Spatial Cognition from comparative, computational, and developmental perspectives

By

Anna Stokhammer Waisman

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Psychology

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Lucia F. Jacobs, Chair
Professor Alison Gopnik
Professor Tom Griffiths
Professor John Campbell

Fall 2010

Copyright

Abstract

Spatial Cognition from comparative, computational, and developmental perspectives

by

Anna Stokhammer Waisman

Doctor of Philosophy in Psychology

University of California, Berkeley

Professor Lucia F. Jacobs, Chair

Spatial memory is critical to the survival of all mobile animals. Using spatial memory animals find and keep valuable resources such as shelter, food and companionship. In a series of three studies, I explored spatial strategies and the use of multiple landmarks from comparative, computational and developmental perspectives.

In the first study, I examined the spatial strategies and landmark use of a diurnal mammalian species, the fox squirrel, *Sciurus niger*. Free-ranging fox squirrels showed a large degree of flexibility both in their use of landmarks and in their use of spatial strategies. Furthermore, their use of landmarks appeared to be sensitive both to changes in the test apparatus and the season in which they were tested. In the second study, I further explored fox squirrel spatial strategies from a computational modeling perspective. Given the squirrels' use of the majority strategy, we specifically investigated the suitability of using a Bayesian model to characterize the squirrels' spatial decisions. The resulting model provides a unifying framework for illustrating different strategies of landmark integration, and a tool for investigating the circumstances under which particular landmarks are used. I show that the best fitting models changed depending on the season at testing and the details of the task. These analyses support my previous claims that squirrels adopt flexible strategies in landmark use.

In the third study, I investigated whether human children develop similar flexible spatial strategies as the fox squirrels and what types of allocentric landmarks they might be using to construct such spatial strategies. In particular, we were interested in the initial development of

such strategies when children first begin to use non-coincident, allocentric landmarks. Thus, all studies were conducted using 3 and 4 year old children since it is at this age that children begin to robustly use non-coincident, allocentric landmarks. I found that 3 year old children rely on a less flexible, hierarchical strategy based on their preferred landmark, but that by four years of age they begin to develop more flexible spatial strategies, similar to those of adult free-ranging fox squirrels.

In sum, both behavioral data and the results of Bayesian modeling support the conclusion that a free-ranging diurnal, mammal uses a flexible, spatial strategy to orient in its environment and that environmental factors may change the expression of such a strategy depending both on the season and properties of the experimental apparatus. At the age of four, human children have begun to develop similar flexible strategies, not long after they have begun to use non-coincident, allocentric landmarks. These results, taken together, suggest that both humans and animals have developed similar strategies to deal with spatial problems and that these strategies develop along with use of more distal landmarks in human children.

Dedication

To my parents, Carlos and Susana,

my beloved husband, Brian,

and

our two darling cats, Shadow and Lady,

for their constant love and support

Table of Contents

Acknowledgments

I would like to thank all those who have made this dissertation possible. First, I would like to thank Dr. Lucia Jacobs, my adviser, whose passionate enthusiasm, creativity and support throughout the graduate process has left an indelible mark upon me. I thank Dr. Alison Gopnik, for her generous support and for introducing me to the wonderful world of children through developmental research. I thank Dr. Tom Griffiths for kindly and patiently assisting me in my first foray into computational models. I also thank John Campbell for his insightful comments and stimulating discussion on my dissertation research.

I would like to thank members of both the Jacobs lab and the Gopnik lab, Tania Bettis, Xiaoqian Chai, Chris Lucas, and Elizabeth Seiver for their encouragement and assistance. I thank Dr. Stephen Lea, the members of the Berkeley Behavior Lunch and the Comparative Cognition Tea for constructive comments on manuscripts and research plans.

I would like to acknowledge the generous contributions of Jose Lopez and Ted Claire in designing and constructing stimuli for many of the experiments. This work could not have been completed without the work of undergraduate research assistants such as Cindy Lau and Gabriella Libin. I thank the University of California at Berkeley Psychology Department for financial support. I also thank Shadow and Lady for their love and attention. Finally, I thank Brian Waismeyer not only for his help in data collection but also for his loving support and unfailing faith in me.

CHAPTER 1: Introduction

Spatial cognition is a necessary cognitive skill for orienting in an already familiar environment, and for venturing forth to explore new environments for potential resources. Diverse animal taxa, including primates such as humans, rely continually on spatial cognition to solve problems in their environment. One of the basic building blocks of such spatial cognition is the ability to encode landmarks for orientation and to use them in the form of spatial search strategies.

To remember a location, one may use a variety of spatial search strategies and types of landmarks to encode that location. Later, when searching for the location, there are a number of spatial strategies available for using those encoded landmarks to find the original location. In his original description of the cognitive map, Tolman (1948) discusses varieties of spatial strategies that can be used to search for a location. He asserts that strategies can vary from simple, narrow strips of knowledge to broad comprehensive theories that will allows animals to make more complicated choices when faced with spatial problems. He also states that both narrow and broad strategies may lead rats to make correct choices to spatial problems, and that the differences between the types of strategies will only appear when there is a change in the environment. The narrow strategy will be less likely to accurately handle the novel problem, while the more comprehensive strategy will be more likely to accommodate it.

The goal of my dissertation is to explore the question of spatial search strategies from an ecological, a computational, and a developmental perspective to get a broad view of spatial cognition across species and across time. From the ecological perspective I examine the spatial search strategies of a scatter-hoarding, diurnal, mammalian species, the fox squirrel, *Sciurus niger,* that relies on spatial memory for survival. I chose this species since, given this species' ecological need for accurate spatial memory, it is likely to have developed the use of multiple landmark types and flexible, comprehensive spatial strategies. From the computational perspective I explore how Bayesian modeling techniques can help us better understand the spatial strategies used by such a species and I evaluate whether a Bayesian model is appropriate as a model of spatial landmark use strategies in the fox squirrel. Finally, from the developmental perspective I investigate at what age, human children begin to develop similar flexible, comprehensive spatial strategies and how their use of different types of landmarks develops as they begin to consistently make use of non-coincident, allocentric landmarks. First, I will review the motivation behind each perspective and current work in the study of spatial strategies.

1.1 Ecological perspective

Previous work has shown that ecological pressures can have strong effects on spatial cognitive abilities (see Smulders, Gould, and Leaver, 2010 for a review). In a study comparing a food-storing bird species (chickadee) to a non-food storing bird species (junco), both species were able to remember and encode a location using multiple types of landmarks, but only the food-storing species showed a persistent, systematic order of preference for the different types of landmarks (Brodbeck, 1994). Additionally, in a study on multiple corvid species with varying ecologies, the species more dependent on a precise use of spatial memory to obtain food (clark's nuctrackers and pinyon jays) outperformed the species less dependent on spatial memory in both a long-term cache recovery task and in a radial arm maze (Balda, Kamil, Bednekoff, and Hile, 1997; Bednekoff, Balda, Kamil, and Hile, 1997; Kamil, Balda, and Olson, 1994). These findings

demonstrate that some food-storing species are more likely to have evolved systematic spatial strategies for re-locating food sites.

Fox squirrels are a diurnal species of food storing mammal and thus an ideal springboard for models of spatial strategies in mammals. Due to their particular ecological pressures, fox squirrels are likely to have developed systematic spatial strategies for orientation. Previous work in a related food-storing squirrel species, the southern flying squirrel (*Glaucomys volans*) has shown that flying squirrels use a flexible spatial strategy called a majority strategy to search for previously rewarded locations (Gibbs, Lea, and Jacobs, 2007). The studies presented in this paper expand on this previous work to determine whether the use of a majority strategy is particular to the ecological niche of the southern flying squirrel, or a more general cognitive ability of the family Sciuridae. The fox squirrel differs from the flying squirrel in that the fox squirrel is a diurnal, non-gliding tree squirrel species. Due to its being diurnal, the fox squirrel is more likely to use distinct visual features than the nocturnal flying squirrel. Furthermore, unlike the previous study in flying squirrels which was conducted in a laboratory setting, I was able to study the fox squirrel in its natural environment. If fox squirrels in their natural environment use similar flexible spatial strategies as southern flying squirrels in a laboratory setting, this suggests that the use of such strategies in neither particular to the flying squirrels' ecological niche, nor an artifact of the laboratory setting. My study of the spatial landmark use strategies of the fox squirrel both expands the work on the spatial cognitive abilities of the Family Sciuridae and establishes a general model for possible flexible spatial strategies in mammals.

1.2 Computational perspective

Bayesian modeling techniques allow us to further specify how such a model for spatial strategy might work at the computational level. From a Bayesian perspective the problem of searching for a location from memory of the landmarks associated with it is ultimately one of probability. An individual's goal is to search in the location that is most likely to be the correct location based on an uncertain set of memories of landmarks associated with the location and the prior probability that a location has contained the sought after resource in the past. For the fox squirrel in a novel experimental task with no established prior probabilities, this means searching for a previously visited location by comparing its memory for the location to the current set of landmarks in the environment. If the memory and the current state differ, then the current landmark information can be combined and compared to the memory to determine the most probable location.

The study of cue combination is well established in human perceptual tasks such as in exploring the ventriloquist effect and other perceptual judgment tasks (Alais and Burr, 2004; Ernst and Banks, 2002). In such cue combination studies, a perceptual judgment such as the height of a stimulus or the location of origin of a sound is measured in the presence of multiple cues. The same judgments are then made based on information from each cue in isolation. The degree to which participants rely on a single cue can be used to calculate the weight that the person has given to that particular cue. This can then be compared to how much a participant relies on one cue versus the other when they are presented in combination. If the cues are used in accordance with Bayesian principles, each cue will be weighted in inverse proportion to its variability, thus consistent with its perceived reliability. If a cue is relied on heavily in single cue tests, then it should also be more relied on in the combined cue tests. Previous work on reliability of landmarks in rats supports the possibility that animals use perceived reliability to weight their

use of spatial landmarks. Rats in spatial tasks that varied the stability of various landmarks, consistently chose to use the most stable landmarks to orient and spatial learning was unlikely to occur without stable landmarks (Biegler and Morris, 1996).

Recent publications have proposed using a Bayesian model to examine spatial cognitive behavior in both animals and humans (Cheng, Shettleworth, Huttenlocher, and Rieser, 2007b; Nardini, Jones, Bedford, and Braddick, 2008). In Cheng et al. (2007b), the authors performed a posthoc analysis of spatial performance data previously collected in pigeons. In a continuous search space, single landmark tests showed a definite preference for some landmarks over others in pigeons (Spetch and Mondloch, 1993). The authors estimated the weight for the preferred landmark that would be predicted by a Bayesian analysis of the results from this data. This weight was then compared to the degree of shift in the search location of the pigeons when their preferred landmark was shifted relative to the other three available landmarks. The predicted weight of the landmark matched the degree of shift in the search location. While, as the authors note, this is not a direct test of a Bayesian model for the spatial decisions of an animal, it suggests that such a model is both possible and valuable.

1.3 Developmental perspective

Given the demonstration of a majority spatial strategy in the fox squirrel, we were interested to see if human children might have similarly flexible spatial strategies. It is well established that during the preschool years, from three to four years of age, children begin to robustly use allocentric rather than egocentric landmarks when searching for a previously visited location (Deloache and Brown, 1983). However, which types of allocentric landmarks and the strategies employed by children for oriented spatial search remain undefined. When tested on four of eight arms of a outdoor radial arm maze, preschool age children performed as well as older children using only the distal landmarks available in the environment (Overman, Pate, Moore, and Peuster, 1996). Preschool age children were also able to locate a hidden object in a spatial relational task in which there were four identical containers arranged in a rectangular array (Gouteux and Spelke, 2001). Additionally, 4 year olds were shown to use both coincident landmarks (landmarks located in the exact target location, such as an object placed on top of the hiding location) and position within an array of objects to locate a hidden object (Lee, Shusterman, and Spelke, 2006). These results suggest that preschool age children can use a variety of types of landmarks, and thus may have the ability to use these in conjunction with another in the form of spatial strategies.

However, in a recent study on cue combination in children, four to five year olds and seven to eight year olds did not average spatial information from self-motion and landmark cues, while adults did (Nardini, et al., 2008). However, in this spatial task, participants visited three locations in succession, and were then tested on the position of the first location they had visited. There is evidence that children at this age are affected by the number of possible locations in a spatial task. As mentioned above, young children perform as well as older children in four arms of an eight arm radial arm maze. In contrast, they performed significantly worse than older children with all eight arms of the radial arm maze (Overman, et al., 1996). This suggests that the cognitive demands of a task need be taken into account when studying young children.

There is also evidence of a possible gap between 3 year olds and 4 year olds that suggests a

cognitive transition at this age. In a table-top version of the classic Cheng box (Cheng, 1986) (a rectangular box in which either of two diagonally opposite corners may be correct if given no distinguishing cues) 3 year olds were found to perform worse than 4 year olds. Furthermore, 3 year olds did not use either a colored wall as a landmark cue or the shape of the space as a geometric cue to orient to the correct location. On the other hand, 4 year olds were able to choose the correct corner or corners regardless of the condition, using either geometry cues alone or both geometry and a landmark cue. The younger children chose at random in either condition (Gouteux, Vauclair, and Thinus-Blanc, 2001). Finally, in two separate circular array tasks in which half of all possible locations were baited, 3 year olds again did worse than 4 year olds at locating the hiding positions (Cornell and Heth, 1983; Foreman, Warry, and Murray, 1990). Even when all the containers of the array were visually distinct from one another, 3 year olds children did not improve (Cornell and Heth, 1983).

1.4 Précis

This paper is organized into four remaining chapters, the first three of which present experimental results related to the perspectives reviewed above. The final chapter concludes with a summary of all results and implications and future directions for the work presented herein.

In the second chapter, I examine to what extent a free-ranging population of fox squirrels is capable of flexible spatial strategy and what types of landmarks they use for orientation. In a series of five experiments, I trained squirrels to a rewarded location within a square array of four feeders and then tested them on transformations of the array that either pitted two landmark types against one landmark type, the majority tests, or all landmark types against each other, the forced-hierarchy test. I also tested squirrels in variations of the original task. In Experiments 2 and 3, I used different trial orders, in Experiment 4, a different apparatus, and in Experiment 5 at different times of the year.

In the third chapter, I further explored how fox squirrels combined information from landmarks of different types from a computational modeling perspective. I define a Bayesian model that indicates how an ideal observer would optimally integrate landmarks, and fit this model to the decisions made by squirrels in the preceding spatial memory task. The resulting model provides a unifying framework for characterizing different strategies of landmark integration, and a tool for investigating the circumstances under which particular landmarks are used.

In the fourth chapter, I investigated whether human children develop similar flexible spatial strategies as the fox squirrels and what types of allocentric landmarks they use to construct such spatial strategies. In particular, I was interested in the initial development of such strategies when children first begin to use non-coincident, allocentric landmarks. Thus, all studies were conducted using 3 and 4 year old children since it is at this age that children begin to robustly use non-coincident, allocentric landmarks.

CHAPTER 2: Flexible landmark use in the fox squirrel (*Sciurus niger*)

2.1 Introduction

Most animals orient in space using redundant sources of information (Schöne, 1984). In some cases, such as when an animal adjusts its magnetic map using information from the setting sun, these redundant sources of information can be used to calibrate each other (Able, 1993; Phillips and Moore, 1992). In other cases, such as on cloudy days when honeybees switch from relying on a sun compass to relying on visual landmarks, it is clear that the redundancy acts as a critical backup for orientation in an unpredictable sensory environment (Dyer and Seeley, 1994). Yet what is not clear - despite many studies in diverse species - is how animals use these different sources of information when they are in conflict with one another.

2.2 Spatial strategies in animals

Several studies suggest that animals may use the information in a linear hierarchical manner. For example, in Brodbeck's study of black-capped chickadees (*Poecile atricapillus*) and dark-eyed juncos (*Junco hyemalis*), birds learned food was available at one of an array of four uniquely decorated feeders (Brodbeck, 1994; Clayton and Krebs, 1994; Herz, Zanette, and Sherry, 1994; Sherry and Duff, 1996). When feeders were shifted, chickadees oriented first to the feeder defined by landmarks outside of the array (i.e., the edges of the walls in the room). Their second choice was the feeder that was in the correct position in the array and their third choice was the feeder with the previously rewarded unique color pattern. Notably, chickadees did not visit the fourth location, which was not predicted by any cues during training. In contrast, juncos, a non-storing passerine, did not show an ordered preference, although they also only visited three of four feeders, ignoring the feeder not predicted by any landmarks. This suggests that both species retained a memory of all available cues but only the chickadees used the cues in a linear hierarchal manner, first searching in the location predicted by one cue type (distal room cues), followed by the location predicted by a second cue type (relative array position), and finally by the location predicted by a third cue type (array features).

More recently, Gibbs, Lea, Jacobs (2007) found that southern flying squirrels (*Glaucomys volans*) chose the location indicated by the greatest number of cue types, rather than having a particular preference for one type of cue. Their behavior was not consistent with a linear hierarchical model of cue use. For example, when the line of feeders was rotated 180°, the feeder in the previously rewarded location relative to distal room cues now displayed a new set of visual features and was in a new array position. The feeder with the correct visual features was now in the previously rewarded array position, but was in a new location relative to the distal room cues. If the squirrels had followed a linear hierarchy, as did the chickadees, they would have first oriented to the location indicated by the distal room cues. Instead, they chose the feeder that was in the correct array position and had the correct visual features.

These results are consistent with a majority cue use strategy by which animals choose the location predicted by the greatest number of cue types rather than relying on an ordered

hierarchy of cue types (Gibbs, Lea, and Jacobs, 2007). This type of strategy would be also be consistent with a Bayesian model in which the two cue types that are least preferred in the linear hierarchy are weighted such that their sum would be greater than the weight given to the preferred cue type. Cheng et al. (2007) have recently proposed using a Bayesian framework to model how animals make orientation decisions. In such a model, sources of spatial information are weighted differentially according to their variance and the prior experience of the animal. Whether the majority strategy is optimal for combining multiple sources of spatial information, as viewed through a Bayesian lens, is clearly an important question and is in fact the focus of current research. The goal here, however, was first to determine the generality of the majority strategy.

2.3 Squirrel spatial cognition

The goal of the present study was therefore to determine if free-ranging fox squirrels (*Sciurus niger*) might also adopt the majority strategy seen in captive flying squirrels. If so, this would suggest that the strategy is not particular to the southern flying squirrel, the design of the Gibbs et al. (2007) experiment, or the conditions of captivity. Squirrels (Family Sciuridae) are suitable subjects for field studies of spatial memory because they are diurnal, habituate easily to human observers and novel experimental objects and have consequently been chosen as subjects in many experimental studies (Cahalane, 1942; Devenport, Luna, and Devenport, 2000; Jacobs and Liman, 1991; Jacobs and Shiflett, 1999; Lavenex, Shiflett, Lee, and Jacobs, 1998; Vlasak, 2006a, 2006b). More important, fox squirrels, like southern flying squirrels, are obligate scatter hoarders (Stapanian and Smith, 1978). Scatter hoarding is a foraging strategy associated with specific cue use strategies, as in the comparison of chickadees and juncos discussed earlier. In general, scatter hoarding bird species rely preferentially on distant visual cues to re-orient to a location (Brodbeck, 1994; Clayton and Krebs, 1994; Herz, et al., 1994; Sherry and Duff, 1996). In contrast, non-storing bird species show no preference (Hodgson and Healy, 2005).

Prior work has demonstrated that free-ranging fox squirrels, like chickadees and other food-storing birds, relied on distant visual cues to orient to a location on an outdoor vertical maze, while ignoring the color of maze pathways (Jacobs and Shiflett, 1999). In another study of free-ranging fox squirrels, Lavenex et al. (1998) also found that squirrels relied on distant cues, and not the unique features of proximate cues, to orient to the spatial distribution of rewards in a large horizontal array of feeders. In field studies of free-ranging Columbian ground squirrels (*Spermophilus columbianus*), Vlasak again found that squirrels relied on distant visual cues to re-orient to a remembered location (Vlasak, 2006a, 2006b). Distant visual cues are large cues in the environment, such as trees and mountains, which are the most stable over time and across different viewing angles. Since these cues would have the least variance in a natural setting, relying on a linear hierarchical strategy that prefers these cues may be optimal when all cue types indicate different locations.

