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Forgetting and the Value of Social Information

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FORGETTING AND THE VALUE OF SOCIAL INFORMATION

A Thesis Submitted to the Graduate School at the University of Missouri-St. Louis in partial fulfillment of the requirements for the degree Master of Biology with emphasis in Ecology, Evolution, and Systematics

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ABSTRACT

Information is everywhere in nature, however it can be deceitful or incorrect, so not all information should be used. Foraging pollinators utilize variable and ephemeral resources so learning about patch quality and nectar replenishment rates are essential to success and survival. However, remembering information after it is no longer relevant is not advantageous. It has been theorized that a pollinator’s memory should reflect their environment. Bumblebees are known to use both personal information (information gathered through trial and error) and social information (information gained through observations of or interactions with other animals or their products) in foraging decisions; however, it is currently unknown how social and personal information are valued in bumblebee memory. We conducted an experiment to illuminate the rate at which bumblebees (*Bombus impatiens*) learn and forget personal and social information. We manipulated the value of social and personal information by varying their reliabilities, and tested the retention of that learned information after 4, 8, and 24 hours. We found that social information is retained better than personal information, and retention decreases as time since learning increases. This experiment is a first step toward elucidating when social or personal information is more valuable to a forager.

CHAPTER 1

I. Foraging in an Ephemeral World

Imagine, for a moment, that you are a foraging pollinator. Every day you must traverse a giant, dangerous, variable and ephemeral world to find enough pollen and nectar to keep you alive and if you're a eusocial bee then you also need to collect enough to take back to the colony before embarking again. Let's think about the actual bees' experience. In any given patch or field of flowers there could be upwards of a dozen species, each presenting you with a different morphology, reward, and even phenology. You need to choose a flower, figure out how to get to the nectar and pollen, assuming it has both available (not all do) and then remember how good that reward was in relation to how difficult it was to access and then use that information when making your next flower choice. At this point you could choose to stay with what you have experience with or try a different flower for a potentially better reward. Keep in mind flying is energetically costly, it takes time to figure out a new flower, and every minute you spend outside the hive you are exposed to predation risks. At this point you might be thinking "just pick a flower that's pretty good and stick with it". But if your chosen flower is not very abundant or has a slow replenish rate you could run out of resources. It's possible to maximize your foraging efficiency by sampling a number of flowers and then remembering which the best are and how to access those rewards. This method takes a lot of time and energy but you can be confident in your information. However, there is a potentially faster way. Upon arrival to a patch, simply scan the area for the presence of other foraging pollinators and then exploit the same resources as those pollinators. It's relatively easy to see where they are and since pollinators don't tend to stay on depleted flowers for too long there is a good chance those flowers will be rewarding. You can even watch to see how they use the flowers and copy them; lessening the time it takes to learn how to access the nectar and pollen. This publically available information, called social information, may not always be as reliable as personal information, information you've learned yourself, because some of the resources have been taken by the pollinators you learned from, but it is easier than using personal information. At this point the question becomes "When you're out foraging, which type of information do you value and rely on more? Information you've learned yourself or information you've learned from others?"

II. Information in Evolutionary Behavioral Ecology

i. What is information, what are the types of information?

Information is the communication or reception of knowledge or intelligence. It can inform the recipient about food or patch quality, the presence or absence of danger, the location of potential mates or competitors, the location and quality of shelters, literally anything that can be known can be transferred as information. Broadly, there is personal information (sometimes called asocial information) and social information. Personal information is gained through trial and error learning; this type of information can be gained in the complete absence of others. Social information is information which is gained through observations of or interactions with either conspecifics or heterospecifics.

Within these two broad categories there are several types of information and various definitions of each type of information that can vary due to differing frameworks or perspectives held by the authors. I will use the information-theoretic definition of information: Information is the reduction of uncertainty, where uncertainty measures the number of states in which a system might be. Central to this definition is the concept of mutual information, which is the measure of how much a cue reduces the uncertainty of an environmental state. Also important is the decision-theoretic value of information, which is defined as the difference between the maximum expected payoff (of a choice) with conditioning on an environmental cue and the expected payoff without conditioning on an environmental cue. (Donaldson-Matasci et al. 2010) The fitness value of information associated with a cue is the greatest fitness cost favored by natural selection in exchange for the ability to detect and respond to said cue. (Donaldson-Matasci et al. 2010)

Information use by animals is key to their adaptive behavior and thus it’s analysis is central to organismal biology. However, an explicit framework is necessary for understanding information use and generating informational hypotheses. This framework has been provided by statistical decision theory, which fits with traditions of both evolutionary and behavioral ecology. Statistical decision theory involves three main elements: priors and posteriors, sampling information, and information and action. It also incorporates Bayes theorem in decision making (Dall et al. 2005). Bayesian reasoning involves incorporating multiple sources of information according to their respective predictive value (Behrens et al. 2007). In realistic situations Bayesian inference can be used to enhance reinforcement learning in an uncertain environment (Doya 2007).

In addition to behavior and organismal biology, information has important ecological significance. Information use and theory is necessary for understanding decision making and phenotypic diversity, breeding and habitat selection, population dynamics, community ecology, predation and landscape connectivity, and interspecific sociality and mutualism among other areas of ecology, see Schmidt et al. (2010) for a detailed review of the topic.

ii. Why is information important?

Information is key in any sort of learning. Learning is a fundamental mechanism for adjusting behavior to a changing environment. Models such as those described by Dunlap and Stephens (2009) recognize different components of environmental change can have different effects on the evolution of learning and information use. Still, many models and experiments find irrational behavior and biases in animal decision making across taxa. These irrational behaviors can be explained by using models that are more similar to the environment the organism evolved in. Models that account for spatiotemporal heterogeneity and autocorrelation can ecologically account for such phenomena as the placebo effect, pessimism and optimism, the “hot hand” fallacy, and intransitive and irregular preference by normalizing errors made due to these phenomena (Fawcett et al. 2014). There is a growing body of research, both experimental evidence and theory, to suggest that the context in which information is acquired is very important to its perceived value, regardless of its actual value. In unknown or sufficiently variable environments social information is valued more than highly reliable personal information if the social information is very convincing (Rieucau & Giraldeau 2011).

The context and order in which information is acquired can be crucial to its salience. A.C. Lewis (1986) found that learning to extract nectar from a second flower species can interfere with the ability to extract nectar from the first species (increases handling time). This could be a cause of floral constancy, the preference for flower types that have already been foraged upon. Insect long term memory is not so small as to necessitate constancy, although short term memory is sensitive to interference during learning of novel stimuli and is possibly limited in capacity. There may be temporal constraints in retrieving long term memory, but experienced bees readily switch between flower species indicating the ability to do so. It is possible that constancy could, at times, be due to larger scale behaviors such as hive location and maximum distance traveled to forage. It is possible that search among multiple parameters is more time consuming than search among a single parameter, and sampling takes time that may be better used foraging on the current flower. Clearly time can have an impact, memory retention of foraging skills in bumblebees is imperfect overnight but does not diminish significantly over several days (Keasar et al. 1996). This could be an example of imperfect memory or adaptive forgetting, which will be discussed later in this review. Time is not the strongest acting force though; the physical state of the animal can have a drastic effect on information retention. Dunlap et al. (2006) found state-dependent sex differences in spatial memory of Pinyon Jays (*Gymnorhinus cyanocephalus*) suggesting that individual life history states can affect the accurate use of information.

III. What Makes Information Valuable?

i. Variability.

Variability can easily affect the value of information. If an environment is too variable an organism may choose to ignore available information in favor of a more static choice. Variability of the environment can also favor different types of information use, when the environment is more variable more value may be placed on social information than personal information because tracking changes in an environment is more accurate on a group level than on an individual level. This behavior of sampling different resources in a changing or fluctuating environment to track their relative quality is known as environment tracking and can occur at both an individual and group level. Pollinators may have to deal with a foraging environment that is variable in many ways. Flowers can be an ephemeral resource varying in combination and reward based on phenology. In addition, flowers replenish their nectar rewards at different rates and some flowers even alter the quality of their nectar rewards over time (Willmer 2011). This amount of variability can decrease the value of information on a floral cue. As time from information acquisition increases, the likelihood the information is correct may decrease (Koops 2004, McLinn& Stephens 2006, Stephens 1989). This environmental uncertainty or variability interacts with signal or cue reliability to affect the value of information, that is, signals should be used when signal reliability exceeds environmental certainty. However, McLinn and Stephens (2006) showed that prior certainty is key in animal information use and blue jays (*Cyanocitta* cristata) tend toward environment tracking over signal use when they are equally reliable. This trend toward environment tracking could be taxonomically widespread as many pollinators use resource tracking as a way to stay informed about rewarding food patches in the environment (Carter 2004). Resource tracking involves frequent sampling of different food patches, remembering differences in patch quality, and choosing appropriately (Shettleworth et al. 1988, Krebs & Inman 1992). Theory suggests that in order to make optimal decisions multiple sources of information, including current sampling information, should be weighed with prior knowledge according to their respective predictive values in what is called Bayesian reasoning or Bayesian updating (Behrens et al. 2007).

ii. Reliability.

