nutritional state has a much smaller effect on exploration than individual nutritional state (as measured by the η2 of the respective main effects; Table 2.2). However, further analysis reveals that individual and colony nutrition both have comparable influences on how bees divide their time between exploration and exploitation, as defined by relative exploration (Table 2.3). The apparent larger effect of individual nutritional state can instead be attributed to the higher overall activity level of Starved bees. This corroborates previous findings that changes in overall activity level is a key behavioral mechanism by which individuals deal with changes in their own nutritional state when confronted with conflicting signals about the nutritional state of the colony (Mayack & Naug, 2013), adding to the growing evidence of individual nutritional state playing a vital role in the regulation of worker behavior in eusocial colonies.

The higher overall activity level of a Dancer led to both more head turns and a longer duration of proboscis extension compared to a Follower (Fig. 2.1A, 2.1E). However, once this difference in overall activity level was accounted for, there was little difference between Dancers and Followers under identical colony and individual nutritional states (Fig. 2.1I). Neither was more exploratory than the other, which is contrary to our prediction that Dancers would be more exploratory. The sole exception to the similar behaviors of Dancers and Followers is in the comparison of Fed Dancers and Fed Followers under mismatched nutrition. Fed Followers from an Empty colony exploit much less than Fed Dancers from an Empty colony (Fig. 2.1A) and Fed Followers from an Empty colony have a much higher relative exploration than Fed Dancers from an Empty colony (Fig. 2.1I). A related trend can be seen in our initial measure of exploration, Dancers explore more in Full colonies than they do in Empty colonies, but Followers explore equally regardless of colony nutritional state (Fig. 2.1F). Dancers therefore altered their behavior in accordance with the colony state to a greater extent than did Followers, and did so in a manner that is consistent with the information primacy hypothesis. This suggests that Followers are more inclined to disregard the colony nutritional state and instead act primarily in accordance with their individual nutritional state, which can be construed as acting in a more 'selfish' manner than Dancers. This is consistent with our prediction that Followers, as a scrounger-type phenotype, would prioritize individual nutrition more than Dancers.

If the allocation of Dancers and Followers within a colony responds to the colony nutritional state as individual bees respond to individual nutritional state (Chapter 1), the information primacy hypothesis predicts that colonies with high food stores will have more Dancers and fewer Followers than colonies with little food stores and vice versa. However in contrast to our prediction, colony nutrition had no effect on the proportion of Dancers in a colony and Dancers were not more exploratory than Followers in the individual behavioral assay. This suggests that either 1) the information primacy hypothesis does not scale to the group level or, 2) Dancers and Followers are equally exploratory, or both. One cannot also completely rule out that our study maybe lacked sufficient power to detect the effect of the treatments on the proportion of Dancers in the colonies, or that our experimental manipulation cannot completely disentangle the effects of individual and colony nutritional state, or that the head turning behavior is influenced by factors besides exploratory tendency. The proportion of Dancers within a colony however increased over the season, which indicates that there are possibly additional mechanisms in the colony that regulate how a colony allocates its efforts into Dancers and Followers, and exploration and exploitation.

Considering the extent to which an individual's behavioral decisions are the product of their own interests and are influenced by the interests of others have widespread application for understanding animal behavior. Several studies have investigated a parallel between the producer–scrounger and the explore-exploit framework (Koops & Giraldeau, 1996; David et al., 2011; Kurvers et al., 2012; Mehlhorn et al., 2015). In the context of social foraging, which provides individuals with the opportunity to either produce (or discover) resources or to scrounge upon the ones produced by others, the payoff to each of these two strategies is defined by a negative frequency dependent relationship. Increased relatedness between such foragers can lead to higher levels of scrounging when producers are kin-selected to be more tolerant of scroungers (Mathot & Giraldeau, 2010). Eusocial insects such as honeybees present extreme examples of such kin groups and one can speculate that higher order sociality and altruistic foraging in these groups might have evolved out of such producer–scrounger systems – with producers becoming increasingly tolerant of scrounging kin to the eventual extreme of promoting and guiding scrounging kin to finding a resource for group-level benefits. The evolution of primate food sharing is sometimes similarly attributed to tolerated theft of food from a producer, especially when a resource patch is too ephemeral or large to exploit by oneself (Bliege Bird & Bird 1997; Blurton Jones, 1984, 1987; Stevens & Cushman, 2004; but see Gurven, 2004).

It has been suggested that there are two different nutritional pathways which regulate foraging behavior in bees (Toth et al., 2005; Toth & Robinson, 2007; Ament et al., 2010). The pathway related to the individual nutritional state is similar to that of solitary animals while the one related to the colony nutritional state is likely a more recent adaptation to group living and may be mediated through social interactions. Our demonstration that the behavioral changes triggered by manipulation of the two nutritional states differ among Dancers and Followers suggests that the Followers may be less sensitive to the pathway related to colony nutritional state than Dancers. This may be adaptive at the colony level as individuals of different sensitivities allow a finer tuning in terms of the exploration–exploitation trade-off rather than when the behavior of all individuals are similarly constrained by a single nutritional state. The difference in the sensitivity of Dancers and Followers to these nutritional pathways may explain the role of Dancers as altruistic producers and Followers as scroungers of information from Dancers. The results from this study show that both individual and colony nutritional states are accounted for in the foraging decisions made by honeybee forager and that individuals of different behavioral phenotypes vary in the degree to which these two states influence these decisions.

TABLES AND FIGURES

Tables

Table 2.1: ANOVA of proboscis extension duration. Predictors are individual nutritional state, colony nutritional state, and behavioural phenotype (N = 178; all predictor df =1). η^2 presented as a measure of effect size.

Predictor	**F**	**P**	η^2
Individual	9.4	0.002	0.030
Colony	5.17	0.02	0.016
Phenotype	10.1	0.001	0.032
Individual * Colony	1.0	0.30	0.003
Individual * Phenotype	6.3	0.01	0.020
Colony * Phenotype	5.5	0.01	0.017
Individual * Colony * Phenotype	5.9	0.01	0.018

Table 2.2: ANOVA of number of head turns. Predictors are individual nutritional state, colony nutritional state, and behavioural phenotype (N = 178; all predictor df =1). η^2 presented as a measure of effect size.

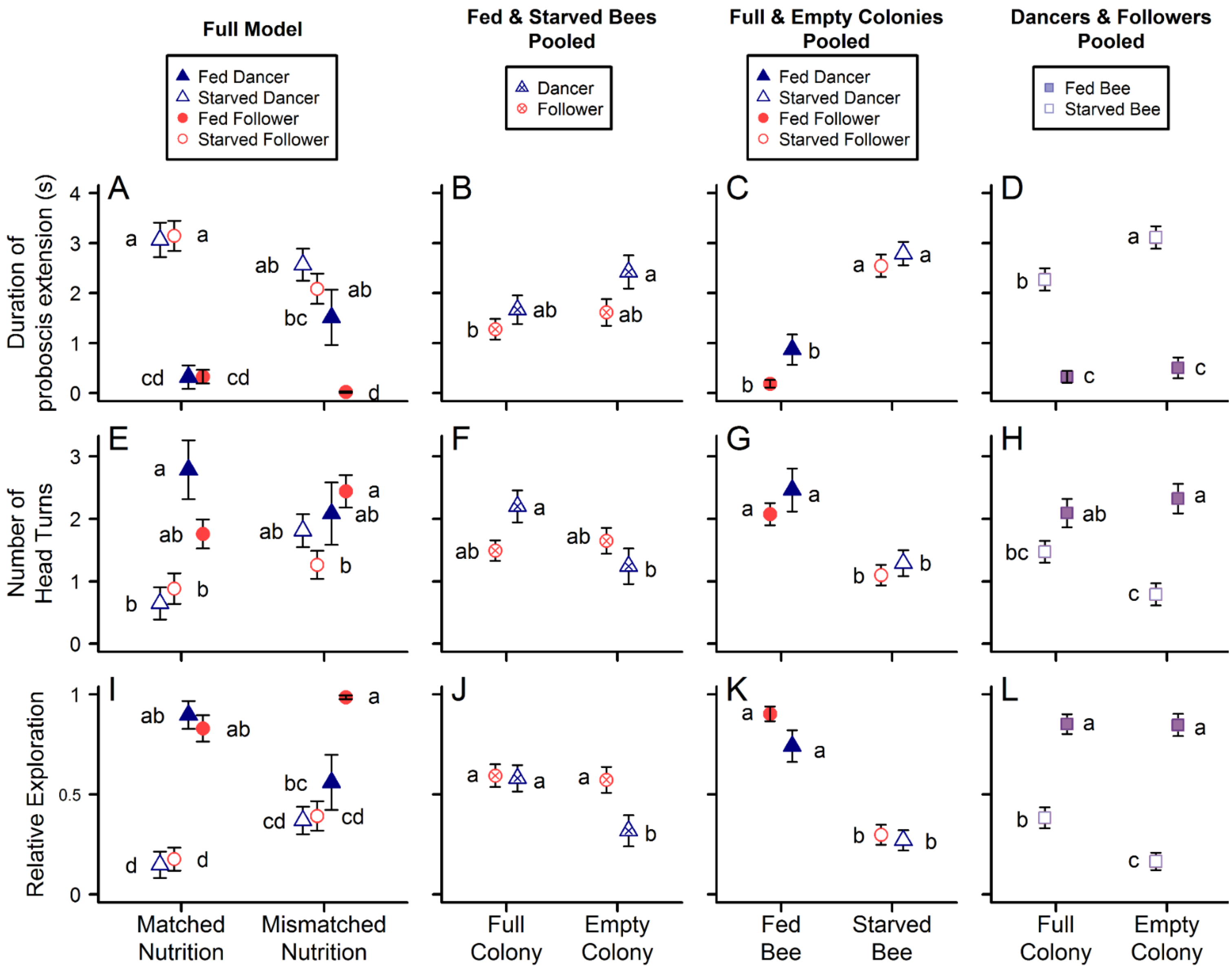
Predictor	**F**	**P**	**η^2**
Individual	32.8	< 0.001	0.145
Colony	2.7	0.09	0.012
Phenotype	1.9	0.16	0.008
Individual * Colony	6.1	0.01	0.027
Colony * Phenotype	8.7	0.003	0.038

Table 2.3: ANOVA of relative exploration. Predictors are individual nutritional state, colony nutritional state, and behavioural phenotype (N = 178; all predictor df =1). η^2 presented as a measure of effect size.