However, none of these studies confronted the study animals with a choice between a location indicated by two cue types and a location indicated by a single cue type. Under these conditions, the majority strategy would seem the most optimal since it is less likely for two types of cues to converge on the same incorrect location, while it is possible that the spatial relationship between a single cue type and the rewarded location might have changed. Relying on a hierarchical preference of cue types would lead the animal to choose the location indicated by the single cue

type when it was the preferred one. We predicted that fox squirrels, as in previous studies, would use a linear hierarchical strategy if given no other option, but would use a majority strategy if available. If they did not, then the previous results with flying squirrels could be the result of species differences or the effect of orientation under captive conditions. If, however, free-ranging fox squirrels also use a majority strategy, then this points to a previously unsuspected degree of flexibility in cue use in scatter-hoarding mammals.

2.4 Experimental design

In our experiments, we trained squirrels to a rewarded location within a square array of four feeders and tested them on transformations of the array. Since it is well documented that squirrels can use a hierarchical strategy, the goal of Experiment 1 was to determine whether squirrels would show the same degree of flexibility as flying squirrels had in previous experiments, by using a majority strategy when available. Experiment 2 examined whether the repetition of training trials might have caused the squirrels to switch from using a less neurologically efficient strategy based on spatial cues to a feature-based strategy in Experiment 1. In Experiment 3, we considered whether the order of testing trials might have caused this switch since we had been unable to counterbalance order of testing due to small sample sizes. Experiment 4 replicated Experiment 1 in the Spring to see whether squirrels were not using a majority strategy in Experiments 2 and 3 due to changes in trial order or seasonal changes. Finally, Experiment 5 replicated Experiment 1 at the same time of year, but using the apparatus from Experiments 2, 3, and 4, to determine if changes in the saliency of objects attached to the feeders or the method of opening the feeders between Experiments 1 and 2 might have caused squirrels to pay less attention to featural cues in Experiments 2, 3, and 4.

2.5 General Methods

2.5.1 Study Sites

All experiments were conducted on four wooded sites on the University of California, Berkeley campus. One site was located within a grove of mature bluegum eucalyptus (*Eucalyptus globules*), redwood (*Sequioa sempervirens*), and coast live oak (*Quercus agrifolia*) trees. The other three sites were located on groomed lawns with redwood and coast live oak (Jacobs and Shiflett, 1999). We conducted Experiments 1 and 5 in late July and early August of 2005 and 2006 and Experiments 2, 3 and 4 in April and May of 2006. Data were collected from late morning to early afternoon. Experiments are presented in the order in which they were conducted.

2.5.2. Study Animals

Adult male fox squirrels ($N = 42$) were individually marked with permanent black fur dye (Nyanzol D). Due to an intervening molt between Experiments 1 and 2, squirrels lost their markings and it is possible that the eight squirrels in Experiment 1 may have also participated in Experiments 2 – 5. After Experiment 2 we were able to continuously track all participants. However, squirrels that had previously participated were immediately obvious to the experimenter since they required no pre-training to learn how to manipulate the apparatus. These squirrels were excluded from participating. Furthermore, due to an increase in the mortality rate possibly as a result of the introduction of West Nile virus to California (Padgett et al., 2007) it is

highly unlikely that the squirrels tested in Experiments 2-5 were the same squirrels that participated in Experiment 1.

Because of the prevalence of male squirrels on these sites, we excluded females from our study to reduce variance in the results. We selected squirrels that were available at the time of testing and that we could test without interference from or interactions with other squirrels. We excluded trials during which participants were interrupted due to social interactions with other squirrels or other disturbances (e.g., dog chases). All squirrels were highly habituated to human observers even at distances of one meter or less.

2.5.3 Experiment Setup

As seen in Figure 1, the array of feeders was presented to study animals on a small table (82 cm x 82 cm x 72 cm high), covered with vinyl sheeting. Feeders were small lockable containers topped with an object of a unique color and pattern, positioned in a square array (28 cm x 28 cm). To preclude the use of orientation to odor cues, all feeders contained chopped nuts (chopped pecans, walnuts, hazelnuts). In addition, the table surface was cleaned with disinfectant wipes between training and testing trials. The table was placed adjacent to a tree trunk, which served as the only access point. This ensured that squirrels always approached the array from the same side.

In preliminary studies, we found that squirrels did not take the same route to the rewarded location, often examining the entire platform before making a choice. We could therefore assume that they were using allocentric information, such as landmarks in the external environment and visual features of the feeders, instead of self-motion cues or path integration. Since the global-local distinction is relative to the size of the experimental setup and is difficult to quantify in the field (Hurly and Healy, 1996; Thiele and Winter, 2005), we classified the available spatial information based on its relationship to the experimental setup which we could control. We decided on three cue types: extra-array cues (EX), intra-array position cues (IN), and unique feature cues (UF). EX included any landmark outside of the testing platform, the testing platform itself, and the tree that provided access to the platform; these cues remained in the same locations throughout training and testing. IN referred to the position of the rewarded feeder as defined by its geometric relationship to the other three feeders in the square array without encoding the specific features of the feeders. UF referred to the features, such as shape and color, of the object located on the feeder and any residual odors on the feeder. The objects included small plastic toys and ceramic salt shakers (Figure 1).
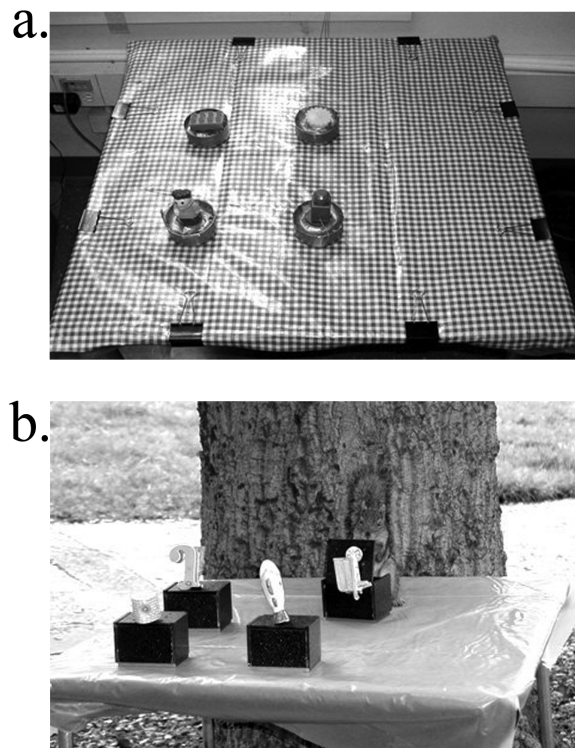
Figure 1: Photographs of the experimental apparatuses in the training configuration. A plastic template was used at the beginning of each session to place the boxes in the correct positions. a. The apparatus used in Experiment 1. b. The apparatus used in Experiments 2-5. See General Methods for more details.

2.5.4 Pre-training

We trained squirrels to approach and eat nuts from an open feeder on the table. The squirrel was then shaped to open a feeder by gradually closing the feeder on subsequent pre-training trials. On average, squirrels were able to open and eat from a closed feeder after 5 minutes of pre-training.

2.5.5 Training

Pre-trained squirrels approached the feeders and were given as much time as needed to find and open the correct feeder through trial-and-error learning. The location of the correct feeder was counterbalanced across subjects. The experimenter then gently urged the squirrel off the table, closed the now open feeder. To avoid experimenter cueing, the experimenter mimed closing the other three feeders in a pseudorandom order. To ensure that all squirrels were trained to the same criterion, training trials were repeated until the squirrel chose the correct feeder first in three consecutive trials. After reaching this criterion, squirrels were given only one testing trial and then retrained to criterion. Across all experiments, squirrels quickly reached criterion in initial training trials (mean $\pm$ standard deviation (SD), 3.6 $\pm$ 1.0; range 3-7; N, 42). After non-rewarded testing, squirrels just as quickly returned to criterion in inter-testing training trials (mean $\pm$ SD, 3.2 $\pm$ 0.8; range, 3 -7; N, 42).

2.5.6 Testing

There were two types of testing trials: the forced-hierarchy test and the majority test. In the forced-hierarchy test, the entire array of feeders was moved horizontally to the other side of the table and the previously rewarded feeder was switched with the diagonally opposite one (Figure 2). Each cue type, EX, IN, or UF, now indicated a different feeder in the array. A fourth feeder served as a distracter. In the majority test, two of the three cue types (e.g., IN and UF) indicated one feeder – the majority location, while the third type (e.g., EX) indicated a second feeder – the minority location. The other two feeders served as distracters. The three possible majority tests are illustrated in Figure 2.
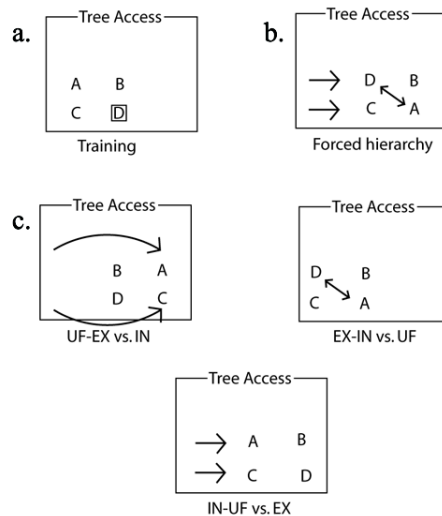
Figure 2: **a**. A schematic of the training trial in which the D position is rewarded. **b**. A schematic of the forced-hierarchy trial based on this training setup. The entire array is moved horizontally to the other side of the table and the previously rewarded box (D) is switched with its diagonal opposite (A). D is now the location indicated by the UF cues, A is the location indicated by IN cues, and C is the location indicated by EX cues. **c**. A schematic of the three majority tests based on this training setup.

Training and testing trials for each subject were conducted in one session on the same day and in the same location. The same procedures were used for all experiments. The order of testing trials was not counterbalanced across subjects to reduce the variance within the small sample sizes. There was no evidence of a decrease in performance between testing trials.

Each squirrel took approximately one hour to complete all trials, including time during which it would sometimes retreat and rest in the tree. The first feeder that the squirrel attempted to open was recorded for every trial. If the squirrel pushed the feeder over or tried to pry it open with its teeth, the behavior was recorded as a choice. All other interactions were noted but were not considered choices.

In each experiment, data were tested against chance using a two-tailed binomial test; the probability of choosing correctly by chance was 0.25. Additional analyses were run using two-tailed Fisher exact tests.

2.6 Experiment 1

Rationale

The purpose of this experiment was to determine what cue types free-ranging fox squirrels would use and whether they would use a majority strategy or a hierarchical strategy in the majority test. We first presented squirrels with all three versions of the majority test. Then we tested them in the forced-hierarchy test to determine what type of cue they would prefer. Based on results from Gibbs et al. (Cheng, et al., 2007a) and Jacobs and Shiflett (Galea and McEwen, 1999) we expected fox squirrels to rely preferentially on EX cues in the forced-hierarchy test and to use a majority strategy in the majority tests.

Methods

We recruited eight adult male fox squirrels at four testing sites. All squirrels were naïve to experimental conditions. We tested squirrels in this order of the three majority tests: EX-UF vs. IN; IN-EX vs. UF; UF-IN vs. EX and then in the forced-hierarchy test (Figure 3). Data were collected from July 23, 2005 – July 26, 2005. All other procedures are as described in General Methods.
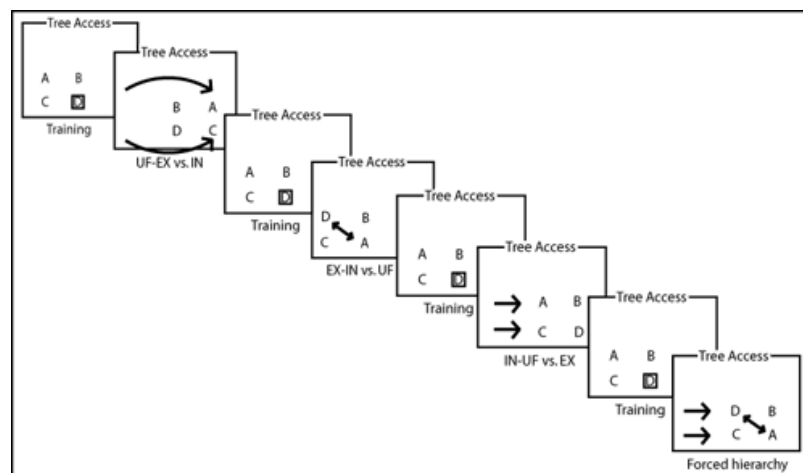
Figure 3: **a.** Schematic of the trial order in Experiment 1, beginning with the initial training trial and including all the inter-training trials. **b.** Schematic of the trial order in Experiment 3, beginning with the initial training trial. The inter-training trials between testing trials are not included. Temporal sequence proceeds from left to right.

Apparatus

As seen in Figure 1a, feeders were shallow circular aluminum containers (tuna cans; 9 cm diameter, 4 cm depth) filled with modeling clay with an inset plastic cup (4 cm diameter, 1.5 cm depth) in the center. A unique plastic object (large Lego™ block) was attached to the side of the aluminum container with steel wire and placed on top of the plastic cup. All four cups were filled with 5 g of chopped nuts. During training, three of the plastic cups were closed with tight-fitting lids, while one was left open; during testing all four cups were closed.

Results and Discussion

In the three majority tests, squirrels significantly re-oriented to the majority and not the minority location (Table 1). In the EX-UF vs. IN and IN-EX vs. UF tests, five of seven squirrels and six of seven squirrels visited the majority location respectively ($n = 7$, $p = 0.013$ and $p = 0.0013$). In the third majority test, UF-IN vs. EX, four of five squirrels visited the majority location ($n = 5$, $p = 0.016$). In the forced-hierarchy test, five of five squirrels re-oriented to the UF location ($n = 5$, $p < 0.001$).

Majority Tests

	Majority location		Minority location		Other locations
Trial type	Cue types	% (Number)	Cue type	% (Number)	% (Number)
EX-UF vs. IN	EX-UF	71.4 (5)	IN	14.3 (1)	14.3 (1)
IN-EX vs. UF	IN-EX	85.7 (6)	UF	14.3 (1)	0 (0)
UF-IN vs. EX	UF-IN	80 (4)	EX	0 (0)	20 (1)

Forced-hierarchy Test

Cue type	EX	IN	UF	Other
% (Number)	0 (0)	0 (0)	100 (5)	0 (0)

Table 1: Results of Experiment 1. Trial and cue types defined in text. The n decreased because of loss of squirrels during testing. Percentages and observed numbers of squirrels choosing are reported.

Data from the majority tests suggest that squirrels are capable of using a majority strategy when orienting to locations. If the squirrels had used a rigid hierarchical strategy they would have chosen the minority location indicated by their preferred cue type in the corresponding majority test. For example, if EX is the preferred cue type in the forced-hierarchy test, they would choose the EX location instead of the UF-IN location in the UF-IN vs. EX majority test. However, they did not. This confirms our prediction that fox squirrels do use a majority strategy.

However, data from the forced-hierarchy test suggest that the preferred cue type for this population of squirrels is UF. This conflicts with previous studies (Jacobs and Shiflett, 1999; Vlasak, 2006a, 2006b) in which squirrels oriented using an allocentric frame of reference based on distal landmarks, i.e., EX in the current experiment. While the small sample size ($n = 5$) limits our ability to generalize from these data, the results of these previous studies would have predicted that the location indicated by UF cues would have been chosen below chance. In both the experiments cited, squirrels seemingly completely disregarded all featural information provided. Therefore the results of Experiment 1 were more surprising than they would have been if the choice of UF had been at chance or at least equal to the other cue types. Instead, we had an overwhelming majority of the squirrels immediately indicate their preference for the UF location over both the EX and AP locations.

It is possible that the squirrels switched from a place navigation strategy by which they oriented using spatial cues, EX and AP, to orienting using an associative, feature-based search strategy by

which they oriented using UF cues. Similar behavior has been previously seen in laboratory rats. It has been argued that this switch could arise because the neural mechanisms underlying a feature-based cue encoding are faster than those of place navigation, making the feature-based search strategy more efficient (Chang and Gold, 2003; Packard and McGaugh, 1996). Thus, over time, if both strategies are equally accurate at solving the training task, the feature-based search may out-compete the slower place navigation (Chavarriaga, Strosslin, Sheynikhovich, and Gerstner, 2005). Given that the forced-hierarchy test followed multiple testing trials, by this trial, the squirrels might have switched to using the feature-based strategy. We tested this hypothesis in Experiment 2.

2.7 Experiment 2

Rationale

To test the hypothesis that over-training through task repetition caused the squirrels to adopt a cue-directed search strategy, we tested each squirrel in the forced-hierarchy test four times in a row. If squirrels preferentially rely on UF cues they should choose the UF location throughout the whole experiment. If, however, they preferentially use spatial cues, but switch to a feature-based search after multiple repetitions of the same task, they should choose either the EX or IN locations in the initial testing trials and the UF location in the final testing trials.

Methods

We recruited eight adult male fox squirrels. All procedures were identical to those used in Experiment 1, except that only the forced-hierarchy test was used. Data were collected from April 8, 2006 – April 30, 2006. All other procedures are as described in General Methods.

Apparatus

To avoid problems with possible remnant odors in the original feeders, we used a new feeder design in this and subsequent experiments (Experiments 2-5). Each feeder was a dark green acrylic box (10.5 cm x 7.5 cm x 7.5 cm high) with a hinged lid and a locking device located on the side (Figure 1b). Boxes appeared identical whether they were locked or unlocked. We fastened ceramic figurines, different in both shape and color, to the top of each box using Velcro™. Each box contained 30 g of nuts.

Results and Discussion

In the first presentation of the forced-hierarchy test, there was no one strategy used by the squirrels. An equal number of squirrels chose the IN as the EX location ($n = 3$ for both), the other squirrels chose the distracter and UF locations ($n = 1$ for both; Table 2). In the second, third, and fourth trials, squirrels chose the EX location. ($n = 8$ for all, $p = 0.0042$, $p < 0.001$ and $p = 0.027$ respectively). Since the squirrels never chose the UF location, the data do not support the hypothesis that task repetition causes squirrels to switch to a cue-directed search, nor do they support the hypothesis that squirrels prefer UF cues.

Forced-hierarchy Test

Trial Number	Cue type: % (Number)			
	EX	IN	UF	None
1	37.5 (3)	37.5 (3)	12.5 (1)	12.5 (1)
2	75 (6)	12.5 (1)	12.5 (1)	0 (0)
3	87.5 (7)	12.5 (1)	0 (0)	0 (0)
4	62.5 (5)	25 (2)	12.5 (1)	0 (0)

Table 2: Results of Experiment 2. Trial and cue types defined in text. Percentages and observed numbers of squirrels choosing are reported.

The results of Experiment 2 suggest that EX is the preferred cue type and that task repetition does not cause squirrels to switch to a feature-based search strategy (i.e., preferring UF). It is also possible that specifically having the majority test trials precede the forced-hierarchy test in Experiment 1 caused squirrels to choose the UF location. Unlike in this experiment, in Experiment 1, the spatial locations were changing in every testing trial. Therefore the UF cue type might have appeared to be the most stable. We tested this hypothesis in Experiment 3.

2.8 Experiment 3

Rationale

The goal of this experiment was to test for the effect of the order of testing trials. We replicated the procedure of Experiment 1, but we introduced a forced-hierarchy test after each majority test. These new forced-hierarchy tests allowed us to assess the preferred cue type throughout the experiment. If the preference for UF in Experiment 1 was due to order effects, then squirrels should initially choose the EX location in the forced-hierarchy trials and switch to the UF location in later trials. Otherwise squirrels should choose the same location in all the forced-hierarchy trials.

Methods

We recruited nine adult male fox squirrels that had not participated in Experiment 2. The order of the majority tests was the same as in Experiment 1, except that after each majority test there was a forced-hierarchy trial (Figure 4). Data were collected from April 30, 2006 – May 21, 2006. All other procedures are as described in General Methods.