Learning about rewards and patch quality is essentially a way for foragers to predict the future, that is, predict which patches will be the most rewarding before they arrive. In order to effectively learn though, the information has to be reliable to some degree. Reliability can be defined as the conditional probability that a signal or cue indicates a specific and known state (Dunlap & Stephens 2009, 2012). In the context of a foraging pollinator a reliable signal could be a floral cue- shape, color, odor, or some combination thereof, that frequently indicates the presence of nectar. The reliability of information is crucial to that information's value. Animals can be quite sensitive to the reliability of information and will switch to an alternate information source if it becomes too unreliable. If information is not reliable then it has no value because there is too much uncertainty as to whether or not the information is correct. This relationship between the value and reliability of information makes several predictions about the circumstances in which information should be used: Individuals should use information that is acquired at zero cost very cautiously (costs of information are usually energetic in nature and will be discussed in the next section). Reliable information should be used even if the cost of misinformation is very high. Misinformation is incorrect information. However, if the cost of misinformation is low relative to the benefit of correct information then unreliable information should still be used. This is because the more beneficial the information the less reliable it can be or the higher the cost can be. If being naïve is worse than having misinformation then it can be said that all information has value, even if misinformation is of less value than correct information. Acquisition costs associated with information have little effect on the value of said information, although there is an effect. If the receiver of information pays for the reliability, then there is an optimal (although less than maximum) and a minimum reliability the receiver is willing to accept. The optimal reliability decreases as acquisition cost increases and the benefit of said information decreases. There can be a struggle when both the sender and receiver of information pay some cost associated with reliability of the information. This is because when the producer pays for information they benefit most from minimum reliability allowed by the receiver but when the receiver pays they benefit most from the optimum reliability. This can create an "evolutionary arms race" over information reliability (Koops 2004). Although determining whether or not information is valuable requires more than just reliability (Koops 2004, Dall et al. 2005).

iii.Costs.

Information may be reliable but also costly to acquire, if this cost is greater than the potential benefit of the information then it is not valuable (Koops 2004). Information can be costly in several ways; costs include risk of predation or injury although in a decision making context we typically think of costs as unnecessary energetic expenses or a decrease in foraging efficacy due to incorrect choices. A central concept in decision theoretic choice models is that foragers are trying to maximize their energy intake, or rewards, and minimize their costs. Experimentation by Irwin and Smith (1957) showed that more information is required to make a confident choice when the reward is more valuable or when information is less costly to acquire. Sampling costs occur when a forager leaves one patch to sample an alternative patch, this alternative patch may be better or worse than the original, but the cost is representative of the reduction from optimal foraging efficiency. Despite this potential inherent cost animals use sampling to track changes in their environment. Random sampling and when animals sample unnecessarily or when they choose a less rewarding patch increases this cost (Shettleworth et al. 1988). Even given these costs foraging animals can sample at least two patches and maintain a near optimal reward intake rate. However, as the similarity between alternate patches increases so do the number of mistakes (Krebs et al. 1978). This is expected by theory and usually considered a recognition error. Theory and models of the costs associated with environment tracking make a few other predictions. Environment tracking is not worthwhile when varying prey levels are unstable and alternate prey have a much greater or much less value. As the value of alternate prey increases, sampling should become less frequent because sampling errors (leaving a patch too early) are expensive compared to overrun errors (leaving a patch too late) (Stephens 1987). The effect of costs on information use and decision making extend past rules for sampling alternate patches, they also effect the value and retention of information. In an experimental study with domestic pigs (*Sus scrofa*), Laughlin and Mendl (2003) showed that small costs, such as time, during sampling decreased errors during recall trials. This suggests that "processes exist that modulate the effectiveness of information acquisition, storage, and retrieval according to the costs to the animal of obtaining or forgetting that information."

IV. The Value of Social Information

One way some animals can decrease the cost of acquiring information is to use social information (Krebs & Inman 1992, Danchin et al. 2004). Social information is information gained through observation of conspecifics or heterospecifics. A variety of information can be acquired socially, including what food resources are rewarding or unrewarding and the presence of danger. Using social information reduces the cost of acquiring information by allowing the observer to learn where food is without having to sample each flower. Similarly, individuals can use the predator avoidance behavior of conspecifics to gauge whether or not it is safe to forage (Coolen et al. 2005, Abbott 2006). Reducing predation risk and the time spent identifying rewarding food patches are just two ways social information can reduce the cost of learning. Although social information may be relatively cheap to acquire, it can also be less reliable than personal information (Danchin et al. 2004, Kendal et al. 2004, Rieucau & Giraldeau 2009, 2011).

Danchin et al. (2004) makes a distinction between Social information, which can provide information about the location of resources a la local enhancement or social attraction, and public information, which can inform quantitatively about patch quality. Public information is used in many of the same ways as social information including in foraging, habitat selection, mate choice, eavesdropping, and predator avoidance. Public information can also spread cultural evolution as seen in birds, cetaceans, and fish (Danchin et al. 2004). Through social learning animals can learn how to deal with a resource (observational learning) or where it's located (local enhancement), this process of social learning can be enhanced through conformity (Kendal et al. 2004). It is theorized and modeled that socially acquired and personally acquired prior information should not be used interchangeably. If there is little cost associated with social information, prior information can interfere with social learning but if there is a cost then prior information can be discounted in favor of social information (Kendal et al. 2004). It has been shown that many animals can consider both asocial and social information when making decisions. There is a lack of evidence for the frequency dependence of social information use, as in the producer-scrounger model. Animals appear to use social information cautiously using it preferentially when asocial information is costly, the forager is naïve, or social information outweighs asocial information (Rieucau and Giraldeau 2011). Classical conditioning provides a powerful tool for studying learning, memory, and emotion. However, studies employing this technique need to be able to distinguish between learning and performance and understand that context is important in accurate memory retrieval (Bouton and Moody 2004).

V. Adaptive Forgetting

Learning can be costly and acquiring social information may be less reliable (Boyd & Richerson 1985, Zentall & Galef 2013) so foragers should be able to remember the location of a rewarding patch when one is found. However, there is an energetic cost to memory so you do not want to remember everything (McNamara & Houston 1987) and due to environmental variability and the ephemeral nature of floral resources it may not be advantageous to remember indefinitely (Dunlap et al. 2009). Therefore, pollinators should remember for an optimally finite amount of time, and it is optimal to only remember useful or valuable information. Information can be considered useful or valuable if it is recalled frequently and thus more likely to be retained (Kraemer & Golding 1997). It has been suggested and modeled that an organism’s memory should reflect their natural history and be shaped by the environment in which they evolved (Anderson & Schooler 1991, Dunlap et al. 2006, Dunlap et al. 2009). For pollinators this means they should ideally remember rewarding flower patches for as long as those flowers produce nectar and pollen (Anderson & Schooler 1991, Carter 2004, Dunlap et al. 2009, Dunlap & Stephens 2012, Kraemer & Golding 1997).

Despite the view that memory is anything but optimal, when considering the patterns of past information presentation in the environment and modeling using a power function, memory does behave close to optimally (Anderson and Schooler 1991). In their review Rosenzweig (2002) explored some of the mechanisms behind long-term potentiation, a process in which memories are stored over time (Bliss and Lomo 1973), and long-term depression, a probable mechanism for the removal of old memories (Lynch et al. 1977). Retrieval-induced forgetting is the consequence of an adaptive mechanism that facilitates remembering by causing forgetting. Indeed, the ability to forget, under certain circumstances appears to reflect the adaptive functioning of memory, not its failure (Storm 2011). Hardt et al. (2013) agreed that forgetting is essential to maintain overall system functionality and demonstrated the beneficial effects of sleep on memory retention in taxa as widespread as honey bees, rats, and humans may reflect net benefit of the processes that eliminate memories and processes that strengthen them. Recent experiments in the fruit fly *Drosophila melanogaster* show that forgetting rate is biochemically adaptive to the environment. Optimal behavior in a stochastically changing environment requires a forgetting rate that is adapted to the time constraints of the changes. These aspects suggest viewing forgetting as a dimension of adaptive behavior that is tuned to the environment to maximize subjective benefits (Brea et al. 2014).

