An Examination of the Role of Associative Learning and Spatial Memory in Foraging in Two Species of Bear (Family: Ursidae)

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An Examination of the Role of Associative Learning and Spatial Memory in Foraging in Two Species of Bear (Family: Ursidae)

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DEDICATION

This thesis is dedicated to my father, one of the smartest people I know, and my mother, one of the strongest, for their encouragement, support and unconditional love.

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SUMMARY

Locating food is one of the most important problems animals face each day. Optimal foraging theory postulates that animals are under strong selective pressure to use efficient foraging strategies when searching for and processing food. However, very little attention has been given to the initial search process for resources or the ways in which foragers can decrease search time for non-randomly distributed food. Moreover, few studies have examined the role of food distribution and foraging ecology on the ability to learn to forage efficiently. It might be expected that closely related species that differ in home range size, diet and the spatial distribution of their resources would perform differently on similar tasks involving association learning and spatial memory. Six experimental foraging tasks were designed to examine differences in the ability of spatial, visual, and olfactory discriminative stimuli to gain control over the foraging behavior of two species of bear and to determine the relative importance of each of these discriminative stimuli in their foraging decisions. The subjects were three male and four female giant pandas (*Ailuropoda melanoleuca*) housed at Zoo Atlanta, the San Diego Zoo, and the Smithsonian National Zoological Park, and one male and one female spectacled bear (*Tremarctos ornatus*) housed at the Smithsonian National Zoological Park. Eight feeders were arranged in a circular array approximately eight feet apart in test areas at each location. The first foraging task was designed to examine the pattern of foraging used by the bears when all eight food sites were baited. The bears used a least-distance strategy, choosing adjacent feeders more often than non-adjacent feeders when traveling between feeders and avoiding previously depleted food sources. In the second task five of the seven giant pandas and one of the spectacled bears relied on spatial cues alone to accurately locate food when four sites were baited. A reversal of the location of the baited feeders disrupted performance, indicating that local olfactory or visual cues were not controlling behavior. Neither the visual or olfactory cues gained control over the foraging behavior of the giant pandas when the spatial location of food was unpredictable between trials. However, the visual cues did gain control of the foraging behavior of the spectacled bears. Because of their frugivorous diet, spectacled bears may be predisposed to learn visual associations. In the final experiment, visual cues gained control of giant panda foraging behavior after being paired with spatial cues and were relied on more heavily for food location when the three cues were dissociated from each other. The spectacled bears made fewer errors (as measured by visits to depleted feeders) in each of the tasks than the giant pandas which may reflect evolutionary species differences in learning ability. This research improves our understanding of the foraging strategies of these species.

CHAPTER 1

THE ROLE OF ASSOCIATIVE LEARNING AND SPATIAL MEMORY IN FORAGING

1.1 Introduction to Optimal Foraging Theory

One of the greatest challenges an animal faces on a day-to-day basis is locating viable food sources and determining the availability and predictability of those food sources in both space and time (Olton, Handelmann, & Walker, 1981). Foraging behavior has become a topic of increasing interest for psychologists working in the field of animal behavior. This is due in part to the emergence of optimal foraging theory (Mellgren, Misasi, & Brown, 1984), which postulates that animals are under strong selective pressure to use efficient foraging strategies when searching for and processing food. Efficient strategies are those that maximize the energetic gains and minimize the energetic costs of foraging (Pyke, Pulliam, & Charnov, 1977). Tests of optimal foraging theory have been conducted in both laboratory, semi-naturalistic, and field situations with both wild and captive animals (Kamil & Sargent, 1981).

One of the major goals of research on optimal foraging theory is to determine what type of information a forager uses to make foraging decisions such as where to forage, when to forage, which food items to consume and how long to stay in a particular food site (Kamil & Sargent, 1981). Some of the issues facing a foraging animal that affect efficiency include choice of prey, handling time, encounter rate, and staying time within a patch (i.e., the amount of time a forager should remain in a patch before moving to another patch). Scientists interested in optimal foraging theory have attempted to incorporate these factors into both patch and prey models designed to predict resource maximization (Stephens & Krebs, 1986). However, most models start with the assumption that the animal has already located a patch and will then forage and travel directly to other patches that are either within sensory range or are in a known location. Very little attention has been given to search time for the initial patch itself and the ways in which foragers can decrease search time between non-randomly distributed patches (Krakauer & Rodriguez-Girones, 1995). Furthermore, few foraging models consider how the spatial distribution of food might influence foraging decisions (Sherry, 1998). Krakauer and Rodriguez-Girones recently developed an optimal foraging model called an area concentrated search model, which assumes that as the distribution of resources becomes more patchy, information becomes more important and profitable for the forager. However, it only predicts the behavior of a forager following the capture of a prey item and does not address the ways in which a forager can increase its likelihood of finding that prey item in the first place.

According to the postulates of optimal foraging theory, a decrease in search time for a food source would result in an increase in the number of prey collected or amount of food that can be processed. For all animals, random foraging is a waste of both time and energy that can be used for the performance of other important activities (Barnard, 1983). Animals that have to actively search for their food, particularly herbivores that forage for sessile "prey" or food patches, can achieve non-random foraging and decrease search time by learning to respond to discriminative stimuli associated with the prey or food patch itself, spatial learning, or a combination of both types of learning to recognize and locate viable patches of food.

1.2 Methods of Non-Random Foraging

1.2.1 Guidance Learning

It would be adaptive for foraging animals to have the ability to learn that certain stimuli in the environment are associated with food. This type of learning is often called guidance or cue learning because a single local discriminative stimulus emanates from the part of the environment that is the goal and serves as a "beacon", causing animals to either approach or avoid the site (Gallistel, 1989, 1990; Lopez, Gomez, Rodriguez, Broglio, Vargas, Salas, 2001). Previously neutral stimuli can become conditioned stimuli that can evoke approach or avoidance behavior through Pavlovian conditioning (Rashotte, O'Connell, & Beidler, 1982). This would be particularly valuable in environments in which the location of food varied with changes in season, making spatial cues irrelevant. This type of associative learning would also be helpful to animals foraging in a new area, allowing the forager to identify new feeding sites more quickly. The ability to form associations between discriminative stimuli originating either from the environment around the food or from the food itself would be valuable in improving foraging efficiency.

Though many studies have been conducted to examine Pavlovian conditioning mechanisms involved in taste aversion learning and to understand how discriminative stimuli can control choice behavior in operant conditioning (Rashotte, O'Connell, & Beidler, 1982), few studies have been conducted to determine if stimuli control behavior in real life foraging situations. It is only recently that researchers have begun to examine how stimuli can come to control behavior in foraging. Foraging has been shown to come under the control of visual stimuli in many species of animal. For example, Menzel (1996) found that macaques (*Macaca fasciluris*) visual stimuli, specifically the shape of objects, can control food-searching behavior in an open field foraging task. This was evidenced by the fact that upon finding food hidden by an experimenter under or near one structure, the macaques were more likely to look for food under or near similar structures that were equally conspicuous. Howery, Bailey, Ruyle, & Renken (2000) found that the presence of a visual signal significantly improved the foraging efficiency of cattle at pasture in that cued animals spent more time feeding and less time standing, had higher overall mean intake of food, and consumed more food per distance traveled than cattle that were not exposed to visual discriminative stimuli. The cattle were also able to associate the cue with the quality of food in the patch. Though it is known that heteromyid rodents relocate cached seeds using both olfactory and spatial discriminative stimuli, visual discriminative stimulus gain control of behavior if it associated with the presence of a seed (Pyare & Longland, 2000). If a cached seed is left for a long enough length of time, seedlings will emerge. Research has shown that heteromyid rodents can use these seedlings as beacons that signal the presence of the seed underneath the soil. Some species have been found to be capable of using the color of a stimulus as a signal for the presence of food. For example, honeybees are capable of navigating through a maze on the basis of color trails alone and can travel through a novel maze on the basis of color trails as easily as bees trained extensively on the maze without discriminative stimuli (Zhang, Bartsch, & Srinivasan, 1996). The color red has been found to control foraging behavior for palatable food in one species of whiptail lizard (*Cnemidophorus murinus*) (Schall, 2000). The lizards were trained using palatable foods containing red dye and unpalatable foods containing green dye. Following training, the lizards consistently preferred red food types even when presented with palatable green food types. Drea (1998) found that macaques (*Macaca mulatta*) were capable of distinguishing between baited and nonbaited feeders on the basis of the color of the feeder.

Some animals are also capable of learning the association between olfactory discriminative stimuli and the presence of food. For example, it has been known for some times that some members of the Canidae family urine mark a cache site upon depletion of the site. Harrington (1981) found that the urine marks of wolves were almost never left when a cache of animal prey was created, presumably because this could not only signal the presence of the animal prey to the individual creating the cache but to other animals as well. However, they almost always urine mark after they have depleted the cache site, perhaps as a signal to themselves that the cache, which presumably still smells of the animal prey, is empty. Animals are also capable using the smell emanating from the food source to locate food when visual discriminative stimuli are unavailable. Laska and Hudson (1993) found that a food-associated odor (banana aroma or peanut aroma) can control foraing behavior of squirrel monkeys (*Saimiri sciureus*) searching for food in a feeding device. Not only can olfactory discriminative stimuli emanating from the food itself signal the presence or absence of food, but arbitrary olfactory discriminative stimuli provided by an experimenter can also signal the presence or absence of food. Lavenex and Schenk (1997) found that learning the location of a food source by rats in a feeding apparatus was potentiated by an arbitrary olfactory discriminative stimulus. Indian short-nosed fruit bats (*Cynopterus sphinx*) rely extensively on olfactory discriminative stimuli to locate fruit (Acharya, Roy, & Krishna, 1998). Research showed that towels soaked in fruit juice were approached by bats in a laboratory situation more often than identical towels soaked in water. Furthermore, the bats were capable of associating a novel, non-fruit odor gained control of foraging for fruit in only three exposures.

To my knowledge, there has been only one study comparing olfactory discrimination learning in two species with different foraging ecologies. Bolen and Green (1997) found that nocturnal owl monkeys (*Aotus nancymai*) were capable of locating hidden fruit at a level greater than would be expected by chance using olfactory discriminative stimuli emanating from the fruit alone. However, diurnal capuchin monkeys (*Cebus apella*) were unable to locate the fruit on the basis of olfactory discriminative stimuli.

1.2.2 Spatial Learning

Though rarely tested experimentally, guidance learning or cue learning is thought to be the simplest form of navigation toward a resource because movement toward a stimulus associated with the resource can be made without regard for a particular pattern of movement (Ellen, 1987). However, if a prey item is not within the sensory range of the forager, then a forager needs some other means for conducting a non-random search. In this case, the capacity for spatial memory can greatly increase foraging efficiency. For example, Benhamou (1994) used computer simulations to compare foraging success in animals using foraging strategies that either did or did not involve the use of spatial memory. It was found that a predator relying on a search mechanism that involved spatial memory was able to harvest 1-6 times more prey items than if it did not use spatial memory. Furthermore, a forager using spatial memory was able to harvest 3-5 times more prey items than if it moved in a straight line with an optimal constant speed. What does he mean by spatial memory or spatial information?

According to Schacter and Nadel (1991), there are three types of spatial knowledge: route, landmark, and map. Route knowledge refers to spatiotemporal relations between specific environmental features. Navigation is accomplished through fairly rigid, strict movements through an environment based on prior learning. For example, an animal may learn to turn left or turn right at particular choice points. This foraging strategy, in which animals follow a consistent route from food site to food site, is sometimes referred to as traplining (Sherry, 1998). Route navigation (also sometimes referred to as path navigation or dead reckoning) is limited by the fact that the route must be traversed in the correct sequence for accurate localization of the goal to take place (Bennett, 1996). In addition, the destruction or change of a portion of the route disrupts the ability of an animal to find the goal. Therefore, this type of search mechanism works well when the relationship between starting point and the goal is constant (Ellen, 1987).

The second type of spatial knowledge, landmark knowledge refers to salient, stationary objects or distinctive features of an environment that are used to identify a location (Schacter & Nadel, 1991; Sherry, 1998). Spetch (1995) sees landmarks as discriminative stimuli that control or signal the location of responding. Landmarks can be distinguished from "beacons" as described above when it can be shown that the animal cannot specify a location in space from a single landmark without additional information from other landmarks or environmental information (Sherry, 1998). The use of landmarks or global stimuli, enable animals to find a goal even in the absence of local discriminative stimuli or beacons (Lopez, et. al., 2001). This type of learning and navigation is only useful when an animal is close enough to the area of the goal to perceive the landmarks that define that goal (Benhamou, 1997).

The third type of spatial knowledge, the cognitive map, has been a heatedly debated topic in psychology in recent years. Tolman first coined the controversial term "cognitive map" in 1948 based on the results of a series of maze-running experiments he conducted with rats. He defined the cognitive map as a representation of the environment which indicates the routes, paths, and environmental relationships that an animal uses in making decisions about where to move. Tolman's research challenged the behaviorist theories of animal learning popular at the time by stating that complex maze learning in rats could not be explained by simple stimulus-response associations, sensory guidance, etc. According to Poucet (1993), there are three functions of cognitive mapping: spatial recognition and identification, spatial localization of the animal itself or its goal and memory, and planning of spatial actions. One of the factors that distinguishes cognitive maps from route based navigation and landmark learning is that cognitive mapping provides the animal with the ability to make novel short-cuts (Vauclair, 1996). Because it is an internal representation, animals can be simultaneously aware of sequentially acquired environmental stimuli even when the environmental stimuli are beyond their perception (Poucet, 1993). Cognitive maps provide the maximum amount of flexibility in movement and behavior because they allow the animal to generate novel routes when landmarks associated with the goal are not visible from the starting point (Poucet, 1993). For these reasons, navigation by reference to a cognitive map is resistant to disruption by the movement of portions of the environment. Cognitive mapping requires knowledge of the spatial relationships among all objects in an area and the ability to understand and use these relationships from different viewpoints (Vauclair, 1996). Knowledge of spatial relationships is believed to be learned through environmental exploration (Ellen, Parko, Wages, & Herrmann, 1982; Thinus-Blanc, 1988). The concept of the cognitive map is highly controversial, particularly when discussing animal behavior and its validity has recently come into question (Bennett, 1996).

CHAPTER 2

EVOLUTIONARY THEORY OF SPECIES DIFFERENCES IN FOOD-SEARCHING BEHAVIOR

Foraging efficiency has been addressed by scientists in many different fields of research. However, the potential for species differences in food-searching behavior and memory has rarely been taken into account. Though Gallistel (1990) stated that the ability to form cognitive maps is ubiquitous across species, he did acknowledge that there may be differences across species in the amount of information that can be retained and the length of time with which that information could be retained in memory. If there are differences within or between species in spatial ability, can we predict where these differences will occur based on the feeding ecology of the animal?

There is reason to believe that animals with similar sensory capabilities may behave differently with respect to searching for food based on their evolutionary and ecological histories. As stated by Olton (1985, p. 482), "The argument goes as follows: Resources in the environment are not distributed randomly. Rather, they occur in patches, which may be temporal or spatial. In any given place, more resources are available at some times than at others. At any given time, more resources are available in some places than at others. These temporal and spatial patterns are predictable. Consequently, an animal can use the memory of previous patterns to make a judgment about the current distribution of resources. An animal that uses this kind of memory should have an adaptive advantage over an animal that does not: access to desirable resources should be enhanced, and exposure to risks should be reduced. To the extent that the environment remains constant for many generations, and the tendency to forage is influenced by genetic variables, animals should develop mnemonic abilities that help them forage efficiently among the resources in their environment."

No formal, comprehensive theory of species differences in food searching behavior has been offered to date. However, Milton (1981, 1988) has proposed an evolutionary hypothesis of the relationship between foraging and primate mental development that may be applicable across many different species. Her hypothesis is based on several factors including body size, diet, home range size, temporal distribution of foods, predictability of food sources in space and time, and food search efficiency. According to Milton (1981), animals with larger body sizes require larger supplying areas of food resources. Similarly, animals that eat mostly young leaves will require a larger supplying area than animals that eat mature leaves. Finally, animals that specialize on fruit (frugivores) will require larger supplying areas than animals that specialize on leaves (folivores) because fruiting trees are more patchily distributed. This last hypothesis is supported by data showing that for 56 primate species, increasing amounts of foliage in the diet was associated with decreasing size of home range (Clutton-Brock & Harvey, 1977; Clutton-Brock & Harvey, 1980; Harvey, Clutton-Brock, & Mace, 1980). This is the result of differences in the distribution between leaves and fruit in the environment.

Most tree species are clumped in nature and can be described as patchy in space. Studies of tropical forests have also shown that fruit trees are not only patchy in space but they are also patchy in time, meaning that young leaves and ripe fruit are only available during certain times of the year (Oates, 1987). Patterns of leafing, flowering, and fruiting in tropical habitats are never synchronized across the whole community in primate habitats. Mature leaves occur in large patches that are encountered more often in a food search than young leaves, fruits, and flowers. These patches are often larger than the metabolic need of the forager, providing them with a highly predictable, nutritious food supply within a relatively small area. Fruit, on the other hand, is much more widely dispersed and less frequently encountered. For frugivores, nutritional food sources that meet their needs are few and far between. Therefore, a primate relying on this resource requires a larger supply area. These aspects of tree and resource distribution would make it difficult for animals to specialize on one type of food. However, the location and seasonality associated with leaf and fruit production in trees has the advantage of being predictable in space and time both daily and seasonally. Once animals have found a particular tree species and learned its location, it becomes a predictable, reliable resource presumably for the entire life of the animal. For those animals living in savannas and deciduous forests, food resources are even more clumped in space and time (Oates, 1997). These species tend to be more terrestrial than those living in tropical forests and have larger home range sizes. According to Milton (1981), all of these characteristics of habitat and resource distribution may have selected for greater cognitive development in consumers that specialize on fruit and flowers for increased foraging efficiency. Milton's hypothesis has been supported by field studies of howler monkeys (*Alouatta palliata*) and spider monkeys (*Ateles geoffroyi*), both of which are large-bodied Neotropical non-human primates. Howler monkeys differ from spider monkeys in several ways. First, they are more folivorous than spider monkeys, focusing more of their foraging time on the leaves of trees than on fruit. Second, howler monkeys forage in cohesive social groups, moving directly as a troop through the forest from areas with low concentrations of preferred foods to areas with high concentrations of preferred foods. Studies conducted in the field by Milton (1981) indicate that howler monkeys do not forage randomly. Rather they are significantly more efficient at locating preferred food sources than would be expected by chance. However, howler monkeys have relatively small home range sizes, limiting the amount of information they would have to know in order to forage efficiently (Milton, 1981). The fruit that they do eat ripens all at once, decreasing the necessity of travel between sites. Finally, howler monkeys display very regular, systematic patterns of behavior. Instead of remembering the locations and type of food found in each preferred food site, they may simply follow strict pathways throughout their home range that increase the encounter rate of preferred food items.