Results and Discussion

In all forced-hierarchy trials, squirrels chose the EX location ($n = 9$, in the last trial $n = 8$, $p = 0.0013$, $p = 0.0013$, $p = 0.027$, for the first, second, and third trials respectively; Table 3). Furthermore, while squirrels chose the majority location in the first two majority tests, EX-UF vs. IN and IN-EX vs. UF ($n = 9$, $p = 0.049$ and $p < 0.0001$, respectively), they chose the minority location (EX) in the third majority test, UF-IN vs. EX ($n = 9$, $p = 0.049$).

Majority Tests

	Majority location		Minority location		Other locations
Trial type	Cue types	% (Number)	Cue type	% (Number)	% (Number)
EX-UF vs. IN	EX-UF	56 (5)	IN	33 (3)	11 (1)
IN-EX vs. UF	IN-EX	100 (9)	UF	0 (0)	0 (0)
UF-IN vs. EX	UF-IN	33 (3)	EX	56 (5)	11 (1)

Forced-hierarchy Test

Trial Number	Cue type: % (Number)			
	EX	IN	UF	None
1	78 (7)	22 (2)	0 (0)	0 (0)
2	78 (7)	22 (2)	0 (0)	0 (0)
3	62.5 (5)	25 (2)	12.5 (1)	0 (0)

Table 3: Results of Experiment 3. Trial and cue types defined in text. Percentages and observed numbers of squirrels choosing are reported.

These data suggest that trial order does not cause squirrels to switch from preferring EX to UF. Squirrels not only visited the EX location in all forced-hierarchy trials, but now there was also no evidence that they were using a majority strategy. In both of the tests in which they chose the majority location, that location was indicated by EX cues. This pattern of data made it impossible for us to determine whether they had used a majority strategy initially and then switched to a hierarchical strategy, or if they had only used a hierarchical strategy with EX as their preferred cue type the whole time. We chose to assume the simpler explanation, that they had used a hierarchical strategy the whole time. Therefore, we concluded from the data that the order of trials in Experiment 1 did not cause squirrels to use a cue-directed strategy; on the contrary, if anything, the order induced them to use only spatial cues (i.e., EX and IN).

Finally, squirrels might have preferred UF cues in Experiment 1 and EX in Experiments 2 and 3 because the feeder construction in Experiment 1 had more salient UF cues than the feeder construction used in subsequent experiments. There were at least three possible sources of increased saliency: differences in the objects placed on the feeders, the manner of opening the feeders, and the feeders themselves. The objects in Experiment 1 were commercial plastic blocks that were simply colored objects with simple shapes, while in experiments 2 and 3 the objects used were more visually complex. In Experiment 1, the squirrels had to remove the object from the feeder to access their reward, while in the later experiments the object did not have to be removed (although many squirrels manipulated the objects prior to opening the feeder). In addition, the feeding containers in the first experiment were made from washed food cans which might have contained remnant odors that would have increased their saliency to the squirrels. We tested the hypothesis that feeder construction had a significant effect on cue use in Experiment 4.

2.9 Experiment 4

Rationale

This experiment replicated Experiment 1 using the new acrylic box feeders from Experiments 2 and 3. If the feeder construction has a significant effect, squirrels should not use UF cues even though we were replicating the procedure of Experiment 1, in which they used UF cues.

Methods

We recruited eight male fox squirrels that had not participated in Experiments 2 or 3. Data were collected from May 20, 2006 – May 21, 2006. All procedures were the same as in Experiment 1 (Figure 3) and as described in General Methods.

Results and Discussion

As in Experiment 3, squirrels consistently chose the EX location in the forced-hierarchy trial and showed no evidence of using a majority strategy. In the first majority test, EX-UF vs. IN, squirrels showed no preference for either the minority or majority location (Table 4). In the second majority test, IN-EX vs. UF, squirrels consistently chose the majority location ($n = 8$, $p < 0.0001$). In the last test, UF-IN vs. EX, six of eight squirrels chose the minority location ($n = 8$, $p = 0.0042$). In the forced-hierarchy trial, five of eight squirrels chose the EX location ($n = 8$, $p = 0.027$) and only one visited the UF location.

Majority Tests

	Majority location		Minority location		Other locations
Trial type	Cue types	% (Number)	Cue type	% (Number)	% (Number)
EX-UF vs. IN	EX-UF	50 (4)	IN	37.5 (3)	12.5 (1)
IN-EX vs. UF	IN-EX	100 (8)	UF	0 (0)	0 (0)
UF-IN vs. EX	UF-IN	25 (2)	EX	75 (6)	0 (0)

Forced-hierarchy Test

Cue type	EX	IN	UF	Other
% (Number)	62.5 (5)	25 (2)	12.5 (1)	0 (0)

Table 4: Results of Experiment 4. Trial and cue types defined in text. Percentages and observed numbers of squirrels choosing are reported.

The results from Experiments 2, 3, and 4 thus suggest that squirrels rely on EX cues and ignore UF cues when using the acrylic box feeders. However, one factor that is prominent in studying cognition in wild, free-ranging animals is that they are undergoing seasonal changes in behavior and physiology associated with reproduction. Such seasonal changes are correlated with

differences in performance on spatial orientation and memory tasks in males and females (Galea, Kavaliers, Ossenkopp, Innes, and Hargreaves, 1994; Gaulin, Fitzgerald, and Wartell, 1990; Jacobs, 1996; Pyter, Trainor, and Nelson, 2006). In California, fox squirrels have two breeding seasons, the first from June to September and a second one from December to March (Byrne, 1979; King, 2004). Changes in cognitive strategies between the summer breeding season (Experiment 1) and late spring which is at the end of the breeding season (Experiments 2-4) may have caused the changes in cue preference that we found. We examined this possibility in Experiment 5.

2.10 Experiment 5

Rationale

To determine whether it was seasonal changes or feeder construction that caused squirrels to prefer UF in Experiment 1 and EX in Experiments 2, 3, and 4, we decided to replicate Experiment 1 with the acrylic box feeders at the same time of year that Experiment 1 had been conducted, late summer.

Methods

We recruited 11 male fox squirrels that had not participated in Experiments 2, 3, or 4. Data were collected from July 28, 2006 – August 5, 2006. All procedures are as described in Experiment 1 (Figure 3) and General Methods.

Results and Discussion

In the three majority tests, squirrels chose the majority location ($n = 11$, $p = 0.007$, $p < 0.00001$, $p = 0.034$, for the EX-UF vs. IN, IN-EX vs. UF, UF-IN vs. EX respectively; Table 5). Five of eight squirrels chose the EX location in the forced-hierarchy trial ($n = 8$, $p = 0.027$). Squirrels used a majority strategy in the majority tests as they had done in Experiment 1, but chose the EX location rather than the UF location in the forced-hierarchy trial.

Majority Tests

| Trial type | Majority location | | Minority location | | Other locations |
	Cue types	% (Number)	Cue type	% (Number)	% (Number)
EX-UF vs. IN	EX-UF	73 (8)	IN	18 (2)	9 (1)
IN-EX vs. UF	IN-EX	100 (11)	UF	0 (0)	0 (0)
UF-IN vs. EX	UF-IN	54.5 (6)	EX	45.5 (5)	0 (0)

Forced-hierarchy Tests

Cue type	EX	IN	UF	Other
% (Number)	62.5 (5)	37.5 (3)	0 (0)	0 (0)

Table 5: Results of Experiment 5. Trial and cue types defined in text. Percentages and observed numbers of squirrels choosing are reported.

These results would be consistent with an effect of seasonal changes since the squirrels now attended to UF cues when using the acrylic box feeders as seen in their use of a majority strategy. However, using the Fisher's exact test we found no significant differences between the pattern of choices in any of the majority tests in Experiment 4 and Experiment 5 (Fisher exact test, two-tailed, $n = 19$, df $= 1$, for all, $p = 0.38$, EX-UF vs. IN; $p = 1$, IN-EX vs. UF; $p = 0.35$, UF-IN vs. EX). Therefore we can not conclude that there were seasonal differences across experiments.

On the other hand, when we compared the patterns of choices from the forced-hierarchy tests in Experiments 1 and 5, we found a significant difference (Fisher exact test, two-tailed, $n = 14$, df $= 3$, $p < 0.001$). There was no difference between experiments in any of the majority tests between Experiments 1 and 5 (Fisher exact test, two-tailed, $n = 55$, df $= 1$, $p = 1.0$). This suggests that the changes made to the feeders after Experiment 1 had significant effect on the weighting given to different cue types, but that the weightings still allowed for use of a majority strategy. Future experiments are needed to ascertain what elements of the feeder construction might have contributed to this effect.

2.11 General Discussion

The goal of this study was to determine which cue types fox squirrels rely on to remember a location and whether they would use a majority strategy if available. In Experiment 1, as predicted from previous work on flying squirrels, squirrels re-oriented to the majority rather than the minority location in all majority tests. However, in the forced-hierarchy test, they chose the UF location indicated by non-spatial features, rather than the IN or EX locations indicated by spatial information. This choice runs contrary both to studies of fox squirrels (Jacobs and Shiflett, 1999) and to those of other bird and mammal species that predictably chose the EX location in forced-hierarchy tests (Brodbeck, 1994; Healy and Hurly, 1998; Spetch and Edwards, 1988; Thiele and Winter, 2005; Vlasak, 2006a, 2006b; Watanabe, 2005). In Experiments 2-5, we tested different hypotheses as to why these squirrels had chosen UF cues as their preferred cue type rather than the predicted EX cues.

These experiments led to the following conclusions: that feeder construction could influence the attention to UF cues, that the time of year was related to trends in the data but its effect was not as strong as that of feeder construction and that finally, squirrels used a majority strategy when available and were most likely to choose the EX location in a forced hierarchy test. Our results are consistent with prior studies showing the use of EX cues in forced hierarchy tests in scatter-hoarding birds and mammals (Brodbeck, 1994; Jacobs and Shiflett, 1999). At the same time, our results confirm the flexible use of the majority strategy when this is an option, as previously demonstrated in southern flying squirrels (Gibbs, et al., 2007).

The choice of the EX location as the preferred location is supported by data from all the experiments, except Experiment 1. In Experiments 2-5, the EX cue type appeared to exert the greatest influence on the squirrels' decision strategy. We found no differences in the results from the forced hierarchy test between Experiments 3, 4, and 5 (Fisher exact test, two-tailed, $n = 58$, df $= 9$, $p = 0.97$). Across all the forced-hierarchy test trials, a majority of squirrels chose the EX location over the other three possible locations. In contrast, when we included the results of Experiment 1 in our comparison, we found a significant difference between the patterns of choices (Fisher exact test, two-tailed, $n = 64$, df $= 16$, $p = 0.03$). Sources of increased saliency in

Experiment 1 might have caused participating squirrels to rely on the more readily available UF cues rather than the spatial cue types (IN and EX).

While EX appeared to be the preferred cue type in the forced-hierarchy tests, we found no evidence for the preference of one combination of cue types over the others in the majority tests. Overall, the combination of IN and EX cue types seemed to exert the most influence on the squirrels' orientation. In all the experiments, a majority of squirrels chose the IN-EX location over the UF location in the IN-EX vs. UF majority test. However, data analyses including only those experiments in which the squirrels were using a majority strategy and therefore clearly attending to UF cues, Experiments 1 and 5, only confirmed a significant difference between the IN-EX vs. UF and the UF-IN vs. EX tests in Experiment 5 (Fisher exact test, $n = 22$, df $= 1$, $p = 0.035$). While this pattern of results implies that EX cues may be more influential than UF cues, we found no evidence that IN cues are more influential than UF cues. There was no difference between the IN-EX vs. UF and the EX-UF vs. IN tests in either Experiment 1 or Experiment 5 (Fisher exact test, Experiment 1: $n = 14$, df $= 1$, $p = 1$, and Experiment 5: $n = 22$, df $= 1$, $p = 0.21$). Thus, although IN-EX seemed to exert the greatest influence across experiments, we were unable to find support for a hierarchy of the different combinations of cue types.

The effect of the feeder construction on their spatial encoding is supported by a comparison of the results of Experiment 1, using the aluminum can feeders, with those of Experiment 5, using the acrylic box feeders. Both experiments were conducted in late summer using the same procedure. In the former, squirrels chose the UF location, indicating UF as their preferred cue type in the forced-hierarchy test, while in the latter, squirrels chose the EX location (Fisher exact test, two-tailed, $n = 14$, df $= 3$, $p = 0.003$). It is possible that remnant odor cues, differences in the squirrels' ability to discriminate between UF objects, and differences in the amount of direct contact with the UF objects may have contributed to this effect. Future work will have to determine the relative contribution of such factors to the squirrels' use of UF cues.

Our pattern of results also suggests that encoding strategy varied by season of study. Although this pattern must be tested in the future with larger sample sizes, there was a remarkable change in the proportion of squirrels using majority strategy across the study. In the spring/summer experiments (Experiments 3 and 4), most squirrels chose a non-majority location (6 of 9 and 6 of 8, respectively). In contrast, in the late summer (Experiments 1 and 5), most squirrels chose the majority location (5 of 6 and 6 of 11, respectively). This suggests a weak seasonal effect that could become statistically significant with a larger sample size and hence higher power of the statistical test.

This pattern of results is also consistent with known seasonal changes in the brain of a congener species, the eastern gray squirrel (*S. carolinensis*). Adult male squirrels showed a significant increase in brain size in October, the height of the caching season, compared to adult squirrels captured in January or June (Lavenex, Steele, and Jacobs, 2000). There was also an absolute increase in the hippocampal subfield (CA1), a structure selectively active during the encoding of small unique objects in the lab rat (Kemp and Manahan-Vaughan, 2007). Thus the male fox squirrel's greater attendance to UF cues in the late summer may be related to seasonal changes in how its hippocampus encodes a location. In addition, such a dissociation of hippocampal functions by cue class is consistent with the parallel map model of spatial encoding (Jacobs and

Schenk, 2003).

In conclusion, the series of experiments reported here on spatial encoding in a free-ranging, scatter-hoarding mammal, the fox squirrel, both complement and challenge earlier studies of this phenomenon. While our results confirm squirrels' preference for distal spatial cues when all cue types are in conflict, they also suggest that there is a large degree of plasticity in the type of strategy used. This degree of plasticity was also recently reported in another scatter-hoarding squirrel, the southern flying squirrel. It appears that a single experiment, at a single time of year or using a single type of apparatus, may not be sufficient to characterize the spatial encoding strategy of a species. The great ecological diversity of spatial ecology among sciurids makes them an ideal group with which to further explore this topic. Future studies can make use of this diversity to systematically study spatial strategy among species with different foraging behaviors (scatter-hoarding vs. non-storing species) and different breeding seasons to determine what role ecological niche has played in the use and expression of spatial encoding strategy.

CHAPTER 3: A Bayesian model of spatial strategies in the fox squirrel (*Sciurus niger*)

3.1 Introduction

Animals of many kinds display remarkable skill at spatial navigation, and formal models of how animals navigate have many potential uses. For example, one can use them to develop robots capable of autonomous movement (Thrun, 2005) and to aid in designing new animal conservation principles (Fevre, Bronsvoort, Hamilton, and Cleaveland, 2006; Simons, 2004). However, to be able to navigate from one location to another, it is first necessary to accurately remember previously visited locations. While animals have been shown to use a number of different types of landmarks to remember locations, understanding the strategies by which animals use these landmarks to re-locate places in their environment is still an active research topic.

The problem facing animals when identifying spatial locations during navigation is one of uncertainty. This uncertainty stems from the inherent imperfections of memory. The animal has a memory of the location it is searching for, but that memory may be inconsistent with the current set of spatial landmarks associated with the location, either as a result of a failure on the part of the animal to remember those landmarks, or because the environment around the location has changed. The decision facing the animal is therefore based on the degree to which the animal believes that a particular location is in fact the location for which it has a memory.

In this paper, we analyze the problem of identifying a spatial location from memory as a kind of Bayesian inference. This approach provides a way to quantify degrees of belief and uncertainty, and thus provides a natural framework in which to develop an "ideal observer" model. In cases where multiple kinds of landmark cues are available, the Bayesian approach allows us to take into account the perceived reliabilities of each landmark or landmark type. This information can be used to identify the location most consistent with the animal's memory.

Formalizing spatial memory in these terms gives us a tool for identifying which types of landmark animals use in navigation, and what factors influence the use of these landmarks. There is evidence that the use of landmarks can change significantly depending on the season in which animals are tested, and the level of salience of different landmark types (Waisman and Jacobs, 2008). Applying our model to data collected from squirrel cue combination tests, we can examine how the posterior probabilities of the locations change in relation to changes of season at testing and in salience of different landmark types across experimental 1 setups. Modeling navigation as a form of Bayesian inference will also allow us to determine what kinds of strategies animals are using by estimating the perceived reliability of landmarks based on how they use those landmarks in combination.

The plan of the paper is as follows. In Section 2, we briefly review the literature on animal landmark use. Section 3 considers the problem of landmark cue combination from a Bayesian perspective, explaining the general structure of a Bayesian model of landmark use. In Section 4, we describe a series of cue combination experiments with squirrels, and the specific model that we used to characterize their behavior. Both experimental and model results are discussed. In Section 5, we demonstrate how the model can be used as a tool to examine seasonal and salience

effects. Section 6 concludes the paper.

3.2 Landmark use by animals

Models of landmark use have varied considerably depending on the class of animal being described and the particular experiments conducted. Invertebrates, in particular honeybees and ants, are commonly thought to navigate by matching stored 2-D images, "snapshots," of locations to current retinal information (Cartwright and Collett, 1983; Collett and Collett, 2002), although recent evidence suggests that honeybees have a much more complex representation of spatial information in their environment than this model had credited them with (Menzel et al., 2005). One model of navigation that has been applied to many classes of animals including invertebrates (Anderson, 1977) is a direction and distance model. In this type of model, animals store both the direction or bearing and distance from landmarks to a goal location. One such model is the multiple-bearings hypothesis (Kamil and Cheng, 2001). This model asserts that spatially specialized birds, such as some species of corvids (e.g., scrub jays) and paridae (e.g., black-capped chickadees), represent goal locations in terms of their distance and direction from multiple landmarks. However, while this may be an apt model for the type of information gained from landmarks, it still leaves unanswered what landmarks the animal will use to gather this information.

Due to natural selection pressures, birds and other animals that are either nectar-feeding or store food have excellent spatial memory abilities, and have often been used in experiments. Some bird families, such as corvids, are famous for the number of nuts they store for consumption during the winter (> 20; 000) (Vanderwall and Balda, 1981). Traditionally, such animals have been described as using landmarks in a hierarchical fashion. In these models of spatial landmark use, when landmarks are in conflict, one type of landmark is prioritized over all other types of landmark. If that type of landmark does not lead to the expected reward, then the animal searches at a location consistent with a different type of landmark. The animal works its way down its preference hierarchy of landmark types until it finds the rewarded location. For example, in spatial memory tasks, food-storing birds are known to first search in the location consistent with remembered far-away global landmarks, then in the location consistent with local array position landmarks, and in the location consistent with remembered local features (Brodbeck, 1994; Clayton and Krebs, 1994; Herz, et al., 1994). Other non-human animals, such as bats, hummingbirds, and squirrels have shown similar preference hierarchies (Healy and Hurly, 1998; Jacobs and Shiflett, 1999; Thiele and Winter, 2005; Vlasak, 2006a).

The traditional hierarchical model has recently been challenged by converging evidence in favor of the plasticity of landmark use in both mammals and birds. For example, while pigeons predominantly use global landmarks when a vertically-oriented array of locations is moved from its trained environment, they rely instead on local landmarks when a horizontally-oriented array is used (Legge, Spetch, and Batty, 2009). Even more surprising, when horizontal arrays are moved far enough away from the trained location, the pigeons revert to relying on global landmarks (Legge, et al., 2009). This demonstrates that pigeons' landmark preferences change depending on spatial context. A similar flexibility in spatial judgments has been observed in chickadees (LaDage, Roth, Fox, and Pravosudov, 2009).