VI. Bumblebees, Information, and Memory

i. How bumblebees learn.

Bumblebees, as well as other hymenoptera, can use both personal and social information when making foraging decisions. Pioneering work by Worden and Papaj (2005) found that bumblebees follow the foraging decisions of non-nest mates or even model bees. Bumblebees can also change their flower choices by observations of non-nest mates. Fast learning bees are also fast to reverse that association. This suggests there is not a tradeoff between learning speed and behavioral flexibility. Differences at the colony level in learning performance and flexibility could reflect more general differences in colony cognitive ability (Raine & Chittka 2012). Bees begin to learn quicker in the presence of experienced conspecifics but the learning process is no quicker when bees forage alone versus with experienced foragers, suggesting that the time it takes to learn a foraging task is the same in the presence or absence of social cues (Leadbeater & Chittka 2007).

ii. Social learning and social information.

Naïve foragers show a preference for occupied flowers, and this preference is a flexible trait that can be positively reinforced through conditioning (Leadbeater and Chittka 2009). Jones et al. (2014) demonstrated a clear interaction between personal information, social information, and innate bias when bumblebees make foraging decisions. They determined social information is used more when personal information is lacking (i.e. they are naïve), when their experience is with flowers with a low quality reward, and when social information directs them toward their innate bias. Social information is not attuned to when prior experience is with high quality resource (Jones et al. 2014). Baude et al. (2010) experimentally manipulated the demonstrator's density and the floral community complexity for foraging bumblebees and found flexibility in the way social information benefits foragers depending on the complexity of the environment. Spatio-temporal scales of decision making appear to determine their response to conspecifics (Baude et al. 2010). Simple positive and negative reinforcement serves as a credible mechanism to promote or adapt this behavior in a foraging context (Leadbeater and Chittka 2009).

iii. Bees and reliability.

Dunlap et al. (2016) found that nectar foraging bumblebees show a preference for social information over personal information when social information is more reliable or equally reliable as personal information. Bumblebee foragers may use a "copy-when-uncertain" strategy for using social information which is adaptive when foragers are naïve and resources are patchily distributed, although this could also be true for experienced foragers (Smolla et al. 2016). Smolla et al. (2016) also experimentally found that non-social cues were learned as readily as social cues but were not attenuated to during testing and that socially salient cues are the most efficient at learning tasks. Leadbeater and Chittka (2009) found that when conspecifics reliably predict reward; foragers prefer flowers with conspecifics significantly to naïve foragers, to solo foragers, or to foragers that learned conspecifics do not predict reward. This joining behavior in bees is a flexible trait that can be reinforced through conditioning and adapted to local circumstances (Leadbeater and Chittka 2009).

CHAPTER 2

Forgetting and the Value of Social information

Introduction

How animals know when to use information and when to ignore information has been studied by ethologists for decades (Dall et al. 2005). Pollinators may have to live in a foraging environment that can vary in many ways. Flowers can be an ephemeral resource varying in combination and reward based on phenology. In addition, flowers replenish their nectar rewards at different rates and some flowers even alter the quality of their nectar rewards over time (Thomson et al. 1989, Willmer 2011). Variability in reward can decrease the value of information as time from information acquisition increases (Koops 2004, McLinn& Stephens 2006, Stephens 1989). Learning about rewards and flower quality is essentially a way for foragers to predict which flowers will be the most rewarding before they arrive. However, to effectively learn, the information should be reliable to some degree. Reliability can be defined as the conditional probability that a signal or cue indicates a specific and known state (Dunlap & Stephens 2009, 2012). However, determining whether information is valuable requires more than just reliability (Gould 1974, Koops 2004, Dall et al. 2005). Information may be reliable, but also costly to acquire. Information is said to be costly when acquiring or learning the information incurs an energetic expense or increases the risk of predation.

One way some animals can decrease the cost of acquiring information is to use social information (Krebs & Inman 1992, Danchin et al. 2004), as this allows the observer to learn where food is without having to sample each flower. This type of information is gained through observation of conspecifics or heterospecifics. A variety of information can be acquired socially, including what food resources are rewarding or unrewarding and the presence of danger. Even though social information may be relatively cheap to acquire, it can also be less reliable than personal information because resources may be depleted and alarm calls can be false (Danchin et al. 2004, Kendal et al. 2004, Rieucau & Giraldeau 2009, 2011).

Foragers should be able to remember rewarding resources when they are found. However, there is an energetic cost to memory so pollinators should not remember everything (McNamara & Houston 1987). Due to environmental variability and the ephemeral nature of floral resources it may not be advantageous to remember indefinitely (Dunlap et al. 2009). Therefore, pollinators should remember for an optimally finite amount of time, and it is optimal to only remember useful or valuable information. Information can be considered useful or valuable if it is recalled frequently and thus more likely to be retained (Kraemer & Golding 1997).

It has been suggested and modeled that an organism’s memory should reflect their natural history and be shaped by the environment in which they evolved (Anderson & Schooler 1991, Dunlap et al. 2006, Dunlap et al. 2009). For pollinators, this means they should ideally remember flower patches if those flowers produce nectar and pollen (Anderson & Schooler 1991, Carter 2004, Dunlap et al. 2009, Dunlap & Stephens 2012, Kraemer & Golding 1997). So memory should be tied to the value of information. Both theory and experiments show that low reliability of information means lower value for that information (Koops 2004, McNamara & Houston 1987). Memory is a good test of the value of information. More valuable information is retained longer, and information that is costlier to acquire is also retained longer. The more important information is to survival the longer it tends to last (Hirvonen et al. 1999). When change increases, memory becomes shorter and as conditions worsen older memories become extinct (Dunlap et al. 2009, Plaçais & Preat. 2013). Social information should be more valuable when foragers are naïve or when the forager is uncertain, possibly due to environmental variability (Kendal et al. 2004, Krebs & Inman 1992). Many theoretical papers have weighed social information against personal information, however direct comparisons are few and none incorporate memory (Danchin et al. 2004, Kendal et al. 2004, Krebs & Inman 1992).

I will test the hypotheses that the presence of conspecifics affects the learning rate of *Bombus impatiens*, and *B. impatiens* forget personal and social information at the same rate. We currently do not know how bumblebees weigh social or personal information in their memory. It could be that one type of information is forgotten faster than the other, or that different types of information are forgotten at the same rate. Discovering how bees forget different types of information can give us insights into which type of information bees find more valuable over time. There is theory to support either personal information or social information being valued more. I believe the value of information is dependent on the amount of environmental variability and the experience of the individual forager. The more variable the environment and the more naïve the forager the more value may be placed on social information. Many more experiments will be necessary to truly elucidate exactly under what contexts different types of information are valued more. This project is a first step toward answering that question.

Methods

Overview

The experiment was set up as a 2X3 factorial with two different levels of environmental reliability and three different retention intervals. The cue was a single artificial flower color or the presence of a conspecific. The non-cue was a different artificial flower color or the absence of a conspecific. Either floral information was entirely reliable and social information was unreliable (all of one artificial flower color was rewarded with sucrose) or floral information was unreliable and social information entirely reliable (only artificial flowers with conspecifics were rewarded with sucrose). The cue was always 100% reliable, while the non-cue was always unreliable (i.e. 50% rewarding and thus random). The retention of information gained after experience with these two different reliabilities was then tested after retention intervals of 4, 8, or 24 hours. 8 blocks of data were collected; each block contains an n=6 (one bee for each environmental reliability at each of the different retention intervals).