In contrast to howler monkeys, spider monkeys are more frugivorous, spending the majority of their time eating fruit. Like howler monkeys, their patterns of movement appear to be goal-directed. However, their home ranges are much larger than that of howler monkeys, which may be due in part to the fact that the fruit trees they prefer only ripen a portion of their fruit each day. This forces spider monkeys to disperse from each other and forage alone or in small subgroups. Because of this, spider monkeys have larger home range sizes than howler monkeys. In support of Milton's (1988) hypothesis that foraging ecology influences mental development, Quirling (1950) found that the mean brain size for spider monkeys was almost double that of howler monkeys. In addition, when taking relativity of brain size to body size into account, the brain size and neural complexity of spider monkeys is double that of howler monkeys (Jerison, 1973). The relationship between brain size and foraging is consistent across a wide variety of species including small mammals (Harvey, Clutton-Brock, & Mace, 1980; Martin, 1986), carnivores (Gittleman, 1986), bats (Eisenberg & Wilson, 1978), and non-human primates (Barton & Purvis, 1994; Clutton-Brock & Harvey, 1980; Sawaguchi, 1988; Sawaguchi, 1990; Sawaguchi, 1992; Sawaguchi & Kudo, 1990). For the 13 families of small mammals tested by Harvey, Clutton-Brock, and Mace (1980), comparative brain size was larger in frugivores than folivores between species within the families Sciuridae, Cricetidae, and Muridae. In fact, those families categorized as being strictly folivorous (Caviidae and Leporidae) had the smallest relative brain sizes than families categorized as being frugivorous, insectivorous, granivorous or generalists (Geomyidae, Heteromyidae, Talpidae, Zaopdidae). These results were corroborated by those of Martin (1986).

Similar to the results from their study on small mammals, Harvey, Clutton-Brock and Mace (1980) found that folivores have smaller comparative brain sizes than frugivores within the Lemuridae, Cebidae, Cercopithecidae, and Pongidae families. In a larger study of 118 species of primate from the Lemuridae, Cebidae, Cercopithecidae, and Pongidae families, Clutton-Brock and Harvey (1980) found comparative brain sizes to be greater in frugivores than folivores. In a similar study of 139 species of primate, Harvey, Martin, and Clutton-Brock (1987) reported that, once the effects of body size were removed from the equation, diet was the only factor that correlated significantly with brain size. Specifically, folivores have smaller brain sizes than frugivores. Although differences in diet have been correlated with relative brain size and are similar for a wide variety of species, the selective pressures that caused these increases in brain size are still unknown and much debated. Most of the hypotheses can be divided into one of two categories (Harvey & Bennett, 1983; Harvey, Martin, and Clutton-Brock, 1987).

The energy hypothesis states that increased brain size in frugivores is related to either basal metabolism (Armstrong, 1983) or to maternal metabolic turnover during gestation (Martin, 1986). However, the most widely offered hypothesis for the relative brain size differences for animals with different diets is similar to that proposed by Milton (1981). This is the foraging hypothesis first proposed by Jerison (1973) and supported by the results of others (Barton, 2000; Eisenberg & Wilson, 1978; Gittleman, 1986; Harvey, Clutton-Brock, & Mace, 1980; Sawaguchi, 1992; Sherry, 1997) which states that larger brain sizes are necessary for animals to locate large pockets of energy-rich food sources that are less predictable in space and time than other food sources. Foraging efficiency would be increased by an animal's ability to store and process large amounts of relatively complex environmental information concerning food distribution.

In addition to the energetics hypothesis and the foraging hypothesis for brain evolution in mammals and non-human primates, there is a third hypothesis that has been offered for the evolution of brain size in non-human primates, the social hypothesis. The social hypothesis contends that primate intelligence evolved with the need for kin recognition and prediction of the action of conspecifics that is necessary in complex social life (King, 1986). This hypothesis is supported by studies that have found that social structure is correlated with brain size such that monogynous species tend to have smaller relative brain sizes than polygynous species when diet is held constant (Clutton-Brock & Harvey, 1980; Sawaguchi, 1990; Sawaguchi & Kudo, 1990).

In the search for answers to the questions concerning the possible cause of brain size evolution in mammals and non-human primates, some researchers have begun to look at specific structures in the brain that may confer benefits to either foraging or social skills. For example, several researchers have examined the neocortex and its relationship to ecological variables. The size of the neocortex has been linked to learning ability and intelligence in non-human primates (Passingham, 1975). As is the case for overall brain size, the size of the neocortex relative to the rest of the brain is larger in frugivores than folivores (Sawaguchi & Kudo, 1990). Researchers have found that the neocortex is associated with a variety of skills such as mental flexibility, the processing of visual and spatial information, the anticipation of future events, and the carrying out of coordinated, sequential and simultaneous movements which may be important the location, recognition, procurement, and manipulation of foods (Barton & Purvis, 1994; Gibson, 1986; Sawaguchi, 1992). According to Gibson (1986), these skills are what separate lower vertebrates from mammals. In addition, portions of the neocortex may be specifically related to spatial memory. The neocortex is functionally divided into lobes. Impairments in or lesions of both the parietal lobe and the frontal lobe have been found to cause a disruption of spatial memory, particularly spatial working memory, spatial navigation, and spatial problem solving (for review see Poucet, 1993).

Another important structure in the brain that is correlated with ecological variables is the hippocampus. The hippocampus of the brain has been linked to spatial memory (for review see Clayton & Lee, 1998) and implicated in the organization of cognitive mapping (for reviews see Chozick, 1985; O'Keefe & Nadel, 1989; Squire, 1992). The size of the hippocampus is larger both in food-storing birds (Basil, Kamil, Balda & Fite, 1996; Clayton & Lee, 1998; Sherry, 1997: Sherry, Vaccarino, Buckenham, & Herz, 1989) and kangaroo rats (Jacobs & Spencer, 1994) than closely related non-food-storing species, and there are species-specific sex differences in brain size among cowbirds based on the nesting behavior of the female brown-headed cowbird (Sherry, 1997). Moreover, studies have shown that the relative size of the hippocampus is correlated with home range size in non-human primates (Barton & Purvis, 1994). However, the hippocampus does not differ significantly between taxa of non-human primates (Stephan, Baron, & Frahm, 1988). In fact, in rats, monkeys and humans it has been found that the hippocampus is involved in working memory (remembrance of places previously visited) and declarative memory, but it does not appear to be related to the formation of cognitive maps (Olton, 1982a; Squire, 1992). In addition, the hippocampus has recently been related to social interdependency in rats (Maaswinkel, Gispen, & Spruijt, 1997).

The debate surrounding the evolutionary origins of increased brain size rages on, with some researchers advocating the foraging hypothesis and some advocating the social hypothesis. This has led to the proposal of a multiple-factor hypothesis which states that multiple, parallel factors associated with diet and social interactions were related to the development and enlargement of multiple, parallel neocortical structures (Sawaguchi, 1992). However, the fact remains that brain size differences can be predicted on the basis of diet and foraging niche. What is yet to be determined is whether these differences in brain size are accompanied by adaptive specializations in learning and cognition for foraging. Though Milton (1981) found correlations between brain size and diet in howler monkeys and spider monkeys, she conducted no research to determine whether those differences actually are correlated with differences in cognitive ability for finding food. According to King (1986, p 368), "We need to find a correlation between frugivory and some facet of intelligence that does not exist in folivores and insectivores". If the evolution of the brain occurred primarily as a result of the demands placed on foraging animals, then it might be expected that species will differ on cognitive tests designed to examine the skills that would be necessary for the location of food sources that are less predictable in space and time than other food sources as well as those necessary for storing and processing large amounts of relatively complex environmental information concerning food distribution.

What I believe is needed is not more correlational information, as suggested by King (1986), but rather experimental data to determine whether animals categorized as frugivores do in fact possess advanced cognitive skills related to foraging that confer advantages in the location of food because, according to Martin (1986, p 88), "no additional evidence is available to demonstrate that the observed correlations have been correctly interpreted". However, it is difficult even with experimental research to directly compare the capabilities of two different species, especially if those two different species are taxonomically distant. Interpretations of differences in performance between two species or even two individuals within the same species tested using an identical task can be difficult. Differences might be found between species for a variety of reasons that have nothing to do with differences in evolution and ecology including hunger level, habituation to the testing environment, sensitivity to the task or stimuli, propensity for distraction by irrelevant stimuli, capability of making the appropriate response (as seen in pigeons foraging on elevated vs. ground feeders, etc., (Shettleworth, 1998). Shettleworth (1998) has stated that meaningful species comparisons can only be made between species for which there is an a priori prediction of species differences based on ecology. Furthermore, comparisons between species should not be made only on tasks designed to tap the presumed adaptive specialization. Rather, a variety of tasks should be tested for which different patterns of responding are predicted. For example, if spatial memory in food storing birds is an adaptive specialization rather than a by-product of a larger brain, then they should perform better than nonstoring birds only on tasks that test spatial memory. This opinion differs from Milton's (1981) proposed theory of intelligence based on foraging niche in that she makes no distinctions between different types of memory systems or cognitive mechanisms. She simply says that one species will use possess more complex foraging skills and have a relatively larger brain size than another. And finally, many different species should be tested to eliminate the possibility that better performance arose by chance.

The examination of species differences in foraging capability needs to be multi-faceted, in that species should be tested on a range of sensory and cognitive capabilities. Arguments surrounding primate brain evolution are beginning to focus on the relationship between visual specialization and brain evolution (for review see Barton, 2000). For example, the size of the neocortex, primary visual cortex, and parvocellular geniculate nucleus are all correlated with the same ecological variables. Visual specialization would confer advantages in both foraging and social situations. If visual specialization was the driving force behind brain evolution, one would not predict differences in spatial memory but rather in visual capabilities that may confer advantages to animals in both social and non-social foraging situations. Therefore, species would need to be tested not only on tasks involving spatial ability but also on tasks involving visual discrimination and memory. These questions cannot be answered through correlational research. They require empirical testing of the relationship between foraging efficiency and food searching behavior either in the laboratory or in the field.

CHAPTER 3

REVIEW OF THE LITERATURE ON FOOD SEARCHING BEHAVIOR

Milton (1988) does not fully outline what might differentiate "complex" foraging strategies from "simple" foraging strategies. However, as suggested by data presented in the first chapter, the ability to remember the location of food that is predictable in both space and time and travel directly to known food sites may confer a great advantage to a foraging animal (Benhamou, 1994). Spatial memory is one of the few areas of psychological research in which differences both within and between species have been studied in relation to foraging ecology and evolution. In many studies of spatial memory, other sensory discriminative stimuli such as visual or olfactory stimuli may control the behavior of orientating towards a goal. It is interesting that, despite the assumption that guidance learning (i.e., the use of a discriminative stimulus as a beacon signaling the presence of food) is the simplest form of navigation toward a resource (Ellen, 1997), many species of animal have been observed to preferentially use spatial information even when both spatial and sensory information are available.

This chapter will review the research that has been conducted on spatial memory in a variety of species, with an emphasis on studies in which other sources of information have been examined or discussed, and direct species comparisons have been made either within species (as in between males and females) or between closely related species known to differ in either their ecological niche or use of the environment. Although the literature on the spatial abilities of insects is substantial (Beugnon, Pastergue-Ruiz, Schatz, & Lachaud, 1996; Cheng, 1999a, 1999b; Dyer, 1994; Dyer, 1998; Gallistel, 1989;

Zhang, Bartsch, & Srinivasan, 1996), to my knowledge there have been no direct comparisons across or within species based on ecology. Therefore, this review will not include data on insects. Instead, it will focus on rodents and small mammals, birds, domesticated animals, and non-human primates. For some species, particularly rats and food-storing birds, there have been many review articles and book chapters summarizing the data. Where extensive reviews are already available, I will provide an overview of the research findings and then direct the reader to the appropriate reviews for a more in-depth discussion. It will be evident that, despite the potential importance of testing niche-related predictions made by Milton and suggested by studies of brain size and foraging strategy for understanding the evolution of species, species differences in spatial learning and performance are very rarely studied and are often relegated to no more than an afterthought in reviews and discussions of empirical studies.

3.1 Rodents and Small Mammals

Rats have been the most studied of all animals in psychology, and studies of associative and spatial learning are no exception. Several types of apparatuses including the T-maze, Hebb-Williams maze, the Maier three-table reasoning task, Morris Water-escape task, the sunburst maze, the holeboard task, and the conefield task have been used in the laboratory to examine spatial memory and its role in foraging decisions in rats (Foreman & Ermakova, 1998; Raaijmakers, Blokland, & van der Stay, 1993). The maze is the oldest and most widely used apparatus, introduced in 1900 by W. S. Small at Clark University (Schultz & Schultz, 1992) and made popular by Tolman and his associates (1948).

Two types of mazes were fashioned after the design of the maze for the entertainment of people in Hampton Court Gardens in England (for historical reviews, see Bowe, 1984; Olton, 1979), alley mazes that had opaque walls to delineate paths and elevated mazes that were composed of raised platforms without walls. Rats perform extremely well in both types of maze, their movements often becoming completely automatic as evidenced by their bumping into blockades suddenly placed onto well-known paths, their falling off of elevated maze alleys when a portion of the alley was suddenly removed, and their running over freely available food placed in a runway as they ran to the location of the pile of food at the end of the goal. These observations led early researchers to view the rat as a "kinesthetic-machine", performing spatial tasks through simple muscle-contractions or by following an inflexible, sequential path through the maze. However, this hypothesis was contradicted by findings of spontaneous alternation, which showed that rats rarely choose the same path or sequence in subsequent trials. Moreover, rats appear to be able to remember where they have been in a maze and where they are going, avoiding making repetitions of alleys or paths and planning ahead so that they choose paths which prevent them from making repetitions. These findings led Tolman (1948) to develop his theory of cognitive maps.

The results of studies conducted with mazes were extremely influential in psychology and inspired researchers to develop variations on the apparatus that were better adapted to answer specific research questions. One of these variations, the radial arm maze, is the apparatus that has become the most prominent in spatial memory testing (Brown, 1993; Foreman & Ermakova, 1998; Olton, 1979). A typical radial arm maze is constructed of a central platform surrounded by a number of runways (usually 8, 12, or

17) that each lead to a food pellet. The animal being tested is allowed to freely explore the apparatus until the food from each of the arms has been depleted. This type of task is known as sampling with replacement. To respond efficiently in a radial maze task, the animal should explore and deplete each of the arms without revisiting previously depleted arms. There are several ways in which an animal can successfully avoid previously depleted sites. One strategy an animal can follow is to always choose adjacent arms until all arms are depleted. Another strategy is to remember the location of previously depleted arms. Finally, visual or olfactory intra- or extramaze stimuli can control the choice behavior sites with food or sites already visited.

The radial arm maze was first used to simulate a foraging situation and examine spatial memory by Olton and Samuelson (1976). In this experiment, an 8-arm maze with interchangeable arms was used to simulate a foraging task. Their study showed that rats rarely revisited arms of the maze, thereby avoiding previously depleted sites. The rats did not seem to rely on intramaze stimuli to avoid previously depleted food sites, as evidenced by the fact that they continued to avoid previously visited arms even when the food sites were re-baited after each choice and the choice sequence was disrupted during testing. Therefore, the rats were not using the absence of olfactory discriminative stimuli to avoid the sites. To experimentally control for intramaze discriminative stimuli, Olton and Collison (1979) modified the radial arm maze such that the food cups at the end of the arms could either be rotated with the arms or remain stationary when arms were rotated. Rats were trained on a standard radial arm maze and then were tested in two groups, an intramaze group and an extramaze group. After each choice, the arms of the radial maze were rotated. For the intramaze group, the food cups remained with the arm.

Therefore, possible intramaze discriminative stimuli such as odor trails deposited by the animal or smells emanating from the food itself were important for accurate performance. For the extramaze group, the food cups remained in the same location while the arms themselves shifted. Therefore, extramaze discriminative stimuli such as features of the testing room or laboratory were important for spatial memory. The results of these manipulations showed that rats in the extramaze group performed significantly better than rats in the intramaze group, suggesting that features of the room outside of the radial arm maze were more important for specifying the location of an arm than intramaze discriminative stimuli. This confirmed that odor and visual discriminative stimuli did not influence behavior. Rather, extramaze discriminative stimuli were the most important for specifying the location of each arm. In fact, rats in early training have been observed to revisit paths that contain feces left by the rat itself on the previous visit (for review of discriminative stimulus use in the radial arm maze, see Foreman & Ermakova, 1998). Furthermore, Zoladek and Roberts (1978) found that performance accuracy decreased for blinded animals but not for anosmic animals, supporting Olton and Samuelson's (1976) conclusion that extramaze discriminative stimuli are more important for learning than intramaze discriminative stimuli.

Further evidence against the use of intramaze discriminative stimuli by rats when locating spatial locations comes from studies using the Morris water-escape task (Morris, 1981). In these studies, rats are placed in a pool of opaque water and are forced to swim to an underwater platform in a fixed location to escape. The platform itself is invisible to the rats, but can be located on the basis of discriminative stimuli outside of the pool environment. This apparatus eliminates visual discriminative stimuli associated with the goal (the platform), olfactory discriminative stimuli or auditory discriminative stimuli in the room. Results of studies conducted with the Morris water-escape task show that rats quickly learn to escape from the pool by swimming directly toward the platform, regardless of their starting point (Morris, 1981). Therefore, visual extramaze discriminative stimuli that can be used as landmarks appear to be important for accurate responding in this task. Recent research has shown that, in this type of task, rats require at least two landmarks to successfully locate an underwater platform. They are unable to locate the platform on the basis of one landmark alone (Prados & Trobalon, 1998). These results should not be taken to imply that the rats do not learn anything from intramaze discriminative stimuli. In fact, it has been found that visual and olfactory local discriminative stimuli can be used beacons to improve discrimination of a goal (Lavenex & Schenk, 1995; Maaswinkel & Whishaw, 1999). Moreover, Brown and Bing (1997) have found that there may be a more complex interaction of intramaze discriminative stimuli and extramaze discriminative stimuli than previously believed. However, it is without doubt that extramaze discriminative stimuli are more important than intramaze discriminative stimuli for learning and remembering the location of a goal (Lavenex & Schenk, 1995).

According to Olton and Samuelson (1976), not only do rats often ignore intramaze discriminative stimuli, they also do not seem to use any particular pattern or sequential sampling when avoiding previously visited arms. Rather, it appears that rats search randomly and are able to remember where they have been during the trial. This tendency to avoid going to sites that have already been visited has been replicated in a variety of apparatuses of differing levels of complexity (Olton, 1982b), even in mazes with as many as 17 arms (Olton, Collison, & Werz, 1977). Within-trial memory for previously depleted arms has been referred to as working memory (Honig, 1978). However, it remains debatable whether rats are actually using some type of memory mechanism for avoidance of revisits. It is possible that they are using a more simple mechanism that is not readily apparent to the experimenters, such as always turn 45 degrees or 135 degrees when returning to the center platform and continue down the arm toward which the body is now facing. Many studies have been conducted with data from some of the original studies of maze learning to determine if, rather than spatial memory, rats are using an algorithm or sequential choice processs to avoid revisits (for review, see Brown, 1993; Foreman & Ermakova, 1998).