Predictor	**F**	**P**	**η^2**
Individual	11.0	0.001	0.034
Colony	6.8	0.009	0.021
Phenotype	13.6	< 0.001	0.042
Individual * Colony	0.4	0.49	0.001
Individual * Phenotype	6.6	0.01	0.024
Colony * Phenotype	9.8	0.002	0.030
Individual * Colony * Phenotype	5.4	0.02	0.016

Figures

Figure 2.1: Exploitation (A - D), exploration (E - H), and relative exploration (I – L) of bees categorized as Dancers (triangles) or Followers (circles), or both pooled together (squares). Bees were manipulated to be Fed (filled shapes) or Starved (open shapes), or both pooled together (crossed shapes). Matched nutrition indicates similar colony and individual nutritional states (e.g. a Fed bee in a Full colony), while mismatched nutritional states indicate dissimilar colony and individual nutritional states (e.g. a Fed bee in an Empty colony). Legends describe the subplots (N = 178) below them. Data consist of means with standard error bars. Means within each subplot that share the same letter are not statistically different at $\alpha = 0.05$ (Tukey post-hoc).


Full Model
Fed Dancer
Starved Dancer
Fed Follower
Starved Follower
Fed & Starved Bees Pooled
Dancer
Follower
Full & Empty Colonies Pooled
Fed Dancer
Starved Dancer
Fed Follower
Starved Follower
Dancers & Followers Pooled
Fed Bee
Starved Bee
Duration of proboscis extension (s)
Number of Head Turns
Relative Exploration
A
B
C
D
E
F
G
H
I
J
K
L
0
1
2
3
4
0.5
Matched Nutrition
Mismatched Nutrition
Full Colony
Empty Colony
Fed Bee
Starved Bee
Full Colony
Empty Colony
a
ab
bc
cd
d
b
c

CHAPTER 3

STABLE WEIGHTS ENHANCE LEARNING PERFORMANCE IN THE HONEYBEE

SUMMARY

Birth weight is correlated with numerous life history traits, and this valuable measure can be expanded upon by examining animal weights throughout life. Changes in weight can provide valuable insights into animal behavior. This has been most notably studied in the context of "compensatory growth" in which low birth weight animals suffer a cost for quickly growing to a more typical weight. One such cost for compensatory growth is reduced cognitive ability. In this study rather than focusing solely on compensatory growth, we seek to determine how the overall stability of animal weight can affect cognition. Our study examines the effect of weight change on the cognitive ability of honeybees by tracking individuals of different birth weights through their late-adult weights and assessing their learning performance. We find that bees with relatively stable body weights show a higher performance on an associative learning task than bees that had more variable weights. This result expands on previous findings of the effects of birth weight and compensatory growth on cognition and indicates that animals which lose weight also pay a cognitive cost.

INTRODUCTION

Birth weight has long been considered as one of the most important variables as an indicator of performance in later life, especially in humans (Wilcox, 2001). It is a variable that has been found to be strongly associated with survival, the risk of various diseases and developmental deficiencies including cognitive deficits during adulthood (Johnson & Breslau, 2000; Kessenich, 2003; Reuner et al., 2009; Walhovd et al., 2016). However, surprisingly, there have been few studies which has looked at the effect of birth weights on later life performance in non-human animals. Animals in natural environments are more subject to environmental fluctuations in resource supply and are therefore more likely to demonstrate variations in birth weights.

Previous work in honeybees, a classic model for learning studies, showed that individuals with low birth weights (weight at the time of adult emergence) have a reduced cognitive capacity, showing a poorer performance on tests of olfactory learning (Scheiner, 2012). Similar findings that low birth weights lead to cognitive deficits have also been found in piglets (Litten et al., 2003; Gieling et al., 2012). However, rather than focusing on birth weight *per se*, more recent work suggests that it is the stability of the developmental state that is a critical indicator of later life performance. This has been associated with various negative outcomes, including metabolic syndrome (Roseboom et al., 2001; Gluckman & Hanson, 2004). One suggested mechanism is the cost of compensatory growth, the price which animals with low birth weights pay to achieve "normal" weights later in life. Amount other consequences, compensatory growth is associated with decreased cognitive performance (Fisher et al., 2006; Estourgie-van Burk et al., 2009).

This presents an interesting case for honeybees and other social insects, which unlike vertebrate models studied in the context of birth weight and adult performance, normally experience a weight loss during early development as they transition from performing in-hive tasks to foraging (Winston, 1987; Tschinkel, 1998; Blanchard et al., 2000; Toth & Robinson, 2005; Ament et al., 2011). However, there is a substantial variation in both birth and late-adult weights seen in honeybees, attributed not only to genetic variability, but also to differences in the colony environment in terms of nutritional availability, number of workers providing care, incidence of various diseases, etc. (Levin & Haydak, 1951; Jay, 1963; Eischen et al., 1982; Lee & Winston, 1985). However, it is not known how birth weight of an individual correlates to its late-adult weight and how the performance of an individual is influenced by these two weights.

Based on the earlier findings related to the effects of catch up growth on cognitive performance (Fisher et al., 2006; Estourgie-van Burk et al., 2009) and the effect of birth weights on learning performance in honeybees (Scheiner, 2012), we therefore developed two competing hypotheses. 1) The performance of honeybee individuals in terms of learning capacity can be predicted by birth weight alone, since honeybees experience a normal weight loss during their early development. 2) The learning performance of honeybee individuals is a function of both their birth and late-adult weights, and the relative stability between them during development in spite of the normal weight loss they encounter during this period. The goal of this study was therefore to examine the pattern of weight change in honeybees during early adult development and test if learning performance in adult honeybees is influenced by their birth weights, late-adult weights, and the change in weight during these two time points.

METHODS

We obtained capped honeybee, *Apis mellifera*, brood frames from three source colonies and hatched them in an incubator. Bees which emerged from the same source colony (N = 3) within 48 hours of each other were said to be within the same "birth cohort" (mean size = 26). We recorded birth weights (defined as mass at time of adult emergence) for the emerging adults, individually tagged them with number tags, and placed them randomly into three foster colonies. We recaptured these tagged bees as returning foragers, stripped them of pollen loads, strapped them into plastic straws, fed them to satiation with 30% (w/w) sucrose solution, and starved them for 24 hours to increase their motivation for an appetitive learning assay.

We used the Proboscis Extension Response (PER) assay to measure the learning performance of each bee (Bitterman et al., 1983) to associate an odor (2-octanone or 1-hexanol) with a 0.4 µl of 30% sucrose reward. Each conditioning trial for a bee consisted of presenting the odor (the conditioned stimulus or CS) for 6 seconds with the sucrose reward (the unconditioned stimulus or US) being presented during the final 2 seconds of the odor pulse. The inter-trial interval (ITI) was 11 minutes. Bees which did not respond to a single presentation of the US immediately before the learning assay and those that spontaneously responded in the first conditioning trial were excluded from the analysis. A bee that showed a PER to the CS before the US was delivered was given a score of one for exhibiting the conditioned response (CR), whereas a bee not showing a PER was given a score of zero, and the total number of CR, called the learning score, was used as a measure of learning. We recorded the weights of all bees after the learning assay and this is defined as the late-adult weight. All weights were recorded to the nearest tenth of a milligram.

Statistical Methods

The weight change of each bee was calculated by subtracting the birth weight of each bee from her late-adult weight. A one-sample t-test was used to compare the weight change of bees with the null hypothesis of no change in weight. The distribution of weight changes was tested for normality using one-sample Kolmogorov-Smirnov test.

The birth and late-adult weights for each bee were converted to a percentile rank by comparing her to all other bees recaptured from the same birth cohort. The weight percentile at birth was then subtracted from the late-adult weight percentile to calculate a “weight change percentile” for each bee. The weight change percentile provides a measure of the relative stability of an individual’s weight and ranges from -100 to +100. A weight change percentile of 0 indicates a bee that did not change its weight percentile rank between birth and late-adulthood and maintained a relatively stable weight. A large negative weight change percentile indicates a bee that lost more weight than typical, and a large positive weight change percentile indicates a bee that lost less than weight than typical, or even gained weight.

The learning scores of bees were analyzed using two Poisson regression models that started with the different weight parameters and the two-way interactions of these weight parameters with our control parameters: age, foster colony, birth cohort, and conditioning odor. The best model was chosen by stepwise Bayesian Information Criterion (BIC) model selection. The first BIC selected model included birth weight, late-adult weight and their interaction, as well as the control parameters and their interactions with each weight parameter. The second BIC selected model included the linear and quadratic terms of the weight change percentile as well as the control parameters and their interactions with each weight parameter. Learning performance, as defined by the acquisition of the conditioned response, was analyzed with a repeated measures logistic regression model that included the linear and quadratic terms of the weight change percentile and their interaction with trial number. A second repeated measures logistic regression model predicting learning performance included the interaction of birth percentile weight and late-forager percentile weight, and trial number. As plotting the interactions of multiple continuous variables with respect to a single dependent variable can be complex, we have chosen to plot some results using binned data but present the statistics with respect to the true continuous form of the data.

RESULTS

Bees lost an average of 21.4 ± 1.5 mg (standard error) between birth and late-adulthood. This weight loss is significantly different than 0 (one-sample t-test: $t = -13.7$, $df = 102$, $p < 0.001$)

and the distribution (Fig. 3.1) is approximately normal (one-sample Kolmogorov-Smirnov test: D = 0.8605, $p < 0.001$).

Learning score of bees (N = 103) was predicted by an interaction between their birth and late-adult weights in the first BIC selected Poisson regression model (BIC = 437; Wald's $\chi^2 = 21.2$, d.f. = 1, $p < 0.0001$; Table 3.1). The model also contained a significant interaction between birth cohort and late-adult weight (Wald's $\chi^2 = 25.9$, d.f. = 3, $p < 0.0001$), but conditioning odor, foster colony and age were not included. In the second BIC selected Poisson regression model, learning score was significantly predicted by the quadratic term of the weight change percentile (BIC = 427; Wald's $\chi^2 = 15.4$, d.f. = 1, $p < 0.0001$; Table 3.2), with no other effects included in the model, besides the linear term. Bees with weight change percentiles close to zero had higher learning scores than bees with high or low weight change percentiles (Fig. 3.2).

The acquisition of the conditioned response was significantly affected by the quadratic term of weight change percentile (Table 3.3; Wald's $\chi^2 = 5.2$, d.f. = 1, p = 0.02). Acquisition increased over trial number (Wald's $\chi^2 = 46.1$, d.f. = 1, $p < 0.0001$), but there was no interaction between weight change percentile and trial number (Wald's $\chi^2 = 1.6$, d.f. = 1, p = 0.19), indicating that the weight change percentile does not influence the rate of acquisition. To more easily visualize the significant effects of both trail and weight change percentile in the above model, bees were divided into two stability categories. Bees with weight change percentiles between -25 and +25 were categorized as "stable" (N = 52, mean |change in weight percentile| = 48.7 ± 2.4) and bees with weight change percentiles less than -25 or greater than +25 were categorized as "unstable" (N = 51, mean |change in weight percentile| = 10.7 ± 0.9). Bees with stable weights displayed the conditioned response more often than bees with unstable weights (Fig. 3.3).