Husbandry

The experimental subjects were captive *Bombus impatiens* purchased from Koppert biological systems, and supplied from Howell Michigan, USA. *B. impatiens* is a readily available native pollinator species commonly used as test subjects for bumblebee cognition experiments. Multiple colonies were used throughout the course of the experiment. Each colony was housed in a 20.5cm X 22.5cm X 10cm tall box with a Plexiglas lid. A thin layer of pine cat litter lined the bottom of the hive box to absorb moisture from the colony. We fed the colony a 20% sucrose solution. Ground fresh pollen, also supplied through Koppert, was delivered to the colony by depositing approximately one tablespoon directly onto the hive. The colonies had a fourteen-hour photoperiod (14L:10D), consistent with the middle of summer in their natural range. Foraging bees were marked with numbered honeybee queen marking tags, fixed with superglue to the dorsal side of the subject’s thorax, between the wings. These tags did not hinder the bee’s movements or activities.

Experimental Setup

All artificial flowers used for pre-training, training, and testing were constructed from craft foam cut into 45mm discs and glued to floral picks. The bottom ~.2ml of a micro centrifuge tube were inserted into the artificial flower as a reservoir and sat flush with the top surface of the artificial flower (figure 1 & 2). During testing and training the arena contained 12 artificial flowers spaced equidistant from each other (figure 3). Two different artificial flower colors were used and half of the artificial flowers had desiccated foragers from other colonies pinned to them, these pinned bumblebees serve as social information and are hereafter referred to as “demonstrators”. The equidistant artificial flower array contained four different artificial flowers: orange without demonstrators, orange with demonstrators, yellow without demonstrators, and yellow with demonstrators. There were three of each artificial flower type in the array. The artificial flowers were arranged semi-randomly and rewarded per the reliability treatment; i.e. either one artificial flower color is rewarded with sucrose, and the other color is unrewarded (contains plain water) (personal information), or only artificial flowers with demonstrators are rewarded with sucrose, and artificial flowers without demonstrators contain plain water (social information). Semi-random order was achieved by first arranging the artificial flowers according to a random number generator, then manually breaking up any groups of four or more similar artificial flowers as needed.

Experimental Procedure

I employed methods that have been used to test the use of social and personal information in bumblebees for a decade (Chittka & Leadbeater 2005, Leadbeater & Chittka 2005, Leadbeater & Chittka 2007, Worden & Papaj 2005). This experiment included three phases: pre-training, training, and testing.

Pre-training

During the pre-training phase, blue or white artificial flowers filled with a 50% sucrose solution were placed in the foraging arena and refilled throughout the day. Blue and white artificial flowers were used in this phase to allow the foraging bees to learn how to use the artificial flowers while preventing them from learning about the color of artificial flowers they experienced in the training and testing phases. Experimental subjects were determined by identifying foragers that repeatedly visited the blue or white artificial flowers in the foraging arena and return to the colony to deposit sucrose.

Training

Experimental subjects were then trained on one of the two reliability treatments by being allowed to forage freely and individually in the foraging arena. During this phase either one artificial flower color was rewarded (personal information) or only flowers with demonstrators were rewarded (social information). Rewarded flowers contained 10µl 50% sucrose solution, unrewarded flowers contained 10µl plain water. I allowed the subject to make as many foraging trips as necessary to reach 80% success, defined as making 16 of the last 20 landings on rewarding artificial flowers. Landings were counted only if the subject attempted to forage from the flower. I then allowed the subjects to return to the hive until the retention interval passed.

Testing

Each bee was tested after one retention interval. During testing the subject were allowed back into the foraging arena where they were presented with a totally unrewarded foraging array and had their first 10 landings recorded. After 10 landings, the subjects were freeze killed. Thorax measurements of all subjects were taken postmortem for analysis as Spaethe & Weidenmuller (2002) found a significant positive correlation between forager size and foraging rate in bumblebees. Forager size may, therefore, be an important covariate in foraging tasks.

Analysis

Behavioral observations

We video recorded both training and testing sessions to analyze time until acquisition of information and number of trials to criterion (80% successful foraging choices) during training; these were determined using video analysis of time spent between artificial flowers, time spent on each artificial flower, and number of foraging choices before criterion is met (Mackintosh, 1974). During both training and testing a foraging attempt was defined as a bee landing on an artificial flower and inserting its head into the nectar well in the flower. Alternatively, if observed, a proboscis extension response into the nectar well in the artificial flower counted as a foraging attempt. Events where the bee landed but did not extend its proboscis or insert its head into the well were not recorded. Video analysis was performed by B.A. as well as undergraduate and high school volunteers. Videos of the training and testing were viewed and the time (to the second) was recorded each time the subject attempted to forage (insertion of head into well or extension of proboscis) and then again when the subject departed the artificial flower. Whether the choice was correct or incorrect was also recorded.

Statistical analysis

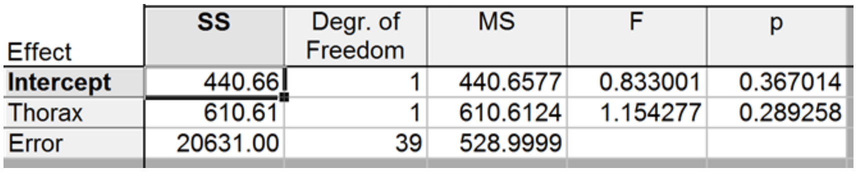
Several statistical methods were used, these varied to accommodate the differences in data analyzed. Linear regression was used to determine the extent to which forager thorax size is correlated with learning speed. We used t-tests to determine the effect of treatment on learning speed. We analyzed percent correct choices during the learning phase by breaking each bee’s trials to criterion into quartiles and performed an analysis of variance (ANOVA) between quartile and treatment. This allowed us to see if there is any difference in the percent correct choices during each quartile of the learning phase. Repeated measures ANOVA was also used to determine the effect treatment had on first five and last five choices during training. We calculated the percentage correct of the first five landings in the memory test and then used an Analysis of Covariance (ANCOVA) to see how the factors of reliability (social or floral) and retention interval (4, 8, or 24 hours) affect performance. A univariate test was performed to look for the effect of treatment and retention interval on errors toward social information.

Results

TRAINING RESULTS

We did a linear regression of thorax size by trials to criterion and found no correlation between thorax size and learning speed (R^2=0.0287, F =1.1542, p =0.2892) (Figure 4).

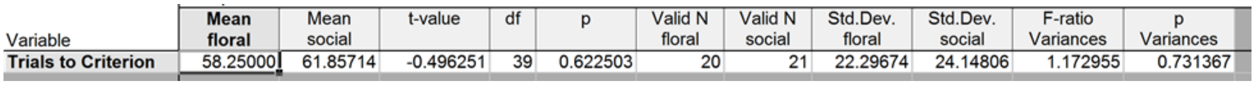
Table 1 Univariate Tests of Significance for Trials to Criterion. Sigma-restricted parameterization. (Thorax size against Trials to Criterion)



Effect	SS	Degr. of Freedom	MS	F	p
Intercept	440.66	1	440.6577	0.833001	0.367014
Thorax	610.61	1	610.6124	1.154277	0.289258
Error	20631.00	39	528.9999		

Finding no relationship between thorax sizes and learning speed, we next looked at the effect of the social cue on learning speed (Fig. 5). Using a t-test we found there is no effect of treatment on learning speed (t= -0.4962, p =0.6225).

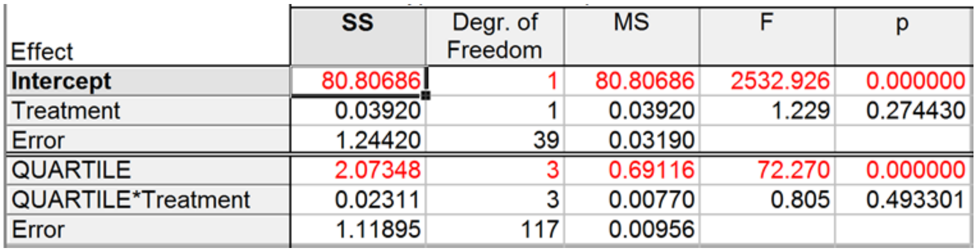
Table 2. T-test; Group 1: floral cue Group 2: social cue. Variable: Trials to Criterion



Variable	**Mean floral**	Mean social	t-value	df	p	Valid N floral	Valid N social	Std.Dev. floral	Std.Dev. social	F-ratio Variances	p Variances
Trials to Criterion	58.25000	61.85714	-0.496251	39	0.622503	20	21	22.29674	24.14806	1.172955	0.731367

With no relationship between treatment and learning speed we wanted to take a more detailed look at training by dividing each bees training session into quartiles based on number of choices made (Fig. 6). We found no correlation between training quartile and treatment (F =0.805, p =0.4933).