Results on landmark use by animals – and in particular vertebrates – are thus beginning to

suggest that traditional ways of understanding how animals use different cues to a location may be too simple. Given that in the field many landmarks remain constant and it may be only one or two types of cues that are in conflict with the rest, we were interested in exploring in more detail how different combinations of landmark types trade off in guiding search behavior. We were especially interested in whether animals might be using Bayesian inference to determine their search strategy. This would explain the flexibility in their search strategies, and predict their strategies in a wide range of novel situations.

3.3 A Bayesian analysis of cue combination in navigation

For simplicity, we will focus on the navigation problem encountered by a single species – the fox squirrel. A squirrel must rely on environmental landmarks and its memory of those landmarks when searching for food. In cases where the landmarks uniquely determine the location of food items and there is no uncertainty (i.e., the squirrel's memory is perfect and the environment is static) the squirrel need only identify the location with the landmarks that match its memory. In practice, environments change and a squirrel's memory has finite precision, leading to a navigational problem for which the ideal solution requires accounting for these sources of error by determining the probability that the food is hidden in a particular location, considering the variability of landmarks including global landmarks, local landmarks, and the perceptual features of candidate locations. More formally, we imagine that the squirrel is choosing between a discrete set of locations L, trying to identify the location $l \in L$ that matches a remembered set of cues m. Locations have a history of being used for storage, with $p(l)$ being the probability of each location being used. The squirrel seeks to compute $p(l|m)$, the posterior probability of each location given the information provided by the memory m. This can be done by applying Bayes' rule,

$$p(l|m) = \frac{p(m|l)\, p(l)}{\sum l \in L\, p(m|l)\, p(l)} \tag{1}$$

where $p(m|l)$ is the probability of the remembered landmarks m given that l was the true location. In order to simplify the problem, we will restrict our attention to the case where the types of cues that comprise the memory m and their associated sources of uncertainty are independent, and no location is more likely a priori. In this case, Equation 1 becomes

$$p(l|m) = \frac{\prod k\, p(m_k|l)}{\sum l \in L \prod k\, p(m_k|l)} \tag{2}$$

where k indexes specific types landmarks and m_k is the part of the memory corresponding to type k.

The distribution of m_k given l – the probability of recalling that landmark k takes its remembered value given that l is where the food is currently hidden – depends on that landmark's tendency to change and the accuracy and granularity of the squirrel's memory. The case where each landmark is normally distributed was analyzed in (Cheng, et al., 2007a), where it was argued that pigeons may combine such landmarks optimally. A similar approach has been used in studies of cue combination by humans, where Bayesian psychophysical models have been developed to explain optimal integration of multi-sensory cues in judgment of object features, such as height and

texture (Ernst and Banks, 2002). We are interested in both continuous cues like those considered in these examples and those better represented using discrete variables, such as visual features of the candidate locations. We defer discussion of the specific landmarks and likelihood functions to after we have discussed the kinds of tasks performed by squirrels in the experimental literature in more detail.

The basic prediction produced by this account is that animals should rely on the perceived reliability of either individual landmarks or landmark categories. Existing evidence suggests that this is the case. For example, animals initially preferring one of two landmarks switched their preference when given evidence that the second landmark was more reliable (Biegler and Morris, 1996). This phenomenon has led researchers to conclude that animals generally prefer the most reliable landmarks or types of landmarks in their environment. In terms of broader categories of landmarks, the most reliable landmarks are considered to be the global landmarks. These are the far away, large landmarks that are not only the most immovable objects in the environment, but are also the ones that are least distorted by changes in visual angle or across seasonal changes to the local environment (Shettleworth, 2003). The evidence that many species of animal prefer to use global landmarks when available, supports these conclusions. However, what would distinguish the behavior of a Bayesian model from that of other models would be the optimal combination of available landmarks based on their reliabilities. In the remainder of the paper, we explore whether this approach can characterize the strategies that squirrels use in identifying spatial locations from memory.

3.4 Applying the model to squirrel navigation

To test the model outlined in the previous section, we analyzed data from a series of experiments in which fox squirrels needed to identify a location based on several different cues, taken from Waisman and Jacobs (2008). These experiments manipulated the environment in which squirrels were making decisions in order to produce conflict in the information provided by different cues, and thus provided a good test of our model.

3.4.1 Experimental setup

We analyzed results from a total of five experiments. All of the experiments we analyzed used the same basic procedure. Free-ranging fox squirrels were trained to feed from a fixed location within a square array of four feeders and then tested on two transformed versions of the array (see Figure 1a). Identification of a location could be done using three types of landmarks, which differed in their relationships to the experimental setup. Extra-array (EX) landmarks were those that were external to the elevated platform on which the squirrels were trained and tested, including objects such as large trees, bushes, and lampposts. Intra-array (IN) landmarks were the non-rewarded boxes in the array of boxes. Unique feature (UF) landmarks were defined as any features unique to the box itself, including scent, texture and the color and shape of ceramic figurines that were placed on top of the boxes.

The experiments used two kinds of tests. In hierarchy tests, all three landmark types were in conflict with one another, with no two cues being consistent in the location they identified (see Figure 1b). This provided a way to see which cue squirrels would follow if forced to choose between the three. In the majority tests, of which there were three permutations, one landmark type was in conflict with the other two landmark types (see Figure 1c). This provided a test of the

majority strategy, examining whether the squirrels always chose the location consistent with the majority of the cues.
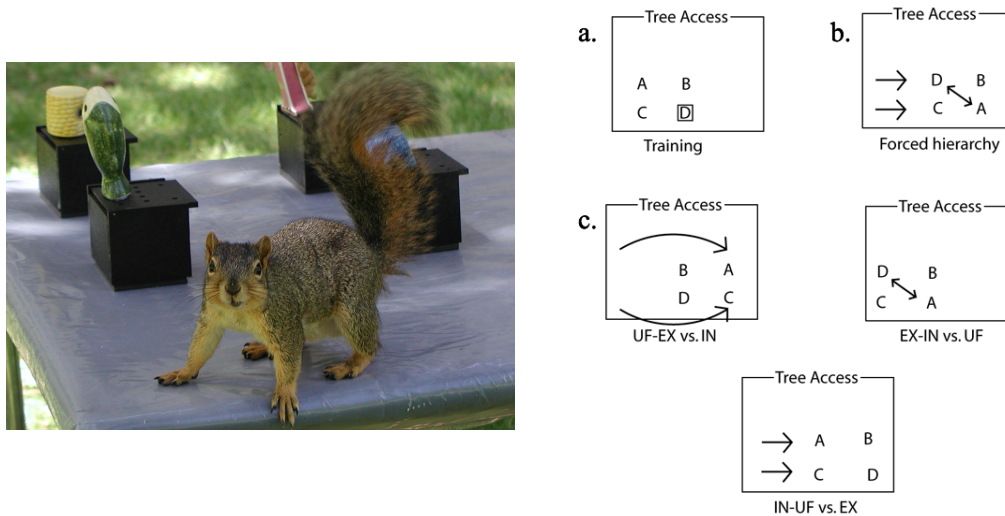

Figure 1: A picture of a squirrel participant and the experimental setup. a. A training trial in which feeder D is rewarded. b. Hierarchy test: the entire array is moved horizontally and feeder D is switched with feeder A. Unique feature (UF) cues indicate search at D, intra-array (IN) landmarks indicate search at A, and extra-array (EX) landmarks indicate search at C. c. Majority tests based on having been trained to feeder D.

3.4.2 Summary of experimental data

Data taken from these experiments were originally analyzed using binomial one-tailed tests. See Waisman and Jacobs (2008) for further discussion of the data. In summary, in Experiment 1, squirrels chose the majority location significantly greater than chance and chose the UF location in the hierarchy test ($p < 0.05$ for all tests). Since fox squirrels are known to prefer EX landmarks in hierarchy tests, the choice of UF in this experiment was perplexing. The contrast suggested that the particular experimental setup had somehow increased the saliency of the UF landmarks. To further explore this possibility, squirrels were tested at the same time the following year, summer, using a different experimental setup and found that, while squirrels continued to choose the majority location in all three majority tests, they now chose the EX location in the hierarchy test ($p < 0.05$ for all tests). From this pattern of data, it was concluded that the experimental setup had indeed increased the saliency of the UF landmarks.

To investigate possible seasonal effects on landmark use, the experiment was also run in the spring, using the second experimental setup, with less salient UF landmarks. In this experiment, squirrels no longer chose the majority location when it was the combination of IN and UF landmarks, and chose the EX location in the hierarchy test ($p < 0.05$). The spring data suggest that squirrels were no longer taking into account UF landmarks when making spatial decisions. Taken altogether, the data are consistent with the proposal that squirrels are using a majority strategy when possible, but that there are both seasonal and salience effects on the use of non-spatial UF landmarks (see Waisman and Jacobs, 2008 for further discussion of these data). The results suggested that rather than being limited to a strict hierarchy, as has been proposed in earlier studies, squirrels switched between using a linear hierarchy and a majority strategy.

3.4.3 Applying the model to the experiment

While traditional statistical analyses provide some insight into the strategies that squirrels used in these experiments, the Bayesian model introduced in the previous section gives us a more sophisticated tool for characterizing these strategies. Again, the squirrel's problem is to determine which location has the highest posterior probability of being correct given its memory of the location. We will use l to denote candidate locations and their associated cues. These cues include extra-array landmarks such as the relative position of the tree, intra-array landmarks, i.e., the position relative to other locations in the array, and visual features, such as a ceramic fish at the candidate location. The squirrel's memory of the location m contains recalled values for extra-array $\left(m_{EX}\right)$, intra-array $\left(m_{IN}\right)$, and feature $\left(m_{UF}\right)$ cues. The squirrels were naive and had no information besides the cues leading them to prefer one particular location over another, and local landmark and feature cues were novel and independently varying, so our earlier formulation (Equation 2) applies, yielding

$$p(l|m) \propto p\left(m_{EX}|l\right) p\left(m_{IN} line\, l\right) p\left(m_{UF}|l\right) \qquad (3)$$

Our model is thus defined by specifying the likelihood terms for each of these cues.

We adopted a slightly different probabilistic model for each cue type. For global landmark cues, EX, we assume that recalled locations are distributed normally around the true location, in accordance with previous cue integration models: $p\left(m_{EX}|l\right) = N\left(m_{EX}|l, \sigma^2 I\right)$, where we represent the cue values as two-dimensional vectors and I is the two-dimensional identity matrix. For intra-array cues, IN, we assume that the most salient difference between a candidate true location and the recalled location is perturbation in grid position, which can occur independently in two orthogonal directions. If we let the probability of a perturbation in each direction be ϵ_{IN}, then $p\left(m_{IN}|l\right) = \left(1-\epsilon_{IN}\right)^{2-p} \epsilon_{IN}^p$, where p is the number of perturbations out of a possible two. For feature-based cues, UF, we assume that all features are equally similar, where the probability that the feature differs between the hypothesized location and the squirrel's memory is ϵ_{UF}, so $p\left(m_{UF}|l\right) = 1-\epsilon_{UF}$ if the recalled and candidate features are identical, else $\epsilon_{UF}/3$ given that there are three other locations with their own distinct features.

Under this specification, the three parameters σ^2, ϵ_{IN}, and ϵ_{UF} capture the reliability of each type of cue, and by extension the strength of the evidence that that cue type provides and the likelihood that the squirrel will prefer that cue when all three are in conflict. The results of the experiment indicate the percentage of squirrels choosing a particular observed location, which can be used to estimate these parameters from the data. We compute the log-likelihood of the choices made by the squirrels by assuming that they used a standard probability-matching decision rule, with the probability of choosing a location being equal to the posterior probability of that location.

3.4.4 Model results for all experiments

We can use this Bayesian model as the basis for defining a nested hierarchy of models that differ in the assumptions they make about the cues that fox squirrels use in choosing locations (see Figure 2). The simplest model sets the parameters to values that make all cue values equally

likely: $\sigma^2 = 1e9$, $\epsilon_{IN} = 0.5$ and $\epsilon_{UF} = 0.25$. This model corresponds to completely uniform choices of location. The fit between this model and the data is represented by its log likelihood value which was -257.92. We can then examine the effects of estimating the parameters associated with each cue. The model that only optimized the UF parameter, ϵ_{UF}, gave a similar log-likelihood of -257.68. Thus, the UF landmark on its own does not provide a significant amount of information for explaining the data. In contrast, the log likelihood values yielded by estimating either the EX parameter σ^2, or the IN parameter, ϵ_{IN}, on their own were significantly different from that of the chance model ($p < 0.01$ for both, by a likelihood-ratio test.).
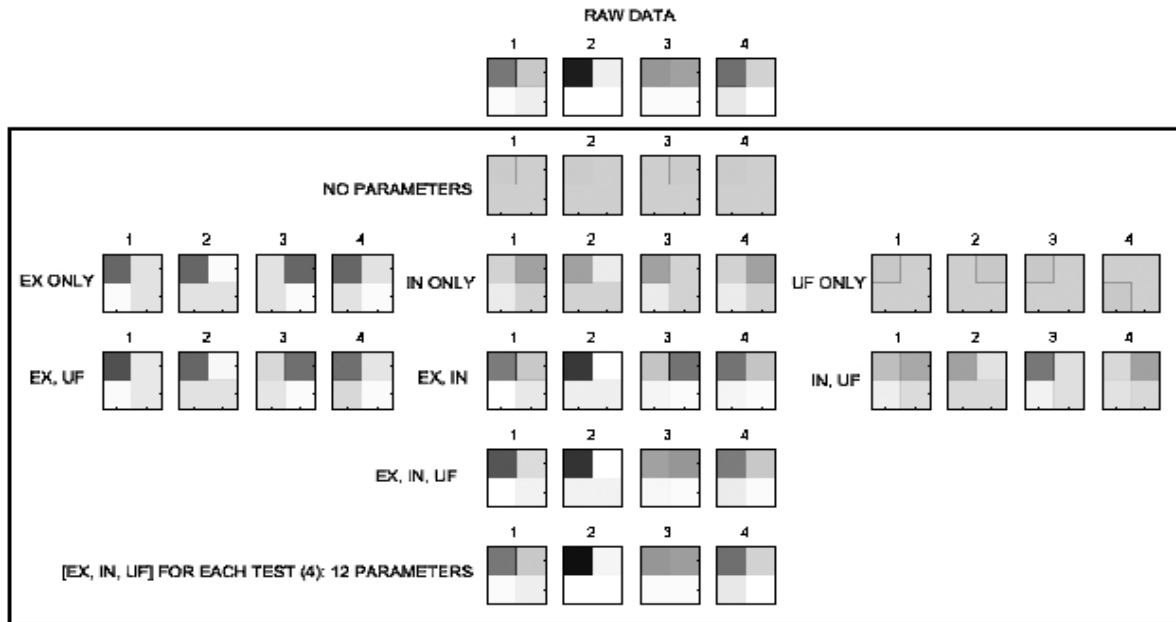

Figure 2: Predictions of each model in the nested hierarchy analysis, labeled with which parameters were estimated and the test type. 1 was the hierarchy test, 2, 3, and 4 represent the majority tests. Each quadrant represents the posterior probability of an observed location, corresponding to the four locations shown in Figure 1. Darker indicates higher probability, while lighter indicates lower probability.

As one can see in Figure 2, of the two optimized parameter models, the model that optimized both the EX and IN parameters most closely fit with the raw data, with a log- likelihood of -160.11. However, most of this fit seems to be captured by the EX parameter, since the model with EX and UF parameters also does well at fitting the data, with a log-likelihood of -172.48. Even so, the log-likelihood of the model that estimated parameters for all three cue types was significantly better at predicting the data than any combination of only two parameters or one parameter on its own ($p < 0.01$ for all comparisons). This model estimated the values of the parameters to be 15.46 for σ^2, 0.30 for ϵ_{IN} and 0.60 for ϵ_{UF}. So while it seems that EX has the greatest influence on the choices of the squirrels, their behavior is consistent with that of a model that uses all three landmark types.

3.5 Further uses of the Bayesian framework

Our Bayesian model suggests that squirrels are sensitive to all three types of landmarks, and

provides information about the relative strength of those landmarks. In this section, we consider how these results relate to the majority strategy, and how the model can be used to explore variation in the importance of cues due to differences in salience and season.

3.5.1 The majority strategy and Bayes

The study from which we took our data found that fox squirrels can switch between relying on one dominant landmark type – a traditional hierarchy strategy – and using a majority strategy. When the squirrels were presented with situations in which each landmark type indicated a different location, they predominantly relied on external, global landmarks. However, when presented with situations in which two landmark types were consistent with one another and in conflict with a third, they chose to search in the location consistent with the greatest number of landmark types. Squirrels chose the majority location even when it was in conflict with the dominant, global landmarks. These results support the idea that, like pigeons and chickadees, squirrels are able to adapt their search strategy to the particular spatial context. This idea of a majority strategy is also supported by previous work in a closely related species, the southern flying squirrel (S. E. B. Gibbs, et al., 2007). Flying squirrels primarily rely on global external landmarks, but they prefer to use information from local landmark types instead when those are consistent with each other and in conflict with global landmarks.

This type of decision strategy can be modeled using a Bayesian approach. Under the same distributional assumptions as before and a maximizing or probability matching decision rule, the squirrel is most likely to visit the location for which $p(m|l)$ is maximal. For this location l_i, $p(m_{EX}|l_i) p(m_{IN}|l_i) p(m_{UF}|l_i) > p(m_{EX}|l_j) p(m_{IN}|l_j) p(m_{UF}|l_j)$ for all $j \neq i$. Equivalently, we can represent this relationship in terms of the evidence provided by each feature, i.e., the log odds of the recalled cue values for location i versus j. For instance, the evidence provided by the intra-array cues is $e_{IN}(i,j) = \log(\frac{p(m_{IN}|l_i)}{p(m_{IN}|l_j)})$. For the majority strategy to apply, no cue may provide evidence dominating the combined evidence from other two: the maximum possible evidence for one cue cannot exceed the sum of the maximum negative evidence provided by the other two, or else conditions may arise in which a Bayesian agent's actions are consistent with hierarchical strategy rather than a majority strategy. We can establish some bounds on σ^2 (in terms of a maximal distance d between candidate and recalled locations), ϵ_{IN} and ϵ_{UF} that determine when a majority strategy will no longer apply: violations of $max \, e_a(i,j) < max \, e_b(j,i) + max \, e_c(j,i)$ for any combination of cues a, b, and c imply that the Squirrel's behavior can deviate from a majority strategy.

Determining whether a set of parameters is consistent with the majority strategy requires computing the maximal evidence that can be provided by each kind of cue. In our model, this is $(2\sigma^2)^{-1} d^2$ for EX, $\log((1 - \epsilon_{IN}^2 \epsilon_{IN}^{-2}))$ for IN, and $\log(\frac{1 - \epsilon_{UF}}{\epsilon_{UF}/3})$ for UF. Plugging these values into the constraints identified in the previous paragraph, we obtain the following inequalities:

$$(2\sigma^2)^{-1} d^2 < \log((1 - \epsilon_{IN})^2 \epsilon_{IN}^{-2}) + \log((1 - \epsilon_{UF}) 3 \epsilon_{UF}^{-1})$$

$$\log((1 - \epsilon_{IN})^2 \epsilon_{IN}^{-2}) < (2\sigma^2)^{-1} d^2 + \log((1 - \epsilon_{UF}) 3 \epsilon_{UF}^{-1})$$

$$\log\left(\left(1-\epsilon_{UF}\right)3\,\epsilon_{UF}^{-1}\right) < \log\left(\left(1-\epsilon_{IN}\right)^2\epsilon_{IN}^{-2}\right) + \left(2\,\sigma^2\right)^{-1}d^2$$

If these inequalities are satisfied, then our Bayesian model will produce behavior consistent with the majority strategy. The parameter estimates computed from the experiments summarized above did not meet these criteria, suggesting that squirrels' cue combination behavior cannot be explained by the use of a majority strategy.