Evidence has been found both in support of algorithmic behavior and in support of the use of some form of working spatial memory. For example, Olton and Samuelson (1976) found that the behavior of rats choosing arms in a radial maze had characteristics that appeared similar to that of working memory studied in non-spatial situations. First, rats were able to remember approximately 12 arms without revisiting (Olton, 1982b). Second, the likelihood of making an error increased with the number of increasing choices. That is, the probability of making an error was greater for arms chosen early in the testing session than for those chosen later in the testing session. This is referred to as a recency effect. It is unclear whether this recency effect is the result of retroactive interference, as it is in other tests of memory (Maki, Brokofsky, & Berg, 1979; Roberts & Smythe, 1979). Some studies have found that there was no indication of a primacy effect in the spatial memory of the rat (Olton, Collison, & Werz, 1977; Roberts &

Smythe, 1979) however, others have found serial position curves similar to those observed in human memory (Kesner, Chiba, & Jackson-Smith, 1994).

Regardless of how rats carry out the task of avoiding revisits, rats in general seem to have an overall tendency to shift rather than stay at a food site, particularly when all resources in an area have been depleted (Olton, 1979; Olton et al., 1981). This behavior of shifting following reward has been referred to as a win-shift strategy. It can be contrasted with a win-stay strategy in which a rewarded animal stays or returns to areas that have been rewarded. It has been found that learning a win-shift strategy is easier for rats than learning a win-stay strategy. However, rats can learn to modify this win-shift strategy of foraging when the environment rewards a win-stay strategy rather than the win-shift (Zeldin & Olton, 1986). Subsequent studies showed that, although shift behavior was the predominant strategy, it was less apparent after reward than non-reward (Gaffan & Davies, 1981; Herrmann, Bahr, Bremner, & Ellen, 1982).

Olton was the first to discuss the behavior of rats on the radial arm maze within an ecological framework, and he made predictions about the performance of rats based on feeding ecology (Olton, 1982b). Specifically, "species that search for changing food sources…ought to have a predisposition to follow a shift strategy in the laboratory, and species that search for reliable food sources ought to have a predisposition to follow a stay strategy" (Olton, 1979). Therefore, this pattern may be adaptive for animals whose prey distribution is nonrandom or takes little time to replenish. Olton (1979, 1982b) reviews work with other species which supports this hypothesis. He discusses the results of an often cited study conducted by Kamil in 1978 on the amakihi, which is a bird that specializes on the nectar of flowers from the mamane tree. On each visit to a flower, the birds deplete all the nectar from that flower. It takes several hours for the nectar to be replenished in that same flower, and as would be predicted by Olton's theory, the birds use a win-shift foraging strategy in which they visit a flower and then shift to another flower. Other birds such as the English thrush and the ovenbird who eat earthworms and grubs that are often found in patches adopt more of a win-stay strategy in that, when a prey item is found they stay in the general area and systematically and methodically search for more in that same area. Unfortunately, experimental studies similar to those conducted by Olton and colleagues have not been conducted with these other species. It would be important to see how these species behave in a similar research paradigm as is normally used with rats.

In support of Olton's theory that environment can influence performance, Takai and Wilkie (1985) found that behavior in the radial arm maze can be modified by rearing environment. Gerbils raised in an environment in which the location of their food and water sources remained constant each day were less likely to use a win-shift strategy in a radial arm maze than those reared in an environment in which the location of their food and water sources changed from day to day. These results suggest that foraging history can influence future behavior on a spatial memory task.

It is generally agreed that rats have very good spatial abilities. But, with the exception of the very early work in apparatus design and Olton's win-shift theory, the spatial abilities of the rat have not been examined within an ecological framework. Many studies have been conducted with other species of rodents and small mammals such as gerbils (Collett, Cartwright, & Smith, 1986; Thinus-Blanc & Ingle, 1985), hamsters (Jones, McGhee, & Wilkie, 1990; Poucet, Chapuis, Durup, & Thinus-Blanc, 1986;

Thinus-Blanc, Bouzouba, Chaix, Chapuis, Durup, & Poucet, 1987) and even shrews (Pierce, 1987) which have confirmed that spatial memory does play a role in the exploratory and foraging behavior of non-rat species. Nocturnal animals that occupy complex tunnel systems such as the blind mole-rat (Kimchi & Terkel, 2001) and the badger (Mellgren & Roper, 1986) have been observed to perform very well on spatial tasks. In addition, spatial memory has been found to play a large role in cache-recovery in seed-caching rodents such as the yellow pine chipmunk (Vander Wall, 1991), fox squirrels (Jacobs & Shiflett, 1999; Lavenex, Shiflett, Lee, & Jacobs, 1998), gray squirrels (McQuade, Williams, & Eichenbaum, 1986), Merriam's kangaroo rats (Barkley & Jacobs, 1998; Jacobs, 1992), and desert kangaroo rats (Langley, 1994). To determine if spatial memory is a specialized trait in food-caching species, they would have to be directly compared to closely related species that are not known to cache food. Few studies have been conducted to directly compare spatial behavior in rodents and small mammals, despite the fact that there are many species that differ widely in their foraging ecology and natural history. Those studies that have been conducted have provided some support for the hypothesis that differences in spatial learning can be predicted on the basis of natural history.

Several studies of mice revealed that they may not be as proficient at spatial memory tasks as are rats, despite the fact that both species are opportunistic generalists and occupy niches with similar food distributions (Mizumori, Rosenzweig, & Kermisch, 1982). For example, Mizumori and colleagues (1982) found that mice were deficient in performance when directly compared with rats. Both rats and mice performed above chance on the first trial of the 8-arm maze. However, whereas rats obtained peak performance of at least seven correct choices (i.e., seven choices to arms that had not previously been visited) by the 8th day of training, the mice were unable to improve their performance after as many as 20 days of testing. The superiority of the rats' performance over that of the mice was evident even when the task was made more difficult for them by adding a delay between choices. The authors acknowledged the possibility that the inferior performance of the mice may have been the result of differences in foraging behavior in the wild that are currently unknown, however, they caution against automatically assuming that there are species differences.

Unfortunately, comparisons between laboratory mice and rats on spatial tasks on the basis of ecological factors are difficult because there are many different strains of mice, some of which are highly inbred. It is, therefore, possible that the difference was due to the strain of the mice used in the study and that other strains may perform as well as rats. In addition, there may have been differences between the species with regard to motivation and differences in reinforcement contingencies. However, it is unlikely that the species difference between rats and mice was due to the particular strain of mouse used in the study (Whishaw, 1995). It is more probable that rats and mice differ on the Morris water maze task because rats in the wild are known to be semi aquatic, whereas mice prefer dry land. This hypothesis has been supported by research showing that, whereas the mice and rats performed equally well on a series of experiments conducted in a standard 8-arm radial maze, the mice performed significantly worse than the rats on a Morris water escape task (Whishaw & Tomie, 1996). Therefore, the differences are more likely related to some non-spatial factor such as ecological validity of the task for mice.

The results of Whishaw and Tomie's (1996) study seem to contradict those of Mizumori and colleagues (1982), who found that the performance of mice was inferior to that of rats in a dry-land radial arm maze. However, the experiments conducted on the maze were very different. Mizumori and colleagues (1982) conducted a typical radial arm maze study in which all eight arms were baited during a trial and the measure of error was the number of revisits to previously depleted arms. In this paradigm, errors are recorded for a failure of the animal to use a win-shift strategy. In contrast, Whishaw and Tomie (1996) performed a series of experiments in which either 4, 2 or only 1 arm was baited during a trial. Animals in this study were considered to have made errors for failure to respond according to a win-stay strategy. Based on the different results of these two studies, it is possible that mice are inferior to rats on tasks involving working memory but not on tasks involving reference memory. In a comparative study of mice and rats similar to that of Whishaw and Tomie's (1996) study, Schenk (1987) also found that woodmice were able to perform very well on a dry-land place learning task, but performed less well on a water-based place learning task. When routes used by mice and rats to get to the goal site were compared across species on both the dry-land and water-based tasks, the mice were observed to use much less efficient and direct routes than the rats to get to their intended goal. Studies such as the one conducted by Schenk (1987) may be considered to be more ecologically valid than that of other experiments because she used mice that were born to wild-caught parents.

Another species that has been directly compared with the rat is the Brazilian short-tailed opossum (Kimble & Whishaw, 1994). Like the rat, the opossum is believed to be nocturnal and omnivorous. The short-tailed opossum and the rat are similar in size, however, the short-tailed opossum has a relatively smaller neocortex than rats. Kimble and Whishaw (1994) compared the behavior of rats and short-tailed opossum on a Morris water maze and a radial arm maze task. They found that the opossum performed significantly worse than the rats on both tasks. They were unable to find a hidden platform without a proximal visual discriminative stimulus in the Morris water maze, and they committed significantly more working memory and reference memory errors than rats on the radial arm maze when four of the eight arms were baited. Similar differences were found between rats and opossum in a very early study using a Hebb-Williams maze conducted by Pollard and Lysons (1967). It is possible that the observed differences between opossum and rats on tests of spatial memory lies in the fact that rats are naturally burrowing animals and may have evolved to be efficient at tasks involving place location. It is unknown whether the difference in neocortex size between rats and opossum is related to spatial memory or possibly to vision. Rats are known to use extramaze discriminative stimuli in finding food, therefore, a difference in vision between the species may cause differences in performance.

The hypothesis that natural selection for or experience with burrowing may affect spatial ability is corroborated by a comparative study recently conducted with laboratory rats, blind mole-rats and the Levant vole (Kimchi & Terkel, 2001). The blind mole-rat is a solitary species that spends its life underground in self-made branching tunnels. The authors hypothesized that natural selection would have favored highly developed spatial orientation abilities in the blind mole-rat (*Spalax ehrenbergi*) and that they would perform better when tested for complex maze-learning than rats (*Rattus norvegicus*) and voles (*Microtus guentheri*). These species of rats and voles use underground tunnel systems but live mostly above ground. The researchers found that, of all three species, the blind mole-rats had the highest learning rate on the complex maze. Furthermore, their memory of the maze was superior to that of rats after delays ranging from 2 to 60 days, and to that of the voles after delays as long as 120 days. The authors attribute the superior performance of the blind mole-rats to the fact that they spend their entire lives in very complex tunnels. Good spatial skills allow the mole-rats to decrease energy expenditure in storing and locating food within their tunnels, locating moist soil where food is more abundant, and in locating and orienting toward potential mates during the breeding season. They suggest that the mole-rats use a combination of route-based behavior, magnetic compass orientation, and internal kinesthetic discriminative stimuli resulting in a mental map of the maze system.

One of Milton's (1981) hypotheses concerning species differences in cognitive ability is that the brains of animals with home range sizes will differ from that of comparably sized animals with smaller home ranges because they have more information to learn in their relatively larger environment. In one of the first tests of the hypothesis that home range size is related to superior spatial ability, Gaulin and Fitzgerald (1986) compared home range size and spatial ability in polygynous meadow voles (*Microtus pennsylvanicus*) and monogamous pine voles (*Microtus pinetorum*). Voles are small rodents, some species of which spend most of their lives in underground burrow systems. Meadow voles spend most of their lives above ground, whereas pine voles spend most of their lives below ground in burrows. Male meadow voles have much larger home ranges than female meadow voles. However, there is no difference in home range size between male and female pine voles. The results showed that male meadow voles, but not male pine voles, had larger home ranges and performed better when tested on a sunburst maze than their female conspecifics. Gaulin and Fitzgerald (1989) found similar results when comparing the performance of meadow voles with another monogamous species of vole, the prairie vole (*Microtus ochrogaster*), on symmetrical mazes. There were no differences in home range size between monogamous male and female prairie voles. Moreover, unlike meadow voles, there were no sex differences in performance in a series of symmetrical mazes. Differences were the result of differences in early experience with complex environments (Gaulin & Wartell, 1990) and differences in activity level between males and females (Gaulin, Fitzgerald, & Wartell, 1990) cannot account for this affect. These results support the hypothesis that sex differences are related to home range size, and that they evolved as a result of selective pressure for males in polygamous mating systems to expand their range as a means of increasing reproductive fitness. However, as with any comparative studies, it is important to use caution when interpreting and generalizing the results. Gaulin and colleagues used open-field type mazes to conduct their research. Other studies have either failed to find sex differences in spatial ability or found only limited evidence of sex differences in spatial ability in voles when using the Morris water-maze task (Galea, Ossenkopp, & Kavaliers, 1994; Sawrey, Keith, & Backes, 1994). This lack of observed sex differences may be dependent on the reproductive state of the animals, as some studies have shown that estrous females or females with high levels of estradiol do in fact perform worse than males on the Morris water-maze task (Galea, Kavaliers, Ossenkopp, & Hampson, 1995; Galea, Ossenkopp, & Kavaliers, 1994; Kavaliers, Ossenkopp, Galea, & Kolb, 1998).

Only one study of small mammals has been conducted with the explicit purpose of relating spatial ability to foraging ecology. Pleskacheva, Wolfer, Kupriyanova, Nikolenko, Scheffrahn, Dell'Omo, and Lipp (2000) conducted a Morris water maze navigation task with two different species of voles, the bank vole (*Clethrionomys glareolus*) and the root vole (*Microtus oeconomus*). They found that bank voles had an infrapyramidal hippocampal mossy fiber projection that was 230% larger than that of root voles, which was accompanied by superior performance on several spatial search pattern tasks in a Morris water-maze. The authors suggest that the observed differences may be due to the feeding ecology of the vole species. Bank voles have larger and more complex home range sizes than root voles, possibly because of their reliance on widely dispersed seeds as a food source. Like Milton (1981), the authors conclude that animals foraging on widely dispersed food sources have larger, more complex home ranges and, therefore, natural selection favored flexible processing of spatial ability and for superior cognitive mapping. Given the wide range of foraging patterns among small rodents and mammals, it would be valuable to use similar methodology to test the generality of these findings.

In conclusion, rats are extremely efficient at performing tasks involving spatial skills. This is not surprising given that they create elaborate underground burrows that resemble mazes used for testing spatial memory. They are able to locate hidden sources of food without using intramaze discriminative stimuli, avoid locations that they have already visited, and make choices on the basis of food quality and quantity in many different types of tasks designed to assess spatial memory tasks. Other species of animals known to use underground systems such as gerbils, hamsters, shrews, blind mole-rats and badgers also have been found to have well-developed spatial skills, though the tests designed to assess those skills have been quite varied making it difficult to compare ability of each species across studies. Furthermore, spatial memory is known to play a role in cache-recovery in seed-caching rodents such as the yellow pine chipmunk, squirrels, and kangaroo rats. However, to determine if spatial memory was specialized in these species, direct comparisons would need to be conducted with closely related non-caching species.

Mice appear to be less proficient at the same types of tasks used with rats, perhaps because of differences in the way they exploit their environment. A priori predictions of superior performance on spatial memory tasks based on living condition and mating system have been supported by results from experimental research. For example, the opossum, which does not live in burrows and has a smaller neocortex size, did not perform as well as the rat in either a Morris water maze or radial arm maze task. However, only one study has been conducted with rodents or small mammals to look specifically at spatial memory with regard to foraging ecology (Pleskacheva et al., 2000). The results supported the hypothesis that animals that forage on more widely dispersed foods will have larger home ranges and display superior performance on tasks designed to test spatial memory than those with smaller home ranges that forage on less dispersed food items.

3.2 Birds

Rodents and pigeons have been the most commonly studied animals in the field of experimental psychology. However, unlike rodents, pigeons were not routinely tested on tasks involving spatial memory. In one of the first comparative studies of spatial memory and spatial abilities, Mackintosh and Cauty (1971) conducted a spatial reversal task with rats, goldfish and pigeons in which the response and location of the reinforcement were similar across studies. The apparatus for all three species had a left and a right key, either of which could be lit by a white light that served as a discriminative stimulus indicating the availability of reinforcement. The animals were first trained by reinforcing presses or pecks to the key on the left. Once trained to consistently press the left key, the researchers reversed the correct response such that the incorrect key was the reinforced key each day for 30 days. The dependent variable was the mean number of errors, defined as presses to the incorrect key, emitted across trials. The researchers found that, in the first 5 days of the study, the pigeons, rats, and goldfish made approximately the same number of errors. Whereas both the pigeons and goldfish did show some improvement throughout the study, neither species improved as rapidly as the rats. The relatively poor performance of the pigeons was surprising given that homing pigeons show remarkable spatial skills in navigation (Gallistel, 1990). This was the first study to suggest that pigeons were less proficient at tasks designed to test spatial learning than rats.

Furthering the notion that the spatial ability of pigeons were deficient compared to that of the rat, similar differences in spatial ability were observed when pigeons were tested using the same type of radial arm maze made popular with rats. Bond, Cook, and Lamb (1981) hypothesized that pigeons would have more difficulty with this type of task than rats on the basis of differences in foraging ecology. According to the authors, pigeons feed on open grasslands and usually use traditional feeding sites. They forage in flocks, relying on the presence of other birds to alert them to abundant food sources. Therefore, they may not have as a great a need for well-developed spatial skills as rats.

Bond and colleagues tested the spatial abilities of both rats and pigeons in an eight arm maze modified to accommodate the body size of the pigeons. They found that, whereas both rats and pigeons performed above chance (as measured by the number of feeders visited to obtain all eight pieces of food) throughout all trials, the performance of the rats was superior to that of the pigeons. The rats required a mean of 8.76 choices to remove the food from each of the arms, whereas the pigeons required 13.33, indicating that the pigeons were revisiting more arms than the rats during each trial. Unlike rats, the pigeons used an adjacency strategy in which they were more likely to turn right or left after returning to the center of the maze. This type of stereotypic movement pattern would not necessarily involve working spatial memory. The authors wisely caution the reader against drawing conclusions from this one study, but point out that these results were as predicted based on the foraging ecology of the animals.

Not all apparatuses produce poor responding in pigeons. Despite the poor performance of the pigeons on the spatial reversal tasks and radial arm tasks, pigeons were found to perform very well on a delayed alternation task in a T-maze (Olson & Maki, 1983). Pigeons were given one forced choice trial in which one arm of the T-maze was baited with food and the other arm was blocked. After obtaining all of the food at the end of the arm, they were returned to the start box and allowed to choose either of the two arms. A choice to the same arm that was baited in the forced choice trial resulted in nonreinforcement. Pigeons performed very well on this win-shift task even after being presented with delays between choices of 8-16 minutes. They did not seem to be using intramaze discriminative stimuli. Though the performance of the pigeons was not directly compared with that of rats, these results suggested that spatial memory in pigeons may not be as different from that of rats as originally thought.