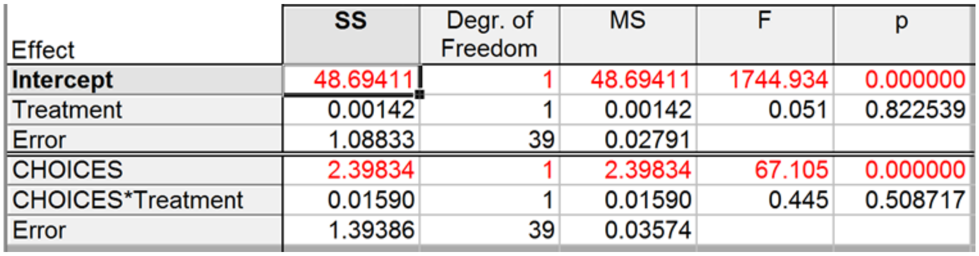
Table 3.Repeated measures ANOVA. Sigma-restricted parameterization (Effect of treatment on learning speed blocked by quartile)



Effect	SS	Degr. of Freedom	MS	F	p
Intercept	80.80686	1	80.80686	2532.926	0.000000
Treatment	0.03920	1	0.03920	1.229	0.274430
Error	1.24420	39	0.03190		
QUARTILE	2.07348	3	0.69116	72.270	0.000000
QUARTILE*Treatment	0.02311	3	0.00770	0.805	0.493301
Error	1.11895	117	0.00956		

Having found no difference in the shape of learning between treatments we looked at the accuracy of the first and last five choices made during the training phase (Fig.7). Although we might expect an interaction between choices and treatment we do not find one (repeated measures ANOVA F =0.445, p =0.5087).

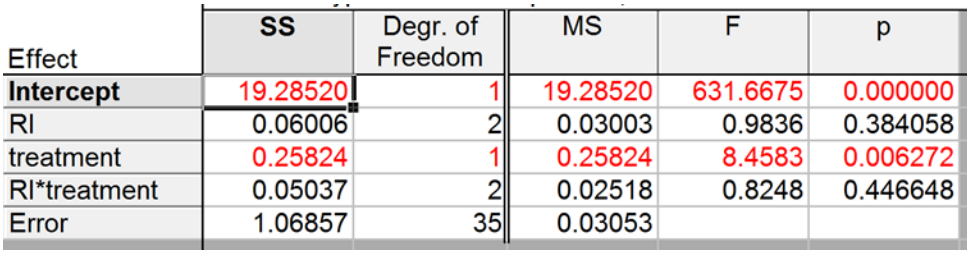
Table 4. Repeated measures ANOVA. Sigma-restricted parameterization. (Effect of treatment on first five and last five flower choices during training)



Effect	SS	Degr. of Freedom	MS	F	p
Intercept	48.69411	1	48.69411	1744.934	0.000000
Treatment	0.00142	1	0.00142	0.051	0.822539
Error	1.08833	39	0.02791		
CHOICES	2.39834	1	2.39834	67.105	0.000000
CHOICES*Treatment	0.01590	1	0.01590	0.445	0.508717
Error	1.39386	39	0.03574		

Determining no difference in learning rate between treatments we wanted to look for differences in how information is forgotten. We found significant differences in the correct choices between treatments with social information being retained better than personal information (univariate test; F =8.4583, p =0.0063) but not among retention intervals (univariate test; F =0.9836, p =0.3840)(Fig 8).

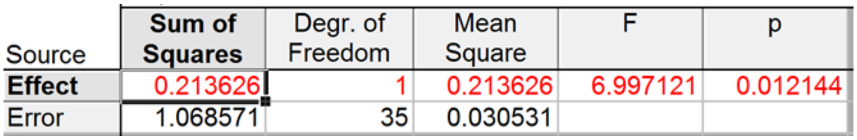
Table 5. Univariate test of significance for first five choices after retention interval. Sigma-restricted parameterization. (Effect of treatment and retention interval on correctness of first five foraging decisions post retention interval)



Effect	SS	Degr. of Freedom	MS	F	p
Intercept	19.28520	1	19.28520	631.6675	0.000000
RI	0.06006	2	0.03003	0.9836	0.384058
treatment	0.25824	1	0.25824	8.4583	0.006272
RI*treatment	0.05037	2	0.02518	0.8248	0.446648
Error	1.06857	35	0.03053		

When we looked at just the 4-hour retention interval though we found it does interact significantly with treatment and performance (univariate test; F =6.9971, p =0.0121).

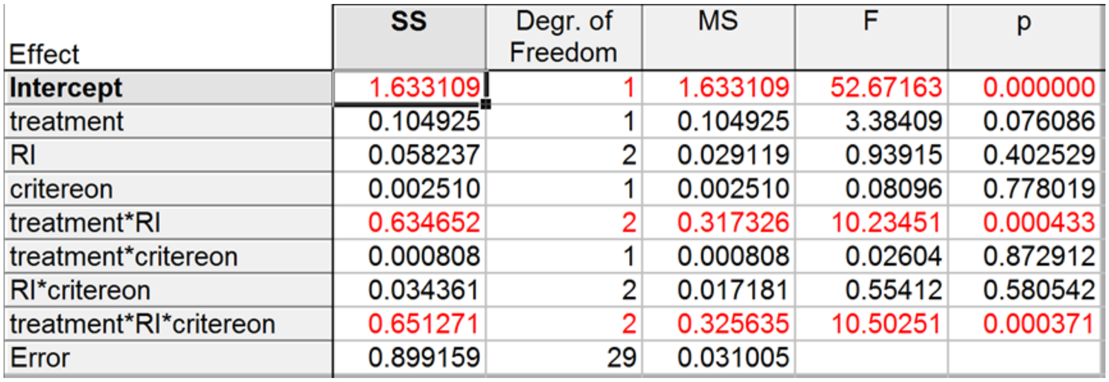
Table 6. Univariate testing of significance. (Effect of treatment and only the four-hour retention interval on correctness of first five foraging decisions post retention interval)



Source	Sum of Squares	Degr. of Freedom	Mean Square	F	p
Effect	0.213626	1	0.213626	6.997121	0.012144
Error	1.068571	35	0.030531		

We next analyzed their choices in terms of whether bees are matching the social cue (Fig. 9). Here we see a non-significant difference between the two training treatments (univariate test; F =3.3841, p =0.0761), and it interacts significantly with retention interval (univariate test; F =10.2345, p =0.0004). In short retention intervals, bees are choosing what they are trained with, but if we look at how that deviates from chance, the effect is stronger for training to social cues.

Table 7. Univariate tests of significance for first five social. Sigma-restricted parameterization. (Effect of treatment and retention interval on errors toward social information)



Effect	SS	Degr. of Freedom	MS	F	p
Intercept	1.633109	1	1.633109	52.67163	0.000000
treatment	0.104925	1	0.104925	3.38409	0.076086
RI	0.058237	2	0.029119	0.93915	0.402529
critereon	0.002510	1	0.002510	0.08096	0.778019
treatment*RI	0.634652	2	0.317326	10.23451	0.000433
treatment*critereon	0.000808	1	0.000808	0.02604	0.872912
RI*critereon	0.034361	2	0.017181	0.55412	0.580542
treatment*RI*critereon	0.651271	2	0.325635	10.50251	0.000371
Error	0.899159	29	0.031005		

Discussion

This study presents a novel method for experimentally testing the value of information. The use of memory as a measure of value of information has, to the authors knowledge, never been published. Our study had two main questions: does the presence of demonstrators affect the learning rate of *Bombus impatiens*, and do *B. impatiens* forget personal and social information at the same rate? Before we addressed our aims we first wanted to address a question about body image. Some studies have shown a strong effect of bumblebee worker body size on foraging performance, with larger foragers gathering more nectar than their smaller coworkers(Spaethe & Weidenmuller 2002). We looked at how the width of subjects' thorax correlates with their trials to criterion, or learning speed (Fig. 4). We found no correlation between thorax width and learning speed. This agrees with Chittka and Niven (2009) who suggested intelligence and cognitive ability is not related to brain size. We then addressed our first aim: does the presence of demonstrators affect learning rate. Previous work suggests that foraging bumblebees should learn social information and personal information at similar rates (Leadbeater & Chittka 2007). Our results support this as we found no statistically significant difference in the trials to criterion between bees that learned from personal information and bees that learned from social information (Fig. 5). This contrasts with previous findings that suggest that learning begins earlier in the presence of conspecifics (Leadbeater & Chittka 2007), however, the present study differs from those other studies in a big way. Previous experiments that have shown bees learn faster from social information did not have complicating floral cues, what that means is unlike my experiment where the reliable cue is 100% rewarding and the unreliable cue is rewarded 50% or random, all previous studies had one cue 100% rewarding while the other is 0% rewarding. There is a real cognitive difference between learning about a world that is either 100% or 0% rewarded and leaning about a world that is either 100% or 50% rewarded. We believe the latter more closely represents natural foraging conditions experienced by pollinators.