3.5.2 Capturing variations in salience and season

The experiments summarized in the previous section incorporated two additional factors that may have affected the results: use of two different sets of stimuli, in which the UF cues may have differed in salience, and testing in two different seasons (Summer and Spring). We analyzed the possible salience and season effects by repeating the analyses from the previous section on two different subsets of the data: one that included only experiments run in the spring, and another excluding Experiment 1, since it was the only experiment that used the experimental setup that seemed to increase the saliency of UF landmarks. Figure 3 summarizes these analyses.
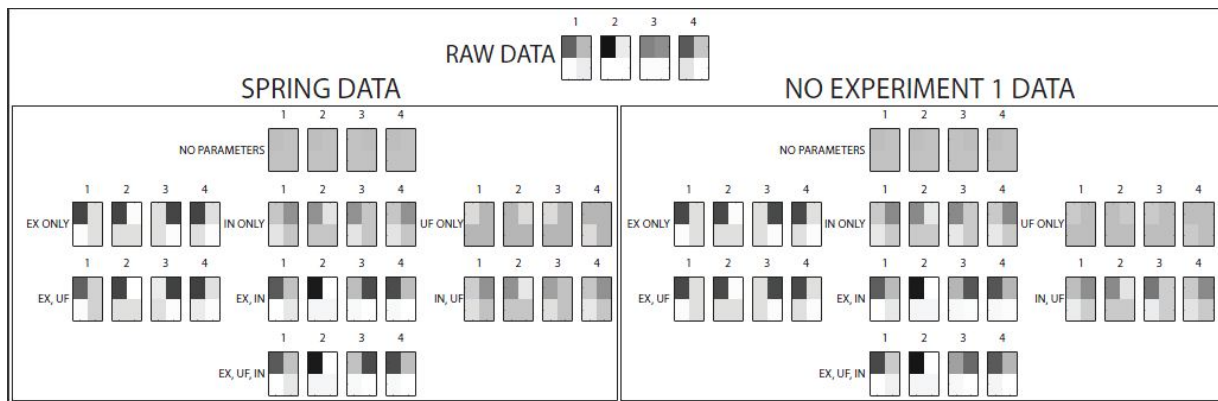

Figure 3: Model predictions for the seasonal and salience analyses. Format is the same as Experiment 1. A. are the analyses using the subset of the data that were collected only in the spring, Experiments 2-4. B. are the analyses using the subset of the data that were collected using the second experimental setup, Experiments 2-5.

Seasonal effects

Using data from only the spring experiments (Figure 3a), the inclusion of ϵ_{UF} , while significantly better than having no parameters ($p < 0.05$), did little to enhance any model in which it was included. The inclusion of both IN and EX parameters was, however, significantly better that including either parameter alone ($p < 0.01$ for both comparisons). Unlike the model using the full data set, these data were predicted just as well by the model that included only the IN and EX parameters as they were by the model that optimized all three parameters. In fact, the log likelihoods of both were identical, with a value of -89.53. The model including the EX and IN parameters estimated the parameters to be 14.46 for σ^2 and 0.30 for ϵ_{IN} . Since the simplest model that best fits the behavioral data of the squirrels during spring this suggests that the squirrels were not taking UF landmarks into account when making spatial decisions at this time, as concluded in Waisman and Jacobs (2008).

Salience effects

In the analyses that excluded Experiment 1 for having a different experimental setup (Figure 3b), the model that optimized the IN and EX parameters was once again not significantly different from the model that included all three parameters. The log- ikelihood values for these models were nearly identical, with values of -121.8 and -120.7 respectively. The model that included the intra-array and extra-array parameters estimated the parameters to be 14.5 for σ^2 and 0.26 for ϵ_{IN} . Since, once again, the model that best matched the squirrels' behavior was the one that did not optimize the parameter for the UF landmark, these analyses support the idea that they were less salient in the second experimental setup.

3.6 Summary and Conclusion

Taken together, the results of these analyses illustrate how our Bayesian framework can be used to characterize the cues used by animals in navigation, and are consistent with previous claims about navigation in squirrels. Across all data sets that we ran, the extra- array parameter, σ^2 , resulted in a statistically significant improvement in fit whenever it was added to a model ($p <$ 0.01 for all comparisons). This agrees with previous research stating that, for squirrels in the field, the global landmarks are the most salient when navigating (Jacobs and Shiflett, 1999; Vlasak, 2006a, b). The fact that for both the spring data set and the data set excluding the first experiment, optimizing the parameter for the unique feature landmarks, ϵ_{UF} , yielded no predictive power beyond that of the other landmark types, corroborates the conclusion that UF landmarks were less salient to the squirrels both in the spring and when using the second experimental setup. From these analyses we can conclude that a Bayesian model is a useful tool for exploring the spatial strategies. The pattern of choices exhibited by the squirrels matched that of a rational model taking into account all three available landmark types. Additionally, model comparisons provided a tool for investigating both seasonal and salience effects in the data.

In light of this Bayesian analysis, there are two future directions that we are currently investigating. One is a single landmark study to confirm the parameter estimates that the models provided, while the other is the effect of priors. While we assumed uniform priors over our observed locations, it is more than likely that priors in the natural environment are not uniform. Some trees may be more abundant seed providers, while others may supply higher quality seeds. However, we do not know whether they learn these parameters over time or whether they are innate biases. In a novel study on pine siskins (Humber, Brodbeck, and Warkentin, 2009), researchers found that when they provided food at a 3:2:1 ratio in a set of three feeders, the birds quickly adapted the number of visits made to each feeder to match the ratio of food. This suggests that priors may play an important role in navigation for at least some species, and are a factor that should be taken into account when modeling spatial memory.

CHAPTER 4: The emergence of allocentric spatial strategies in preschool age children

4.1 Introduction

Studies looking at how adults give directions have shown that most adults will actually use multiple spatial strategies when giving one set of directions, such as, go north on shattuck avenue (cardinal direction), turn right at the fast food restaurant (egocentric, route-based), and look for the green awning (feature-based) (Bell, 2002). However, not all of these strategies come naturally to young children. Spatial cognition is not considered fully mature until around 10 years of age. In part this is due to the long maturation process of both the medial temporal lobe and the pre-frontal cortex which are considered two of the primary brain regions responsible for memory in general and spatial memory in particular. As children develop, these regions increase both in their specialization for particular tasks, including spatial ones, and are recruited more reliably during those tasks (Ghetti, DeMaster, Yonelinas, and Bunge, 2010). Similar developmental changes are well established in the lab rat (Jarrard, 1993). However, experiential factors also exert strong control over the maturation of spatial cognitive abilities (Clearfield, 2004; Kermoian and Campos, 1988) .

Therefore, for children to accurately orient in their environment, they must develop spatial strategies to remember previously visited locations. One way to explore the initial stages of spatial strategy formation is by understanding how children use landmarks to make decisions about novel spatial problems. Previous research has devoted itself to exploring when children begin to use landmarks (e.g. Acredolo, 1978; Acredolo and Evans, 1980; Bremner, 1978; Bremner and Bryant, 1977) and which landmarks are then used both in oriented and disoriented spatial search tasks (e.g. Foreman, et al., 1990; Laurance, Learmonth, Nadel, and Jacobs, 2003; Learmonth, Nadel, and Newcombe, 2002). However, what remains to be explored is how and when children integrate those landmarks into spatial search strategies.

Cue integration has only recently been directly explored in the area of spatial cognition in children (Nardini, et al., 2008). Results showed that preschool age children did not integrate self-motion information with landmark information when searching for a hidden object, while adults did. However, the landmarks were distal landmarks on the walls of the experimental arena. Although there is evidence that preschool age children will use distal landmarks to orient in some instances (e.g. Bullens et al., 2010), the studies in which preschool age children do not use distal landmarks predominate (Laurance, et al., 2003; Overman, et al., 1996).

4.2 The development of spatial cognition in children

The first major cognitive transition necessary for a more comprehensive spatial strategy starts in infancy, around the physical locomotor transition. This transition revolves around the ability to encode a location in reference to landmarks external to oneself (allocentric) rather than in reference to one's own body position (egocentric). One must be able to encode locations using an allocentric frame of reference to construct a comprehensive, flexible spatial strategy, or as Tolman (1948) would have labeled it, a broad cognitive map. For example, when trying to remember one's parking location, one could take a look at the spot and encode it as to one's left. However, once you move in space, the location in reference to your body position would change and this information would no longer be useful. Encoding the location in reference to local

landmarks would be more useful, since it is unlikely that lampposts will change position frequently. Many studies have shown that prior to 8 months infants use egocentrically encoded action sequences when searching for locations. Between 9 and 11 months infants begin to transition to an allocentric, external frame of reference (Acredolo, 1978; Acredolo and Evans, 1980; Bai and Bertenthal, 1992; Bremner, 1978; Bremner and Bryant, 1977). This transition has been attributed both to physical maturation and to transition from the relatively sedentary lifestyle of a pre-crawling infant to the more spatially experienced crawling or even walking lifestyle of older infants.

Nonetheless, the ability to use allocentric landmarks at this age is tenuous at best. Three factors greatly affect the number of egocentric behaviors that are displayed: the saliency of the landmarks, the distance between the landmark and the target location, and whether the child rotates themselves around a space or whether the space is rotated around the child. First, using very salient landmarks such as neon lights and large objects, 11 month old infants have been shown to use allocentric landmarks. However, those same infants opt for the egocentric strategy when less salient landmarks are used (Acredolo and Evans, 1980)). Second, landmarks that are in the same place or even a feature of a target location, such as a marker on top of a covered hole in the ground or the color of the target box are considered coincident with the target location. 12 month old infants have been shown to consistently rely on such coincident landmarks. However, when the landmarks are located even a small distance away from the target location, the same infants perform poorly (Bushnell, McKenzie, Lawrence, and Connell, 1995).

Furthermore, when 8 month old post-crawling infants are asked to make a spatial choice after moving themselves around a two-choice experimental setup, they pick the allocentric position. However, those same infants choose the egocentric position when the setup is rotated in front of them (Bai and Bertenthal, 1992). Infants need to experience rotational cues to update their spatial strategies. Thus, the egocentric frame of reference at this age seems to be the default strategy. If landmarks are not salient, and not coincident with the target location and when the infant does not experience rotational cues, the child is more likely to adopt an egocentric search strategy. However, even 11 month old infants did show improved performance with salient, indirect (non-coincident) landmarks when compared to their search in a no landmark condition (Acredolo and Evans, 1980). This suggests that even very young children can, in some circumstances, encode locations using non-coincident, allocentric, landmarks.

As infants move into toddler-hood, it is well established that they are able to use landmarks that are non-coincident with a target location to find a hidden object from memory both in large-scale and small-scale environments (Deloache and Brown, 1983; Ratner and Myers, 1980). When target locations in a delayed response task were placed adjacent to natural landmarks (e.g. a couch), older toddlers (24-29 months) performed better than younger toddlers (18 – 22 months) (Deloache and Brown, 1983). Performance of children over 21 months old in a spatial search task was also improved by the presence of non-coincident landmarks, while there was no improvement for younger children (16-21 months) (Newcombe, Huttenlocher, Drummey, and Wiley, 1998). Yet, as determined by their use of landmarks toddlers, like younger infants, use a fairly limited or narrow spatial strategy, relying primarily on proximal, nearby, allocentric landmarks, rather than more distal, further away, allocentric landmarks. It is not until the preschool years (3-4 years) that children begin to show evidence of using more distal landmarks

which would allow for more comprehensive, flexible strategies. 2, 3, and 4 year olds in a touch-screen search task all showed decreased performance in a proximal landmark based task when compared to their performance in a coincident landmark task. However, 2 year olds did significantly worse than the older children in the proximal landmark-based task. Only when the number of distractors was reduced to one did the 2 year olds perform as well as the older children (Sutton, 2006). This suggests that around the two to three year transition, children begin to develop a more robust use of non-coincident landmarks and accordingly a more comprehensive and flexible spatial strategy.

Thus, by three years of age, children have started to reliably use allocentric, non-coincident landmarks, the basis of a comprehensive and flexible spatial strategy. Evidence suggests that it is also at this time, between the ages of two and five, that spatial cognition begins a significant period of development (Foreman, et al., 1990). In one study, children younger than 5 years old did not perform as well as older children in 3 different spatial tasks (Overman, et al., 1996). The authors concluded that spatial relational solutions were not mature until six years of age, but that younger children were in a period of transition since a small but significant percentage of the younger children were able to use external landmarks to solve spatial problems. The preschool ages of three and four are therefore ideal ages at which to study the beginning of the formation of a comprehensive, adult-like spatial strategy. We chose a small-scale table-top task for ease of use at various preschools. We have reason to believe that 3-4 year olds will use allocentric coding on a small table top task since previous research found that preschool age children learn faster in an allocentric condition than in an egocentric condition in a small table-top task (Haun, Call, Janzen, and Levinson, 2006).

4.3 Experimental design

To determine the spatial strategies of preschool age children we turned to recent work in a diurnal mammal, the fox squirrel, that has shown that squirrels can use a flexible spatial strategy, called a majority strategy (Waisman and Jacobs, 2008). Using this strategy, squirrels choose locations based on the number of landmark types indicating a particular location, rather than choosing based on the particular type of landmark indicating a location. It is possible that while children at this age may have a rudimentary map of space, they, like the squirrels, may be able to use that map in flexible ways to solve novel spatial problems. On the other hand, one argument for using a flexible strategy is that relying on a single landmark type in natural habitats can be detrimental since the landscape and its landmarks can change drastically from season to season and from year to year. Since, in contrast with the world of squirrels, man-made landmarks rarely move around, a more rational option for children may be a hierarchical strategy based on preference for a single type of landmark. Using the methods previously established in fox squirrels we explored children's use of landmarks and landmark strategies in two experiments.

In Experiment 1, we explored children's landmark type preference in a hierarchical test and their majority strategy use in a majority test that pitted their preferred landmark type against the two remaining landmark types. We also included three single landmark tests to determine if children at this age were truly encoding all three landmark types. In Experiment 2, we explored how moving the previously coincident landmark to a proximal, adjacent location to the possible locations would affect children's choices in all the tests. We predicted that simply by making the coincident landmarks non-coincident and therefore not intrinsic to the hiding locations, children

would rely less on a cue-based strategy and on more distinctly spatial strategies. We believed that this could prompt children to pay attention to all the available spatial landmark types which could change their decision strategy in the majority test. We also included a second condition in Experiment 2 to determine whether children were using egocentric or allocentric strategies.

4.4 Experiment 1: spatial cognition using coincident and non-coincident landmarks

The purpose of this study was to determine which types of landmarks preschool age children encode when attempting to remember a discrete location and how they use those landmarks when they are in conflict with one another. Children were taught to find a toy in one of four discrete locations. The locations were marked by green plastic boxes set up in a square array on a child-sized table. Each box was distinguished by a unique ceramic figurine attached to the top of it. The target location could be encoded using any one or a combination of three landmark categories. One way children could encode the location is by using the associated figurine as a coincident landmark (coincident landmark position). They could also encode the position of the target location relative to the positions of the other three boxes (array position). Finally, they could encode the position of the target location relative to its position on the table or in the room (absolute position) (see Figure 1b for an example of these three encoding strategies). During testing, the locations and all landmarks associated with them were shifted to determine which of three possible sets of landmarks children were relying on and whether children were using a narrow or broad spatial strategy.

We used three types of tests: the forced-hierarchy test, the majority test, and the single landmark tests. The child's choice in the forced-hierarchy test indicated their preferred landmark type when all three landmark types were in conflict with one another. In the majority test, one location remained consistent with the child's preferred landmark type, while another location was consistent with both the remaining two landmark types. If the child continued to choose based on their preferred landmark type this would indicate a spatial strategy based on hierarchy of preference for landmark types. However, if the child chose the majority location over their preferred landmark type, this would indicate that they were using a majority spatial strategy. In the single landmark tests only one location was consistent with the tested landmark type and all remaining locations were distractors. We hypothesized that children in the hierarchy test would primarily choose the location consistent with the coincident landmarks, but would choose the majority location over their preferred landmark type in the majority test. The single landmark trials were present to determine whether children were in fact paying attention and remembering all three types of landmarks.
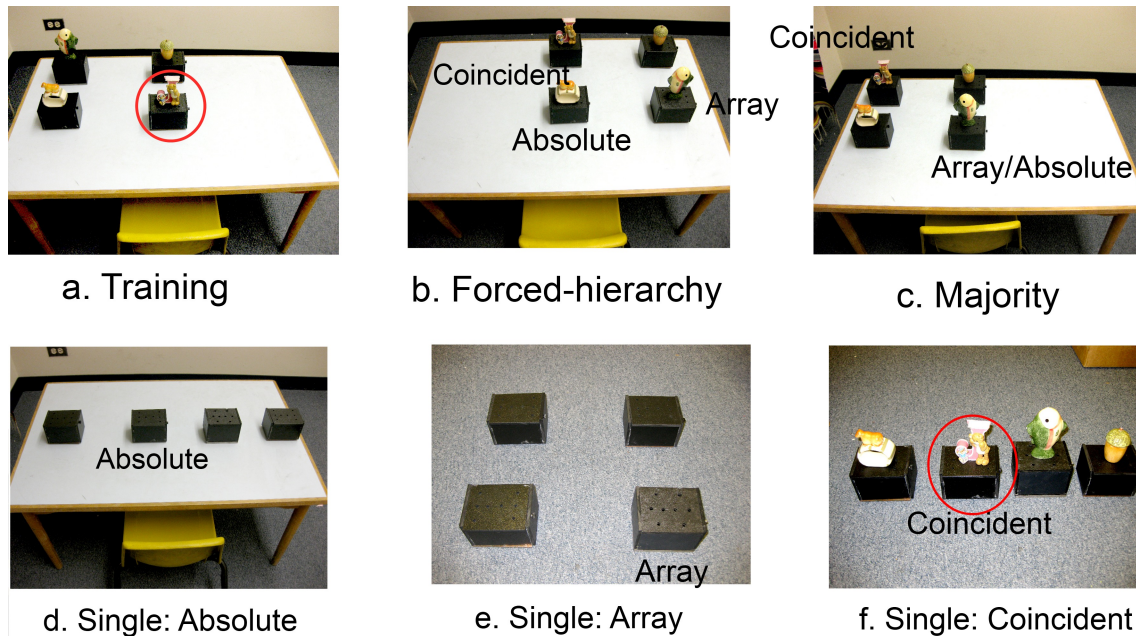
Figure 1: Photographs of the experimental setup in Experiment 1, a. starting with one of two possible training setups b. The forced-hierarchy test for the specified target location. c. The majority setup pitting the coincident landmark against both the array position and absolute position landmarks. d.-f. The three possible single landmark test setups.

4.4.1 Experimental methods

Participants

The sample consisted of 25 preschool age children ($M = 48.80$ months, $SD = 7.81$, range = 36.53 - 59.21 months) recruited at preschools affiliated with the University of California at Berkeley. Participants were tested during the school day in study rooms located at the preschools. The sample was primarily middle- to upper-middle class based on previous analysis of the schools, but no formal demographic data were collected in this study. 12 participants were female, 13 were male. 11 participants were 3 years old ($M = 41.06$ months, $SD = 3.27$, range = 36.53 – 46.42) and 14 were 4 years old ($M = 54.89$ months, $SD = 3.71$, range = 48.36 – 59.21). Three additional participants were recruited but were excluded from the final sample because of experimenter error (2) and unwillingness to participate (1). All children were naive to the experimental procedure. Parents gave written permission prior to testing and children were asked for verbal consent immediately prior to participation.

Test Environment

The study took place at the preschools in testing rooms with uniform wall coloring. Children sat across from the experimenter at a small rectangular play table (table dimensions varied slightly depending on the school). A single video camera recorded each session, focusing on the child's upper body and torso and the table with the experimental stimuli. A second experimenter sat in a corner of the room taking notes. The setup consisted of four identical green, acrylic boxes (10.5cm x 7cm x 7cm) in a square-shaped pattern (range: 30 cm. – 35 cm. square) on the table with one edge of the square aligned at the center of the table. One ceramic figurine was attached to the top of each box with Velcro®. All figurines were different from one another in both shape and color (Figure1a).