Though pigeons were initially found to perform poorly when tested using the radial arm maze, with specialized training they seem to be able to perform at a level comparable to that of rats. In their study, Roberts and Van Veldhuizen (1985) gradually introduced pigeons to the radial arm maze by allowing them access first to only two of the arms and to more arms in subsequent phases. Once trained in this manner, the pigeons performed just as well as rats on tasks involving both working memory and reference memory. Moreover, they were able to make efficient choices based on the quantity of food in each of the arms. The response accuracy of the pigeons decreased, however, when delays over 6 minutes were imposed between choices, which is considerably less than that observed for rats. Rats have been reported to be capable of remembering the location of four forced choices for as long as 4 hours (Foreman & Ermakova, 1998). Despite the decrease in accuracy with increasing delays, performance in these tasks was better than had previously been attributed to pigeons. According to Roberts and Van Veldhuizen, these results suggest that the differences observed in previous studies between rats and pigeons may not necessarily indicate that spatial memory in pigeons is inferior to that of rats. It may simply mean that pigeons are not as well prepared initially to navigate a maze like environment. Unfortunately, the design of the study made it impossible to know if the pigeons were using spatial working or reference memory in any of their experiments. Each arm of the maze was differentiated by a different color discriminative stimulus placed at the end of the arm on the cup.

When these stimuli were rearranged within a task, performance was disrupted suggesting that the pigeons had been using these stimuli as beacons all along.

In support of the idea that pigeons are not as well prepared for radial arm mazes and hence show seemingly poor performance, Spetch and Edwards (1986) showed that an apparatus designed to more closely simulate a pigeons' natural environment can reduce the degree of difference between rats and pigeons on tests of spatial memory. They developed a multiple-goal, open-field test environment to examine pigeons' spatial working memory abilities. Eight food sites were arranged in a square spatial configuration in the test room. Unlike radial arm mazes, this open-field environment allowed the birds to make choices about how to travel from one food site to another. In the first portion of the study, all eight food sites were baited with food and the pigeons were allowed to choose freely among the sites. The results showed that the pigeons were able to accurately locate baited food sites and avoid revisiting previously depleted sites. As observed by Roberts and Van Veldhuizen (1985), the performance of the pigeons decreased after retention intervals of 5 minutes or more. In the second portion of the study, the pigeons were forced to choose from four randomly determined sites at the beginning of the test session. After visiting all four sites, a variable delay period was imposed after which the pigeons were allowed to search from among all eight sites. The pigeons were very accurate at this task, rarely revisiting previously depleted sites despite being disrupted during their travels. Therefore, like the rats in Olton and Samuelson's (1976) study and the pigeons in Olson and Maki's (1983) study, pigeons in this study were predisposed to follow a win-shift foraging task. It is unknown whether the pigeons were using working memory to avoid depleting previously depleted sites because they developed an adjacency strategy. That is, they were more likely to travel to adjacent feeders than non-adjacent feeders. Similar results have been found in other open-field studies conducted with pigeons (Roberts, 1988). Whereas this type of foraging pattern may preclude making determinations on the use of working memory, it does indicate that pigeons are highly efficient in their foraging, using an adjacency mode of travel. The pigeons did not seem to rely on intramaze stimuli to perform accurately on the task. When choice accuracy was compared between an environment with ground feeders and an environment with elevated feeders (which required flight), the pigeons performed better with ground feeders (Spetch & Edwards, 1986). Pigeons in the wild normally feed on the ground. Therefore, their superior performance on tasks requiring them to find food on the ground provides further support for the idea that preparedness to respond to a task can play a role in performance. However, Spetch and Honig (1988) found they found that pigeons' memory for baited food sites on forced choice trials could persist for as long as 2 hours, after which it began to deteriorate. This retention interval is still shorter than that observed for rats and food-storing birds.

More recent studies are beginning to show that the strength of spatial memory in pigeons may depend on both the task and the experience of the pigeons. Willson and Wilkie (1993) and Wilkie and Willson (1995) tested spatial memory in pigeons using a standard operant chamber. These pigeons had considerable testing experience in operant chambers. In these studies pigeons were exposed to four illuminated response keys, only one of which had been randomly chosen at the beginning of each trial to provide grain on a variable schedule. Each day the pigeons initially responded to the key that had provided reward on the previous day, indicating that they had remembered the relationship between food and location of the key for 24 hours. Rather than follow a win-shift strategy, the pigeons followed a win-stay strategy in which they returned to the locations that had previously provided reinforcement. Two-day breaks in testing did not disrupt performance, indicating that memory for associations between spatial location and food can persist for as long as 72 hours. Furthermore, pigeons were found to be capable of remembering more than one food-place association. The predisposition of pigeons to follow a win-stay strategy in these studies contrasts with the results of Olson and Maki (1983) and Spetch and Edwards (1986) who found that pigeons, like rats, were predisposed to follow a win-shift strategy. The response of pigeons following reward may be flexible and dependent on the task. For example, Randall & Zentall (1997) found that pigeons only showed a predisposition to use a win-stay strategy after experimental delays were imposed during the study.

From the early studies reporting inferior spatial memory to more recent studies reporting at least comparable spatial memory, it is clear that it is difficult at best to directly compare distantly related species such as pigeons and rats in comparative psychology. More valid comparisons based on foraging ecology would be those made between pigeons and another species of bird. Plowright, Reid, and Killian (1998) tested pigeons (*Columba livia*) and mynahs (*Gracula religiosa*) on a visible displacement task in which the birds learned to find hidden food. In each trial, food was dropped into one of four compartments in view of the bird. Pigeons pecked holes in paper towel covering the opening of the compartment and mynahs lifted lids to recover the hidden food. The mynahs learned the visual displacement task more quickly than the pigeons, performing at above chance levels on the first few trials of the study. Mynahs feed on fruit and nectar, in addition to insects and small animals. In contrast, pigeons feed mostly on grains and seeds. Based on differences in feeding ecology, it was expected that the mynahs would outperform the pigeons. Because of logistical problems discovered early on in the task, the tasks differed slightly between the pigeons and mynahs making it difficult to draw conclusions. However, the results were in the direction predicted on the basis of differences in foraging ecology.

Other species of bird also seem to be able to perform at higher levels than the pigeon. For example, a study of Clark's nutcrackers (*Nucifraga columbiana*) conducted in a testing situation analogous to that of a radial arm maze showed that these food-storing birds are able to remember the location of hidden food for intervals much longer than those previously recorded for pigeons or rats (Balda & Kamil, 1988). In a search phase, Clark's nutcrackers were forced to visit four of eight baited holes. Following a retention interval ranging from five minutes to twenty-four hours, the experimenter baited the other four holes, leaving the original four holes empty. The birds were tested for their ability to avoid previously depleted sites. All birds performed above chance at intervals as long as 6 hours. However, they were unable to perform as well at intervals of 24 hours.

Olson (1991) directly compared the behavior of pigeons to that of Clark's nutcrackers and scrub jays, both species of the corvid family that cache seeds in the fall and recover them throughout the winter. It was predicted that Clark's nutcrackers would outperform scrub jays on a spatial nonmatching to sample task because in the wild they are much more dependent on caching than scrub jays. Similarly it was predicted that scrub jays would outperform pigeons, a species not known to cache food in the wild. In the nonmatching-to-sample procedure, the subjects were placed in an operant chamber that had two response keys. In each trial, one of the two response keys was illuminated and served as the sample stimulus. Following five pecks to that sample stimulus, the lights were darkened and one of the two response keys was again illuminated. A correct response was to the stimulus that was not the sample stimulus. Delays increasing by 0.1 seconds were imposed between the illumination of the sample stimulus and the comparison stimulus in the subsequent trials when the subject made a correct choice. The results supported the predictions based on feeding ecology. Clark's nutcrackers performed significantly better than both scrub jays and pigeons at delays as long as 70 seconds. There were no significant differences in performance between the pigeons and the scrub jays.

Some of the most interesting and productive comparative work in spatial cognition using the ecological approach has been conducted with food-storing birds. Food-storing parids and corvids such as the North American black-capped chickadee (*Parus atricapillus*), the Eurasian marsh tit (*Parus palustris*), Clark's nutcracker (*Nucifraga columbiana*), and the Eurasian nutcracker (*Nucifraga caryocatactes*) are known to store large quantities of food during periods of food shortage and are able to relocate these caches over long periods of time (Shettleworth & Hampton, 1998). For example, an individual Clark's nutcracker will store between 22,000 and 33,000 seeds in 6000-8000 caches each year. It is estimated that they are able to successfully recover 60-86% of their caches (Balda & Kamil, 1998), sometimes as long as 285 days after first creating the cache (Clayton & Lee, 1998). Cache recovery in birds and other animals could be alternatively explained by many factors totally unrelated to memory including discriminative stimuli emanating directly from seeds, preferences for storing in particular sites, or systematic patterns of movement (Kamil & Roitblat, 1985). Each of these must be ruled out as possible explanations before it can be assumed that the animals are using spatial memory. However, any regularity in seed caching for particular sites (i.e., at the base of a trees) or recognizable stimuli (i.e., displaced soil) that could be used by the animal that is caching the seeds could also be used by other animals to locate and exploit those caches. Therefore, it would be advantageous for a food storing bird to leave as little evidence and be as unpredictable as possible. Spatial memory for the location of the caches would make the food in the cached available only to the individual bird that created the cache (Balda & Kamil, 1998).

Though different species are known to differ in the number of caches they create, in the amount of food stored in individual spatial locations, and in the time between cache and recovery (for review see Sherry, 1984b), both field and laboratory studies have shown that they all appear to use a combination of spatial memory and visual landmarks to recover their caches (for review, see Sherry & Duff, 1996). Although they are able to use the sun as a compass for large-scale orientation toward cache sites, food-storing birds use distal discriminative stimuli and landmarks for small-scale orientation toward cache sites (Sherry & Duff, 1996). Food storing birds are capable not only of accurately remembering a larger number of caches, but also of remembering the quality (Sherry, 1984a) and quantity of the food in these sites (Smith & Sweatman, 1974). Whereas these findings certainly indicate that food-storing birds have well-developed spatial memory skills, they do not tell us whether they are inherently different from non-storing birds.

Research has shown that the brains of food-storing birds are different from those of other birds (for review see Clayton & Lee, 1998). Specifically, the hippocampal formation, which includes both the hippocampus and the parahippocampus, is enlarged and contains more neurons in bird species that are known to store food. This hippocampal formation in birds appears to be involved specifically in the development of new spatial memories, particularly long-term memories. The enlargement of the hippocampal formation appears to be experience dependent, as evidenced by the fact that nestlings of food-storing birds do not have larger hippocampal formations than nestlings of non-storing birds. Furthermore, preventing food-storing birds from storing and retrieving caches results in much smaller hippocampal volumes. There does not seem to be a critical period in development for enlargement of the hippocampal formation. The brain size differences between food-storing and non-storing birds seem to be accompanied by differences in performance on tasks designed to assess spatial memory, but not on tasks designed to assess other types of memory.

Comparisons of several different species of food-storing birds in the corvid family have revealed significant differences on tests of spatial memory between species that correlate with the caching of food in the wild. For example, Clark's nutcrackers (*Nucifraga columbiana*) and Pinyon jays (*Gymnorhinus cyanocephalus*), the species of birds in the Corvid family that most rely on food storing in the wild, have been shown to outperform Western scrub jays (*Aphelocoma californica*) and Mexican jays (*Aphelocoma ultrimarina*) on many different spatial memory tasks (Balda & Kamil, 1989; Balda, Kamil, Bednekoff, & Hile, 1997; Bednekoff, Balda, Kamil, & Hile, 1997; Kamil, Balda, & Olson, 1994; Olson, 1991; Olson, Kamil, Balda, & Nims, 1995). Balda and Kamil

(1989) used an open-field testing situations in which Pinyon jays, Clark's nutcrackers, and Western scrub jays were allowed to store seeds in a caching session and then tested recovery accuracy seven days later. The Pinyon jays and Clark's nutcrackers performed similarly to each other, both species recovered cached seeds more accurately than the Western scrub jays. Bednekoff and colleagues (1997) followed this experiment with one in which Clark's nutcrackers, Pinyon jays, Western scrub jays and Mexican jays were allowed to cache seeds and recover them 10, 60, 150, and 250 days later. They found that, whereas all species were more accurate than chance in all intervals, Clark's nutcrackers and Pinyon jays made significantly fewer errors at both the 10 and 60 day retention intervals. There were no differences between species following 150 or 250 day intervals.

It could be argued that the Clark's nutcrackers and the Pinyon jays performed better on an open-field food storing task because it tested a response with which they were very proficient. However, similar differences between species were also found in analogues of the traditional radial arm maze used with rats. This task does not involve caching. Kamil, Balda, & Olson (1994) tested Clark's nutcrackers, Pinyon jays, Mexican jays and Western scrub jays on a task in which the birds were required to retrieve food hidden by an experimenter. At the start of the session, four of twelve holes were opened and baited and the birds were allowed to deplete those sites. After a 5 minute retention interval, another four randomly chosen holes were opened and baited, the four previously baited holes were left empty and opened, and the birds were allowed to deplete the food in each site. The results showed that Clark's nutcrackers and Pinyon jays learned the task more rapidly and performed more accurately than either of the other two species.

Moreover, when delays were increased to 30, 60, 120, and 210 minutes in ascending order in subsequent sessions, Clark's nutcrackers and Pinyon jays performed more accurately than the other two species at each retention interval. After a 24 hour retention interval, only the nutcrackers performed above chance. These results were corroborated by Balda and colleagues (1997) in a test of Clark's nutcrackers, Pinyon jays and Western scrub jays using a similar testing situation. However, a recent study in which both working memory and reference memory were simultaneously tested using an analog of the radial arm maze, Gould-Beierle (2000) found that Western scrub jays and Pinyon jays performed better than the Clark's nutcracker and the Eurasian jackdaw (a nonstorer) in both components of the task. Therefore, species differences may not be absolute in all tests.

Studies conducted in operant chambers using a non-matching-to-sample spatial task have found that Clark's nutcrackers remember spatial locations longer than any of the scrub jays (Olson, 1991). When Clark's nutcrackers, Pinyon jays, Mexican jays, and Western scrub jays were tested on both spatial non-matching-to-sample tasks and non-spatial non-matching-to-sample tasks, species differences were apparent only in the spatial non-matching-to-sample task (Olson, Kamil, Balda, & Nims, 1995). Specifically, all four species performed equally well on a task in which the birds were required to respond to a comparison stimulus that was different in color from a sample stimulus. However, when they were required to respond to a comparison stimulus presented in a different location than the sample stimulus, Clark's nutcrackers performed significantly better, particularly at long retention intervals, than the three other species, including Pinyon jays. This study was the first to discover a difference between Pinyon jays and

Clark's nutcrackers. The authors interpreted the result as possibly indicating that food-storing represents convergent evolution between New World Pinyon jays and Old World Clark's nutcrackers but divergent evolution between Pinyon jays and other New World jays.

Comparative spatial cognition research been conducted not only with members of the food storing family Corvidae, but also with members of the food storing avian family Paridae (chickadees and titmice). The results of studies conducted with parids have not been as clear-cut as those conducted with the corvids. Despite the fact that food-storing parids have larger hippocampal complexes than non-storing parids (Krebs, Clayton, Healy, Cristol, Patel, & Jolliffe, 1996), not all tests have found robust differences in spatial behavior in the laboratory. Krebs, Healy and Shettleworth (1990) did find some differences in spatial ability between the food-storing coal tit (Parus ater) and the non-storing great tits (P. major). When the birds were rewarded for returning to sites that had originally contained unobtainable food, the food-storing coal tit learned the task faster than the great tits. However, the differences observed between the species were not as large as differences found in previous studies of storing and non-storing corvids. Healy and Krebs (1992) compared the performance of food storing marsh tits (*Parus palustris*) and nonstoring blue tits (*Parus caeruleus*) on a task in which the birds were required to return to a location in which it had partially deplete food following a retention interval (i.e., a win-stay task). The experimenters failed to find differences between the two species of tit even after intervals as long as 24 hours. Similarly, Healy and Suhonen (1996) predicted that food-storing British marsh tits (*Parus palustris*) would outperform food-storing willow tits (*Parus montanus*), which have a smaller hippocampus and retrieve their stores sooner, when retention intervals between storing and retrieving were long. However, the results showed that both species performed equally well even after retention intervals as long as 17 days.

There may be several explanations for these seemingly aberrant results. First, the quality of the food items typically offered for caching may affect behavior. Hampton , Sherry, Shettleworth, Khurgel, and Ivy (1995) tested black-capped chickadees (*Parus atricapillus*), Mexican chickadees (*P. sclateri*) and bridled titmice (*P. wollweberi*) on two food-storing tasks and found that not only did the black-capped chickadees have a relatively larger hippocampus, they also cached more food than the other two species. This difference may be related to the fact that the researchers allowed the birds to choose the type of food they wanted to cache. Other studies did not allow the birds to choose their reward. Second, Clayton and Krebs (1994) found that the design of the search phase of a task may affect behavior. In their study two conditions were established, one in which the food item was visible in the pre-retention but hidden in the post-retention phase and one in which the food item was hidden in both phases. The results showed that, whereas there were no species differences between marsh tits and blue tits when the food was visible in the pre-retention phase, the food storing marsh tits outperformed the blue tits when the food was hidden in both phases. In Healy and Kreb's (1992) study, the food item was also hidden in the pre-retention phase, however, the location of the food item was signaled by a brightly colored piece of tape. Finally, the lack of species differences in the Healy and Suhonen (1996) study may have resulted from the fact that both species were allowed to store the food themselves, which may have made it easier for them to make the association between the presence of food and spatial location. It is possible that species differences are apparent only when the food is stored by the experimenter and recovered by the bird.

In conclusion, research has shown that pigeons may not be as deficient at tasks involving spatial memory as once believed. Testing pigeons in a more species-appropriate manner resulted in behavior similar to that of rats. The performance of the pigeons is sensitive to the spatial configuration of the food goals, affecting working memory within trials. Most of the direct species comparisons conducted with birds have supported the hypothesis that spatial memory performance can be predicted on the basis of feeding ecology. Pigeons perform worse than both mynahs and food-storing birds on tasks involving spatial memory. The multi-disciplinary approach taken to understand the relationship between food-storing, spatial memory, and neural specialization has provided the most thorough understanding to date of the relationship between brain size, habitat, and behavior. This research should be used as a model for comparative research with other species.

3.3 Non-human primates

Most researchers of non-human primates in the field have reported that the animals in their study seem to make highly directed movements to food and other resources suggestive of goal- oriented behavior and the use of some type of mental map (Oates, 1997). For example, Boesch and Boesch (1984) analyzed the way chimpanzees transported tools for nut cracking and found that they seem to be able to remember not only the location of tools but also the quality of tools. Once a choice is made they travel directly to the nuts using an adjacency strategy. However, most evidence for the existence of mental maps in non-human primates comes from descriptive and observational research conducted in the field. As pointed out by Janson and Di Bitetti (1997), it is impossible to know if visits to the nearest available resources and the ability to travel to resources in a direct, straight line are evidence for cognitive maps without knowing information about the ability of non-human primates to detect those resources. For example, many non-human primates in the wild seem to preferentially choose and use goal-directed travel to visit larger resources. However, most researchers do not measure or test the distance over which non-human primates can detect those resources. When detection fields for resources are large, as might be expected for large resources, animals do not need prior knowledge of their location to make an encounter when traveling in a straight line.