The same effect can also be seen in terms of the interaction between percentile weight at birth and percent weight as a late-adult which also has a significant effect on acquisition of the conditioned response (Table 3.4; Wald's $\chi^2 = 11.9$, d.f. = 1, $p < 0.01$). As expected, trial number also continuous to have a positive effect on learning (Wald's $\chi^2 = 60.4$, d.f. = 1, $p < 0.01$). To more easily visualize the significant effects of both trail and the interaction between the two percentile weights in the above model, bees were divided into four percentile weight change categories: "consistently heavy" (weight percentile in the top third at birth and as a late-adult; N = 13), "consistently light" (weight percentile in the bottom third at birth and as a late-adult; N = 14), "light to heavy" (weight percentile in the bottom third at birth and in the top third as a late-adult; N = 9), and "heavy to light" (weight percentile in the top third at birth and in the bottom third as a late-adult; N = 9). Bees which did not meet one of the four criteria (those with medium weight percentiles) were dropped from this plot. As seen in our previous analysis, bees with stable weight percentiles have higher learning scores than those with unstable weight percentiles (Fig. 3.4).

DISCUSSION

It is well known that the mean birth weight of bees is lower than the mean late-adult weight (Winston, 1987; Tschinkel, 1998; Blanchard et al., 2000; Toth & Robinson, 2005; Ament et al., 2011). However, our study provides the first measurements of weight loss for individually tracked bees (Fig. 3.1). We found substantial variation in the amount of weight lost by individuals. This allowed us to assess the effect of the weight stability of individual bees on cognitive performance.

Our results most notably show that the learning performance of a bee was influenced by an interaction between its birth and late-adult weight and that bees which maintain most stable weights during their development show the highest learning performance. The interaction between the birth cohort of an individual and her late-adult weight suggests that genetic differences between source colonies or different developmental environments could also influence learning score. The use of percentile ranks allowed us to correct for any such differences in our second model (Fig. 3.2), which is likely the reason that it leads to a better model fit by BIC than the raw weights model. While a stable weight rank leads to an overall higher acquisition of the conditioned response, it does not influence the rate of acquisition (Fig. 3.3). When our data are analysed in terms of birth weight percentile and late-adult weight percentile (Fig. 3.4), the results are consistent with those found in terms of a change in weight percentile. Our data support our second hypothesis; rather than birth weight alone, the relative stability of body weight is the critical factor in determining learning performance. These results extend previous findings of the effect of birth weight on learning performance in honeybees (Scheiner, 2012). This result is also consistent with the finding that a higher reliability in the environment, the likelihood that prior experiences can accurately guide decision making, is important for promoting learning in animals (Dunlap & Stephens, 2009). As optimal strategies can differ between environment types (Cartar & Dill, 1990), animals in less reliable environments may apply sub-optimal strategies based on past information (such as using a strategy best suited for use in poor environment in a rich environment or vis versa) while animals in reliable environments will be able to apply strategies that match their current environment.

As the weight of a bee can be influenced by its nutritional status both at birth (Wang et al., 2016) and in adulthood (Hoover et al., 2006), it is possible that the increase in cognitive performance of bees with relatively stable weights is a result of experiencing relatively consistent nutritional conditions. The positive effects of stable nutritional conditions are consistent with the Predictive Adaptive Response hypothesis, which states that animals develop a phenotype best suited for the environment under which they mature (Bateson et al., 2014). Therefore, animals which experience matching nutritional conditions (good or bad) during development and adulthood may outperform animals which experience a nutritional mismatch between development and adulthood. Physiological predictive adaptive responses have been previously found in honeybees (Wang et al., 2016) and other nutritional factors have been shown to effect honeybee behaviour (Chapter 1; Toth & Robinson, 2005), but further research would be required to determine if nutritional differences play a causal role in the cognitive differences observed here.

Our results indicate that weighing animals at a single time point may be insufficient for behavioural studies. While weight at key time points may be informative alone, the relative stability animal weight can provide vital insights, as shown by our finding that the cognitive abilities of honeybees are highest when they have relatively stable weights. Future studies should seek to incorporate multiple measures of weight and other factors expected to change during an animal's life in order to better evaluate behavioural outcomes.

TABLES AND FIGURES

Tables

Table 3.1: Type III ANOVA results based on a Poisson regression predicting the overall learning score, including all effects in the BIC selected model (N = 103, BIC = 437.3).

Predictor	**Wald's χ^2**	**df**	**P**
Intercept	19.3	1	< 0.0001
Birth weight	21.1	1	< 0.0001
Late-adult weight	18.8	1	< 0.0001
Birth cohort	23.4	3	< 0.0001
Late-adult weight * Birth cohort	25.9	3	< 0.0001
Late-adult weight * Birth weight	21.2	1	< 0.0001

Table 3.2: Type III ANOVA results based on a Poisson regression predicting learning score, including all effects in the BIC selected model (N = 103, BIC = 427.3).

Predictor	**Wald's χ^2**	**df**	**P**
Intercept	76.4	1	< 0.0001
Weight change percentile			
Linear	2.0	1	0.15
Quadratic	15.4	1	< 0.0001

Table 3.3: Type III ANOVA results based on a repeated measures logistic regression predicting the probability of a bee extending her proboscis over six learning trials (N = 103).

Predictor	**Wald's χ^2**	**df**	**P**
Intercept	46.2	1	< 0.0001
Trial	46.1	1	< 0.0001
Weight change percentile			
Linear	2.5	1	0.11
Quadratic	5.2	1	0.02
Linear * Trial	1.6	1	0.19
Quadratic * Trial	1.0	1	0.30

Table 3.4: Type III ANOVA results based on a repeated measures logistic regression predicting the probability of a bee extending her proboscis over six learning trials (N = 103).

Predictor	**Wald's χ^2**	**df**	**P**
Intercept	1.5	1	0.20
Trial	60.4	1	< 0.01
Birth weight percentile	10.6	1	< 0.01
Late-adult weight percentile	8.4	1	< 0.01
Late-adult weight percentile * Birth weight percentile	11.9	1	< 0.01

Figures

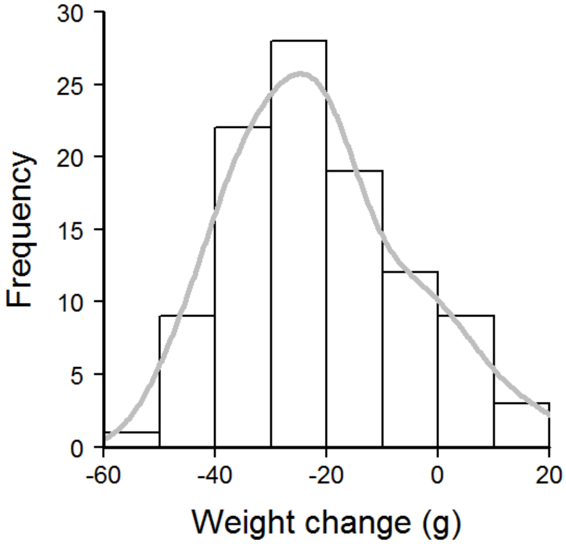


Figure 3.1: The distribution of weight change of individuals between birth and late-adulthood (N = 103). Density curve shown in gray.

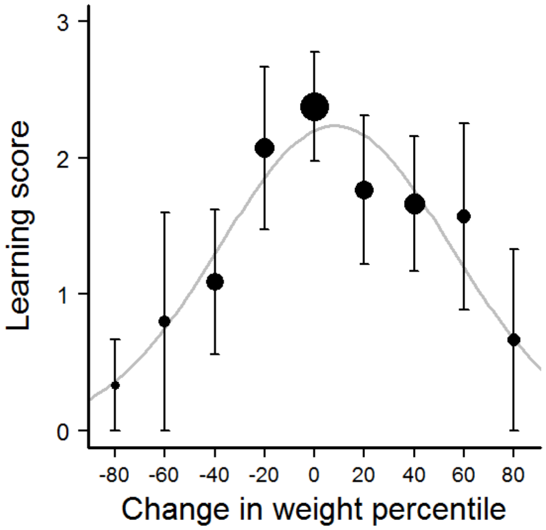


Figure 3.2: The effect of change in weight percentile on learning score in honeybees. Changes in weight percentile were rounded to the nearest 20 (for plotting purposes only) and mean learning score of each grouping is shown with standard error bars. Circle areas are proportional to the number of bees binned in each group (N = 103).

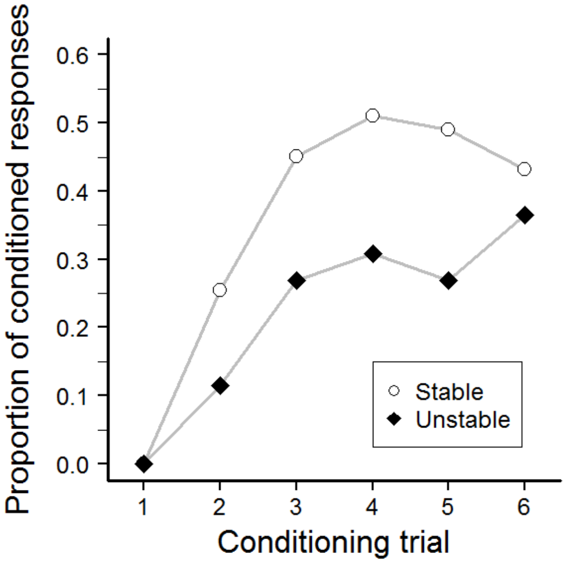


Figure 3.3: The effect of weight stability on the proportion of bees displaying the conditioned response across six learning trials. To divide bees into stability categories (for plotting purposes only), bees with weight change percentiles between -25 and +25 were categorized as “stable” and bees with weight change percentiles less than -25 or greater than +25 were categorized as “unstable”. Unstable bees (N = 52, mean |change in weight percentile| = 48.7 ± 2.4) are shown as black diamonds and stable bees (N = 51, mean |change in weight percentile| = 10.7 ± 0.9) are shown as white circles.

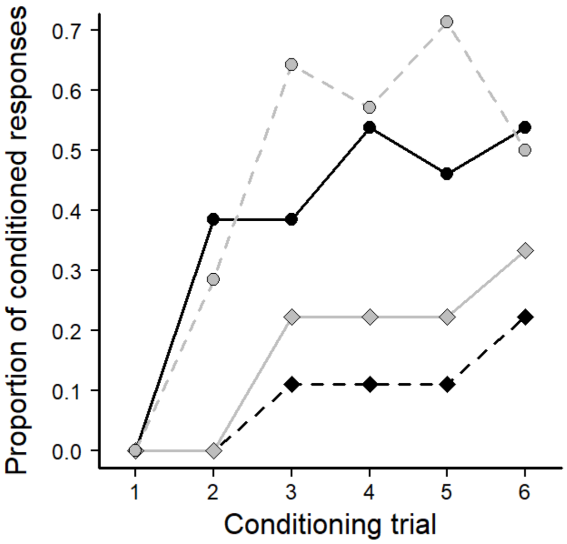


Figure 3.4: The effect of weight percentiles at birth and as a late-adult on the proportion of bees displaying the conditioned response across six learning trials. Here bees are divided into four weight change categories: “consistently heavy” (weight percentile in the top third at birth and as a late-adult; plotted a solid black line; N = 13), “consistently light” (weight percentile in the bottom

third at birth and as a late-adult, plotted a dashed grey line; N = 14), “light to heavy” (weight percentile in the bottom third at birth and in the top third as a late-adult; plotted a solid grey line; N = 9), and “heavy to light” (weight percentile in the top third at birth and in the bottom third as a late-adult; plotted a dashed black line; N = 9). Bees which did not meet one of the four criteria (those with medium weight percentiles) were dropped from this analysis. Bees with stable weight percentiles are plotted using circles, while bees with unstable weight percentiles are plotted using diamonds.