In addition to no difference in the trials to criterion, we also found no difference in the overall shape of learning (Fig. 6), that is, there is no difference in learning rate between the treatments over the course of training. The literature on social information use in bees and local enhancement would suggest that all bees may be attracted to the presence of other bees but that bias should be erased with experience. We looked at the first and last five choices during training to get an idea of how attraction to conspecifics might affect choices at the beginning and end of training (Fig. 7). While bees' attraction to forage on flowers with conspecifics can be seen non-significantly in their first five choices, learning is clearly occurring; local enhancement does not explain their final choices (Fig. 7). Similarly, there is no difference between how many choices are required to learn that social cues or floral cues are rewarding (Fig. 5).

Having found no difference in learning rate between personally and socially acquired information, we'd like to address our second aim: are personal and social information forgotten at the same rate?

After four hours, social information is retained at a higher rate than personal information, which does not differ from chance. However, that preference for social information decreases, with no difference after 24 hours (fig. 8). We were most surprised by the poor performance of the subjects in the personal information treatment. We wanted to see if their poor retention could be explained by an attraction toward conspecifics. We analyzed the memory choices in terms of going toward social information (Fig. 9). Figure 9 shows that the bees trained to learn from personal information are not going toward social information at any retention interval. This is what we expect to see if those bees are ignoring the presence of demonstrators.

In our experiment bee trained to use the presence of conspecifics as an indicator of reward retained that information significantly better than chance after four and eight hours, only being non-significantly different from chance after 24 hours. This is significantly better than bees trained to use personally acquired information, which did not do better than chance after even four hours. When we looked to see if this could be explained by errors toward social information we found it could not. This means bees trained to use personal information were not remembering what they had recently learned and were not following the foraging choices of others. This finding is contrary to what behaviorists may expect. The poor foraging retention of bees trained to personal information could be more easily explained by the variability of the environment they experienced than by a general lack of memory. The switch from pretraining array to training array back to pretraining or other feeder then to the testing array may be too much variation for a bee to experience in 4-24 hours. When that amount of change is paired with a training phase where the presence of conspecifics is an unreliable cue then random may be the most efficient choice. This would account for the apparent absence of memory of personally acquired information, which is in contrast to some studies. This also allows that both personally acquired and socially acquired information to be learned at the same rate, as we found.

In summary, we present a novel method for testing the value of information, using memory as a proxy for value. Our findings support previous work suggesting that there is not a difference in information acquired socially and information acquired through trial and error learning. We have novelly shown that socially acquired information is retained better than personally acquired information after up to 8 hours. We have also shown that personally acquired information may be forgotten as quickly as 4 hours after information acquisition. Although this last finding may be connected to the methodologies used and the subsequent environmental variability our subjects may have experienced. Our results provide new information about the value of social information in a variable environment and the importance of context in foraging decision making.

Future directions

One of the biggest questions to come from this research is how can we be sure that foraging bees are treating the social cues as social information and not simply a form of floral complexity. Several studies since Worden and Papaj (2005) have used bumblebee models as a proxy for social information. Leadbeater and Chittka (2007) compared bumblebees learning from model bees or learning from "complex" flowers. They found that model bees were a more salient cue than floral complexity. These studies did not account for the 3D structure of the models versus the 2D structure of the flowers or directly compare the retention of this information. A second experiment is underway to elucidate what aspects of our demonstrator bees are salient to the foragers. Similar methods to the experiment presented in this paper will be used, individual bumblebee foragers are trained in a foraging array to attend to augmented flowers over non-augmented flowers. Once the forager has reached 80% correct choices they are returned to the colony until a 4-hour retention interval has passed. They are then tested on the same array and their first 10 choices are recorded. This data will be analyzed to determine if there are retention differences between a desiccated bee pinned to the flower and other types of 2D and 3D floral complexity.

Acknowledgments

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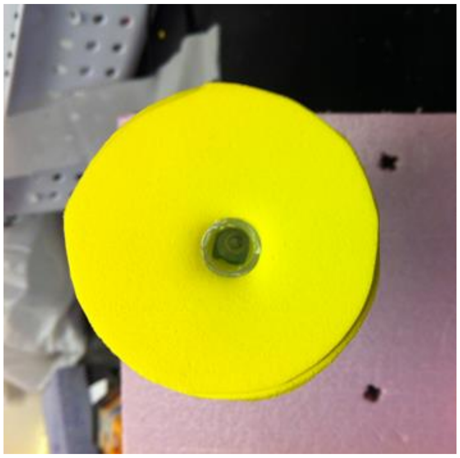
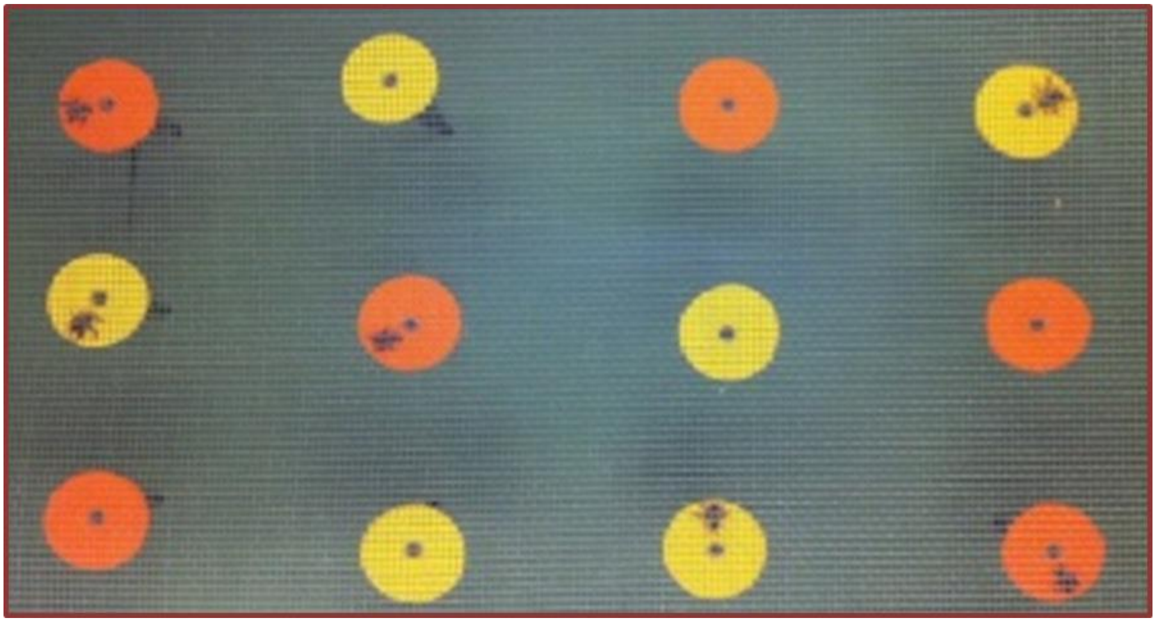
Figures