Compared with other types of cognition, such as learning and problem–solving skills, spatial memory has long been an understudied topic of experimental research with non-human primates (Garber & Dolins, 1996; Meador, Rumbaugh, Pate, & Bard, 1987). This is surprising in light of the fact that Milton's theory of primate intelligence hypothesizes that increased brain size is the result, not of the selective pressures of group-living, but of the distribution patterns of preferred food sources in tropical forests (Milton, 1988). As previously outlined, according to Milton's theory primary consumers such as non-human primates were under strong selective pressure to increase foraging efficiency and evolve highly complex problem-solving skills as a result of the distribution and predictability of their resources in space and time. This is particularly true of larger-bodied non-human primates such as great apes that exhibit both a high encephalization quotient and a high degree of neural complexity.

Several field studies of non-human primates provide evidence for the use of spatial memory in foraging. Garber and Hannon (1993) compared the results of their field study with the results of computer-generated foraging patterns based on random foraging, olfactory foraging and spatial memory foraging. According to the authors, the results of this comparison suggest that the foraging patterns of both species of these monkeys are best explained by their ability to maintain a spatial map of the distribution of resources in their home range. Similar results were found in a more controlled study with wild capuchin monkeys (*Cebus apella*) (Janson, 1998). Janson (1998) placed feeding platforms throughout the home range of the monkeys and compared their movements from one site to the next with the movements predicted by a model of random foraging. The results showed that capuchins moved in a straight-line fashion toward feeding platforms and preferred to travel from one platform to the next nearest platform. Although spatial memory was hypothesized to be the primary method for locating platforms, visual and olfactory discriminative stimuli emanating from the platforms were not controlled in this experiment.

Field experiments designed to have greater experimental control have provided further evidence that spatial memory is important in foraging for non-human primates. Garber and Dolins (1996) designed a series of experiments to examine the ability of wild mustached tamarins (*Saguinus mystax*) to locate food on sixteen feeding platforms on the basis spatial, visual and olfactory information associated with the presence or absence of food. Four feeding stations comprised of four platforms each were created and installed in an open space just at the edge of a forested area. The results of these studies indicate that the tamarins were able to learn the location of viable food sources on the basis of both spatial and visual information. They did not appear to use olfactory discriminative stimuli emanating from the food source to locate food. Furthermore, when both types of information were available, spatial information appeared to be more important. A similar study conducted by Garber and Paciulli (1997) with wild capuchin monkeys (*Cebus capucinus*) in Costa Rica also found that capuchins rely preferentially on spatial information to locate viable sources of food, even when olfactory and visual discriminative stimuli are available.

The above studies are important in that they describe the behavior of wild populations of non-human primates foraging in their home range. However, controlled experiments conducted in the laboratory or in semi-naturalistic conditions can also provide important information concerning the variables involved in the development of efficient foraging strategies. Several experiments have been designed to further test the spatial memory of other non-human primates in semi naturalistic foraging tasks. MacDonald and Wilkie (1990) examined the spatial abilities of two wild-caught yellow-nosed monkeys (*Cercopithecus ascanius whiteidei*) housed at the Stanley Park Zoo in Vancouver, British Columbia. In MacDonald and Wilkie's study, eight plastic cups baited with food arranged in a fashion similar to that of a radial arm maze served as food sites. Like rats, the yellow-nosed monkeys were able to successfully avoid previously visited food sites. In contrast to studies using rats and pigeons as subjects, the performance of the yellow-nosed monkeys on the win-stay task was similar to their performance on the win-shift task. In each of the experiments, the subjects were observed to use a least-distance foraging strategy similar to that observed in chimpanzees.

MacDonald, Pang and Gibeault (1994) conducted a similar study of nonhuman primate spatial memory with marmosets (*Callithrix jacchus jacchus*) housed at the Metropolitan Toronto Zoo. The results showed that, as observed with the yellow-nosed monkeys, the marmosets avoided previously depleted food sites. However, the marmosets differed from the yellow-nosed monkeys in that the marmosets' accuracy on the win-shift task was much lower than their accuracy on the win-stay task. This suggests that win-stay strategies may be more adaptive for this species in the wild, perhaps because a large proportion of the diet of marmosets is gum exudate, which is a renewable resources that could be exploited repeatedly on return visits.

Despite Milton's (1988) theory of primate intelligence, which makes specific hypotheses about differences that should be evident between different primate species, very few comparative studies have been conducted using an ecological approach. Those that have been conducted have provided mixed results with respect to species differences in spatial ability. For example, Andrews (1988) examined the choice behavior of eight titi monkeys (*Callicebus moloch*) and eight squirrel monkeys (*Saimiri sciureus*) using a modified 8-arm radial maze. Both species are frugivorous, however, titi monkeys have larger home ranges than squirrel monkeys and may therefore have a greater need for spatial memory in the location of food sources. The results of their experiments showed that, unlike the rats in Olton and Samuelson's (1976) study, neither species avoided previously visited food sites when food was replaced between trials. However, the monkeys were observed to avoid previously depleted food sites when the food rewards were not replaced between trials. No significant species differences were found.

Other studies, however, have found species differences on at least some types of spatial memory tasks. Platt, Brannon, Briese, and French (1996) compared the foraging skills of individual Wied's tufted-eared marmosets (*Callithrix kuhli*) and golden lion tamarins (*Leontopithecus rosalia*) on tests of spatial memory requiring one-trial associative learning. They hypothesized that, because golden lion tamarins have larger home ranges than Wied's marmosets and return to feeding sites only after days or weeks, they would be able to retain information over longer intervals. Individual subjects were allowed to visit eight feeding sites. In the search phase, four feeding sites were randomly baited with food. Following a 5 min, 30 min or 24 hour delay period, the other four feeders were baited, requiring that the monkeys use a win-shift strategy for efficient foraging. The results showed that both species performed at above chance levels when the ability to make a choice was delayed by 5 or 30 minutes. However, only the tamarins performed above chance level at the 24-hour delay period. The tamarins were also found to outperform Wied's marmosets at long delays on a spatial delayed matching-to-sample task that required a win-stay strategy for efficient foraging. Finally, the color of a baited feeder gained control of behavior more quickly for the tamarins than it did for the marmosets in tests involving longer delay intervals. The results of this study suggest that, whereas both species were capable of locating food at levels better than expected by chance, the golden lion tamarins performed more accurately and made better use of the beacons than the marmosets at longer delay intervals. These results support the hypothesis that animals with larger home range sizes perform better on tests of spatial memory than those with smaller home range sizes.

In an early study by Fischer and Kitchener (1965), the learning abilities of young orangutans and gorillas were directly compared using a variety of tasks. In a test of perceptual-learning ability, there were no significant differences between the two species. However, in a test of delayed spatial response, gorillas did not perform as well as orangutans. In this task, a piece of food was hidden in two visually discriminable wells and the subjects' task was to learn and recall the location of the hidden food after a variety of delay intervals. Whereas the increasing delay period caused decreasing performance levels in both species, the decrease was significantly more pronounced in the gorilla. Gorillas are considered to be much more folivorous than orangutans. Therefore, these results of this study are in keeping with Milton's prediction that folivores will perform worse than frugivores on tests of spatial ability.

CHAPTER 4

PROPOSED RESEARCH ON THE FORAGING SKILLS AND SENSORY CAPABILITIES OF BEARS

As can be seen from the review of the above literature, few studies have been designed to test a priori predictions of species differences in foraging skill on the basis of the foraging ecology of the subjects. Of those that have been conducted on the basis of a priori predictions, most seem to support Milton's theory postulating a relationship between foraging ecology and cognitive ability. However, few species of mammal other than rats and food-caching small mammals have been tested to examine their sensory and cognitive skills in foraging, particularly within the Order Carnivora (Bacon & Burghardt, 1974). Not all species within the Order Carnivora are strictly meat-eaters. In fact the diets of carnivores can be characterized as omnivorous, insectivorous, frugivorous and, in the case of the giant panda, almost entirely folivorous. Because of their wide range of dietary habits and home range sizes, differences in foraging skills or cognitive ability might be predicted between carnivores. This is particularly true for members of the bear family (Ursidae).

Bears are descended from a small family of tree-climbing carnivores that have been evolving for approximately 40 million years (Brown, 1993). There are currently eight species of bear living on every continent except Africa, Australia, and Antarctica. Though their ancestors were carnivorous, most bear species are considered to be omnivorous and are often characterized as wandering opportunistic generalists (Brown, 1993). However, they consume a wide range of diets from almost entirely carnivorous as observed in polar bears to almost entirely folivorous as observed in the giant panda. Despite the fact that the largest proportion of their time is devoted to searching for food, there have been virtually no experimental studies to determine what type of information control the foraging decisions of bears. Brown (1993, p. 160) states that "they remember size, shape, (and) color of objects that have produced a food reward", however, he provides no reference for this statement. There has been only one experimental study of bear vision and discrimination. Bacon and Burghardt (1974) found that American black bears were capable of discriminating food sites on the basis of the hue of a visual signal, learning the discrimination task more quickly than chimpanzees tested with a similar paradigm. From these results, the authors concluded that American black bears most likely rely on vision to locate and obtain food.

Bears in general are believed to be highly intelligent. According to Domico and Newman (as quoted by Brown, 1993, p. 96) they are "capable of as many responses in a given circumstance as a human. Some biologists believe the highly adaptable bear is intelligent enough to be ranked with primates, like monkeys and baboons". Bears in general are known anecdotally for their skill at navigating through their home ranges, however, it is unknown whether they use fixed travel routes, orient to goals or foraging sites using sensory beacons, or if they have the ability to orient toward a goal that is beyond sensory contact using spatial memory (Brown, 1993). It appears that, like other species tested, relative brain size may be correlated with foraging niche in the bears. Among the seven different species of bear included in a study conducted by Gittleman (1986) (only the spectacled bear, *Tremarctos ornatus*, was not included), the three species with the highest brain/body ratio are the sloth bear (*Melursus ursinus*, 0.30%), the sun bear (*Helarctos malayanus*, 0.44%) and the Asiatic black bear (*Selenarctos thibetanus*, 0.31%). Each of these species is considered to be omnivorous, however, sloth bears specialize on termites, the location of whose mounds would be highly predictable. Sun bears are considered to be the most frugivorous of the bear species. Those species that had either a folivorous diet such as the panda (*Ailuropoda melanoleuca*, 0.20%) or strictly carnivorous diet such as the polar bears (*Ursus maritimus*, 0.13%) had the smallest brain/body size ratios.

Most of the information, anecdotal or otherwise, on bears comes from only three of the eight species, specifically the American black bear, the brown bear, and the polar bear. No research on the sensory or cognitive capabilities used in foraging has been conducted with the Asiatic black bear, giant panda, sloth bear, sun bear and spectacled bear. This study attempts to compare the sensory and cognitive abilities that may be used for foraging between two species of the family Ursidae. As outlined above, Milton's (1988) research suggests that organisms with the most complex strategies for efficient foraging will be those animals that 1) forage on resources that are both patchy and predictable in space and time, 2) have larger home ranges, and 3) are solitary or disperse from their group for foraging. Giant pandas and spectacled bears are solitary species but differ from each other in home range size and predictability and distribution of their resources, making them appropriate subjects for comparative purposes.

4.1 Foraging Ecology of Giant pandas (*Ailuropoda melanoleuca*)

The first species included in this study is the giant panda (*Ailuropoda melanoleuca*). Though they were once distributed throughout China, giant pandas are currently found only in the temperate forests of the eastern edge of the Tibetan plateau (Schaller, Jinchu, Wenshi, & Jing, 1985). Like most bears, they are solitary except when raising cubs (Schaller et al., 1985). The giant panda is somewhat of an anomaly in the animal kingdom in that it is a carnivore that subsists almost exclusively on an herbivorous diet. Bamboo comprises approximately 99% of the diet (Schaller et al., 1985). Most herbivores are equipped with a complex foregut, which facilitates digestion of otherwise indigestible plant cellular components. However, giant pandas have a simple stomach, short straight colon, and a small gall bladder (Raven, 1936). Because of their digestive system, giant pandas are only able to digest approximately 12-23% of the bamboo they consume, which requires them to spend the majority of their time eating to maintain adequate nutrition (Dierenfeld, Hintz, Robertson, Van Soest, & Oftedal, 1982; Mainka, Zhao, & Li, 1989; Schaller et al., 1985). For this reason, optimal foraging may be particularly important for the giant panda.

Giant pandas have several morphological, physiological, and behavioral adaptations that presumably help them increase their foraging efficiency on a food source like bamboo. For example, they have a unique pseudo-thumb which helps decrease handling time and manipulation of bamboo stalks. They also are large in size, giving them a lower metabolic rate and allowing them to subsist on a poor diet (Schaller, et al., 1985). Behaviorally, Schaller and colleagues (1985) state that giant pandas remain inactive for much of their waking hours to conserve energy. However, little is known about the sensory and cognitive abilities of the giant panda and what role they may play in foraging.

Schaller and colleagues (1985) found that the giant pandas in their study fed predominantly on two types of bamboo, *Sinarundinaria* and *Fargesia*. After eating in one site, giant pandas shifted to the next closest site. It was found that the mean distances between patches of each of these types of bamboo were 6.6 and 9.0 meters respectively and that a panda had to travel only a mean distance of 2.3-2.8 meters to reach the next nearest food site. This suggests that after the depletion of one patch, the giant pandas are almost always in sight of another patch of bamboo. The ability to use visual discriminative stimuli such as leaf shape or size of the culms may increase the foraging efficiency of the giant panda. A recent study found that giant pandas may prefer bamboo species with large leaves because larger leaves take less time to process than smaller leaves (Tarou, Williams, Powell, Tabet, & Allen, submitted for publication).

It has also been suggested that olfactory discriminative stimuli control choice behavior among available food items in giant pandas. Olfaction is known to play an important role in social behavior and reproductive behavior in giant pandas (Schaller, et al., 1985), with recent evidence indicating that giant pandas are able to discriminate the odors of individual conspecifics (Swaisgood, Lindburg, & Zhou, 1999). Schaller and colleagues hypothesized that giant pandas may also use olfaction to discriminate food items, observing that they often sniff a shoot or stem of bamboo in the wild before eating. He speculated that this may be particularly important when foraging at night when visibility is low. This suggests that giant pandas may be able to learn to use olfactory discriminative stimuli to locate viable food sources.

As reviewed earlier in this paper, a growing body of research concerning foraging and choice behavior shows that spatial memory plays an important role in foraging in a variety of animals, particularly rodents and birds. It is unknown whether giant pandas are capable of using spatial information to locate food sources. However, given the abundance and close proximity of food patches in their environment, spatial memory may be unimportant for efficient foraging by giant pandas. For example, Schaller and colleagues (1985) observed that giant pandas in the Wolong Nature Reserve only traveled a mean of 418 m each day. Their home ranges are the smallest of all members of the family Ursidae. Gittleman and Harvey (1982) report that giant pandas have a home range of only 2.5 km^2 (though see Reid, Hu, Dong, Wang, & Huang, 1989), whereas the compared the American black bear and American brown bear have home ranges sizes of 56.3 km^2 reported for and 53.1 km^2 respectively. As stated by Brown (1993, p. 121), "one would not expect a giant panda to experience much difficulty (in navigation) when its home area is approximately one to three square miles". Though feeding sites were sometimes well-spaced and the giant pandas seemed to selectively choose only certain patches even when surrounded by potential food, giant pandas were observed to travel a mean of only 2.3-2.8 meters to the next nearest patch of bamboo (Schaller, et al., 1985). Wei, Fung, Wang, and Jinchu (2000) reported that of the five species of bamboo that occurred in the Yele Natural Reserve, Mianning County, southwestern Sichuan Province, the preferred bamboo species of giant pandas and red pandas (*Bashania spanostachya*) was the most prolific, covering entire hillsides. Therefore, giant pandas might not have much need for spatial memory in locating bamboo.

4.2 Foraging Ecology of Spectacled Bears (*Tremarctos ornatus*)

The second species of bear that will be included in this study is the spectacled bear (*Tremarctos ornatus*), so named for the light markings around the eyes that resemble glasses or goggles. Spectacled bears are the only species of bear found in South America, distributed throughout the Peruvian and Venezuelan Andes, Ecuador, Columbia, and Bolivia (Brown, 1993; Mondolfi, 1989). Their habitats in both Peru and Venezuela are characterized as being dense, humid montane forest, ranging in elevation from 1,000 to 3600 m (Mondolfi, 1989; Peyton, 1980). There have been very few published studies of the foraging ecology of the spectacled bear. However, aside from the giant panda, they are considered to be the most herbivorous of all the bear species. In Venezuela, spectacled bears have been reported to feed on the fruits of several species of trees, the unopened petioles of palm trees, and the heart of both terrestrial and tree-dwelling bromeliads (Mondolfi, 1989). Peyton (1980) reported a similar diet for spectacled bears in Peru. The bears in his study consumed the fruit from 31 species of tree, particularly those of the genus Ficus, 22 species of Bromeliaceae, 11 species of Cactaceae, the bulbs of orchids, shrub berries, young bamboo shoots, corn stolen from farms, insects such as ants, and mammals including deer, goats and rodents. Only 4.1% of the scats analyzed in Peyton's (1980) study contained animal parts, indicating that spectacled bears are almost entirely herbivorous.

Unfortunately, neither Peyton's (1980) nor Mondalfi's (1989) study used radio-telemetry to track the movements of the bears through their habitats. Therefore, they were unable to give estimates of home range size. However, spectacled bears are believed to travel seasonally, following the cycle of ripening of the different species of plants and fruit that they eat (Peyton, 1980). According to Peyton (1980), spectacled bears repeatedly climb the same trees year after year, as evidenced by healed scars from bear claws on the bark, suggesting that home range size may be defined by known groves of trees. There has been only one study of the home range. Paisley (personal communication) recently conducted the first study of the home range size of spectacled bears using radio-telemetry. Unfortunately, because of the difficult terrain, the bears could only be found two-thirds of the time. However, two small males used an area approximately 9 km^2. She suspects that they had traveled outside the core study area at the times during which they could not be located. This purported home range size is much larger than that reported for the giant panda.

Many people living in or near spectacled bear habitat believe that the spectacled bear is more intelligent than primates. The local inhabitants refer to them as "El Salvaje", which means the savage. They believe that spectacled bears are creatures both physically and mentally on a level between monkey and man. There is some evidence from the field to suggest that these bears are in fact highly intelligent. One potential indicator of intelligence in primates is extractive foraging (Gibson, 1986). Spectacled bears do engage in extractive foraging, particularly for the hearts of bromeliads. Further evidence for their intelligence comes from research suggesting that these bears build foraging platforms. According to Peyton (1980), the majority of the trees in which the spectacled bears feed are over 25 m in height, and they will sometimes build feeding platforms of leaves and branches to help them reach smaller branches laden with fruit that would not be able to support their weight. This could be considered to be a kind tool for build to maximize foraging efficiency after climbing into the canopy of the trees.