CHAPTER 4

MODELING HOW METABOLIC RATE INTERACTS WITH RESOURCE AVAILABILITY TO INFLUENCE FORAGING SUCCESS AND LIFESPAN

SUMMARY

Metabolic rate, the biological rate of energy processing, is often considered to be the fundamental determinant of life history and pace of life in biological systems. We modeled the behavior of groups composed of individuals with different metabolic rates in environments of various resource configurations, with or without group-level behaviors such as information sharing and division of labor. Our results show how metabolic rate interacts with the resource environment to determine the energy gain and lifespan in individuals. The results also suggest that in a group context, rather than the average MR of the group, it is the composition of the group that matters such that metabolically diverse groups outperform metabolically homogenous groups. These findings bring new insights to possible gene environment interactions that may be involved in the evolution of intraspecific differences in metabolic rates and how metabolic diversity may contribute to the evolution of group living.

INTRODUCTION

Energy is the primary driver of all life processes and therefore metabolic rate (MR), the biological rate that determines the acquisition and expenditure of energy, has been proposed as the fundamental driver of structure and function at all levels of biological organization (Brown et al. 2004; Hou et al., 2010). Interspecific differences in MR have long been a topic of interest, with most of these studies focusing on how MR scales with body size and temperature (Sibly et al., 2012; White & Kearney 2013). In contrast, the adaptive rationale for intraspecific variation in MR is less clear and the fitness consequences of such differences have only recently become a major research focus (Burton et al 2011, Nilsson & Nilsson 2016). The observation that differences in life history traits can be correlated to differences in MR (Ricklefs & Wikelski 2002) has led to the hypothesis that MR is the fundamental driver of "Pace of Life" (POL) - a suite of correlated traits that define differences in animal personality (Careau & Garland 2012; Houston 2010; Réale et al. 2010; Biro & Stamps 2010; Burton et al. 2011; Le Galliard et al. 2013; Dammhahn et al. 2018). However, it has been repeatedly pointed out that the majority of evidence for the POL hypothesis is correlational (Glazier, 2015; Mathot & Dingemanse, 2015), and there is an urgent need for experimental and theoretical investigations into the functional mechanisms through which MR can influence behavior and life history (Mathot & Frankenhuis, 2018).

MR and life history, arguably, are most fundamentally linked through foraging, an energetically expensive activity, which provides the energy required to run all the life processes that constitute the so-called "metabolic engine", including foraging itself (Biro & Stamps 2010). This can result in a positive feedback loop between MR and foraging such that a higher MR provides a benefit in terms of higher energy acquisition. However, a higher MR also comes with a maintenance cost, both while active and at rest, requiring increased energetic allocation or expenditure, which can overshadow any acquisition benefits from it. This complex relationship probably underlies observations of MR showing both a positive and a negative correlation with POL (Arnqvist et al. 2017) and that of individuals with higher MR showing an advantage only in resource rich environments (Auer et al. 2015). Thus, while MR can be expected to have a significant influence on POL and performance, the exact nature of the functional relationship between them is far from clear.

The complexity of the functional relationship between MR and performance is further compounded when one considers the fact that a biological unit can be made up of lower level organizational units that vary in their MR. It has been proposed that the emergent properties at a higher level of organization can be fundamentally explained by the metabolic properties of its components (Brown et al. 2004), but empirical tests of such metabolic principles of biological organization are difficult and rare (Speakman et al. 2004; Konarzewski & Książek 2013). Social insect groups, which are characterized by a high degree of behavioral variation (Jeanson & Weidenmuller 2014) and can be experimentally taken apart and reassembled in different configurations to study individual and group level properties, are therefore ideal models for understanding how interindividual variation in behavior and POL might be associated with variation in MR and how these parameters scale up to determine life history and POL at a higher organizational level.

Experimental approaches to understanding the influence of MR on behavior and performance are fraught with various confounds and in some cases MR may only be correlated with other traits rather than being their causal driver (Krams et al. 2017). It therefore can be instructive to take a modeling approach to understand how the costs and benefits associated with a variation in MR can influence performance and life history parameters and generate testable predictions, but such models are rare (Sibly et al. 2013). Since foraging can be considered as the central link between MR and fitness, we take an individual based modeling approach to examine how MR can influence resource acquisition while paying out its allocation costs. We simulate groups of agents with different MR foraging under specific resource configurations, which allows us to test how variation in MR interacts with the environment to influence performance both at the individual and the group level. We quantify rates of resource collection and lifespan as our two measures of performance because they are arguably the two most primary life history parameters and also because they can be calculated as a function of MR from our model with the least number of assumptions.

METHODS

Model description

We built an agent-based model (using NetLogo v.5.3.1) to simulate the behavior of groups of central place foragers, in environments with non-depleting energy resources available in patches of large or small patch value, distributed in a random or a clumped fashion. An agent leaves its central place to forage with a fixed amount of energy, required to complete a foraging trip. It spends this energy, at a rate dictated by its active metabolic rate (AMR), to move randomly in the foraging environment, at a speed dictated by its AMR, and collects all the energy resources it encounters. The agent returns to the central place when it has used its allocated foraging energy. Upon its return, the agent deposits all the energy it has collected into a common pool called the energy store. The agent then collects a fixed amount of energy from the store and consumes it at a rate dictated by its resting metabolic rate (RMR). It leaves for a new foraging trip, with a fixed amount of energy allocated for foraging, when it has spent this between-trip energy. An agent has a fixed limit of lifetime maximum energy expenditure, $E_{max,}$ and it dies upon reaching this value (defined as death due to senescence), or if the value of the energy store goes to zero (defined as death due to starvation). Each run of a simulation continues until all agents in a group are dead, a period which defines the lifespan of the group. Derivations and definitions of all parameters are summarized in Table 4.1.

Agent characteristics

There are three types of agents, defined by their distinct MR, those with low MR or MR_L, medium MR or MR_M, and high MR or MR_H. These three types of agents are used to create four types of groups with 20 agents each, “pure low” (all MR_L), “pure medium” (all MR_M), “pure high” (all MR_H) and “mixed” (half MR_L and half MR_H).

Since locomotion and activity of all animals are known to be strongly influenced by their MR (Nachtigall et al. 1995; Reinhold 1999; Chappell et al. 2004; Gębczyński and Konarzewski 2009; Lovegrove 2004; Skandalis and Darveau 2012; Darveau et al. 2014), we assume the most parsimonious positive relationship between MR and movement velocity in this model,

$$V_X = AMR_X$$

where V_X is the movement speed and AMR_X is the active metabolic rate of an agent of a given type. Each agent also has a resting metabolic rate, RMR_X, assumed to be ¼ of its active metabolic rate.

$$RMR_X = \frac{1}{4} AMR_X$$

An agent initiates a foraging trip carrying an amount of energy, E_0, the trip energy available for use and the energetic cost of movement, C_M, for a single time step was defined as:

$$\mathrm{C_M = AMR_X + E_t \cdot C_E}$$

where E_t is the total amount of energy being carried by the agent at time t and C_E is a constant representing the energetic cost imposed by each unit of energy being carried by the agent. C_M is subtracted from E_t at each time step the agent spends moving in the environment. Therefore, at the beginning of a foraging trip (time step 0), E_t is equal to trip energy E_0 and it decreases at each time step as the agent moves through the environment and it increases at each time step the agent encounters a patch and picks up the energy load from it. The rate at which E_t is reduced is higher when E_t is large due to the increased energetic expenditure required to carry larger amounts of energy.

When an agent encounters a food patch, the energy value of the patch, E_P, is instantaneously added to its current energy, E_t, and it continues its movement uninterrupted. At the start of each time step, an agent calculates the energetic cost to return to the central place from its current location in a straight-line and once the total energy spent foraging ($\sum C_M$) including the return trip is greater than or equal to E_0, the agent ceases foraging and returns to the central place by moving in a straight line. The net energetic gain from a foraging trip, E_G, can therefore be summarized as:

$$E_G = N \cdot E_P - \sum C_M$$

where N is the number of food patches encountered during the foraging trip. The gross energy foraged ($N \cdot E_p$) is added to the current value of the energy store at time t, S_t.

When the gross energy foraged is greater than the cost of the trip ($\sum C_M$), E_G is positive and the foraging trip has a net positive effect on the energy store. However, the cost of the trip can also be greater than the gross energy foraged, in which case E_G is negative and the trip has a net negative effect on the energy store.

Upon its return to the central place and after depositing E_G into the energy store, the agent draws an amount of resting energy, E_R, from the energy store and remains in the central place, spending E_R at a rate dictated by its RMR, and once the value of E_R equals zero, it draws E_0 from the energy store and leaves the central place on another foraging trip. Agents with higher RMR spend this resting energy, E_R, more quickly and therefore engage in more frequent foraging trips. Agents have activity cycles divided into an active time, T_A, during which they forage and they spend the remaining time resting, T_R, and an entire activity cycle of $T_A + T_R$ is referred to as a “day”. During T_R, agents draw energy from the energy store, reducing it by a value equal to their RMR at each time step.

Simulations

At the start of each simulation run, all agents have 0 energy ($E_t = 0$) and the value of the energy store, S_t, is set to an amount of energy enough for 10 foraging trips per agent. The model environment and agent characteristics described above refer to the 1) “basic environment”. We modified the environment and agent characteristics in the following manner to evaluate five additional environments that investigate further aspects of how MR may influence performance. 2) “temporal variation environment”, where the energy value of the food patches, E_P, switches from large to small or *vice versa* during the rest period of each day (T_R), while mean Ep remains the same as in the basic environment. The large and small patch values were calculated such that the coefficient of variation from the mean was always 1, which ensures that variability is constant across different patch values. 3) “spatial variation environment”, where food patches are distributed in the environment in clumps, instead of at random. These clumped environments were defined as having a dispersion index equal to 3 ± 0.1. 4) “information environment”, where an agent has the ability to share information about the location (in terms of distance and direction) of the last food patch it encountered in its previous foraging trip. After every foraging trip, an agent compares its foraging gain, E_G, to the average foraging gain (G_{avg}) across all trips by all agents in the group and adds the location as an information unit to a group-level information pool with a probability (P_I) defined as:

$$P_I = \frac{E_G}{2 \cdot G_{avg}}$$

This results in a probability of 1 for information sharing when $E_G \geq 2\ G_{avg}$ (last encountered food patch by an agent is twice as good as the average of what other agents have found) and a probability of 0 for information sharing when $E_G << G_{avg}$ (last encountered food patch is much poorer than the average of what other agents have found). Any P_I values less than 0 or greater than 1 were set to 0 and 1 respectively. Agents leaving on a foraging trip have a fixed probability of 0.9 for randomly selecting an information unit from the information pool to use - a high probability of using information while still allowing for some agents to not use previously gathered information and explore new areas of the environment. Once used, the information unit is removed from the information pool, which simulates the temporal decay of information. An agent using information travels in a straight line from the central-place to the specified location, after which it reverts to moving randomly for the remainder of the foraging trip. 5) "spatial variation with information environment", a combination of the second and the third environments. 6) "division of labor environment", where half the agents within a group are randomly designated as foragers each day while the other half act as non-foragers who remain at the central place. Non-foragers represent agents dedicated to within-nest tasks and they deplete the energy store according to their RMR, in a manner identical to the behavior of all agents during T_R.