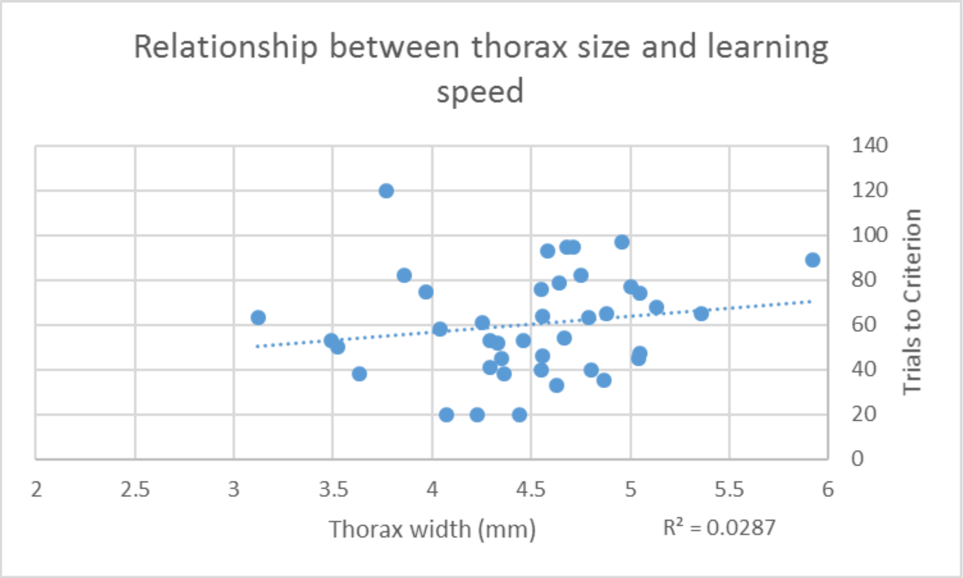


(Figure 1. Artificial flower- top view)

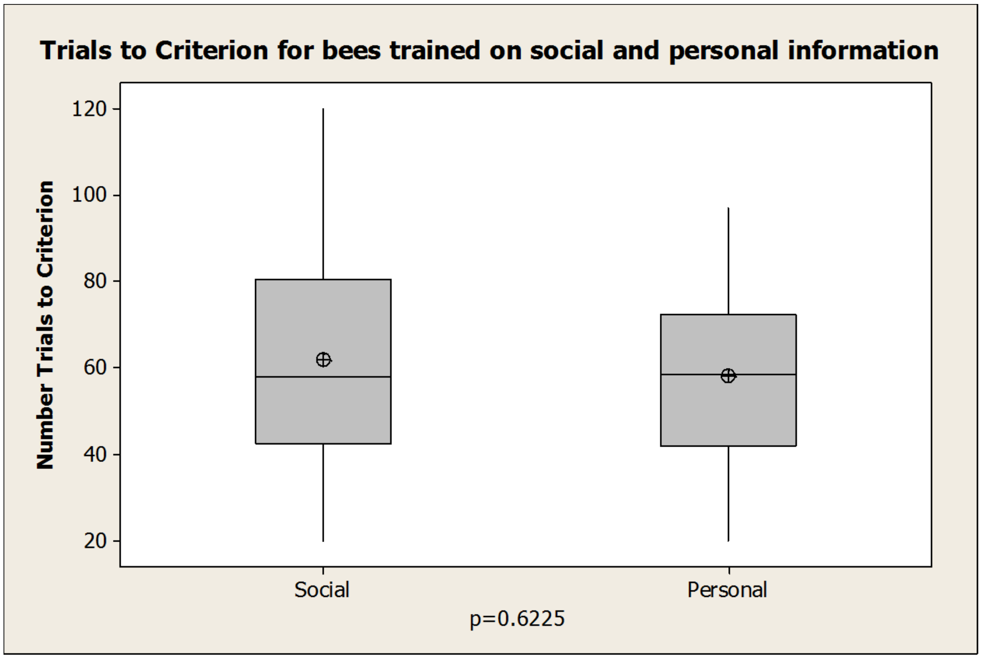
(Figure 2. Artificial flower- side view)



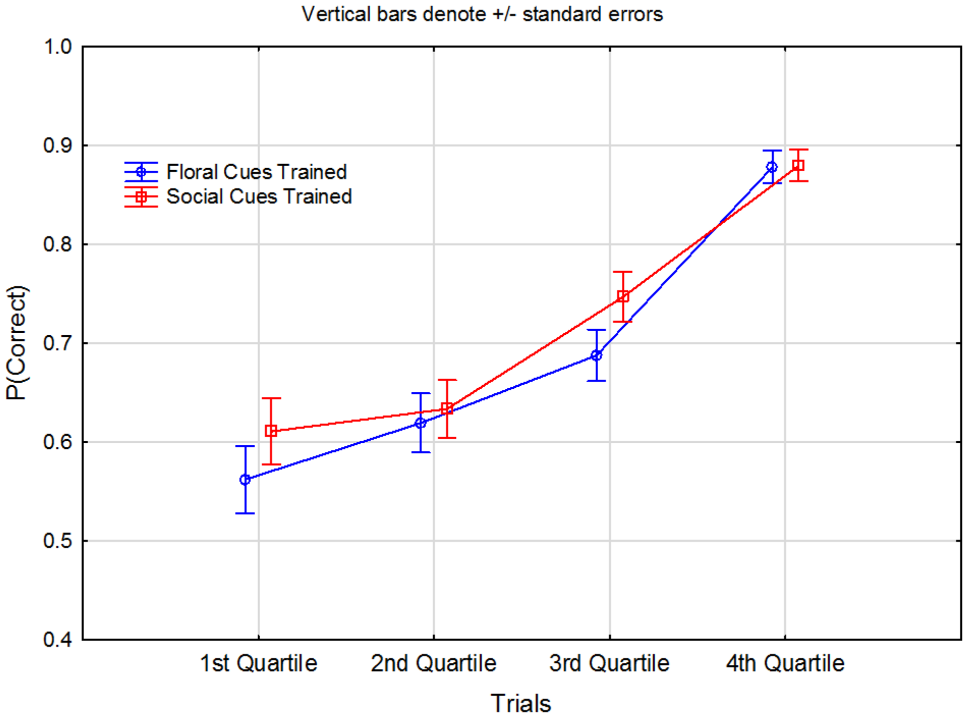
(Figure 3. Training/testing example array in place.)



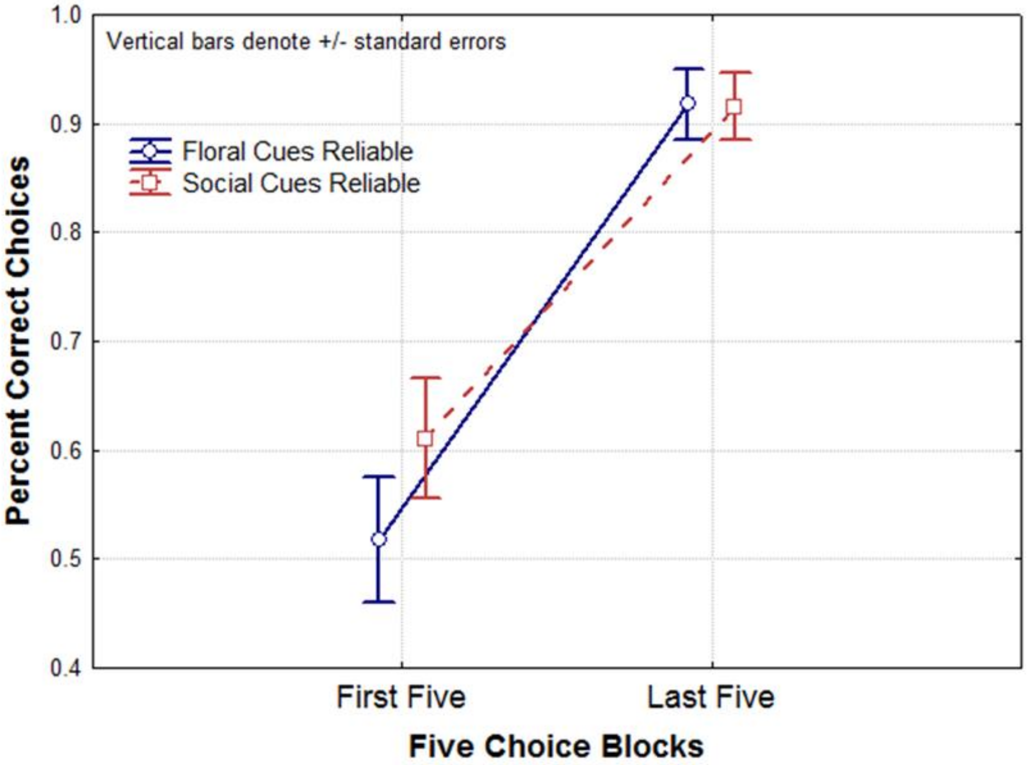
(Figure 4. Thorax size plotted against number of foraging decisions made before criterion. R^2= 0.0287F =1.1542, p =0.2892 . Thorax width in mm is on the X axis and the number of foraging trials before learning criterion was met is on the Y axis. The absence of a strong relationship between forager size and learning speed is exemplified by the low R^2).