Little is known about the sensory capabilities of the spectacled bear. It possible that the bears use visual or olfactory discriminative stimuli as beacons to locate the food in their environment. This has been shown to be true for other animals that consume a large proportion of fruit and foliage. For example, owl monkeys (*Aotus nancymai*), a nocturnal species of primate, are able to locate hidden fruit at a level greater than would be expected by chance on the basis of olfactory discriminative stimuli emanating from the source (Bolen & Green, 1997). According to Peyton (1999), olfaction is the dominant sense of the spectacled bear in regulating social behavior. However, it is unknown what role olfaction might play in foraging. It is also possible that spectacled bears use visual discriminative stimuli such as fruit color, leaf size and shape of preferred bromeliad species, etc., to locate food (Lucas, Darvell, Lee, Yuen, & Choong, 1997). Peyton (1999) suggests that spectacled bears may create visual discriminative stimuli at the entrance of a trail leading to concentrated food sources. It is unknown whether this discriminative stimulus is used as a territorial advertisement to conspecifics signaling ownership of a food source or if that discriminative stimulus can also be used as a visual discriminative stimulus signaling the presence of the food patch to improve search at a later time.

Given that spectacled bears travel seasonally with ripening fruit, Milton (1988) would predict them to have very good knowledge of their environment. The ability to remember the location of fruit-bearing trees and travel directly to these food sources would be very valuable for these animals. According to Milton (2000), fruiting trees such as those of genus *Ficus* that are consumed by primates (and incidentally also consumed by spectacled bears) native to Latin America and South America are often widely distributed. For example, in Panama there were only 21 individuals of the *Ficus* tree within 0.32 km^2. Though the patterns of leafing and flowering are not synchronized across all species of tree consumed by spectacled bears, the locations of these large, widely distributed fruit trees would be predictable over the lifetime of the spectacled bear. Therefore, it might be predicted that, of the two bear species being examined in this study, the spectacled bear would be capable of learning a spatial task more quickly than the giant pandas.

The purpose of this study was to determine the types of information that giant pandas and spectacled bears are able to use to locate viable sources of food using six foraging tasks similar to those conducted previously with primates in the field (Garber & Dolins, 1996; Garber & Paciulli, 1997) and semi-naturalistic foraging situations (MacDonald, Pang, & Gibeault, 1994; MacDonald & Wilkie, 1990). The subjects were three male and four female giant pandas housed at ZA, the San Diego Zoo, and the Smithsonian National Zoological Park, as well as two male and one female spectacled bears (*Tremarctos ornatus*) housed at the Smithsonian National Zoological Park. Six tasks were designed to test the foraging capabilities of the bears using an analog of the traditional radial arm maze. It was assumed that abstract stimuli, whether they be local or global, would gain control of the foraging behavior of an optimal forager.

The first foraging task was an exploratory task designed to examine the pattern of foraging used by the bears when depleting food sites. Efficient foragers often visit adjacent food sites, minimizing travel time between sites (Pyke, Pulliam, & Charnov, 1977). It will also be determined if working memory is involved in the bears' ability to avoid previously depleted food sites. Foraging Tasks 2-5 were designed to examine the ability of the bears to use spatial or global stimuli, visual stimuli, and olfactory stimuli to locate the presence of food in a feeding site. Finally, Foraging Task 6 was designed to determine the relative importance of each of these discriminative stimuli in their foraging decisions. Few studies have examined the differential ability of discriminative stimuli to control foraging behavior. For example, visual, olfactory, and spatial stimuli can gain control of foraging by rats, but until recently their relative reliance on these discriminative stimuli was unknown. Maaswinkel and Whishaw (1999) found that rats have a hierarchical preferance for using visual, olfactory, and spatial discriminative stimuli when foraging in the laboratory. In contrast, McQuade, Williams, and Eichenbaum (1986) found that visual and spatial discriminative stimuli, but not olfactory discriminative stimuli, control the location of caches in gray squirrels (Sciurus carolinensis). Visual discriminative stimuli were relied upon more than spatial discriminative stimuli. This difference in preference may be attributable to the foraging ecology of the animal. For example, Brodbeck and Shettleworth (1995) found that, whereas nonstoring birds had no preference for visual or spatial discriminative stimuli in foraging, food storing birds exhibited a strong preference for the use of spatial discriminative stimuli. Therefore, species differing in their foraging ecologies may differ in their use of information associated with food.

CHAPTER 5

GENERAL METHODOLOGY

5.1 Subjects

The subjects were three male and four female giant pandas (*Ailuropoda melanoleuca*) housed at Zoo Atlanta, the San Diego Zoo, and the Smithsonian National Zoological Park, as well as one male and one female spectacled bear (*Tremarctos ornatus*) housed at the Smithsonian National Zoological Park. All were experimentally naïve at the start of the study. The male, "Yang Yang", and female, "Lun Lun", giant panda at Zoo Atlanta (ZA) were both born in the Fall of 1997 at the Chengdu Research Base of Giant Panda Breeding, in Chengdu, Sichuan Province, People's Republic of China. At the time of the study they were 3 years of age and were housed together on exhibit either in outdoor yards or indoor day rooms between the hours of 0830 and 1700. They were housed separately in an indoor holding facility during the remaining hours of the day. They were fed a diet of mostly bamboo, supplemented with leafeater biscuits and produce. When the giant pandas first arrived at ZA, they were hand-fed the biscuits and produce to ensure that both were consuming the desired amount. Water was available ad libitum.

One adult female, "Bai Yun", one subadult female, "Hua Mei", and one male giant panda, "Shi Shi", were tested at the San Diego Zoo (SDZ). The male was rescued from the wild in 1992 in the Qionlai Mountains of Sichuan Province, People's Republic of China. He was given medical attention at the Wolong Giant Panda Breeding Center in Wolong, People's Republic of China, for injuries sustained presumably in a fight with another male over access to a female. He was estimated to have been between the ages of 20 and 25 years at the time of the study. The adult female was born on September 7, 1991, at the Wolong Giant Panda Breeding Center in Wolong, People's Republic of China. She was 10 years of age at the time of testing. She gave birth to the subadult female on August 21, 1999. All three animals were housed separately with little visual contact, no tactile contact, and only occasional olfactory contact with the other giant pandas.

The giant pandas at SDZ were housed on exhibit either in naturalistic yards or off-exhibit in exercise pens ranging for approximately 8-12 hours a day depending on the time of year. Both the outdoor yards and exercise pens contained live bamboo, a pool, trees, logs and stumps. They were housed off exhibit in indoor holding facilities consisting of small indoor bedrooms, outdoor "sunrooms" with cement floors, and small outdoor grassy areas. All giant pandas at SDZ were fed 4-6 different species of bamboo, leafeater biscuits, carrots and yams. The adult female also received apples. The adult male was given honey daily as a method to deliver medication (Clavamox) for bacterial infections. The giant pandas had access to water ad libitum.

One male giant panda, "Tian Tian", and one female giant panda, "Mei Xiang", were tested at the Smithsonian National Zoological Park (NZP) in Washington, DC. Both giant pandas were born at the Wolong Giant Panda Breeding Center in Wolong, Sichuan Province, People's Republic of China. The male was born on August 27, 1997, and the female was born on July 22, 1998. They were on loan to NZP where they were housed in large outdoor enclosures from approximately 0800 to 1700. The outdoor yards contained several different species of trees, pools of water, cooling caves, and deadfall for climbing. During the summer, the yards were cooled by either misters or foggers. Both giant pandas were housed from 1700-0800 in indoor rooms with rockwork, pools, and a small den with a platform. The male had access to one large room and the female had access to two slightly smaller rooms. The giant pandas at NZP were fed approximately 20 kg of bamboo per day. This was supplemented with leafeater biscuits, yams, carrots, and apples fed out in 4-5 feedings per day. The biscuits and produce were fed by scattering them throughout the yard or night quarters. The bamboo was fed in relatively fixed locations. Water was available ad libitum.

One male, “Willie”, and one female, “Bandit”, spectacled bear were also tested at NZP. The male was born on September 22, 1982, and the female was born on February 7, 1977. They were 21 and 26 years of age at the time of testing and were housed separately throughout the study with some visual and olfactory access to one another. The female was housed with another male, Roger, who was not included in the study for health reasons. All bears had access to both the indoor holding facility and outdoor yards throughout the day. Both outdoor yards had grass, rockwork, and concrete. The female’s yard also had a large pool. The bears were separated from the public by a dry moat. The spectacled bears were fed a diet of dry-food mixture specifically formulated for omnivores and produce including sweet potatoes, carrots, apples, oranges and grapes. Water was available ad libitum.

5.2 Apparatus

The apparatus consisted of feeders constructed of PVC pipe. Each feeder was approximately 12 inches in diameter. An opaque piece of plexiglass was attached to each feeder with a spring-loaded hinge to form a lid. The bears were able to obtain a food reinforcer by lifting the lid using either their muzzle or paw. The lid was designed to fall closed when the bear removed its muzzle or paw, ensuring that the outward appearance of the feeder was retained after being opened. In addition, the feeders were mounted in each test area in such a way that they could not be displaced or overturned during foraging. This is important because an open lid or overturned feeder could serve as a signal to the animal that the feeder had been exploited. The feeders were baited with either leafeater biscuits (giant pandas), omnivore biscuits dipped in honey (spectacled bears), or carrots (San Diego adult and juvenile females).

5.3 Test Area

Testing of the giant pandas at each of the three institutions at ZA took place in each of two dayrooms measuring 63 m^2. The giant pandas were very familiar with these rooms, because they were housed there when the temperature outside or some other factor prevented them from being able to use the outdoor yards. The feeders were bolted approximately 8 feet apart from each other around the walls of the day rooms. This prevented the giant pandas from removing or displacing them during testing. Each panda was tested in the dayroom that is attached to their night quarters and the location of testing for each panda remained constant throughout the study. The substrate of the rooms was mulch. The dayrooms contained a number of items that could be used as global landmarks, such as the doors leading to and from the night quarters, the location of the other dayroom and outdoor yard, the drinkers, the windows to the public, and the climbing structures in the center of the room. One wall of each of the dayrooms was a window through which the giant pandas could be viewed by the public. All data were collected from the public viewing area. The order in which the male and female were tested was counterbalanced. The giant pandas had access to this room outside of the testing situation, therefore, the feeders were removed following each trial.

All three giant pandas housed at SDZ were tested in an outdoor area adjacent to the indoor bedroom of the male. The room measured approximately 60 m^2. It was familiar to the male, but novel to both females. The feeders were bolted to cement blocks and spaced approximately 8 ft apart from one another. All three giant pandas were tested in the same room. It was not possible to counterbalance across subjects or to test all three animals in one day. Therefore, the male and subadult female were both tested during the same time period. For ease of shifting the giant pandas and putting them on exhibit, the male was always tested first and the subadult female was always tested second. The adult female was tested at times outside of the breeding and potential birthing seasons. The testing area was not on exhibit. The room used for testing had several features that could be used as landmarks including a drinker, a large log for climbing, a platform or shelf in the corner of one of the walls, and doors leading to and from the keeper and animal areas. The giant pandas did not have access to the test room outside of the testing situation. All data were collected from the roof of the test area

Testing of the giant pandas at NZP took place in one of the large, outdoor enclosures of the giant pandas. The giant pandas were housed in these yards throughout most of the day, therefore, they were familiar with the testing environment. The feeders were arranged in a circular array on flat portion of grass toward the back of the enclosure which was near the indoor holding facility. The feeders were spaced approximately 8 feet apart from each other. Before each trial, the feeders were mounted onto 95 lb steel metal plates to discourage the giant pandas from moving the feeders during a session.

Because the giant pandas had access to this room outside of the testing period, the feeders were removed from plates after each trial. The metal plates, however, remained in the yards and their location remained constant throughout the study. There were many possible landmarks in the testing area, including two large willow trees, other smaller willow trees, deadfall, a pool, the panda house building, and the walls of the exhibit. The male panda was always tested first. All of the data were collected from an indoor room equipped with 21 cameras that allowed the giant pandas to be viewed from any part of the indoor or outdoor exhibits.

Finally, testing of the spectacled bears took place in one of their outdoor enclosures. The female had access to this yard both during the day and at night. The male only had access to this yard during the test period. The feeders were arranged approximately 8 ft apart in a somewhat circular array as the shape of the yard and ground space permitted on a flat area of grass. The feeders in the spectacled bear yards were mounted on 95 lb steel plates to discourage the bears from displacing them. Because the female had access to this yard during the day, the feeders were removed between trials. Potential landmarks in the testing area included the indoor holding facility, the public viewing area, trees and shrubs. All data were collected from the roof above the test area.

5.4 General Procedure

Because zoo housed animals cannot be food deprived to increase motivation for working in a study, testing of the giant pandas took place before the first morning meal between 0700 and 0900. Bamboo was provided before a trial in small amounts to prevent the giant pandas from being anxious. This did not seem to influence their motivation to retrieve the food reward during the test sessions. Because of the schedule of the zookeepers, the spectacled bears were tested between 1030 and 1200. They received a small meal of omnivore biscuits at 0700.

Between all trials, the feeders were thoroughly cleaned with antibacterial soap to eliminate or reduce odors that may have been left on the feeders by a bear in a preceding trial. During each trial the experimenters were careful to physically touch each feeder and wipe down each feeder even if the feeder had not been touched or opened by a bear in a previous trial. Moreover, the experimenter walked around the perimeter of the feeders even in foraging tasks in which not all of the feeders were to be baited with food. These measures were taken to reduce the chance of the bears using odor trails left by people to localize baited feeders.

The bears at each of the three institutions were tested first on the exploratory foraging task. The order in which the giant pandas were tested on the spatial/reversal, visual and olfactory tasks was counterbalanced to across institutions, with the exception that the reversal foraging task always followed the spatial task. The giant pandas at Zoo Atlanta were tested first on the spatial/reversal task, followed by the olfactory and visual tasks. The SDZ giant pandas were tested first on the olfactory task and then on the visual and spatial tasks. Finally, the NZP giant pandas were tested first on the visual task and then on the spatial/reversal and olfactory tasks. The order of testing of the spectacled bears was visual, spatial/reversal, and olfactory. All bears were tested on Foraging Task 6 after the completion of all other tests.

Data were collected using The Observer program, by Noldus. At both Zoo Atlanta and the San Diego Zoo, data were collected using hand-held Psion computers. At the National Zoological Park, data were collected using a laptop computer. Continuous focal animal sampling was used to record the following behaviors: self-directed behavior, locomotion, inactivity, feeding, object manipulation, scent-marking, vocalization, stereotypic behavior, and visits to feeders. The ethogram used for the giant pandas in the study can be seen in Appendix 1. Because of the presence of high-voltage hot wire in close proximity to the site of data collection on the roof of the spectacled bear exhibit, we were unable to use a computer to collect data. Therefore, the ethogram was pared down to include only two behaviors: exploring of the feeders and visiting the feeders. Data were collected by hand using a stopwatch and pen and paper. A visit to a feeder was defined as the placement of a subject's muzzle or paw under the lid of the feeder. Trials began when the bear entered the test area and ended after either 15 minutes or, if the bears seemed anxious, two minutes after the last visit to a feeder. The feeders (and plates at NZP and concrete base at SD) were thoroughly cleaned with a sponge and soap both within and across test sessions to decrease the chance that the bears could use the scent of the food or the scent of another bear to find food. Five volunteers at Zoo Atlanta, 4 volunteers at the San Diego Zoo and 13 volunteers at the National Zoological Park assisted in data collection. They were trained and reliability tested before the start of the study. All were allowed to collect data on the project if they scored above 85% on a reliability test.

CHAPTER 6

SPECIFIC METHODOLOGY, DATA ANALYSIS, RESULTS, AND DISCUSSION

6.1 Foraging Task 1: Exploratory Task

6.1.1 Methods

In Foraging Task 1, all eight feeders were baited with one leafeater biscuit. This is a commercially available, high fiber biscuit used as a nutritional supplement for folivores. The bears were allowed to explore and deplete the feeders. Of interest in this task was the length of time it took the giant pandas to visit all of the feeders in each session, the pattern of foraging in each trial, the number of correct choices of the first eight choices made during a session, the total number of feeders visited in each session, and the ability of the bears to avoid re-visiting previously visited sites. The ability to avoid re-visiting previously depleted sites has been referred to as working memory (Honig, 1978). Many studies that have been conducted using a similar methodology as that used in the present study have been unable to examine the potential for working memory in avoiding revisiting previously depleted sites. For instance, the displacement of a feeder after visitation (MacDonald & Wilkie, 1990), or the removal of a lid that was once covering a feeder (Laska & Hudson, 1993) can be used as cues by a forager to avoid visiting previously depleted sites. In the present study, the lids of the feeders were spring-loaded so that the appearance of the feeders was unchanged after visitation. One session was conducted each day for a total of 15 days.

6.1.2 Data Analysis

Data collected in Foraging Task 1, the exploratory foraging task, was examined to determine the length of time between the first visit to a feeder and the last visit to a feeder. A significant decrease in the amount of time taken to visit all 8 feeders as determined by a regression analysis was indicative of learning of the task. In addition, I was interested in the pattern of foraging used by the bears and its relation to foraging efficiency. To examine whether the bears were using an efficient pattern of foraging in Foraging Task 1, the percentage of visits in which the bears bypassed 0, 1, 2, or 3 feeders to visit successive feeders was calculated. The foraging pattern of the bears was considered optimally efficient when the bears visited adjacent feeders and least efficient when 3 feeders separated successive choices, which would indicate that the bears traveled across the room to visit the next food site. Assuming that the bears made seven subsequent choices after visiting the first feeder in their search for food during a trial, a forager traveling randomly would be expected to visit 5 non-adjacent feeders for every 2 adjacent feeders. Over the course of five trials the bears would be expected to make a total of 35 choices. Twenty-five would be expected to be to non-adjacent feeders and 10 would be expected to be to adjacent feeders. The mean number of visits to adjacent and non-adjacent feeders was calculated across the first five and last five trials. For the giant pandas, a one-sample t-test was used to determine if the number of visits to adjacent feeders in the first five trials was significantly different from that expected by a forager traveling randomly. A one-sample t-test was also used to determine whether the number of visits to adjacent feeders by the giant pandas in the last five sessions was significantly different from that expected by chance. Performance in the first 5 sessions and last 5 sessions was compared using a paired sample t-test to examine learning across trials.

For the spectacled bears, the mean number of visits to adjacent feeders in both the first five sessions and the last five sessions was compared to that expected by a randomly traveling forager using one-sample Komolgorov-Smirnov tests. This non-parametric test is used to determine if a particular distribution differs significantly from a normal distribution with a specified mean and standard deviation. The Kolmogorov-Smirnov test was chosen rather than a t-test or z-score for the following reasons: the sample size was small, the test does not require normality, and it is distribution free (Tille, Newman, & Healy, 1996). Visits to adjacent feeders in the first five sessions and last five sessions were compared using a Wilcoxon Signed-Rank test. Species differences in the mean number of visits to adjacent feeders in the first block of five sessions and in the last block of five sessions was determined using Mann-Whitney *U* tests.