For the simulation of each environment, a single group of each type (pure high, pure medium, pure low, or mixed) is placed by itself into a randomly generated environment of the given type. Each of these simulations was run across a range of food patch values ($1 \leq E_P \leq 100{,}000$) and repeated 1000 times and we report each of our performance measures as the average of 1000 simulated groups. Additional simulations were run to assess the sensitivity of the model and the functional importance of some of the parameters. The mathematical relationship between AMR and velocity was tested at $\mathrm{V} = \mathrm{k}.\sqrt{\mathrm{AMR_X}}$, $\mathrm{V} = \mathrm{k}.\mathrm{AMR_X}$, $\mathrm{V} = k.\mathrm{AMR_X}^2$, $\mathrm{V} = \mathrm{k}.\mathrm{AMR_X}^3$, and V = 6 (a constant value unrelated to AMR). The effect of load cost, C_E, was examined at $C_E = 0.0001$, $C_E = 0.001$, and $C_E = 0.01$. Various rules based on different currencies that might dictate when a forager leaves for a foraging trip were also evaluated, including, after spending a constant amount of energy ($E_R = 10$), after spending a random amount of energy (E_R = a random number between 0 and 20 with an average of 10), after spending a constant amount of time steps (60), and after spending a random amount of time steps (a random number 20 and 120 with an average of 60). Supplemental results can be found in Appendix II.

RESULTS

The total energy collected by a group (S_t) over its lifetime expectedly increases with patch value in all environments (Fig. 4.1A). To more easily compare results across patch values, we divided the lifetime energy storage by the patch value (E_P), which reveals that the pure low groups collect more energy than other groups at smaller patch values while the pure high groups collect the most amount of energy when patch values are large (Fig. 4.1B, 4.S1). The parabolic shape of this measure is a result of higher survival of agents due to decreased starvation risk with the initial increase in patch value and a decrease in agent lifespan from the energetic cost of movement with large loads at large patch values, given the limit on lifetime energetic expenditure. In terms of daily energy storage, the pure high groups store more energy across nearly all patch values and all groups show a peak in daily collection at intermediate patch values (Fig. 4.1C).

To determine the relative advantage of the different groups over each other, we calculated their relative foraging success by dividing the lifetime energy storage of each group at each patch value by the mean lifetime energy storage of all groups across all environments at that patch value. The relative foraging success is a unitless measure where a score of 1 indicates an average performance, a score of 2 indicates a performance twice as good as average, and so on. In all environments, the pure low groups have a higher relative foraging success than pure high groups for small patch values and this trend reverses at large patch values (Fig. 4.2). At very large and very small patch values, the performance of the pure medium groups falls between the pure low and the pure high groups, but at intermediate patch values the pure medium groups show a small advantage over all other groups in the majority of the environments. In the division of labor environment (Fig. 4.2F), the mixed groups show a distinct advantage across all but the largest patch values. The overall decrease in foraging success for all groups in the division of labor environment is expected because only half the agents forage on any given day. Information has little effect on relative foraging success in a spatially random environment (Fig. 4.2A, 4.2D), but when information is used in a spatially variable environment (Fig. 4.2E), all groups show an increase in foraging success.

Pure low and mixed groups have substantially longer lifespans than both pure high and pure medium groups under all patch values, but the advantage is reduced at extreme patch values, both small and large (Fig. 4.3). All groups show a sharp increase in lifespan as patch value initially increases, which marks the threshold at which agents begins to live until senescence, rather than dying of starvation (Fig. 4.S2). This threshold patch value is smallest for the pure low group and largest for the pure high group, which follows from their respective energetic demands. The large difference in lifespan between the mixed and the pure medium group is interesting since both groups have identical energetic requirement at the group level. However, the presence of low MR individuals in the mixed groups allows them to survive longer than the homogeneous pure medium groups. Mixed groups have very similar lifespans as pure low groups, except in the division of labor environment where all groups live somewhat longer (Fig. 4.3F), presumably because division of labor allows agents to forage half as often which saves energy and takes them longer to reach the maximum lifetime energetic expenditure. The decline in lifespan in the richest environments is somewhat counterintuitive but is attributable to the energetic cost of carrying large energy loads and the model constraint that requires the agents to always fully exploit a patch.

The difference in group lifespan between low and high MR groups fundamentally arises from the longer individual lifespan of low MR agents (Fig. 4.4A). Interestingly, when low and high MR agents live in mixed groups, their lifespans approach the lifespan of the medium MR agents. These observed differences in lifespan can be further explored in terms of what we define as realized lifespan. As agents die of senescence when they have used a fixed amount of energy and their MR determines the pace at which they reach this energy maximum, each MR has a specific maximum life expectancy associated with it. We defined life expectancy for each MR as the age at which an agent would die if it only rested and did not forage. In terms of realized lifespan, calculated as actual lifespan / life expectancy, all three types of agents (low, medium, high) have very similar patterns (Fig. 4.4B) with a sharp increase with the initial increase in patch value and an eventual decrease at large patch values as seen earlier. The frequency distribution of lifespan is bimodal for agents of all three MR types (Fig. 4.4C), with an initial peak for agents that die of starvation and a second peak for those that die of senescence. Low MR agents in mixed groups die less frequently of senescence (a shorter second peak) and more frequently of starvation while those in pure groups show the opposite pattern. In contrast, high MR agents in mixed groups die less frequently of starvation and more frequently of senescence (a taller second peak) while those in pure groups show the opposite pattern (Fig. 4.4C).

Load cost (C_E), has a strong negative influence on the total amount of energy harvested and stored. At small patch values, a reduced load cost resulted in pure low groups gathering more energy than pure high groups and an increased load cost resulting in a reversal of fortunes (Fig. 4.5A). The negative effect of increased load cost on low MR groups is correlated to a reduction in lifespan advantage experienced by them compared to high MR groups (Fig. 4.S3A). At large patch values, a change in load cost has little effect on the relative performance of the different groups (Fig 4.5B). Load cost is expected to have a stronger effect on foraging in poor resource environments as the load cost would represent a larger proportion of the total cost of a foraging trip. Load cost has a strong effect on lifespan in rich environments (Fig. 4.S3B), due to the multiplicative relationship between load cost and the amount of resources gathered on a trip. A single trip can represent a much larger portion of an individual's maximum lifetime energy expenditure when patch value is large. This is consistent with the general decline in lifespan observed at larger patch values (Fig 4.3).

The relationship between active metabolic rate and movement velocity is a critical assumption in the model and different relationships lead to significantly different results. The difference in energy storage due to different assumptions made between AMR and movement velocity is more prominent in poor environments. The assumption of a simple linear relationship provides the least advantage to a group of any specific metabolic type (Fig. 4.5C, 4.5D), while low MR groups perform better when movement velocity is a saturating function of MR, and high MR groups do better when movement velocity is an accelerating function of MR. When velocity is unrelated to MR (a constant), low MR groups consistently outperform high MR groups. Overall, high MR groups outperform low MR groups when the cost of a high MR is compensated for by a velocity advantage.

The model is more sensitive to whether a currency of energy or time is used as a foraging rule rather than whether it is a random or a constant value of the specific currency (Fig. 4.5E, 4.5F).

A foraging rule based on time gives an advantage to low MR groups at both small and large patch values while a foraging rule based on energy gives a smaller advantage to low MR groups at small patch values and high MR groups at large patch values. When agents leave on foraging trips based on a time rule, high MR agents pay a higher energetic cost of unproductive waiting than low MR agents and both MR types forage at similar frequencies. Using an energy based foraging rule, which is more consistent with individuals foraging to meet an energetic need, leads to high MR agents foraging more frequently than low MR agents.

DISCUSSION

Our model demonstrates that differences in MR can interact with the resource environment to impact the foraging success and lifespan of individuals and groups. Broadly, the pure low MR groups had an advantage in lifespan in all environments and in energy storage in resource poor environments while the pure high MR groups stored more energy than other groups in rich environments. This finding is consistent with both theoretical and empirical work suggesting that both a high MR and a fast POL are more likely to be adaptive only when resources are abundant, while a slow POL has an advantage when resources are scarce (Biro & Stamps 2010; Burton et al. 2011; Auer et al. 2015). The pure medium groups outperformed all other groups in term of energy storage in environments of intermediate richness while division of labor allowed the mixed groups to take the lead in all environments except in the very richest ones.

Division of labor resulted in an advantage to mixed groups consisting of low and high MR individuals over other groups. This is an interesting result because at the group level, the mixed group is similar to the pure intermediate MR group as both groups have identical MR when averaged across all agents. This outcome arises in spite of our parsimonious assumption that labor is divided randomly across individuals of different MR, although in reality division of labor is a non-random process (Beshers & Fewell, 2001). This supports the idea that diversity among the units that constitute a higher level phenotype can be adaptive by allowing a larger range of response to a complex and dynamic environment (Piersma & Drent 2003; Liao 2012; Woods 2014), an idea especially relevant for social insects (Myerscough & Oldroyd 2004; Oldroyd & Fewell 2007). While behavioral variation and division of labor are considered to be the primary mechanisms that allow social groups to adjust for variations in the resource environment, our results show that interindividual variation in MR can be a primary mechanism underlying this advantage. Understanding such energetic principles of biological organization and the links between MR and POL at the individual and the group level can contribute to fundamental questions regarding social evolution such as how variation in MR drives division of labor and contributes to the extraordinary ecological success of social groups.

Variability in the environment reduced the performance of all groups to an extent and the ability to use information in such environments, not too surprisingly, allowed them to compensate for this variability. Interestingly, the pure low groups showed the largest influence of information use in these environments, extracting a great advantage from it when the environment was poor but also showing the highest decline in relative performance when the environment was rich. This indicates that the ability to share information amplifies the foraging advantage of all groups, but does not provide an advantage to foragers of any particular MR. Somewhat counterintuitively, mixed groups or those with intermediate MR did not show any particular advantage over the other groups in a variable environment, suggesting that division is labor is the critical factor that can provide an advantage to mixed groups, rather than metabolic diversity alone.