Procedure
Child enters the room and is introduced to the second experimenter, pre-training begins.

Pre-Training:
The child sits opposite an experimenter on one of the two long sides of the rectangular play table. The boxes and ceramic figurines are already in place on the table. The experimenter tells the child that they are going to play a hide-and-seek or memory game and explains the "rules" of the game. First, a toy will always be hidden in the same place on the table. The experimenter then places a toy in one of the boxes and the child is asked to open the box and retrieve the toy. To establish motivation, the child is told that they will collect toys throughout the experiment that they can play with.

Second, the other boxes are always locked and do not have toys inside. The child is encouraged to try to open the locked boxes for themselves to avoid their desire to explore them during the study. Third, there are times when the child will be allowed to open the box to retrieve the toy, "I will say, go ahead, find the toy", while at other times the child will only be allowed to point to the boxes, "I will say, this is a no-touching part, you can point to which box you think the toy would be in." Once the child is familiar with the experimental procedure, the experimenter starts the first training trial.

Training:
All objects are removed from the table and then placed back on the table in the same configuration as before. The child is told to, "find the toy, it's in the same place." Once the child has opened the correct box without visiting any other boxes first on two consecutive trials, the experimenter runs the first test trial. Between all test trials, there is at least one training trial in which the child is asked to find the toy in the original training configuration. If the child chooses correctly, the experimenter moves on to the next test trial. If the child chooses incorrectly, the experimenter repeats training trials until the child chooses correctly once. In between trials, the child is encouraged to play with the toys they have collected.

Tests:

We used three different testing setups to determine landmark use strategies:

The first was a completely dissociated *forced hierarchy* test. In this test, the boxes were shifted such that one box remained in the same position relative to the room and the table as the original target location had been (absolute position), a second box was in the same position relative to the three other boxes as the original target location had been (array position), a third box was located coincident with the same ceramic figurine as the original target location had been as the original target location had been (coincident landmark position), and the remaining box was a distractor. The first choice the child made in this test was considered their preferred landmark type.

The second test was a *majority dissociated* test dependent on the child's choice in the hierarchy test. In this test, two types of landmarks were consistent with one location, while the preferred landmark indicated a different location. For example, if the child had chosen the array position first in the hierarchy test, in the majority test, one box would continue to be in the correct array

position, while another box would be both in the correct absolute position and associated with the correct coincident landmark (i.e. with the correct figurine on top of it). The remaining two boxes were distractors.

Finally, children participated in a series of three *single landmark* tests in which only one type of landmark was available (Figure 1d-f). For example, in the array position only test, the four boxes without figurines were placed in a square array on the floor of the testing room. In this configuration one box is in the correct array position, while there are no coincident landmarks to use and no box on the table in the absolute position.

In test trials, children were not allowed to touch or interact directly with the boxes and children received no feedback about their choices since no boxes were opened. Children were asked to point to, "where do you think the toy would be?" That box was then removed from the table and the child was asked, "if the toy was not there, where else would you look?" In piloting it was determined that children would not tolerate making more than two choices during test trials. After the child's two choices, the experimenter removed all the boxes and figurines from the table and set up the next inter-test training trial. Test trials were run with the hierarchy test first to determine the dominant landmark type of the child, then the majority test, then all single landmark tests. Gender, age, the target location and the order of the single landmark tests were counterbalanced across all children.

Data collection

All children's actions during testing were coded both in real-time by a second experimenter who remained uninformed of the experimental hypotheses and by experimenter one from videotape of the session. A child was coded as having made a choice if they attempted to raise the lid, pick up, or pointed to any one of the boxes. Inter-coder agreement was 100%. Since there were 4 possible hiding locations, chance was 25%. All analyses were run using first choice data. One child was excluded from the majority test analysis due to experimenter error in the setup. All data were tested using either two-tailed binomial tests or Fisher exact tests.

4.4.2 Results and Discussion

Children did exceptionally well in the training trials. Most children reached criterion in the minimum number of trials needed to reach criterion (Mode = 2), and most children (18 of 25) chose correctly on all inter-testing trials (binomial test, $p < 0.001$). There were no significant age or gender differences, so we pooled the data from both 3 and 4 year olds and males and females. Children primarily relied on the coincident features of the location in the hierarchy test (i.e. the individuating ceramic figurine) (20 of 25 children, $p < 0.001$, binomial test). 19 of 24 children chose to continue using their preferred landmark type in the majority test trial. Since they did not switch to the location indicated by a majority of landmark types in the majority test trials, this suggests that are not using a majority strategy. However, while children did appear to be remembering the array position and the intrinsic, coincident landmarks in the single landmark test trials ($p < 0.05$ and $p < 0.0001$ respectively) they did not appear to be paying attention to or remembering the possible absolute position landmarks (8 of 25 children chose the correct location in this single landmark test trial, $p > 0.10$, binomial test). For the majority location to be a majority, one would have to be encoding using all three types of landmarks. Given that children were not paying attention to all three possible landmark types, it is unlikely that they would have

chosen the majority location.

a. Hierarchy Test
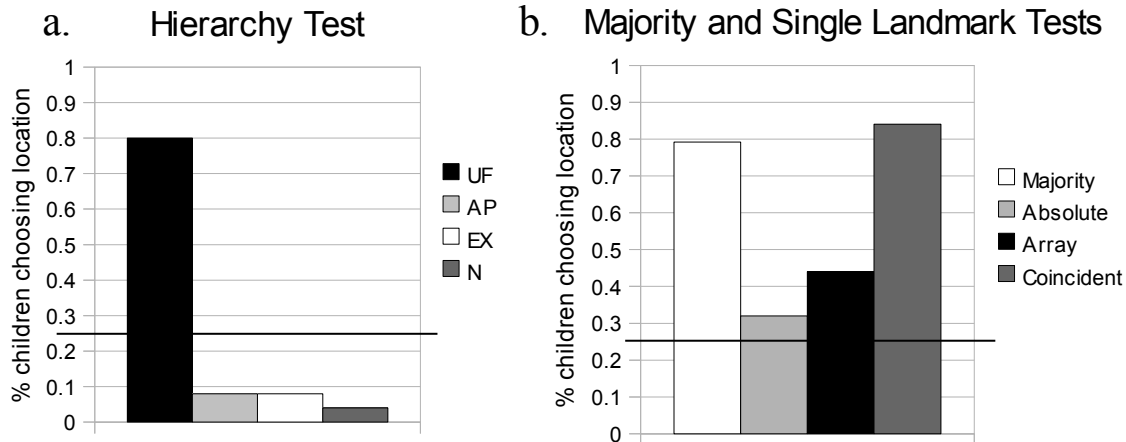
b. Majority and Single Landmark Tests

Figure 2: a. The % of children choosing each location in the hierarchy test b. The % of children choosing the target location in the majority and the three single landmark tests. Chance is marked by a line at 25%.

These results suggest that preschool age children prefer to use coincident landmarks over non-coincident landmarks. Related work has also demonstrated that 3 year old children were more likely to use a beaconing strategy based on coincident landmarks when available to them over a relational or place strategy (Horn and Myers, 1978; Sutton, 2006). However, it is possible that by having landmarks coincident with the locations, these landmarks overshadow learning of non-coincident landmarks. Studies in rats have demonstrated robust reciprocal overshadowing in spatial tasks (Chamizo, Aznar-Casanova, and Artigas, 2003; Sanchez-Moreno, Rodrigo, Chamizo, and MacKintosh, 1999).

In these studies, rats perform better in spatial tasks that test for the use of either of two possible cues for orientation when trained with those cues in isolation rather than when they are trained with those cues combined. For example, if trained with an object that emits a constant sound as a landmark, rats perform poorly in tests with either the sound or the object alone. In contrast, rats perform well if they are initially trained using either the sound or the object in isolation. Thus, the rats are able to use these cues in isolation, but do not learn the cues as well if during training they are presented in combination. Each cue overshadows the learning of the other. Furthermore, similar results in both clark's nutcrackers (Goodyear and Kamil, 2004), pigeons and adult humans (Spetch, 1995) have shown that overshadowing in spatial tasks can occur based on relative distance of landmarks to the target location. The closer a landmark is to the target location, the more likely it is going to overshadow the learning of other landmarks further from the target location. Along these lines, since a coincident landmark has no distance between it and the target location it is highly likely that learning based on this landmark will overshadow the learning of other landmarks.

This possibility is further supported by the fact that young children did not choose the correct location in the absolute position test. While neither 3 nor 4 year old children are considered particularly adept at using distal landmarks for orientation, we would have expected them to be able to orient using the absolute position. Both in three large-scale spatial tasks (eight arm RAM,

Dry Morris maze, and open field search) and a virtual reality environment (circular room with distal wall cues) 3 and 4 year olds regularly performed worst in conditions in which they had to rely only on distal spatial information (Laurance, et al., 2003; Overman, et al., 1996). However, In the same eight arm RAM study mentioned above, when only four of the eight arms were made available, the same young children performed as well as the older children (Overman, et al., 1996). This suggests that if the cognitive demands of a task are taken into account, young children may be capable of limited use of distal landmarks.

Even young infants are sensitive to absolute position. In a two-choice, table-top search task, creeping, 8 month old infants searched at random between absolute position and coincident landmark position when the table setup was rotated in front of them (Bai and Bertenthal, 1992). If the infants had been sensitive only to the coincident landmarks they should have chosen those in the table displacement condition over the absolute position. Furthermore, when they were rotated around the table, they chose the location that was both in the absolute position and associated with the correct coincident landmarks, demonstrating that they do have a preference when both positions are in concordance with one another. To explore whether providing children with salient coincident landmarks caused them to adopt a cue-based strategy, we ran a second experiment in which the ceramic figurines were placed a few inches to the side of the boxes rather than coincident with them. Thus all landmarks in the second experiment were non-coincident with the locations.

4.5 Experiment 2: spatial cognition using only non-coincident landmarks

The purpose of this experiment was to determine whether children were using a cue-based strategy in Experiment 1. The coincident landmarks from Experiment 1 were moved adjacent to the hiding locations and all tests were run as in Experiment 1. In this *non-coincident* condition there were three types of landmarks, the now adjacent landmarks, the array position landmarks, and the global position landmarks. Additionally, since pilot work suggested that children were now choosing correctly in the absolute position test, a second condition, the *rotation* condition, was included to established whether children were using an egocentric or allocentric strategy in the. In the test itself, the correct absolute position was also the correct position in terms of egocentric cues since the child did not change position and thus the location was in the same position relative to the child during training and testing.

To ascertain which strategy children used in the absolute position test, in the rotation condition, the array position and coincident landmark position tests were replaced with a rotation test in which children were asked to trade places with the experimenter before making a choice in the absolute position test setup. If children chose the same location relative to their body-position that they had chosen in the original absolute position test, they were labeled as using an egocentric strategy. If they chose the same absolute position that they had chosen in the original absolute position test, they were labeled as using an allocentric strategy. There is evidence that at this age, children are much more likely to use an allocentric frame of reference rather than an egocentric one (Haun, et al., 2006).

4.5.1 Experimental methods

Participants

The sample consisted of 42 preschool age children (*M* = 49.69 months, *SD* = 6 months, range =

36.36 – 61.32 months) recruited at preschools affiliated with the University of California at Berkeley. There were 24 participants in the relative replication condition ($M = 48.95$ months, $SD = 6.71$ months, range = 36.36 – 61.32 months). There were 18 participants in the rotation condition ($M = 50.69$ months, $SD = 4.91$ months, range = 44.88 – 59.28 months). Participants were tested during the school day in study rooms located at the preschools. The sample was primarily middle- to upper-middle class based on previous analysis of the schools, but no formal demographic data were collected in this study. Of the total sample, 25 participants were female and 17 were male, 16 participants were 3 years old ($M = 53.51$ months, $SD = 3.47$ months, range = 36.36 – 47.52 months) and 26 were 4 years old ($M = 43.49$ months, $SD = 3.48$ months, range = 48.84 – 61.32 months). Three additional participants were recruited but were excluded from the final sample because they did not reach criterion in training (1), experimenter error (1), and unwillingness to participate (1). All children were naive to the current procedure. Parents gave written permission prior to testing and children were asked for verbal consent immediately prior to participation.

Test Environment and Procedure
All experimental stimuli and setup were the same as described in Experiment 1, except that the unique ceramic figurines were placed to the sides of the boxes, between 2 and 6 cm away from each box, depending on the specific figurine (adjacent landmarks). The figurines were placed in a non-square array pattern to help children distinguish between array position landmarks and adjacent landmarks. Each figurine remained closest to one box (Figure 3). Gender, age, and the target location were counterbalanced across all children in both conditions. As in Experiment 1, the order of the single landmark tests in the non-coincident condition was also counterbalanced.
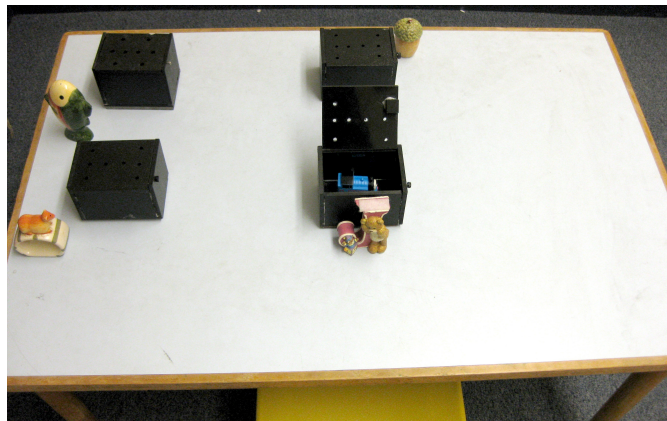
Figure 3: Photograph of the setup in Experiment 2 with the adjacent landmarks to the side of the hiding locations.

Tests

In both conditions, as in Experiment 1, children were initially run in the hierarchy and majority test trials. The children in the non-coincident condition then received exactly the same procedure as the children in Experiment 1.

Rotation condition
After the initial hierarchy and majority tests, children were first tested in the absolute position

test to establish their non-rotated choice for the absolute position. After an inter-test training trial, children were tested in the rotation test. In the rotation test, children were first asked to trade places with the experimenter. Once the child sat in the experimenter's seat, they were asked, "Can you point to where you think the toy would be?" That box was then removed from the table and the child was asked, "If the toy wasn't there, where else would you look?"

All other procedures are as described in Experiment 1.

Data collection
All children's actions in the test phase were coded both in real-time by the second experimenter who remained uninformed of the experimental hypotheses and by experimenter one from videotape of the session. A child was coded as having made a choice if they attempted to raise the lid, pick up, or pointed to any one of the boxes. Inter-coder agreement was 100%. Since there were four possible hiding locations, chance was at 25%. All data were tested using either two sided binomial tests or Fisher exact tests. All analyses were run using first choice data unless otherwise noted.

4.5.2 Results and Discussion

There were no significant differences between conditions in either the hierarchy, majority, or absolute position tests, so the data for those tests was pooled across conditions. For the remaining tests: the array position, the adjacent landmark and the rotation test, only the participants from each condition were used for analysis.

As in Experiment 1, children excelled at the training for this task. Most children took the minimum number of trials required to reach criterion and no more (Mode = 2). Also, most children (31 of 42) chose correctly on all inter-testing trials on their first try. In contrast with the results from Experiment 1, children with all non-coincident landmarks primarily relied on the array position in the hierarchy test trial (28 of 42, $p < 0.0001$). In the majority test trial, children continued to choose their preferred landmark type as in the previous experiment (22 of 41, $p < 0.001$). However, the pattern of data suggests that children were indeed more likely to use landmarks other than their preferred landmark type in the majority test as compared to the responses of children in Experiment 1. In Experiment 1, only 5 of 24 children chose a location other than the one indicated by their preferred landmark. Of those 5, only 2 chose the majority location. In this experiment, 19 of 41 children chose a location other than the one indicated by their preferred landmark type. Of those, 14 chose the majority location instead. The distribution of the children's responses was marginally significantly different between children in experiment 1 and 2 (2 tailed Fisher exact test, $p = 0.05323$). This pattern of data suggests that children with all non-coincident landmarks are more likely to use a majority strategy.

a.

Overall Results
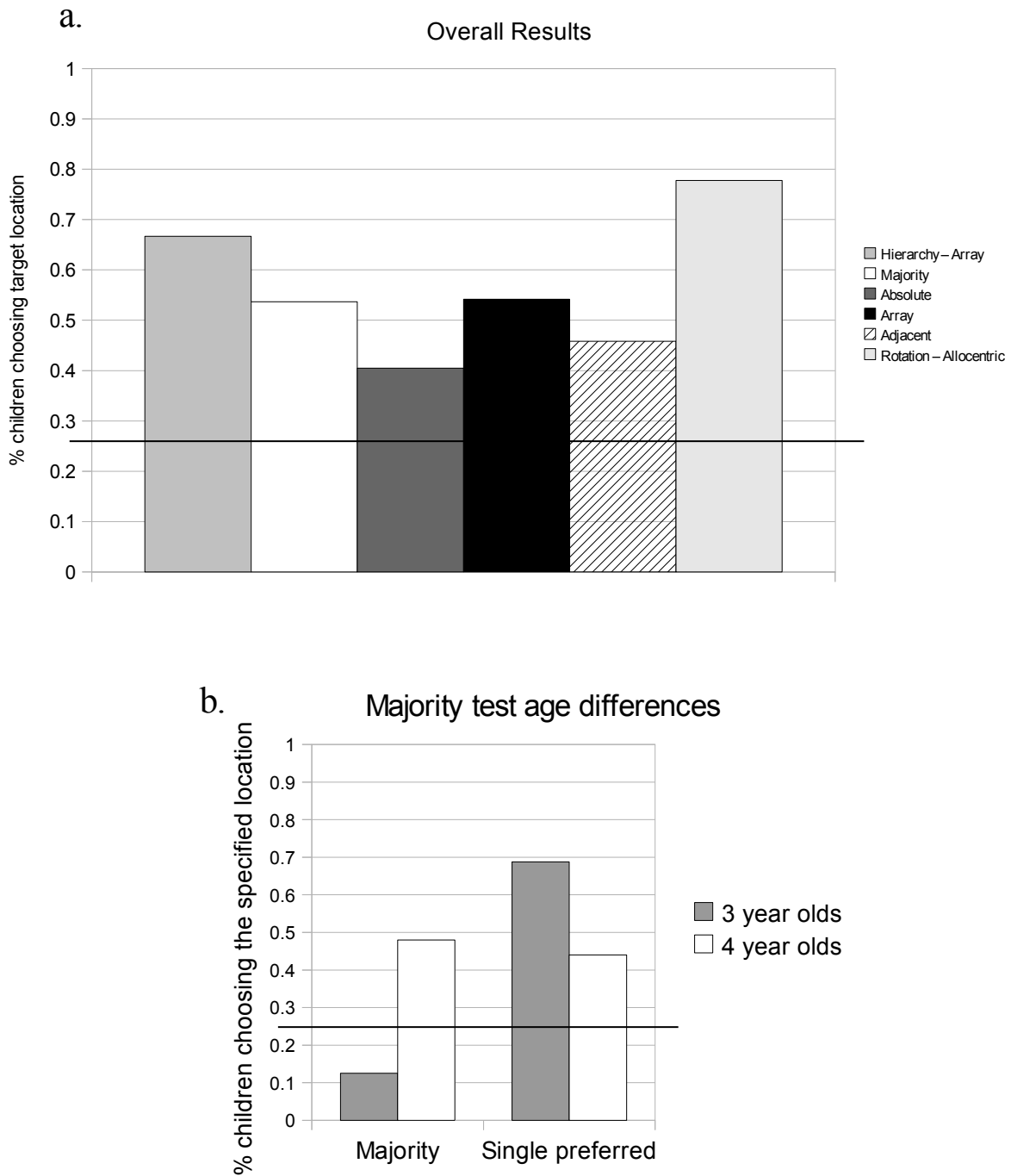

b.