A randomly traveling forager would be expected to visit 5.252 baited feeders in their first 8 visits by chance, assuming that each site is equally likely to be chosen. The number of correct visits in the first eight visits was calculated for each trial. For the giant pandas, the mean number of visits to baited feeders in the first eight visits in both the first 5 sessions and last 5 sessions was compared to that expected by chance using one-sample t tests. To assess improvement across sessions, performance in the first five sessions was compared to performance in the last five sessions using a paired sample t test. For the spectacled bears, the mean number of visits to baited feeders of the first eight visits in both the first 5 sessions and last 5 sessions was compared to that expected by a randomly traveling forager using a one-sample Komolgorov-Smirnov test. Differences in performance between the first five sessions and the last five sessions were tested using a Wilcoxon Signed-Rank test. Mann-Whitney U tests were used to determine if there were species differences in the mean number of visits to baited feeders in the first 5 and last 5 sessions.

To obtain all of the food in a session, the bears only needed to visit a total of 8 feeders. Anything less than 8 visits would indicate that the giant pandas had failed to deplete all of the feeders. More than 8 visits would indicate that the bears were revisiting feeders they had already visited in a trial. The total number of visits to feeders was summed in each session for each of the giant pandas and the mean was calculated across the first five and last five sessions. One sample t tests were used to compare the mean number of visits by the giant pandas in the first five and last five sessions with the total necessary to obtain all of the food in a trial. An examination of the graph of the data suggested that there might be differences across institutions in the number of visits to feeders. Therefore, a Kruskal-Wallis one way analysis of variance was used to further examine the possibility of differences in performance between the giant pandas at the three institutions. One sample Komolgorov-Smirnov tests were used to compare the mean number of visits by the spectacled bears in the first five and last five sessions with the total necessary to obtain food in a trial. A Mann-Whitney *U* test was used to determine if there were species differences in performance in the first five and last five sessions.

Finally, I was interested in whether the bears were able to avoid feeders they had already depleted within a trial. Therefore, the frequency of visits to previously depleted food sites was calculated for each session. For the giant pandas, a regression analysis was used to determine if there was a decrease in the frequency of revisits across sessions. The data were then averaged across the first five sessions and last five sessions, and the performance of the giant pandas was compared to that of the spectacled bears using Mann Whitney *U* tests.

6.1.3 Results

The giant pandas required no training to open the lids of the feeders. On the first day of exposure to the feeders, the giant pandas learned to use either their pseudothumb or nose to lift the lids. The giant pandas at both ZA and NZP readily responded to the task, consuming all of the biscuits provided during each session. Both females at SDZ were reluctant to participate in the first few trials. It was hypothesized that their reluctance resulted from the novelty of the test room and the fact that it was a room used by the male, Shi Shi. To reduce the affect of novelty on their behavior, both giant pandas were allowed several days of access to the room without the presence of the feeders. When they seemed more comfortable being in the room and were shifting easily from their dayrooms to the test room, trials were started again. However, neither of the giant pandas visited all of the feeders during the sessions, sometimes leaving biscuits even after opening the lids of the feeders and seeing the food inside. The decision was made to switch the reinforcer to carrots, which the keeper staff believed the giant pandas preferred to the biscuits. After changing the reinforcer, both giant pandas began visiting all of the feeders and consuming all of the hidden food. Therefore, carrots were used throughout all of the tasks for the SDZ females.

The spectacled bears also did not require explicit training on the task. Even though the feeders were completely novel to them on the first trial, both bears readily approached and opened the lids with their paws to reveal food. Grapes were initially used as reinforcers in the first trial, however neither bear seemed motivated to open all of the feeders. In the second trial I used omnivore biscuits, which still did not sustain consistent responding. On the third trial, the biscuits were dipped in honey. This resulted in sustained performance, therefore, honey-coated biscuits were used as the reinforcer throughout the rest of the study. The feeders and plates were thoroughly cleaned between all trials.

The length of time it took the giant pandas to visit all of the feeders (as measured from examination/lifting lid of the first feeder to examination/lifting lid of the last feeder) and obtain food during a trial decreased across the 15 sessions of the exploratory task for each of the seven giant pandas (see Figures 1-3). As can be seen in Figure 4, the mean length of time between the giant pandas' first and last visits to feeders during a session decreased from 6.3 minutes in the first session to 3.9 minutes in the last session. A regression analysis indicated that this decrease was statistically significant [$R = 0.23$, $p = 0.02$]. The length of time it took the giant pandas to visit all of the feeders in the first session varied widely across individual giant pandas, ranging from 3.4 minutes (204.2 seconds) for the adult male at NZP (Figure 2) to 11.8 minutes for the adult female at ZA (705.9 seconds) (Figure 1). By the last session, the adult male at NZP was visiting all feeders in only 1.8 minutes and the adult female at ZA was visiting all feeders in only 3.3 minutes. Trials 2 and 3 are missing for the adult male at SDZ (Figure 3). In trial 2 he visited 0 feeders and in trial 3 he only visited 1 feeder.

The amount of time it took for the spectacled bears to visit all of the feeders during a trial also decreased significantly across the 15 sessions. Figures 5 and 6 depict the length of time it took both spectacled bears to visit all feeders during a session, as well as the overall mean for both spectacled bears. The mean length of time between the spectacled bears' first and last visit to a feeder during a session decreased significantly from 9.1 minutes in the first session to 3.3 minutes in the last session [$R = 0.68$, $p < 0.001$]. There was no significant difference between the mean length of time it took the giant pandas ($X = 270.9$ sec) and spectacled bears ($X = 271.1$ sec) to finish the task across trials [$U = 2.0$, $p = 0.14$].

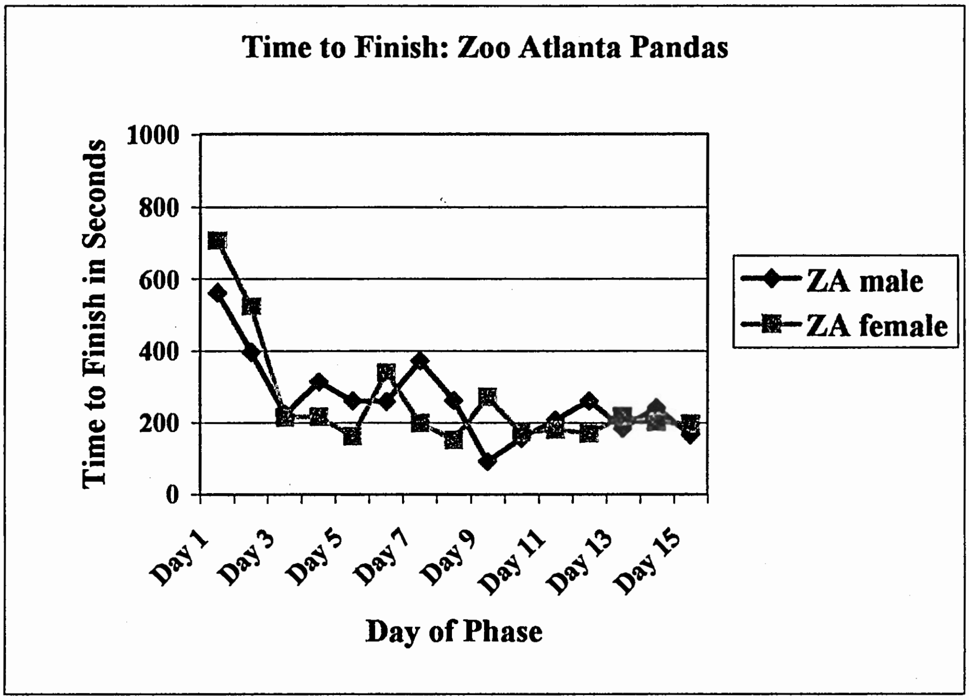

Figure 1. The length of time in seconds it took the Zoo Atlanta pandas to visit all of the feeders, as measured from examination/lifting lid of the first feeder to examination/lifting lid of the last feeder, in each trial.

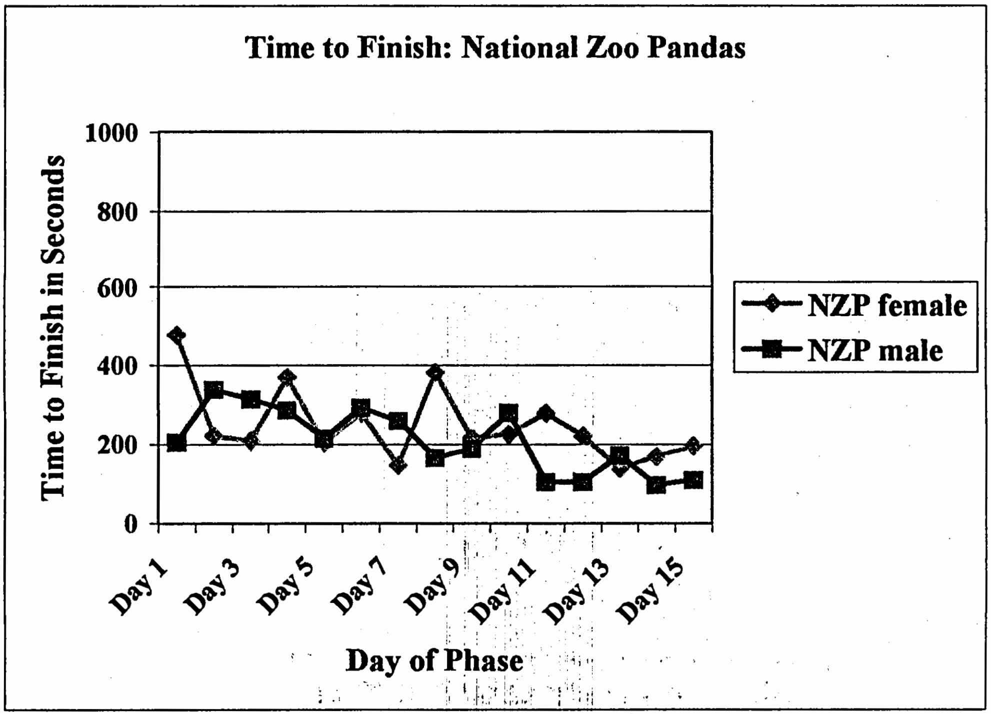

Figure 2 The length of time in seconds it took the National Zoological Park pandas to visit all of the feeders, as measured from examination/lifting lid of the first feeder to examination/lifting lid of the last feeder, in each trial.

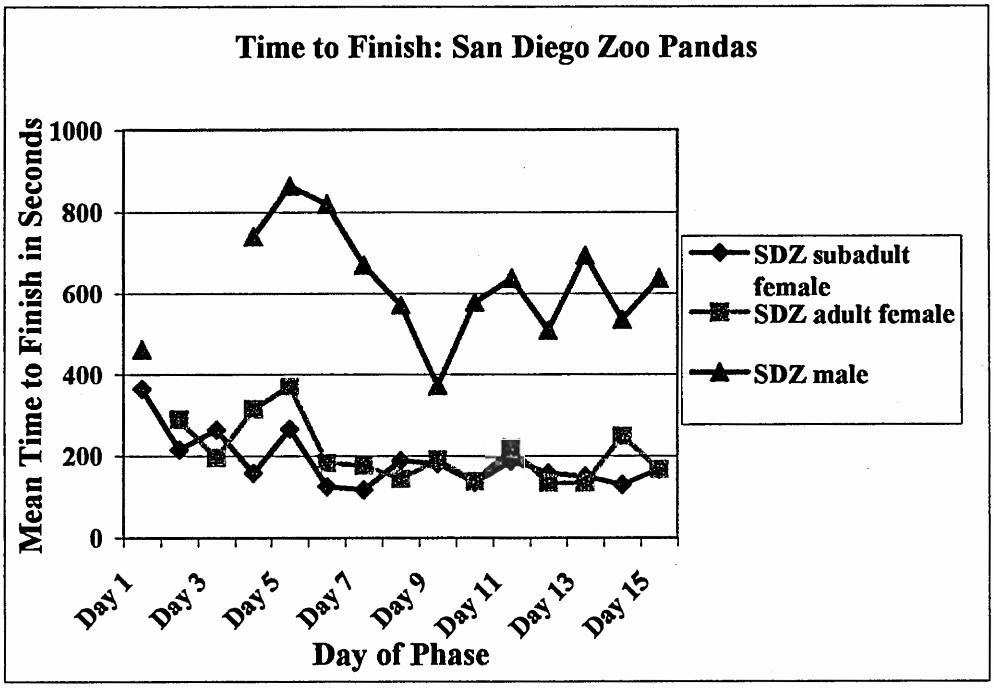

Figure 3 The length of time in seconds it took the San Diego Zoo pandas to visit all of the feeders, as measured from examination/lifting lid of the first feeder to examination/lifting lid of the last feeder, in each trial.

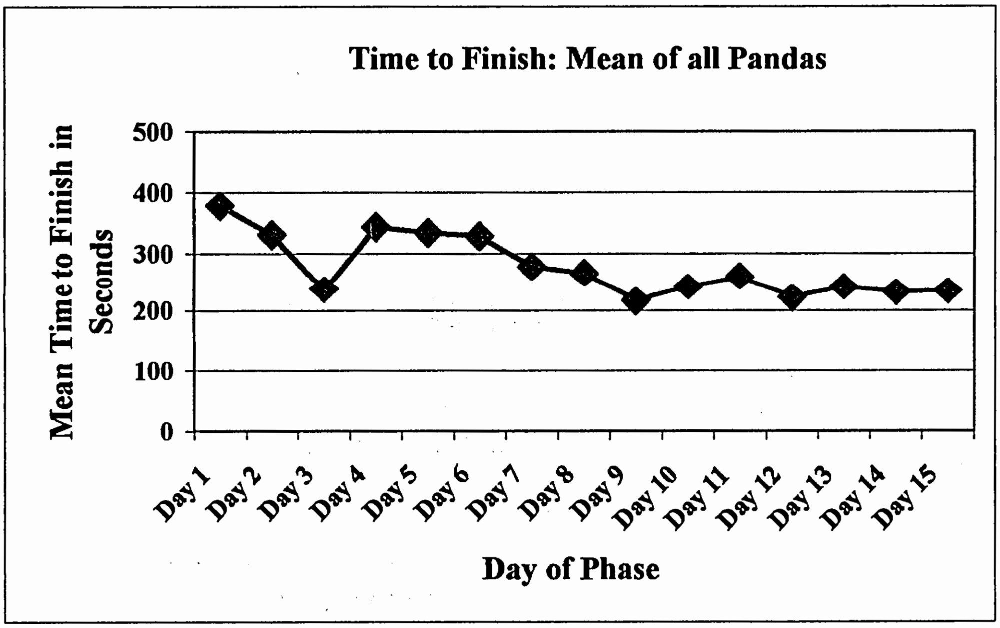

Figure 4 The overall mean length of time in seconds it took the pandas to visit all of the feeders, as measured from examination/lifting lid of the first feeder to examination/lifting lid of the last feeder, in each trial

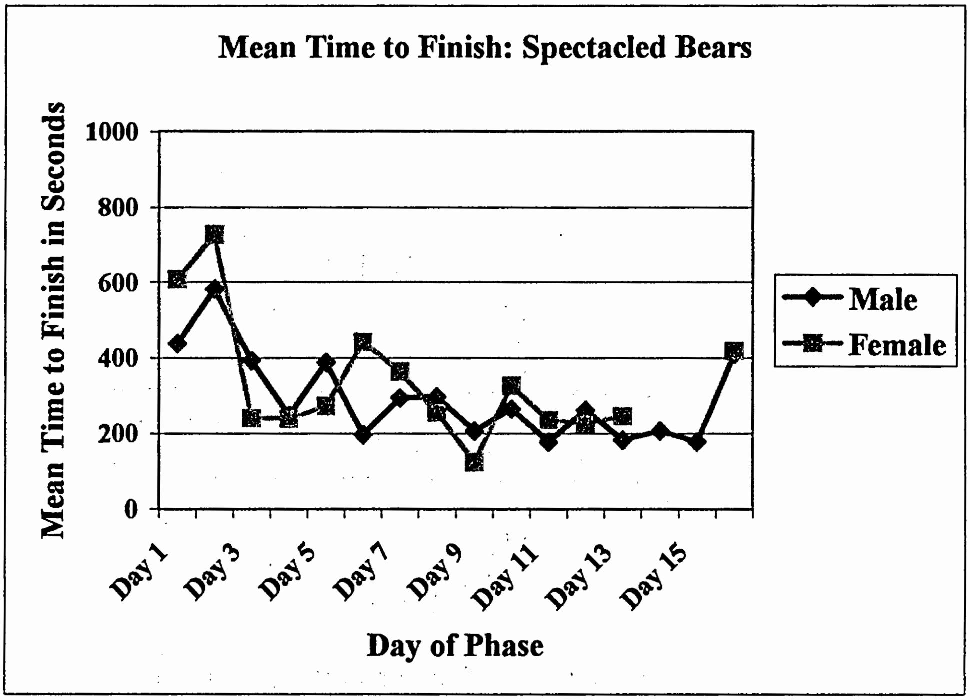

Figure 5 The length of time in seconds it took the spectacled bears to visit all of the feeders, as measured from examination/lifting lid of the first feeder to examination/lifting lid of the last feeder, in each trial.

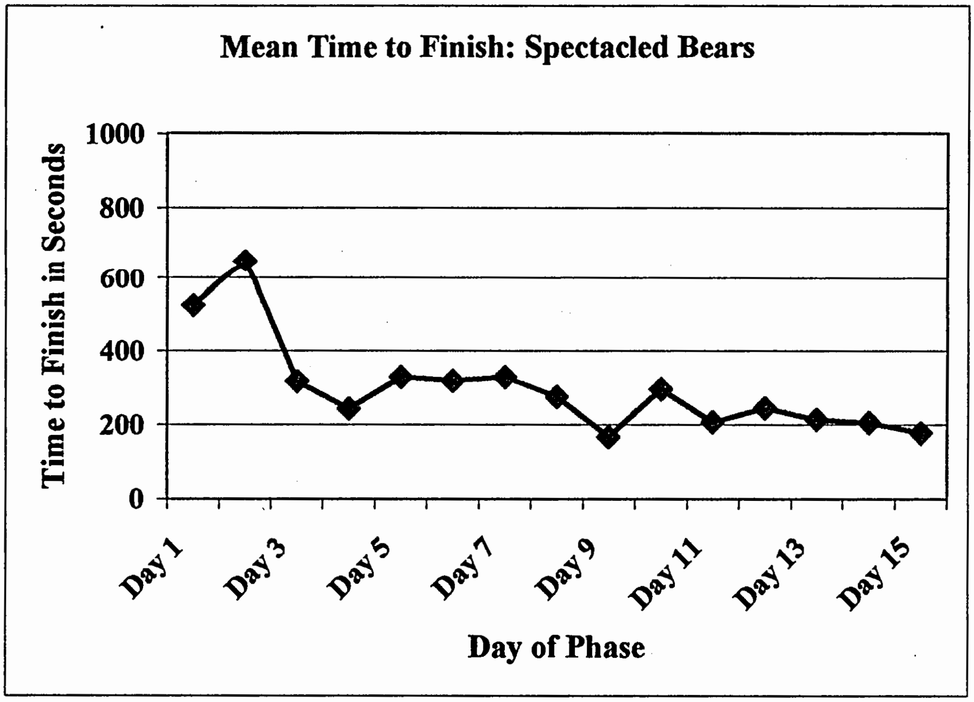

Figure 6 The mean length of time in seconds it took the spectacled bears to visit all of the feeders, as measured from examination/lifting lid of the first feeder to examination/lifting lid of the last feeder, in each trial.