The mechanisms underlying lifespan is one of the most important and unresolved question in biology and our use of a maximum lifetime energy expenditure to determine senescence is consistent with both the POL and the rate of living hypotheses (Careau & Garland 2012; Kirkwood & Austad 2000; Speakman 2005). Empirical findings on the effect of MR on lifespan are quite mixed, with studies reporting the association of longer lifespan with a low MR (Wikelski et al. 2003) being often confounded by other factors (Duarte & Speakman 2014). Our results show a consistent lifespan advantage for individuals with low MR, but individuals of all MR types show an increase in lifespan as the environment becomes richer due to the accompanying decrease in starvation risk. Somewhat counterintuitively, individuals also show a decline in lifespan in the richest environments due to the energetic cost of harvesting large energy loads as they are maximizing energetic gain. This is however consistent with the observation that individuals which forage more or work harder have reduced lifespans (Schmid-Hempel & Wolf 1988). Such energetic constraints and the need to preserve lifespan may be responsible for why animals choose to maximize foraging efficiency as a currency rather than rate of gain (Schmid-Hempel et al. 1985; Houston et al. 1988; Nolet 2002).

Our results also show an interesting influence of group context on the lifespan of individuals with different MR. Low MR individuals in mixed groups die less frequently of senescence than those in pure low MR groups, while high MR individuals in mixed groups die more frequently of senescence than those in pure high MR groups. Death due to starvation has exactly the opposite pattern in mixed versus pure groups. This suggests that the fitness of different MR types can be subject to frequency dependent selection and such mechanisms can play an important role in the dynamics of social evolution. The frequency distribution defining the interindividual variation in MR within a group, by setting the rates of resource acquisition, allocation and expenditure, can therefore have a complex effect in determining its life history trajectory and POL. This also means that in a eusocial context, individuals of different MR types may not contribute equally to colony performance measures, which may underlie the workload based reproductive conflicts in social insect colonies (Schmid-Hempel 1990). These results therefore suggest that diversity in MR can create the scope for both cooperation and conflict in social groups and understanding these dynamics can provide a metabolic or energetic basis for social evolution.

Our model was found to be sensitive to the assumptions regarding the energetic cost of carrying a load, the relationship between MR and movement velocity and the rule based on which foragers leave the nest on a foraging trip. It is therefore important that these relationships are tested in different species to get a comprehensive understanding regarding how MR can be expected to influence life history parameters and POL. Since intraspecific variation in MR can have a genetic component (Wikelski et al. 2003; Arnqvist et al. 2010), the observed interaction between the resource environment and MR on our performance measures can be depicted as behavioral or metabolic reaction norms (Fig. 4.6), which can then be used to make testable predictions regarding how MR may influence POL in different environments.

Since our model spans across different levels of biological organization, social insects can serve as excellent experimental systems to test the predictions of this model at both the individual and the group level. Social insect colonies, which are characterized by a high degree of behavioral and physiological variation (Jeanson and Weidenmuller 2014) and can be experimentally taken apart and reassembled in different configurations to study individual and group level properties, are ideal for understanding how variation in MR might be associated with interindividual variation in behavior and POL and how these parameters scale up to determine life history and POL at the colony level (Dornhaus et al., 2012; Sibly et al., 2012). Prior experimental work shows that interindividual differences in energetic demand and MR have a significant influence on behavioral variation (Chapter 1 & 2; Mayack & Naug 2011; Mayack & Naug 2013; Reade & Naug 2016). Since there are known and ecologically relevant genetic markers for MR in honeybees (Harrison & Fewell 2002), it is possible to test the performance of individuals of known MR as well as create experimental groups that differ in their composition with respect to the frequency of different MR types. Using such experimental colonies and measuring various behavioral and life history parameters in different types of resource environments can allow us to test how interindividual variation in MR can influence energy acquisition and allocation characteristics at the individual and the colony level and how this contributes to life history and POL at different levels of biological organization.

TABLES AND FIGURES

Tables

Table 4.1: Descriptions and definitions of model parameters and derived quantities

	Description	
Parameters		
E_t	Energy of an agent at time t	
E_P	Energy value of a food patch	
S_t	Energy in energy store at time t	
N	Number of food patches encountered	
Constants		
AMR_X	Active metabolic rate of an agent of a given type	$L = 2; M = 6; H = 10$
E_0	Trip energy with which an agent starts each foraging trip	$E_0 = 100$
T_D	Total time steps in an activity cycle, or day	$T_D = 24 \cdot 60$
C_E	Cost of carrying 1 energy unit	$C_E = 0.001$
E_R	Resting energy spent between successive foraging bouts	$E_R = 10$
E_{MAX}	Maximum lifetime energy expenditure	$E_{MAX} = 10000$
Derived quantities		
V_X	Velocity of an agent	$V_X = AMR_X$
RMR_X	Resting metabolic rate of an agent of a given type	$RMR_X = 0.25 \cdot AMR_X$
C_M	Energetic cost of movement for one time step	$C_M = AMR_X + E_t \cdot C_E$
E_G	Net energic yield of a foraging trip	$E_G = N \cdot E_P - \sum C_M$
T_A	Time steps spent active each day	$T_A = 0.5 \cdot T_D$
T_R	Time steps spent resting each day	$T_R = T_D - T_A$

Figures

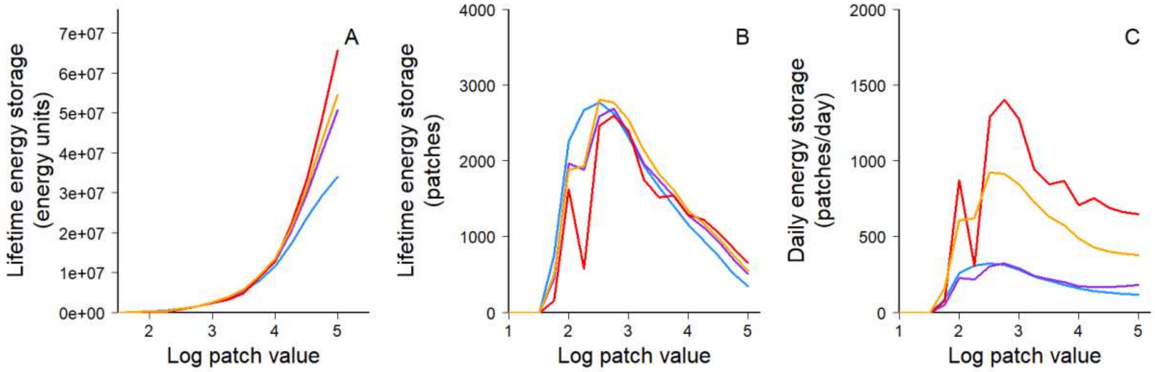


Figure 4.1: Performance of different groups in the basic environment, shown as (A) Lifetime energy storage in energy units (S_t), (B) Lifetime energy storage in number of patches (obtained by dividing S_t in energy units by the energy value of the patches), and (C) Daily energy storage, the lifetime energy storage in number of patches divided by the lifespan of the group. Groups are represented as pure high (red), pure medium (orange), pure low (blue), and mixed (purple).

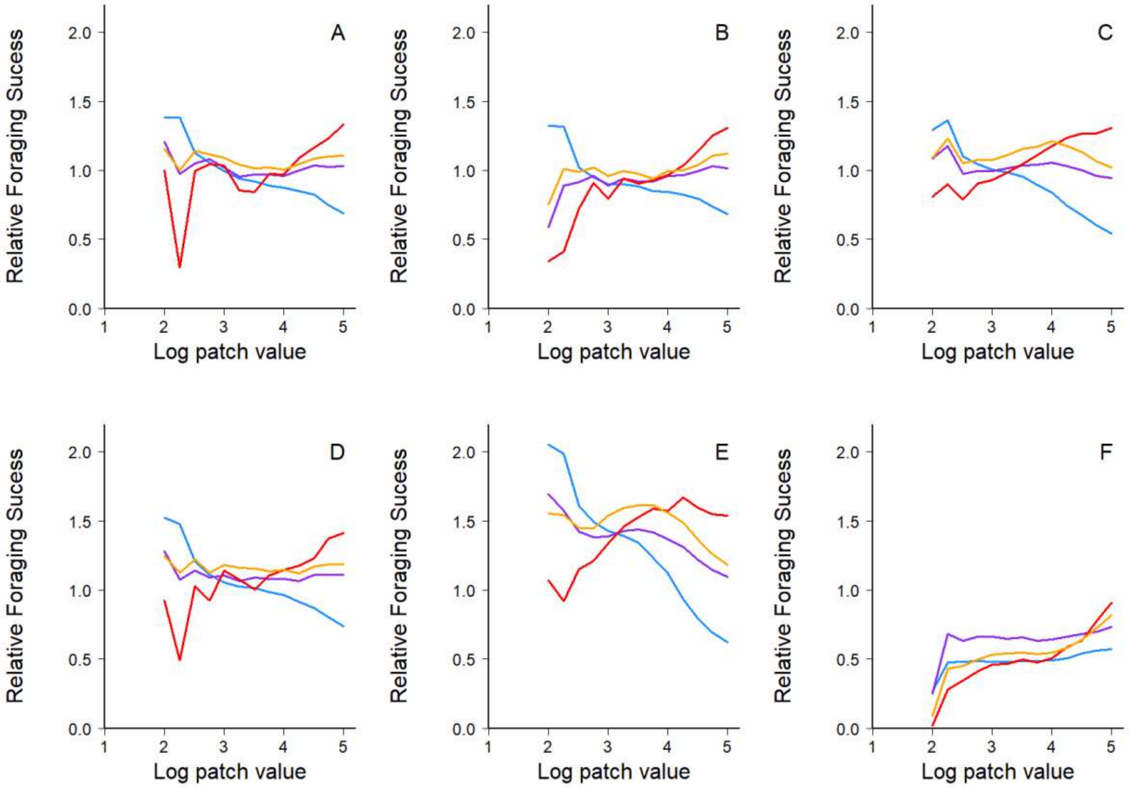


Figure 4.2: Relative foraging success of groups, calculated as the lifetime energy storage of a group divided by the average lifetime energy storage collected at that patch value across all groups and simulation environments. Groups are represented as pure high (red), pure medium (orange), pure low (blue), and mixed (purple). Each panel represents one of the six simulation environments: (A) basic environment, (B) temporal variation environment, (C) spatial variation environment, (D) information environment, (E) spatial variation with information environment, and (F) division of labor environment.