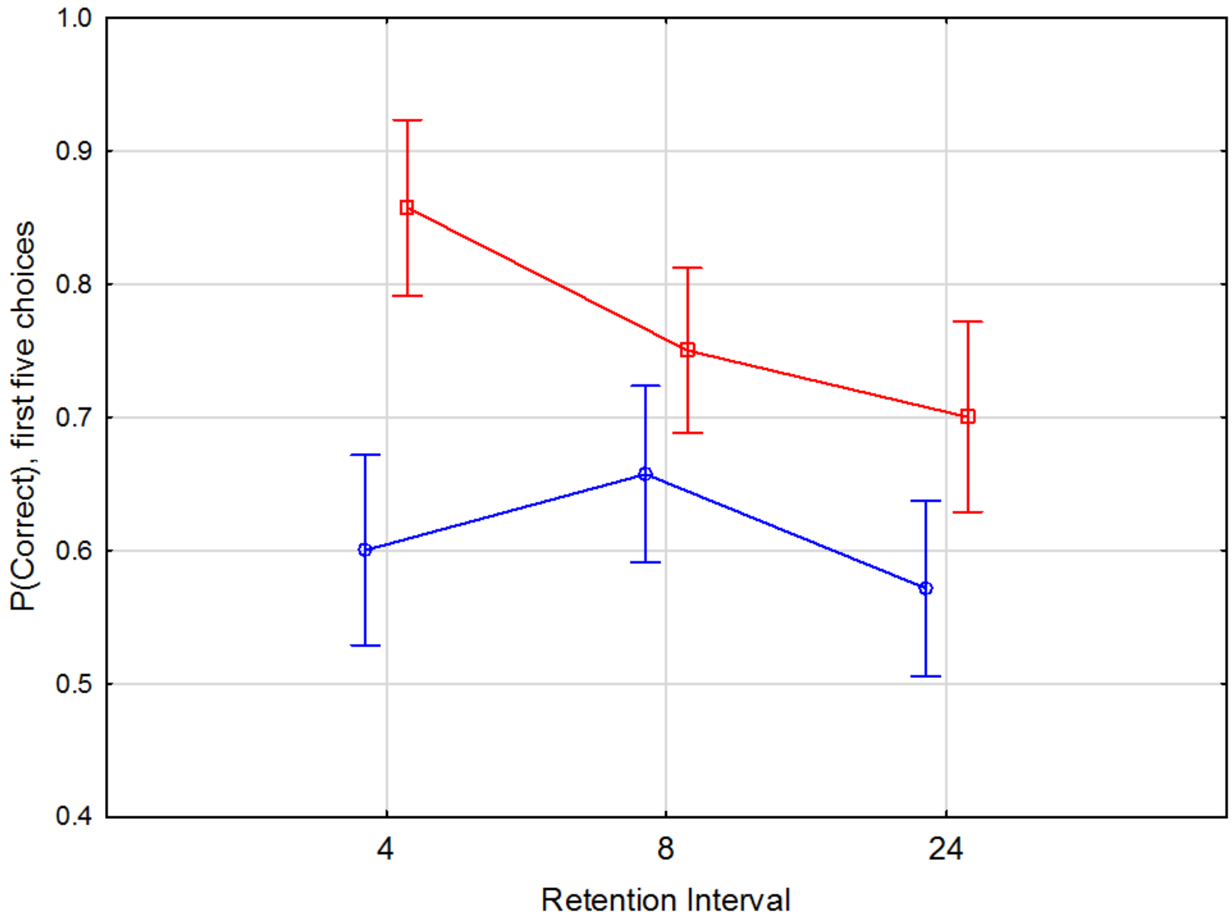
(Figure 5.Average number of trials to criterion for each treatment. p =0.6225. Number of foraging decisions before learning criterion was met is on the Y axis and learning treatment, either floral cue or social cue, is on the X axis. This shows that bees learned the social cue faster, although not significantly t_{35}=11.06, p=0.296).



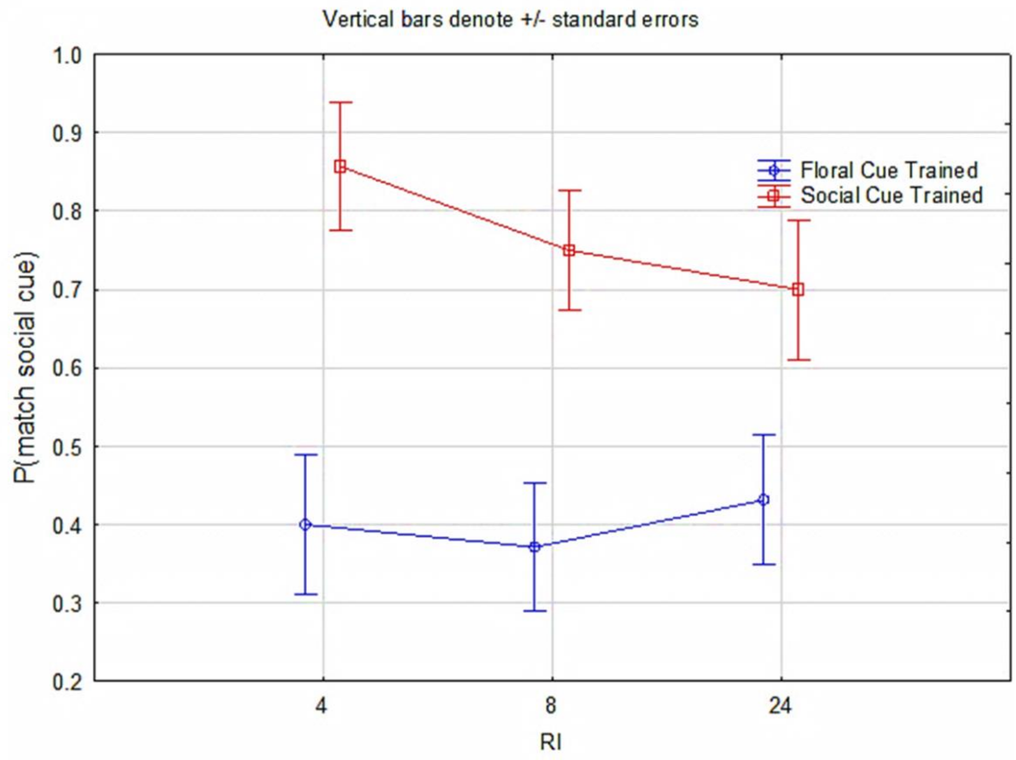
(Figure 6. Percent correct choices during training blocked by quartile. Repeated measures ANOVA F =0.805, p =0.4933 Percent correct foraging decisions during training is on the Y axis and training phase divided into quartiles is on the X axis. This shows there is no significant difference in the speed of learning for bees trained on floral cues versus bees trained on social cues.)



(Figure 7. Percent correct first five and last five choices during training. Repeated measures ANOVA F =0.445, p =0.5087 Percent correct foraging decisions during training is on the Y axis and first five and last five choices are on the X axis. Bees trained to use personal information are represented by the blue circles. Bees trained to use social information are represented by the red squares. This shows there is no significant difference between treatments and bees in both treatments are learning.)



(Figure 8. Percent correct choices after retention interval. Bees trained on social cues are represented in red. Bees trained on floral cues are represented in blue. `ANCOVA F =8.4583, p =0.0063.` *Just the 4-hour retention interval: ANCOVA F =6.9971, p =0.0121. Percent correct of the first five foraging decisions in the testing phase is on the Y axis, Retention interval, 4 hours, 8 hours, 24 hours later, is on the X axis. Floral cues trained are in blue, Social cues trained are in red. This shows the significant difference [p=0.0063]in retention between bees trained to social cues and bees trained to floral cues. This difference is non-significant when retention interval is used as a covariate [p=.4466] but when just the 4 hour RI is considered we do get significance [p=0.0121])*



(Figure 9. Percent choices matching the social cue. Bees trained on social cues are represented by red squares. Bees trained on floral cues are represented by blue circles. ANOVA F=28.8350, p<0.0001. This shows that bees trained to the floral cue did not deviate from chance regarding the social cue (T-test: 4 hour RI- p=0.3144, T=1.118. 8 hour RI- p=0.345, T=1.0247. 24 hour RI- p=0.8968, T=0.1353). This is what we expect to see if the bees trained to the floral cue are ignoring the demonstrators.

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