Majority test age differences

Figure 4: a. Results of all tests; hierarchy, majority and absolute tests include data from both conditions, while array, adjacent tests only include data from the non-coincident condition, and the rotation test only includes data from the rotation test. The locations indicated for the hierarchy test and the rotation test are the array position and the allocentric position respectively. b. Graph of the age differences found in the majority test between 3 and 4 year olds. Chance is represented by a line at 25%.

Data from the single landmarks test trials further supports this conclusion, since children in this experiment were attending to all three landmark types: absolute position (17 of 42, $p < 0.05$),

array position (13 of 24, p < 0.01), and adjacent landmark position (11 of 24, p < 0.05). This indicates that simply by breaking the direct physical connection of coincident landmarks to the hiding locations, shifted the children's strategy from a narrow, cue-based strategy to a more comprehensive spatial strategy. It is also interesting to note that children using the cue-based strategy in Experiment 1 had encoded the array position successfully, but that only when using a more comprehensive spatial strategy did children encode the more distal absolute position. Given that children were encoding all three landmark types as evidenced by the results of the three single landmark test trials, it would have been possible for them to use a majority strategy in the majority test trial. Nevertheless, they did not. This suggests that preschool age children prefer to use a hierarchical strategy rather than a more flexible majority strategy when searching for a location in space.

However, there were significant age differences that may account for this effect. In the majority test trial, 4 year olds chose the majority location as often as the preferred landmark location (12 and 11 of 25 respectively). On the other hand, 3 year olds overwhelmingly chose the preferred landmark location in the majority test trial (11 of 16, $p < 0.001$). Of the five 3 year olds that did not choose the preferred landmark location, only two chose the majority location. The distribution of the two groups was significantly different from one another (2-sided Fisher exact, $p < 0.05$). Older children appear to use more comprehensive and flexible spatial strategies than younger children. Moreover, while there were no significant differences between age groups in the single landmark tests, the pattern of data indicates possible age differences in the use of each landmark type that in the future could be discovered through more sensitive tests. While 4 year olds chose the single landmark location above chance in all single landmark test trials, 3 year olds did not choose any specific location above chance in any of the single landmark test trials.

Both males and females chose the array position as their preferred landmark type in the hierarchy test trial, and then the preferred landmark location in the majority test trial. The only significant difference between males and females occurred in the absolute position single landmark test trial (2 sided Fisher exact test, $p < 0.01$). Males chose the correct absolute position (11 of 17, $p < 0.001$), while females showed no preference for any position. Many prior studies in spatial tasks have found no significant sex differences in young children (e.g. Lehnung et al., 1998; Overman, et al., 1996). The work that has found sex differences prior to puberty has varied considerably depending on the specifics of the task. Girls were found to have an advantage in a outdoor radial arm maze task (Mandolesi, Petrosini, Menghini, Addona, and Vicari, 2009), while boys were found to perform more accurately and faster both when learning a novel route based on landmarks and when learning to search for a hidden object between two landmarks (Beilstein and Wilson, 2000; Spetch and Parent, 2006). Future work is needed to clarify in which situations sex differences apply to young children.

All children used a distinctly allocentric strategy when choosing in the rotation condition. Of the 18 children who participated, 14 chose the same location relative to its absolute location in both the absolute position and the rotation tests (14 of 18, $p < 0.001$). Two children chose egocentrically, choosing the same location relative to their own body-position (e.g. nearest on the right) in both tests. The remaining two children appeared to choose at random in both tests. There were no age or sex differences in the rotation condition.

4.6 General Discussion

In sum, when coincident landmarks are present, preschool age children primarily rely on those landmarks to find a hidden object. This preference for coincident landmarks continues even in testing situations in which a majority of other landmark types indicate a position different from that of the coincident landmarks. This is contrast with recent evidence in a diurnal mammal (the fox squirrel) that chooses locations based on a majority strategy – choosing the location indicated by a majority of landmark types, rather than primarily relying on a single landmark type. When the coincident landmarks were shifted a few centimeters from the hiding locations and were therefore not coincident with the locations, all children switched to a different search strategy primarily relying on array position landmarks. In this case, 3 year olds and 44% of the 4 year olds continued to use a narrow spatial strategy based on a single preferred landmark type rather than using the information from other landmark types to make novel choices. Thus preschool age children, especially 3 year olds, will switch spatial search strategies depending on the nature of the landmarks available to them, but do not use a more comprehensive, majority strategy to make spatial decisions.

These conclusions are consistent with previous research indicating that while 3 year old children can use allocentric landmarks to orient they continue to have difficulty with far away more distal landmarks and relational encoding, such as center search strategies and large-scale place learning strategies until 7 – 10 years of age (Lehnung, et al., 1998; Spetch and Parent, 2006). When proximal and distal search strategies were placed in conflict with one another, even 5 year old children only used proximal landmarks to relocate hidden targets in a large-scale environment with non-coincident landmarks. Older children, were either in transition (7 year olds) or only ever used a place strategy based on more distal landmarks (10 year olds) (Lehnung, et al., 1998).

Our data suggests a younger age of transition for landmark use. Older children were more likely to choose the majority location than younger children. This indicates a developmental transition in the use of comprehensive, flexible, spatial strategies at this age. Our results are consistent with similar transitions in preschool age children. Hermer-Vazquez and Moffet (2001) have shown that children before the age of five do not integrate geometric information with featural cues in a rectangular shaped arena. By the age of five however, children have begun to integrate these two sources of information as human adults do. Moreover, in a landmark-based touch-screen search task in which one unique landmark was located adjacent to a non-distinct hiding location (i.e. a picture of a cow was located near the target bush in an arena with many bushes). When those landmarks were pitted against each other (i.e. the cow was moved to a different location near a non-target bush on the screen), 3 and 4 year old children were split in their responses between following the adjacent landmark (the cow) or choosing to search in the absolute position (the target bush)(Sutton, 2006). The authors concluded that both 3 and 4 year olds used nearby landmarks when searching, but that 3 year olds' search patterns in landmark shift trials, while not significantly different from either 2 year olds or 4 year olds, were more similar to the 2 year olds, who did not follow the landmark when it was shifted.

However, our results are in contrast with recent work showing that children do not integrate sources of spatial information. In Nardini et al. (2008) 4 to 5 year old children did not integrate self-motion and distal landmark information when orienting to a location. There are at least two differences between our studies and those of Nardini et al. (2008) that may explain this

discrepancy. First, the task demands in Nardini et al. (2008)'s study were higher than those of our study. In Nardini et al. (2008), children visited three locations in succession and then were tested on their memory for the position of the first location. As previously mentioned, there is evidence that the number of total possible locations in a spatial task can have a significant effect on the performance of young children. Specifically, the larger the number of possible locations, the poorer the performance of young children on a variety of tasks. In a radial arm maze, preschool age children performed poorly in a spatial task when there were eight possible hiding locations, however they performed as well as older children when the number of locations was reduced to four (Overman, et al., 1996). Additionally, toddlers performed poorly in a non-coincident landmark-based task when there were seven identical distractor locations. When the number of distractors was reduced to one, 2 year olds performed as well as 3 year olds in the landmark task (Sutton, 2006). These studies indicate that young children may not show evidence of more complex spatial landmark use if task demands are too high.

Second, to children at this age, there may be a functional difference between self-motion cues and landmarks that does not enable the integration across these two broad types of spatial information. In Acredolo (1977), 3 year olds responded egocentrically when they re-oriented to a previously visited location from the opposite side of a room with no landmarks of any kind. In this condition, children had to update their orientation based only on self-motion cues. In contrast, when children were provided either direct or indirect landmarks for orientation, they chose to visit the correct allocentric location. In this situation, 3 year old children clearly treat self-motion and landmarks cues very differently. When presented with the same experimental setup in the form of a model, 3 year old children were now able to choose the correct allocentric location. Since children at this age use self-motion cues and landmarks differentially, it is possible that, while children at this age may have begun to integrate information from multiple types of landmarks, they do not integrate information from self-motion cues and landmarks.

Another factor that may have encouraged both older and younger children to use more landmarks in the non-coincident condition was the variability introduced in the coincident landmarks by moving them to the side of the hiding locations. This is especially true since in Experiment 1 when the landmarks were coincident, they were always located on top of the boxes. In the non-coincident condition, the adjacent landmarks changed in their position relative to the boxes to ensure that each landmark was only ever associated with one box.

Bayesian inference may provide an interesting framework for such a hypothesis. Bayes theorem proposes that the probability of an event having occurred can be determined by combining information from both the prior probability of that particular event occurring and the likelihood of the event having occurred given the observed data. In terms of spatial decision making, the children are attempting to determine if a location is the one that they remember from the training trials. All positions should have the same prior probability since there is no reason to presume that children expect any one box out of the four to contain the hidden object without any experience. As for the likelihood, it can be calculated based on the landmark information provided in the environment. Bayes theorem also proposes that when information from multiple sources is combined to compute the likelihood of an event, each cue should be weighted in inverse proportion to its variability. Thus, less variable (more reliable) sources will be weighted more heavily.

Examining the present results from a Bayesian perspective, when noise was introduced into the coincident landmarks by disconnecting them from the hiding locations, this resulted in that particular type of landmark being more variable and thus less reliable. A Bayesian model would predict that the children would weight that type less than they had when it had been more reliable. The data support the idea that children are sensitive to reliability and that they do weigh the landmark type less when it is perceived as more variable. Children opted to use the less noisy array position landmarks instead of the their more preferred, but now less reliable coincident/adjacent landmarks. Comparing the single landmark test for the coincident landmarks in Experiment 1 to the single landmark test for the adjacent landmarks in Experiment 2, children were more likely to choose correctly in experiment 1, when the landmarks were more reliable (two-tailed fisher exact test, $p = 0.00715$). For older children it would also seem that including this noise might have encouraged them to take into consideration other landmarks in the majority test. Future studies are needed to confirm these predictions using Bayesian modeling techniques.

It would be of interest to determine if there is a transitional stage at which children use a type of landmark or a source of spatial information without including it in integrated spatial search strategies, such as the use of self-motion cues without integrating them with landmarks (Nardini et al., 2009), and the use of geometric cues without combining them with featural cues (Hermer-Vazquez and Moffit, 2001) and our own work showing that 4 year olds use all three types of landmarks without always incorporating them into an integrated search strategy. Children may have to first learn how to use a specific landmark type before integrating it with other landmarks for use in spatial search strategies. Following from this line of reasoning, it is possible that children may be capable of integrated spatial strategies within landmark types at younger ages. For example, while the 3 year olds in the studies presented herein did not integrate information from multiple landmark types, it is possible that they could integrate information from individual landmarks of the same type with one another. The majority strategy may develop earlier within specific landmark types and as it develops, it may encompass more and more landmark types, eventually including other types of spatial information, such as the self-motion cues. Furthermore, studies in larger scale, natural spaces suggest that a similar version of this task in large-scale may yield results that demonstrate both broader landmark use and broader spatial strategies in younger children (Deloache and Brown, 1983; Gouteux, et al., 2001).

One question that remains is why this shift occurs at the age of three. A similarly important transition occurs in infancy when children first learn to locomote. Infants that have transitioned to locomoting (i.e. crawling or walking), begin to prefer allocentric over egocentric strategies. Studies have shown that while maturation may play a role in this transition, the experience of self-locomotion is a much better predictor of spatial abilities than age alone. Success on spatial tasks, such as an adapted Morris water maze task using both direct and indirect landmarks, is best predicted by locomotor experience rather than age. The pattern of success even follows the developmental trajectory closely by showing decreased success rates initially after the transition from crawling to walking, showing latent learning by increasing much faster with walking experience than it had with crawling experience (Clearfield, 2004). Moreover, giving prelocomotor infants self-locomotion experience in a walker intervention improves their performance on spatial tasks so that there are no differences between the intervention group and a group of age-matched crawling infants (Kermoian and Campos, 1988). These results indicate

that experience in the world can aid and even induce changes in spatial cognition.

If we examine the 3-4 year transition for experiential changes, one important experiential shift that occurs at this age is that of the false belief task. At the age of three, children are less likely to understand that others hold beliefs that are false according to their own knowledge. By the age of four they have gained an understanding of other's perspectives that allows them to under stand that others may hold false beliefs (Wellman, Cross, and Watson, 2001). This is an interesting developmental shift to occur at the same time as children are also gaining a better understanding of more distal landmarks. Both transitions suggest a shift to a wider mental perspective. One theory of the development of spatial cognition specifically predicts that as infants gradually expand their attentional fields, they will move from using more proximal to more distal landmarks (Pick, Yonas and Rieser, 1979). Future research should be done to explore the possibility that cognitive shifts in attention may bring about such dramatic changes in both social and spatial cognition.

In conclusion, we propose that just as children develop physical skills starting from the proximal (central body parts) to the distal (extremities), that cognitive development may follow a similar trajectory across cognitive domains, moving from a more proximal perspective to a more distal one. We also propose that in using a more distal perspective, children use more comprehensive, flexible strategies in solving novel spatial problems. Furthermore, spatial, social, and other cognitive experiences may both motivate and mediate general developmental processes that underlie the expansion of allocentric thought to include further distal perspectives. Future studies are needed to determine what experiential factors, if any, may play a role in such changes of perspective throughout the maturational process.

CHAPTER 5: Conclusion

The goal of this dissertation was to present a broad and integrated view of spatial cognition from ecological, computational, and developmental perspectives. To this end, I investigated the spatial search strategies of both a mammalian species whose ecology is associated with more comprehensive search strategies and those of human children at the age when children begin to demonstrate the use of more distal landmarks and hence more comprehensive search strategies. I also related this to computational work in models of cue integration by exploring the appropriateness of a Bayesian model of the reported squirrel behavior.

In sum, there appear to be multiple factors that affect spatial reasoning and these factors can be tied to the needs of the species being examined both in terms of evolved adaptations and in terms of developing cognitive abilities in children. First from the ecological perspective, Fox squirrels predominantly oriented using distal, extra-array landmarks to find a previously rewarded location. They also used a majority strategy in majority tests, indicating an ability to use different types of landmarks flexibly and in combination with one another. However, their use of coincident landmarks varied both by the season in which they were tested and differences in the experimental setup.

The connection between ecological needs and cognitive abilities is based on the assumption that improved memory is a costly attribute that is best maintained only when necessary (Dukas, 1999). In the studies presented here, the season at testing influenced fox squirrels' use of specific landmark types. In spring, when male fox squirrels are not longer primarily caching nuts (Byrne, 1979; King, 2004), they did not use all three available landmarks, instead relying only on the most distal, stable extra-array landmarks to orient to a previously visited location. In summer, during the mating season and when squirrels are beginning to cache nuts for the winter season (Byrne, 1979; King, 2004), male squirrels relied on all three landmark types to orient. Fox squirrels appear to have evolved cognitive adaptations in their spatial landmark use that allow for more accurate spatial memory for cache locations at times of the year when it is most needed.

This is in accordance with recent work exploring the connection between ecological factors and spatial performance. Smulders et al. (2010) propose that a detailed analysis of the ecology of an individual species must be examined in terms of its ecological needs to be able to predict spatial memory specializations in a species. They specifically present the argument that scatter-hoarding species may vary in their spatial cognitive abilities in ways that correspond to details of their ecologies, as in the present case. The fox squirrels' spatial orientation appears to shift to the use of other cues in the late spring when precise localization is unnecessary given an abundance of food resources. Future studies are needed to confirm the seasonal changes in squirrel landmark use presented here and to determine what factors may be motivating this change.

From the developmental perspective, the work I have presented here supports the conclusion that as children expand their perspectives, they are also expanding their spatial cognitive abilities. This is most readily apparent at the locomotor transition ages, when infants shift from an egocentric to an allocentric spatial strategy dependent on their locomotor status (Acredolo, 1978; Bremner, Knowles, and Andreasen, 1994; Clearfield, 2004; Kermoian and Campos, 1988). The studies presented here demonstrate an important shift between the ages of three and four. Both 3

and 4 year old children primarily relied on coincident landmarks for orientation when they were present. However, when the coincident landmarks were moved to adjacent rather than coincident positions, both 3 and 4 year olds preferred to rely on array position landmarks instead.

Additionally, the pattern of results from the 4 year old children suggests that they are in a state of transitioning from more rigid to more flexible spatial strategies. While 3 year olds only chose the preferred landmark location, 4 year old children were as likely to choose the majority location as their preferred landmark location in the majority test. In general, there is a considerable degree of evidence for a slow but constant increase in performance across many spatial tasks between the ages of three and nine (Acredolo, 1977; Foreman, et al., 1990; Laurance, et al., 2003; Lehnung, et al., 1998). However, in some studies, a more specific transition centered between the ages of three and five has been reported (Cornell and Heth, 1983; Gouteux, et al., 2001). In these studies, 5 year olds have been found to have both a larger spatial memory capacity, and an ability to combine featural and geometric cues and thus improve the accuracy of their spatial searches. These results support my conclusion that the three to four year transition is an important initial stage for the development of spatial strategies.

From the computational perspective, the results of my analyses demonstrated how a Bayesian framework could be used to characterize the landmarks used by animals in navigation, and were consistent with both the seasonal and saliency effects that were found in the squirrels. Also, all models that included the extra-array parameter resulted in an improvement in fit, supporting our conclusion that the squirrels primarily oriented using these distal landmarks. Thus, I have shown that a Bayesian model can be a useful tool for exploring spatial strategies in animals; studies examining squirrels' weighting of different landmark types in single landmark tests to confirm the predictions made by the Bayesian model are in progress (Waisman, unpublished data).

Taken together, these results demonstrate the use of a majority strategy in both non-human and human animals. They also indicate that such a strategy can be illustrated using a Bayesian model of spatial search strategies. These results are in accordance both with previous papers that proposed the use of averaging strategies in animals (Cheng, et al., 2007a; Smulders, et al., 2010) and studies in reorientation of preschool age children that have shown a similar developmental shift in the ability to integrate spatial information between the ages of three and five (Hermer-Vazquez and Moffit, 2001). Some have even proposed that the reliance on geometric features in children prior to the age of five is due to a learned Bayesian weighting of the individual cues that leads to a heavier weighting for geometric cues (Ratliff and Newcombe, 2008), much like the model that we and others have proposed for the landmark integration of the squirrels (Cheng et al., 2007; Smulders et al., 2010). Thus both animals and human children appear to develop flexible spatial strategies that can be described using a Bayesian model of cue combination.

Future research into the flexible, spatial strategies of both animals and children is needed to examine the onotogenetic and phyolgenetic trajectories of such strategies. The work presented here both expands upon and adds to the growing literature that integrates multiple perspectives to increase accuracy in our search for and understanding of spatial cognition. An integrated approach can allow us to draw parallels between phylogeny and ontogeny in diverse species. Given that spatial memory is a cognitive ability common to all animals for survival, it is not surprising that animals from diverse taxa may have homologous spatial search strategies. The

work here supports the idea that both phylogenetic and ontogenetic development of spatial cognition is influenced by environmental factors. In both children and squirrels, the use of flexible search strategies appears to occur when it would be needed, such as when children begin to take on more distal perspectives to their own and when squirrels are in greater need of spatial memory accuracy during the caching season. Furthermore, our work suggests that such flexible spatial search strategies can be represented using a Bayesian model of cue combination. Continued work in both humans and non-human animals can and should be done to determine what experiential factors may influence both the evolution and the human development of spatial cognitive abilities, and to investigate how Bayesian models of cue combination can be used to represent the effects of such factors.

REFERENCES

Able, K. P. (1993). Orientation Cues Used by Migratory Birds - a Review of Cue-Conflict Experiments. *Trends in Ecology and Evolution, 8*(10), 367-371.

Acredolo, L. P. (1977). Developmental-changes in ability to coordinate perspectives of a large-scale space. *Developmental Psychology, 13*(1), 1-8.

Acredolo, L. P. (1978). Development of spatial orientation in infancy. *Developmental Psychology, 14*(3), 224-234.

Acredolo, L. P., and Evans, D. (1980). Developmental-changes in the effects of landmarks on infant spatial-behavior. *Developmental Psychology, 16*(4), 312-318.

Alais, D., and Burr, D. (2004). The ventriloquist effect results from near-optimal bimodal integration. *Current Biology, 14*(3), 257-262. doi: 10.1016/j.cub.2004.01.029

Anderson, A. M. (1977). Model for landmark learning in honeybee. *Journal of Comparative Physiology, 114*(3), 335-355.