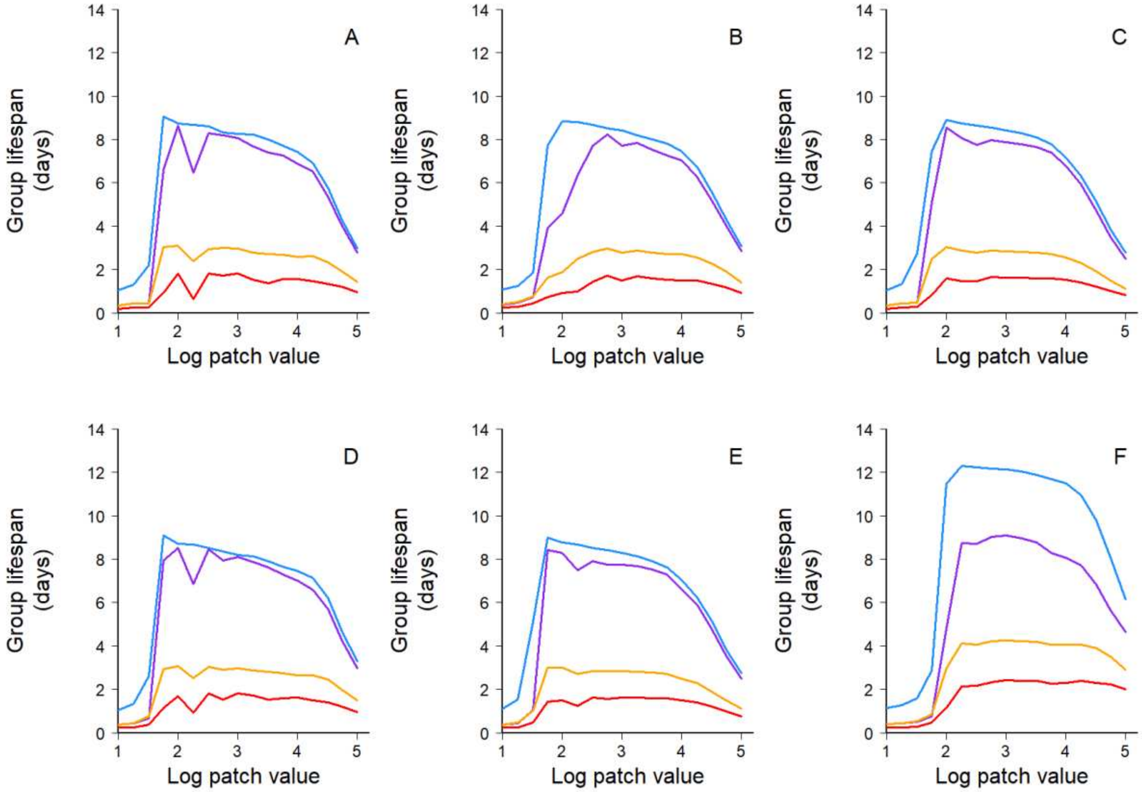


Figure 4.3: Group lifespan, the day at which the last member of a group dies, as a function of patch value. Groups are represented as pure high (red), pure medium (orange), pure low (blue), and mixed (purple). Each panel represents one of the six simulation environments: (A) basic environment, (B) temporal variation environment, (C) spatial variation environment, (D) information environment, (E) spatial variation with information environment, and (F) division of labor environment.

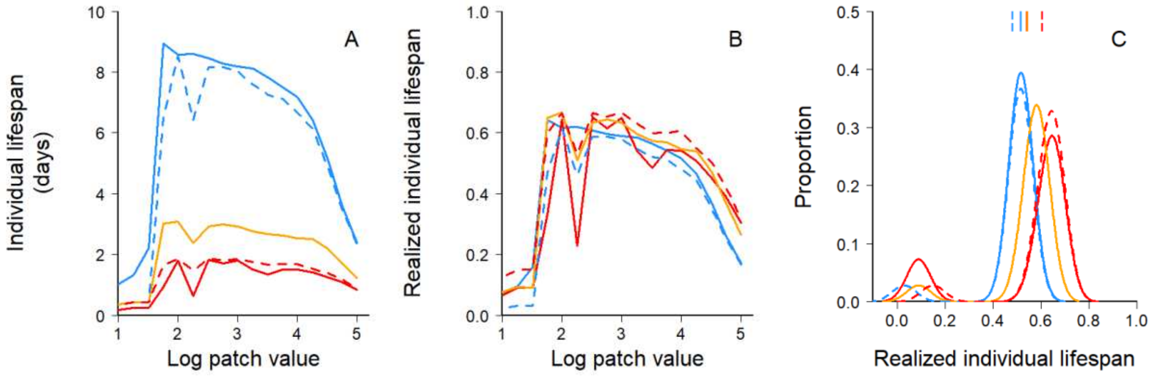


Figure 4.4: (A) Individual lifespan and (B) realized lifespan, calculated as actual lifespan divided by life expectancy, as a function of patch value in the basic environment, and (C) as a frequency distribution at a large patch value (10,000). Agents of different metabolic rates are represented as high (red), medium (orange), low (blue). Agents from pure colonies are shown with solid lines and those from mixed colonies are shown with dashed lines. Vertical lines at the top of panel C show mean values of the distributions.

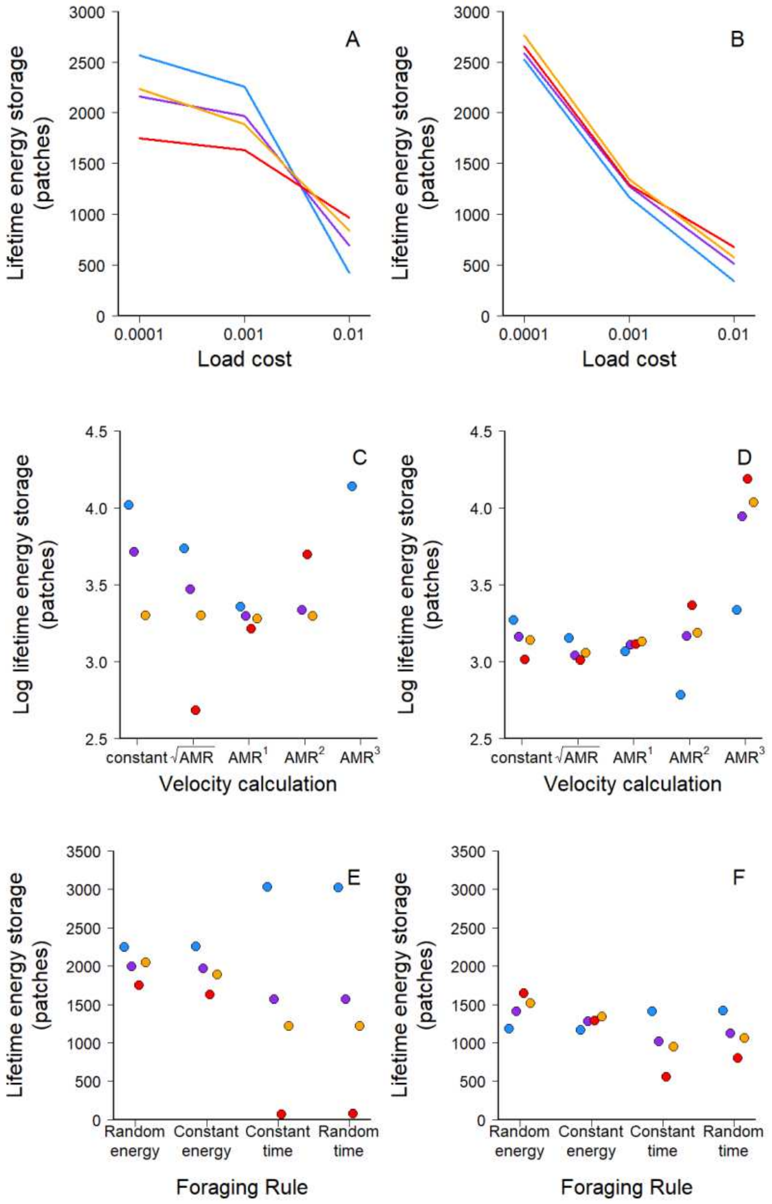


Figure 4.5: Model sensitivity tested for the effects of (A & B) load cost, C_E, (C & D) relationship between AMR and movement velocity, and (E & F) foraging rule, simulated for the basic environment measured at small (100 energy units per patch) and large (10,000 energy units per patch) patch values in the basic environment. Groups are represented as pure high (red), pure medium (orange), pure low (blue), and mixed (purple).

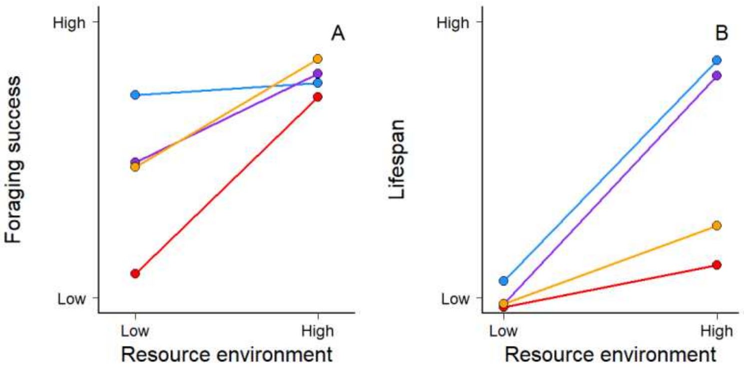


Figure 4.6: Metabolic (rate) or behavioral reaction norms in response to the quality of resource environment in terms of (A) Relative foraging success and (B) Group lifespan. Groups are represented as pure high (red), pure medium (orange), pure low (blue), and mixed (purple).

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APPENDIX I

NOVELTY EXPERIMENT

The number of head turns made by a bee was not significantly influenced by the specific odor associated with each reward during conditioning (GLM: Wald's $\chi^2 = 2.02$, d.f. = 1, $p = 0.15$) or the colony from which a bee came from (Wald's $\chi^2 = 3.12$, d.f. = 6, $p = 0.79$). The duration of proboscis extension was not significantly influenced by odor type (Wald's$\chi^2 = 0.24$, d.f. = 1, $p = 0.61$) or colony identity (Wald's $\chi^2 = 6.41$, d.f. = 6, $p = 0.37$). The choice made by a bee was also not affected by odor type (Wald's $\chi^2 = 1.78$, d.f. = 1, $p = 0.18$) or colony identity (Wald's $\chi^2 = 6.64$, d.f. = 6, $p = 0.35$).

PARTIAL UNCERTAINTY EXPERIMENT

The number of head turns made by a bee was not significantly influenced by specific odors (GLM: Wald's $\chi^2 = 1.07$, d.f. = 1, $p = 0.29$) or colony identity (Wald's $\chi^2 = 2.60$, d.f. = 4, $p = 0.62$). The total duration of proboscis extension was not significantly influenced by odor (Wald's $\chi^2 = 0.24$, d.f. = 1, $p = 0.61$) or colony identity (Wald's $\chi^2 = 1.77$, d.f. = 4, $p = 0.77$). The choice made by a bee was not significantly influenced by odor (Wald's$\chi^2 = 0.01$, d.f. = 1, $p = 0.91$) or colony identity ($\chi^2 = 1.42$, d.f. = 4, $p = 0.84$).Acquisition to the two rewards was significantly affected by reward size (Repeated Measures Logistic Regression: Wald's $\chi^2 = 10.31$, d.f. = 1, $p = 0.001$) but not by colony identity ($\chi^2 = 0.26$, d.f. = 1, $p = 0.60$) or odor type ($\chi^2 = 0.008$, d.f. = 1, $p = 0.92$; Fig. 1.S1).

WELL-BEING ASSAY

The number of head turns made by a bee was not significantly influenced by odor type (GLM: Wald's $\chi^2 = 1.47$, d.f. = 1, $p = 0.22$), but was significantly influenced by colony identity (Wald's $\chi^2 = 18.89$, d.f. = 4, $p < 0.01$). The duration of proboscis extension was not significantly influenced by odor type (Wald's $\chi^2 = 0.65$, d.f. = 1, $p = 0.41$), but was significantly influenced by colony identity (Wald's $\chi^2 = 11.75$, d.f. = 4, $p = 0.01$). The choice made by a bee was not significantly influenced by odor type (Wald's $\chi^2 = 0.59$, d.f. = 1, $p = 0.44$) or colony identity ($\chi^2 = 4.6$, d.f. = 4, $p = 0.32$).

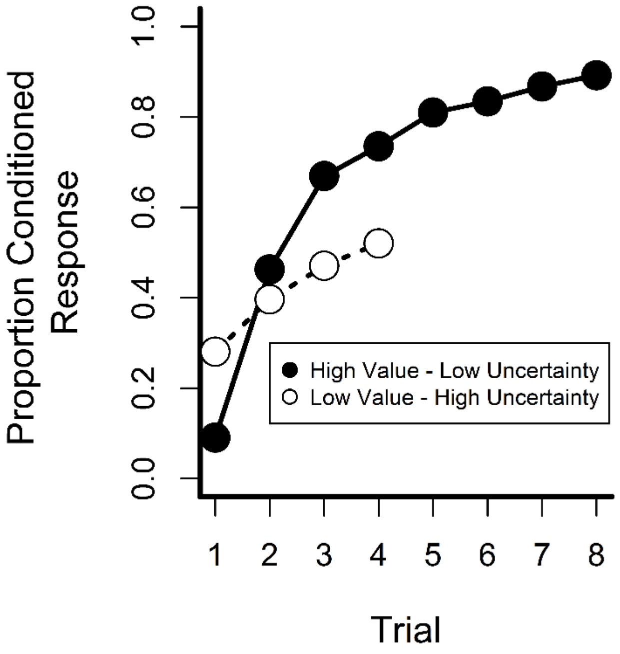

Figure 1.S1: Acquisition of the two odor-reward pairings in the Partial Uncertainty Experiment. Data consist of means. Bees learned the High Value-Low Uncertainty pairing at a significantly higher rate.

APPENDIX II

TABLES

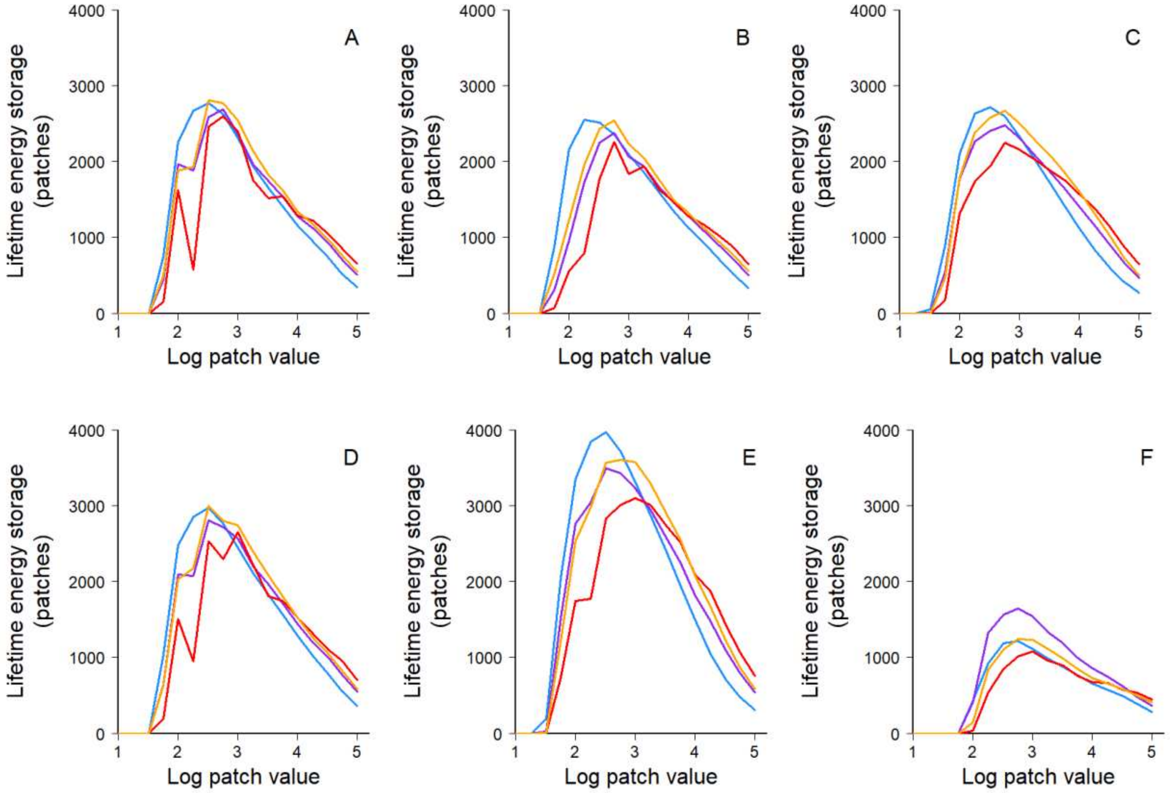

Figure 4.S1: Lifetime energy storage (in number of patches) as a function of patch richness. Groups are represented as pure high (red), pure medium (orange), pure low (blue), and mixed (purple). Each panel represents one of the six simulation environments: (A) basic environment, (B) temporal variation environment, (C) spatial variation environment, (D) information environment, (E) spatial variation with information environment, and (F) division of labor environment.

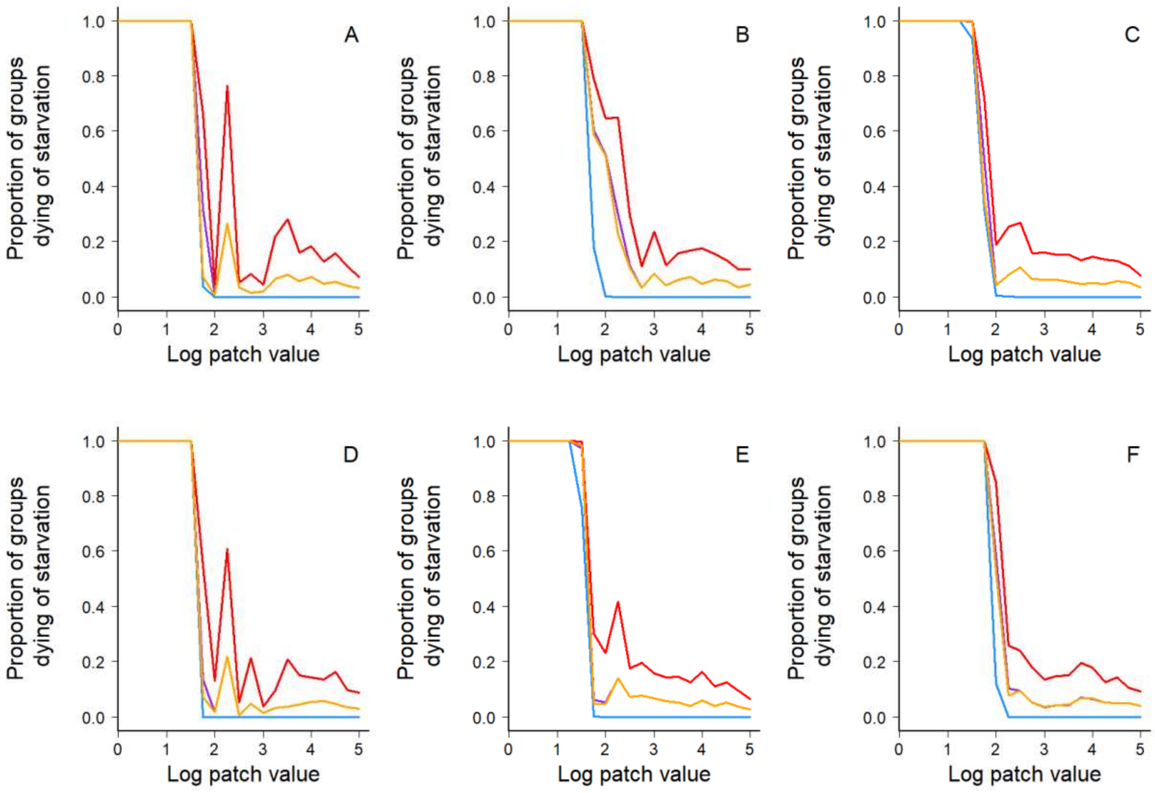

Figure 4.S2: Proportion of groups dying of starvation as a function of patch richness. Groups are represented as pure high (red), pure medium (orange), pure low (blue), and mixed (purple). Each panel represents one of the six simulation environments: (A) basic environment, (B) temporal variation environment, (C) spatial variation environment, (D) information environment, (E) spatial variation with information environment, and (F) division of labor environment.

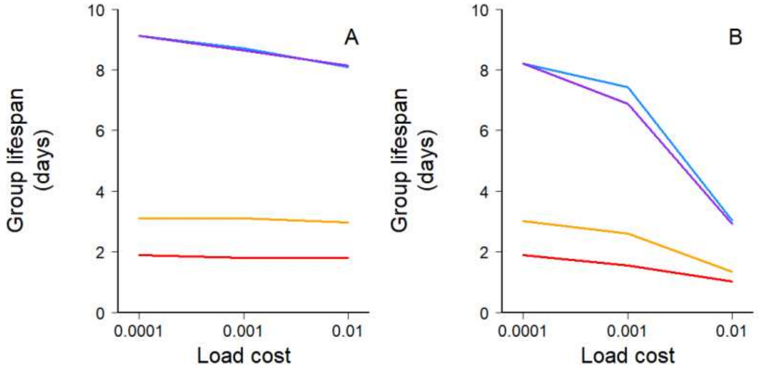

Figure 4.S3: The effect of different values for load cost (C_E) on group lifespan measured at (A) small (100 energy units per patch) and (B) large (10000 energy units per patch), patch values. Groups are represented as pure high (red), pure medium (orange), pure low (blue), and mixed (purple) and simulated for the basic environment.