Bai, D. L., and Bertenthal, B. I. (1992). Locomotor status and the development of spatial search skills. *Child Development, 63*(1), 215-226.

Balda, R. P., Kamil, A. C., Bednekoff, P. A., and Hile, A. G. (1997). Species Differences in Spatial Memory Performance on a Three-dimensional Task. *Ethology, 103*(1), 47-55. doi: 10.1111/j.1439-0310.1997.tb00006.x

Bednekoff, P. A., Balda, R. P., Kamil, A. C., and Hile, A. G. (1997). Long-term spatial memory in four seed-caching corvid species. *Animal Behaviour, 53*, 335-341.

Beilstein, C. D., and Wilson, J. F. (2000). Landmarks in route learning by girls and boys. *Perceptual and Motor Skills, 91*(3), 877-882.

Bell, S. (2002). Spatial cognition and scale: A child's perspective. *Journal of Environmental Psychology, 22*(1-2), 9-27. doi: 10.1006/jevp.2002.0250

Biegler, R., and Morris, R. G. M. (1996). Landmark stability: Studies exploring whether the perceived stability of the environment influences spatial representation. [Article]. *Journal of Experimental Biology, 199*(1), 187-193.

Bremner, J. G. (1978). Egocentric versus allocentric spatial coding in 9-month-old infants - factors influencing choice of code. *Developmental Psychology, 14*(4), 346-355.

Bremner, J. G., and Bryant, P. E. (1977). Place versus response as basis of spatial errors made by young infants. *Journal of Experimental Child Psychology, 23*(1), 162-171.

Bremner, J. G., Knowles, L., and Andreasen, G. (1994). Processes underlying young childrens spatial orientation during movement. *Journal of Experimental Child Psychology, 57*(3), 355-376.

Brodbeck, D. R. (1994). Memory for spatial and local cues - a comparison of a storing and a nonstoring species. *Animal Learning and Behavior, 22*(2), 119-133.

Bullens, J., Nardini, M., Doeller, C. F., Braddick, O., Postma, A., and Burgess, N. (2010). The role of landmarks and boundaries in the development of spatial memory. [Article]. *Developmental Science, 13*(1), 170-180. doi: 10.1111/j.1467-7687.2009.00870.x

Bushnell, E. W., McKenzie, B. E., Lawrence, D. A., and Connell, S. (1995). The spatial coding strategies of one-year-old infants in a locomotor search task. *Child Development, 66*(4), 937-958.

Byrne, S. (1979). The distribution and ecology of the non-native tree squirrels, *Sciurus carolinensis* and *Sciurus niger*, in Northern California. *unpublished Ph. D. Dissertation, University of California, Berkeley.*

Cahalane, V. H. (1942). Caching and recovery of food by the western fox squirrel. *Journal of Wildlife Management, 6*(4), 338-352.

Cartwright, B. A., and Collett, T. S. (1983). Landmark learning in bees - experiments and models. *Journal of Comparative Physiology, 151*(4), 521-543.

Chamizo, V. D., Aznar-Casanova, J. A., and Artigas, A. A. (2003). Human overshadowing in a virtual pool: Simple guidance is a good competitor against locale learning. *Learning and Motivation, 34*(3), 262-281. doi: 10.1016/s0023-9690(03)00020-1

Chang, Q., and Gold, P. E. (2003). Switching memory systems during learning: Changes in patterns of brain acetylcholine release in the hippocampus and striatum in rats. *Journal of Neuroscience, 23*(7), 3001-3005.

Chavarriaga, R., Strosslin, T., Sheynikhovich, D., and Gerstner, W. (2005). Competition between cue response and place response: a model of rat navigation behaviour. *Connection Science, 17*(1-2), 167-183.

Cheng, K. (1986). A purely geometric module in the rats spatial representation. [Article]. *Cognition, 23*(2), 149-178.

Cheng, K., Shettleworth, S., Huttenlocher, J., and Rieser, J. (2007a). Bayesian integration of spatial information. *Psychological Bulletin 133*(4), 625-637.

Cheng, K., Shettleworth, S. J., Huttenlocher, J., and Rieser, J. J. (2007b). Bayesian integration of spatial information. [Review]. *Psychological Bulletin, 133*(4), 625-637. doi: 10.1037/0033-2909.133.4.625

Clayton, N. S., and Krebs, J. R. (1994). Memory for Spatial and Object-Specific Cues in Food-Storing and Nonstoring Birds. *Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology, 174*(3), 371-379.

Clearfield, M. W. (2004). The role of crawling and walking experience in infant spatial memory. *Journal of Experimental Child Psychology, 89*(3), 214-241.

Collett, T. S., and Collett, M. (2002). Memory use in insect visual navigation. *Nature Reviews Neuroscience, 3*(7), 542-552.

Cornell, E. H., and Heth, C. D. (1983). Spatial cognition - gathering strategies used by preschool-children. *Journal of Experimental Child Psychology, 35*(1), 93-110.

Deloache, J. S., and Brown, A. L. (1983). Very young childrens memory for the location of objects in a large-scale environment. [Article]. *Child Development, 54*(4), 888-897.

Devenport, J. A., Luna, L. D., and Devenport, L. D. (2000). Placement, retrieval, and memory of caches by thirteen-lined ground squirrels. *Ethology, 106*(2), 171-183.

Dukas, R. (1999). Costs of Memory: Ideas and Predictions. *Journal of Theoretical Biology, 197*(1), 41-50. doi: DOI: 10.1006/jtbi.1998.0856

Dyer, F. C., and Seeley, T. D. (1994). Colony Migration in the Tropical Honey-Bee Apis-Dorsata F (Hymenoptera, Apidae). *Insectes Sociaux, 41*(2), 129-140.

Ernst, M. O., and Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature, 415*(6870), 429-433.

Fevre, E. M., Bronsvoort, B., Hamilton, K. A., and Cleaveland, S. (2006). Animal movements and the spread of infectious diseases. *Trends in Microbiology, 14*(3), 125-131. doi: 10.1016/j.tim.2006.01.004

Foreman, N., Warry, R., and Murray, P. (1990). Development of reference and working spatial memory in preschool-children. *Journal of General Psychology, 117*(3), 267-276.

Galea, L. A. M., Kavaliers, M., Ossenkopp, K. P., Innes, D., and Hargreaves, E. L. (1994). Sexually Dimorphic Spatial-Learning Varies Seasonally in 2 Populations of Deer Mice.

Brain Research, 635(1-2), 18-26.

Galea, L. A. M., and McEwen, B. S. (1999). Sex and seasonal differences in the rate of cell proliferation in the dentate gyrus of adult wild meadow voles. *Neuroscience, 89*(3), 955-964.

Gaulin, S. J. C., Fitzgerald, R. W., and Wartell, M. S. (1990). Sex-Differences in Spatial Ability and Activity in 2 Vole Species (Microtus-Ochrogaster and Microtus-Pennsylvanicus). *Journal of Comparative Psychology, 104*(1), 88-93.

Ghetti, S., DeMaster, D. M., Yonelinas, A. P., and Bunge, S. A. (2010). Developmental Differences in Medial Temporal Lobe Function during Memory Encoding. *Journal of Neuroscience, 30*(28), 9548-9556. doi: 10.1523/jneurosci.3500-09.2010

Gibbs, Lea, and Jacobs. (2007). Flexible use of spatial cues in the southern flying squirrel (Glaucomys volans). *10*(2), 203-209.

Gibbs, S. E. B., Lea, S. E. G., and Jacobs, L. F. (2007). Flexible use of spatial cues in the southern flying squirrel (Glaucomys volans). *Animal Cognition, 10*(2), 203-209. doi: 10.1007/s10071-006-0059-y

Goodyear, A. J., and Kamil, A. C. (2004). Clark's nutcrackers (Nucifraga columbiana) and the effects of goal-landmark distance on overshadowing. *Journal of Comparative Psychology, 118*(3), 258-264. doi: 10.1037/0735-7036.118.3.258

Gouteux, S., and Spelke, E. S. (2001). Children's use of geometry and landmarks to reorient in an open space. [Article]. *Cognition, 81*(2), 119-148.

Gouteux, S., Vauclair, J., and Thinus-Blanc, C. (2001). Reorientation in a small-scale environment by 3-4-, and 5-year-old children. *Cognitive Development, 16*(3), 853-869.

Haun, D. B. M., Call, J., Janzen, G., and Levinson, S. C. (2006). Evolutionary psychology of spatial representations in the hominidae. *Current Biology, 16*(17), 1736-1740.

Healy, S. D., and Hurly, T. A. (1998). Rufous hummingbirds' (Selasphorus rufus) memory for flowers: Patterns or actual spatial locations? *Journal of Experimental Psychology-Animal Behavior Processes, 24*(4), 396-404.

Hermer-Vazquez, L., Moffet, A., and Munkholm, P. (2001). Language, space, and the development of cognitive flexibility in humans: the case of two spatial memory tasks. [Article]. *Cognition, 79*(3), 263-299.

Herz, R. S., Zanette, L., and Sherry, D. F. (1994). Spatial Cues for Cache Retrieval by Black-Capped Chickadees. *Animal Behaviour, 48*(2), 343-351.

Hodgson, Z. G., and Healy, S. D. (2005). Preference for spatial cues in a non-storing songbird species. *Animal Cognition, 8*(3), 211-214.

Horn, H. A., and Myers, N. A. (1978). Memory for location and picture cues at ages 2 and 3. [Article]. *Child Development, 49*(3), 845-856.

Humber, J. M., Brodbeck, D. R., and Warkentin, I. G. (2009). Use of spatial and colour cues by foraging pine siskins (Carduelis pinus): A field study. *Behavioural Processes, 80*(3), 233-237. doi: 10.1016/j.beproc.2008.12.009

Hurly, T. A., and Healy, S. D. (1996). Memory for flowers in rufous hummingbirds: Location or local visual cues? *Animal Behaviour, 51*, 1149-1157.

Jacobs, L. F. (1996). The economy of winter: Phenotypic plasticity in behavior and brain structure. *Biological Bulletin, 191*(1), 92-100.

Jacobs, L. F., and Liman, E. R. (1991). Gray Squirrels Remember the Locations of Buried Nuts. *Animal Behaviour, 41*, 103-110.

Jacobs, L. F., and Schenk, F. (2003). Unpacking the cognitive map: The parallel map theory of

hippocampal function. *Psychological Review, 110*(2), 285-315.

Jacobs, L. F., and Shiflett, M. W. (1999). Spatial orientation on a vertical maze in free-ranging fox squirrels (Sciurus niger). *Journal of Comparative Psychology, 113*(2), 116-127.

Jarrard, L. E. (1993). On the role of the hippocampus in learning and memory in the rat. *Behavioral and Neural Biology, 60*(1), 9-26.

Kamil, A. C., Balda, R. P., and Olson, D. J. (1994). Performance of 4 seed-caching corvid species in the radial-arm maze analog. *Journal of Comparative Psychology, 108*(4), 385-393.

Kamil, A. C., and Cheng, K. (2001). Way-finding and landmarks: The multiple-bearings hypothesis. *Journal of Experimental Biology, 204*(1), 103-113.

Kemp, A., and Manahan-Vaughan, D. (2007). The hippocampal CA1 region and dentate gyrus differentiate between environmental and spatial feature encoding through long-term depression. *Cerebral Cortex, (in press)*.

Kermoian, R., and Campos, J. J. (1988). Locomotor experience - a facilitator of spatial cognitive-development. [Article]. *Child Development, 59*(4), 908-917.

King, J. (2004). The current distribution of the introduced Fox Squirrel (*Sciurus niger*) in the greater Los Angeles metropolitan area and its behavioral interaction with the native Western Gray Squirrel (*Sciurus griseus*). *unpublished M.S. thesis, University of California, Los Angeles*.

LaDage, L. D., Roth, T. C., Fox, R. A., and Pravosudov, V. V. (2009). Flexible cue use in food-caching birds. *Animal Cognition, 12*(3), 419-426. doi: 10.1007/s10071-008-0201-0

Laurance, H. E., Learmonth, A. E., Nadel, L., and Jacobs, W. J. (2003). Maturation of Spatial Navigation Strategies: Convergent Findings from Computerized Spatial Environments and Self-Report. *Journal of Cognition and Development, 4*(2), 211 - 238.

Lavenex, P., Shiflett, M. W., Lee, R. K., and Jacobs, L. F. (1998). Spatial versus nonspatial relational learning in free-ranging fox squirrels (Sciurus niger). *Journal of Comparative Psychology, 112*(2), 127-136.

Lavenex, P., Steele, M. A., and Jacobs, L. F. (2000). Sex differences, but no seasonal variations in the hippocampus of food-caching squirrels: A stereological study. *Journal of Comparative Neurology, 425*(1), 152-166.

Learmonth, A. E., Nadel, L., and Newcombe, N. S. (2002). Children's use of landmarks: Implications for modularity theory. [Article]. *Psychological Science, 13*(4), 337-341.

Lee, S. A., Shusterman, A., and Spelke, E. S. (2006). Reorientation and landmark-guided search by young children: Evidence for two systems. *Psychological Science, 17*(7), 577-582.

Legge, E. L. G., Spetch, M. L., and Batty, E. R. (2009). Pigeons' (Columba livia) hierarchical organization of local and global cues in touch screen tasks. *Behavioural Processes, 80*(2), 128-139. doi: 10.1016/j.beproc.2008.10.011

Lehnung, M., Leplow, B., Friege, L., Herzog, A., Ferstl, R., and Mehdorn, M. (1998). Development of spatial memory and spatial orientation in preschoolers and primary school children. [Article]. *British Journal of Psychology, 89*, 463-480.

Mandolesi, L., Petrosini, L., Menghini, D., Addona, F., and Vicari, S. (2009). Children' s radial arm maze performance as a function of age and sex. *International Journal of Developmental Neuroscience, 27*(8), 789-797. doi: 10.1016/j.ijdevneu.2009.08.010

Menzel, R., Greggers, U., Smith, A., Berger, S., Brandt, R., Brunke, S., et al. (2005). Honey bees navigate according to a map-like spatial memory. *Proceedings of the National Academy of Sciences of the United States of America, 102*(8), 3040-3045.

Nardini, M., Jones, P., Bedford, R., and Braddick, O. (2008). Development of cue integration in

human navigation. *Current Biology, 18*(9), 689-693.

Newcombe, N., Huttenlocher, J., Drummey, A. B., and Wiley, J. G. (1998). The development of spatial location coding: Place learning and dead reckoning in the second and third years. [Proceedings Paper]. *Cognitive Development, 13*(2), 185-200.

Overman, W. H., Pate, B. J., Moore, K., and Peuster, A. (1996). Ontogeny of place learning in children as measured in the radial arm maze, Morris search task, and open field task. *Behavioral Neuroscience, 110*(6), 1205-1228.

Packard, M. G., and McGaugh, J. L. (1996). Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place and response learning. *Neurobiology of Learning and Memory, 65*(1), 65-72.

Padgett, K., Reisen, W. K., Kahl-Purcell, N., Fang, Y., Cahoon-Young, B., Carney, R., et al. (2007). West Nile virus infection in tree squirrels (Rodentia: Sciuridae) in California, 2004-2005. *American Journal of Tropical Medicine and Hygiene, 76*(5), 810-813.

Phillips, J. B., and Moore, F. R. (1992). Calibration of the Sun Compass by Sunset Polarized-Light Patterns in a Migratory Bird. *Behavioral Ecology and Sociobiology, 31*(3), 189-193.

Pyter, L. M., Trainor, B. C., and Nelson, R. J. (2006). Testosterone and photoperiod interact to affect spatial learning and memory in adult male white-footed mice (Peromyscus leucopus). *European Journal of Neuroscience, 23*(11), 3056-3062.

Ratliff, K. R., and Newcombe, N. S. (2008). Reorienting When Cues Conflict: Evidence for an Adaptive-Combination View. [Article]. *Psychological Science, 19*(12), 1301-1307. doi: 10.1111/j.1467-9280.2008.02239.x

Ratner, H. H., and Myers, N. A. (1980). Related picture cues and memory for hidden-object locations at age 2. [Note]. *Child Development, 51*(2), 560-564.

Sanchez-Moreno, J., Rodrigo, T., Chamizo, V. D., and MacKintosh, N. J. (1999). Overshadowing in the spatial domain. [Article]. *Animal Learning and Behavior, 27*(4), 391-398.

Schöne, H. (1984). *Spatial orientation : the spatial control of behavior in animals and man / by Hermann Schöne ; translated by Camilla Strausfeld*. Princeton, N.J. :: Princeton University Press.

Sherry, D. F., and Duff, S. J. (1996). Behavioural and neural bases of orientation in food-storing birds. *Journal of Experimental Biology, 199*(1), 165-171.

Shettleworth, S. J. (2003). Memory and hippocampal specialization in food-storing birds: Challenges for research on comparative cognition. *Brain Behavior and Evolution, 62*(2), 108-116.

Simons, A. M. (2004). Many wrongs: the advantage of group navigation. *Trends in Ecology and Evolution, 19*(9), 453-455. doi: 10.1016/j.tree.2004.07.001

Smulders, T. V., Gould, K. L., and Leaver, L. A. (2010). Using ecology to guide the study of cognitive and neural mechanisms of different aspects of spatial memory in food-hoarding animals. [Review]. *Philosophical Transactions of the Royal Society B-Biological Sciences, 365*(1542), 883-900. doi: 10.1098/rstb.2009.0211

Spetch, M. L. (1995). Overshadowing in landmark learning - touch-screen studies with pigeons and humans. *Journal of Experimental Psychology-Animal Behavior Processes, 21*(2), 166-181.

Spetch, M. L., and Edwards, C. A. (1988). Pigeons, Columba-Livia, Use of Global and Local Cues for Spatial Memory. *Animal Behaviour, 36*, 293-296.

Spetch, M. L., and Mondloch, M. V. (1993). Control of pigeons spatial search by graphic

landmarks in a touch-screen task. *Journal of Experimental Psychology-Animal Behavior Processes, 19*(4), 353-372.

Spetch, M. L., and Parent, M. B. (2006). Age and sex differences in children's spatial search strategies. *Psychonomic Bulletin and Review, 13*(5), 807-812.

Stapanian, M. A., and Smith, C. C. (1978). A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. *Ecology, 59*(5), 884-896.

Sutton, J. E. (2006). The development of landmark and beacon use in young children: evidence from a touchscreen search task. *Developmental Science, 9*(1), 108-123.

Thiele, J., and Winter, Y. (2005). Hierarchical strategy for relocating food targets in flower bats: spatial memory versus cue-directed search. *Animal Behaviour, 69*, 315-327.

Thrun, S., -. (2005). *Probabilistic robotics / Sebastian Thrun, Wolfram Burgard, Dieter Fox*. Cambridge, Mass. :: MIT Press.

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review, 55*(4), 189-208.

Vanderwall, S. B., and Balda, R. P. (1981). Ecology and evolution of food-storage behavior in conifer-seed-catching corvids. *Zeitschrift Fur Tierpsychologie-Journal of Comparative Ethology, 56*(3), 217-242.

Vlasak, A. N. (2006a). Global and local spatial landmarks: their role during foraging by Columbian ground squirrels (Spermophilus columbianus). *Animal Cognition, 9*(1), 71-80.

Vlasak, A. N. (2006b). The relative importance of global and local landmarks in navigation by Columbian ground squirrels (Spermophilus columbianus). *Journal of Comparative Psychology, 120*(2), 131-138.

Waisman, A. S., and Jacobs, L. F. (2008). Flexibility of cue use in the fox squirrel (Sciurus niger). *Animal Cognition, 11*(4), 625-636. doi: 10.1007/s10071-008-0152-5

Watanabe, S. (2005). Strategies of spatial learning for food storing in scrub jays. *Journal of Ethology, 23*(2), 181-187.

Wellman, H. M., Cross, D., and Watson, J. (2001). Meta-analysis of theory-of-mind development: The truth about false belief. [Review]. *Child Development, 72*(3), 655-684.