As can be seen in Table 1, the bears developed preferences for both direction of travel and the feeder from which to begin searching. In approximately 80% of the trials, four of the seven giant pandas were observed to travel between the feeders in a clockwise direction. The other three giant pandas traveled predominantly in a counterclockwise direction. The giant pandas were most likely to start their travel at either the feeder designated as being in position 1 (3 giant pandas in 84% of trials) or the feeder designated as being in position 8 (4 giant pandas in 76% of the trials). In each of the testing areas at the three institutions, feeders 1 and 8 were the feeders located closest to the entrance of the test area, and were therefore the most likely to be encountered first in travel toward the array of feeders.

The pattern of foraging became relatively fixed for four of the seven giant pandas (ZA female, NZP male and female, and SDZ adult female). These giant pandas started on the same feeder and traveled in exactly the same direction in each of the last five sessions of the task. The SDZ subadult female panda started on the same feeder in each of the last five sessions, but traveled counterclockwise in four sessions and clockwise in one session. The SDZ male did not use a consistent pattern of foraging in any of the last five sessions of the exploratory task. The ZA male started with the feeder in position 1 and traveled clockwise in 3 of the last five sessions, and he started with the feeder in position 8 and traveled counterclockwise in 2 of the last five sessions.

The spectacled bears also had preferences for direction of travel and feeder from which to start their search. However, these preferences were not as pronounced as those of the giant pandas. Approximately 64% of the female's search patterns were in a clockwise direction. She started with the feeder in position 8 50% of the time. The male traveled in a counterclockwise direction 66.7% of the time and preferred to start with the feeder that was in position 1 53.3% of the time.

Table 1 Percentage of trials in which the bears traveled in either a clockwise or counterclockwise direction, and percentage of trials in which either feeder 1 or feeder 8 was visited first.

		Direction of Travel		First Visited Feeder	
Subject	Species	% clockwise	% counter	% Feeder 1	% Feeder 8
ZA female	Panda	93.3	6.7	86.7	6.7
ZA male	Panda	73.3	26.7	73.3	26.7
SDZ adult female	Panda	85.7	14.3	92.9	7.1
SDZ subadult female	Panda	33.3	66.7	26.7	66.7
SDZ male	Panda	72.7	27.3	18.2	63.6
NZP female	Panda	20	80	0	93.3
NZP male	Panda	6.7	93.3	6.7	80.0
NZP female	Spectacled	64.3	34.7	21.4	50.0
NZP male	Spectacled	33.3	66.7	53.3	0.0

To examine whether the giant pandas were using an efficient pattern of foraging in the exploratory task, I calculated the proportion of visits in which the giant pandas bypassed 0, 1, 2, or 3 feeders to visit successive feeders. The foraging pattern of the giant pandas was considered optimally efficient when 0 feeders were bypassed (i.e., the giant pandas visited adjacent feeders) between successive choices and least efficient when 3 feeders separated successive choices. A bypass of 3 feeders indicated that the giant pandas traveled across the room to visit the next food site. Figures 7-9 present the mean proportion of visits in which 0, 1, 2, or 3 feeders separated successive choices during the first 5 trials and last five trials of the study for each of the giant pandas at the three institutions, as well as the mean for all giant pandas (Figure 10). With eight possible choices to find food, a randomly foraging animal would be expected to visit 5 non-adjacent feeders and 2 adjacent feeders in their 7 visits following the first visit to a feeder. There were some sessions in which the giant pandas did not make 7 subsequent visits after visiting the first feeder. These sessions were not used for the analysis, and the expected number of visits to non-adjacent and adjacent feeders was adjusted accordingly.

The giant pandas were efficient in their pattern of travel between feeders, even in the first five sessions of the exploratory task, rarely visiting non-adjacent feeders. As can be seen in Figure 7, the ZA male was optimally efficient both in the first five sessions and last five sessions of the task. All of his visits were to adjacent feeders. One-sample t tests were used to compare the observed mean number of visits by all giant pandas to adjacent feeders with the number expected if the giant pandas were foraging at random. During the first five sessions, the mean number of visits to adjacent feeders was 5.98 of 7 choices, which was significantly greater than would be expected by chance [t(6) = 14.13,

$p < 0.001$]. This increased to a mean of 6.91 visits in the last five sessions, which was also different than would be expected had they been foraging randomly [t(6) 110.96, $p < .001$]. A paired samples t test indicated that the difference between the mean number of visits to adjacent feeders in the first five sessions ($X = 5.98$) and last five sessions ($X = 6.91$) was statistically significant [$t(6) = -3.32$, $p = 0.016$], suggesting that the giant pandas learned to travel more efficiently over time.

The spectacled bears were also very efficient foragers. Figure 11 presents the mean proportion of visits in which either 0, 1, 2, or 3 feeders separated successive choices during the first 5 trials and last five trials of the study for each of the spectacled bears as well as the mean for both bears (Figure 12). In the first five sessions of the study, the spectacled bears visited a mean of 6.05 adjacent feeders in their first 7 visits. A one-sample Komolgorov-Smirnov indicated that the difference between the observed and expected number of visits was statistically significant [$D_{max} = 1.0$, $p < 0.001$]. Visits to adjacent feeders increased to a mean of 6.9 in their first 7 visits in the last five sessions, which was also significantly different than that expected had they been searching randomly [$D_{max} = 1.0$, $p < 0.001$]. A Wilcoxon Signed-rank test indicated that there was no significant difference between the mean number of visits by the spectacled bears to adjacent feeders in the first five sessions and the mean number of visits to adjacent feeders in the last five sessions [$Z = 1.34$, $p = 0.18$]. They were equally efficient in the first five trials of the study as they were in the last five trials. Mann-Whitney U tests indicated that there were no significant differences between the giant pandas and the spectacled bears in the mean number of visits to adjacent feeders in either the first five sessions [$U = 7.5$, $p = 0.88$] or the last five sessions [$U = 7.0$, $p = 1.0$].

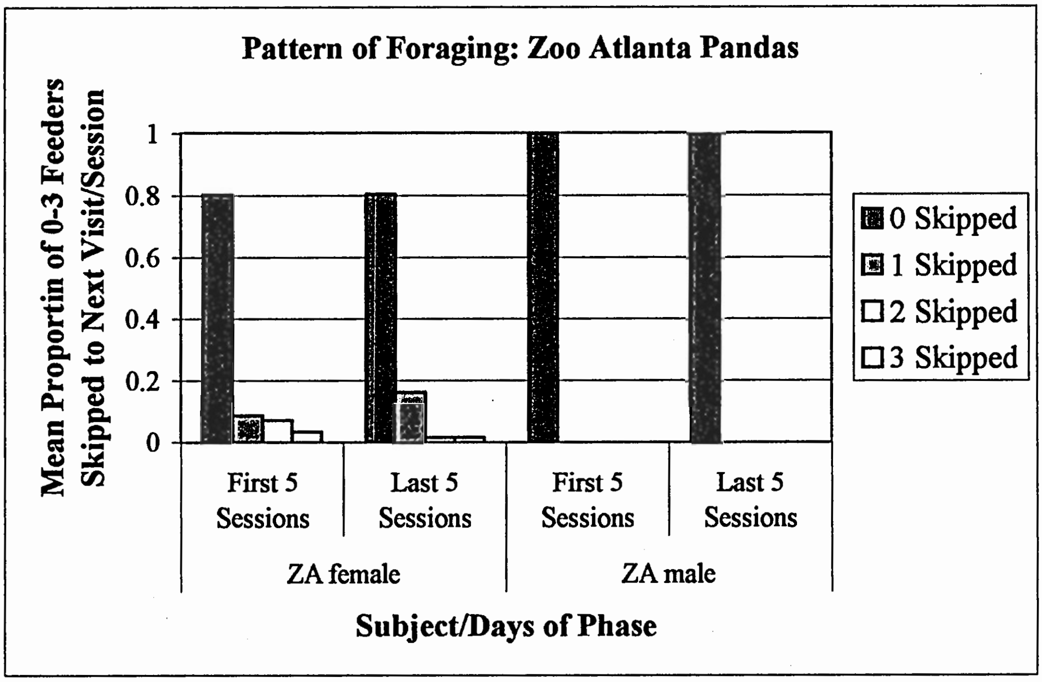

Figure 7 The mean proportion of visits in which the Zoo Atlanta pandas bypassed 0, 1, 2, or 3 feeders to visit successive feeders in the first five and last five sessions of the exploratory task.

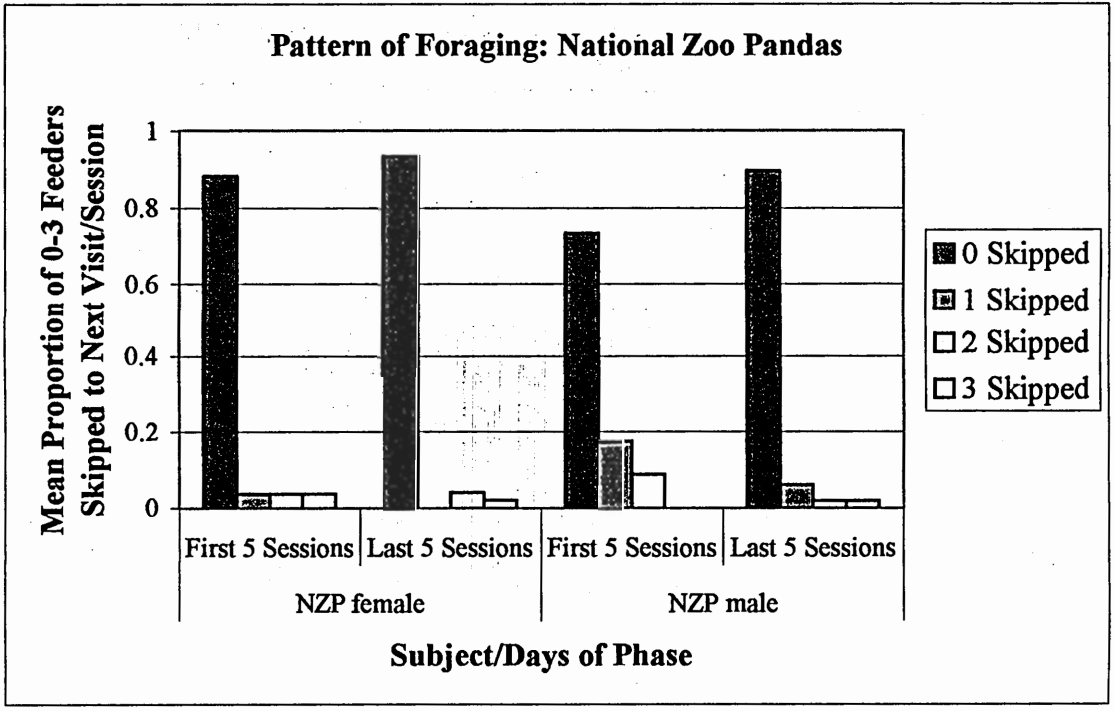

Figure 8 The mean proportion of visits in which the National Zoological Park pandas bypassed 0, 1, 2, or 3 feeders to visit successive feeders in the first five and last five sessions of the exploratory task.

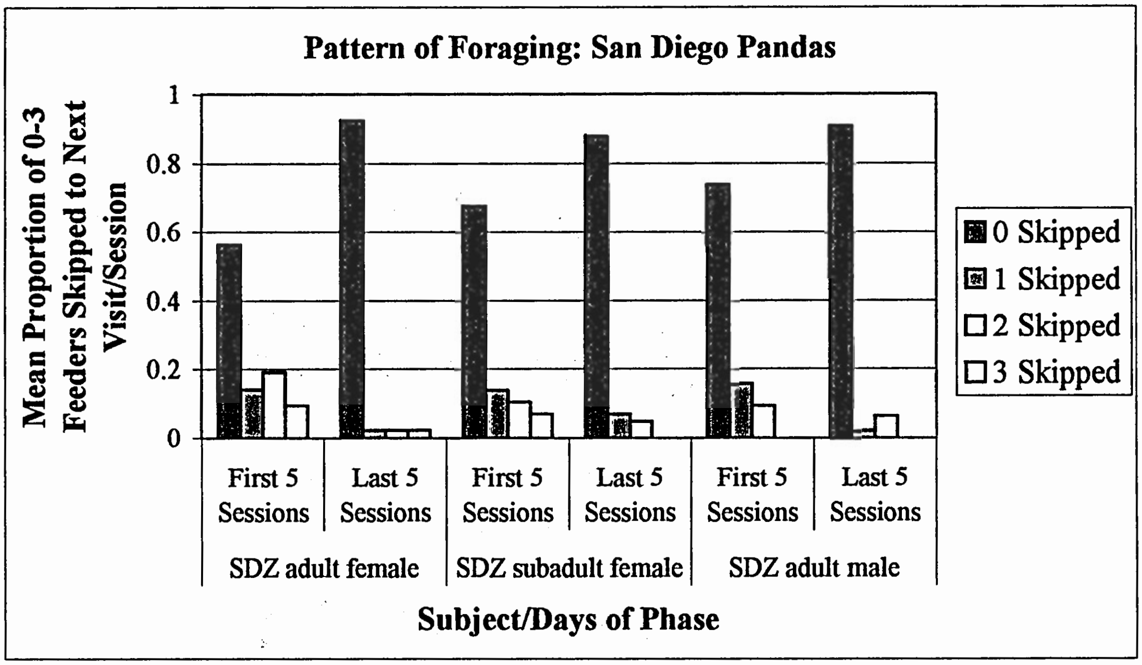

Figure 9 The mean proportion of visits in which the San Diego Zoo pandas bypassed 0, 1, 2, or 3 feeders to visit successive feeders in the first five and last five sessions of the exploratory task.

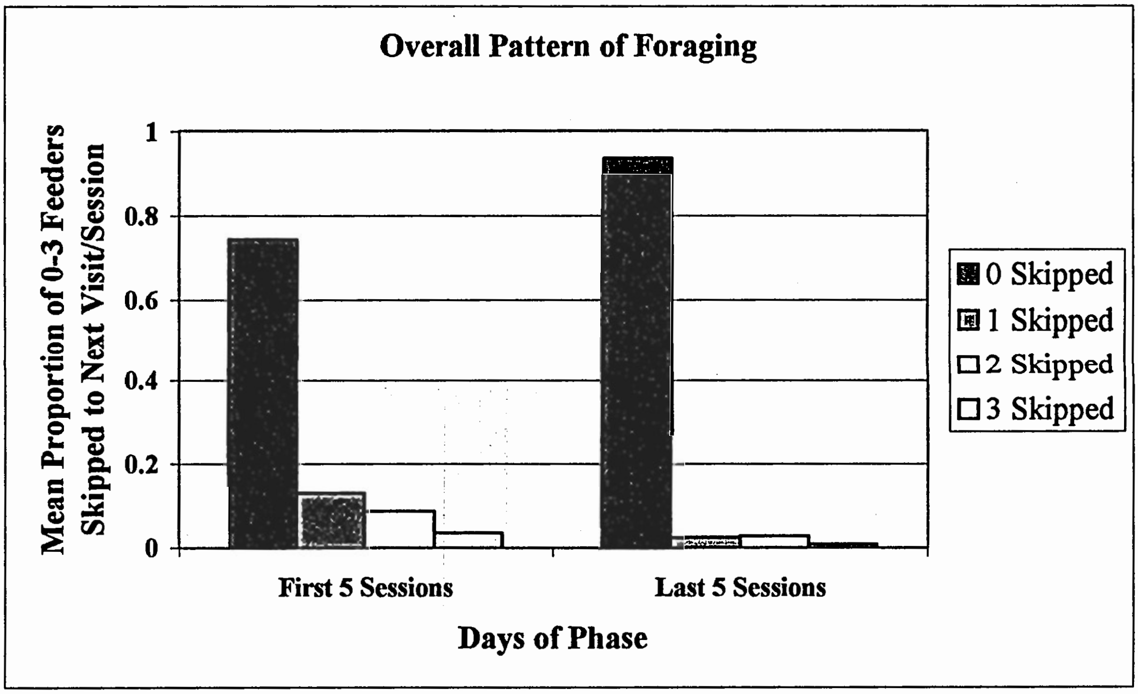

Figure 10 The mean proportion of visits in which the pandas bypassed 0, 1, 2, or 3 feeders to visit successive feeders in the first five and last five sessions of the exploratory task.

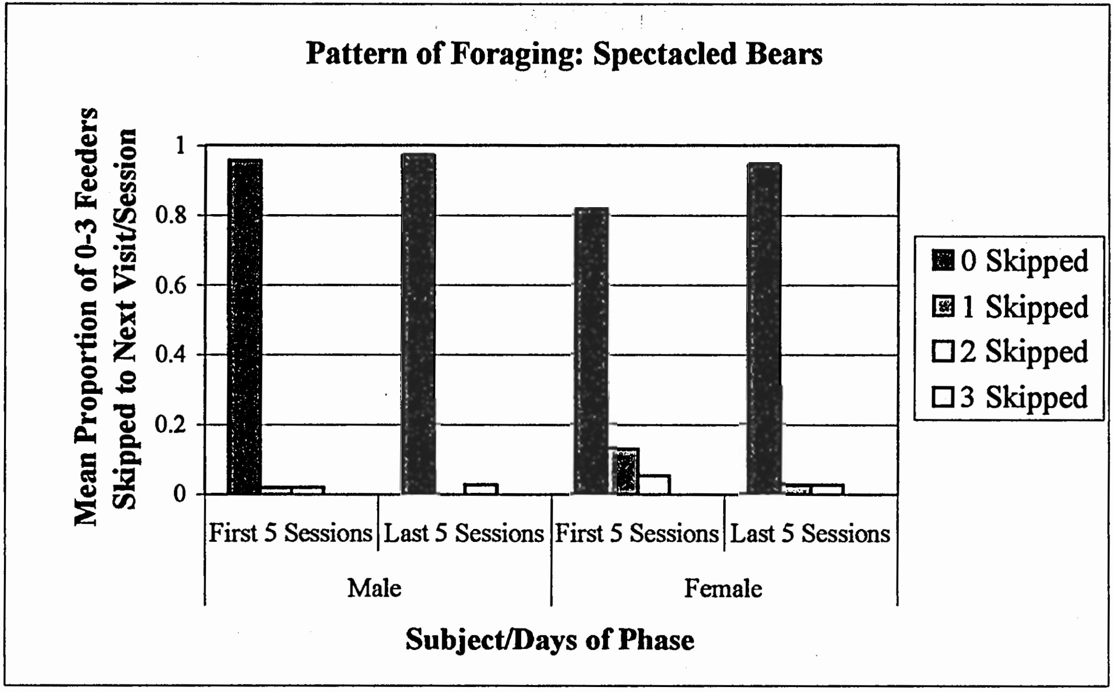

Figure 11 The mean proportion of visits in which the spectacled bears bypassed 0, 1, 2, or 3 feeders to visit successive feeders in the first five and last five sessions of the exploratory task.

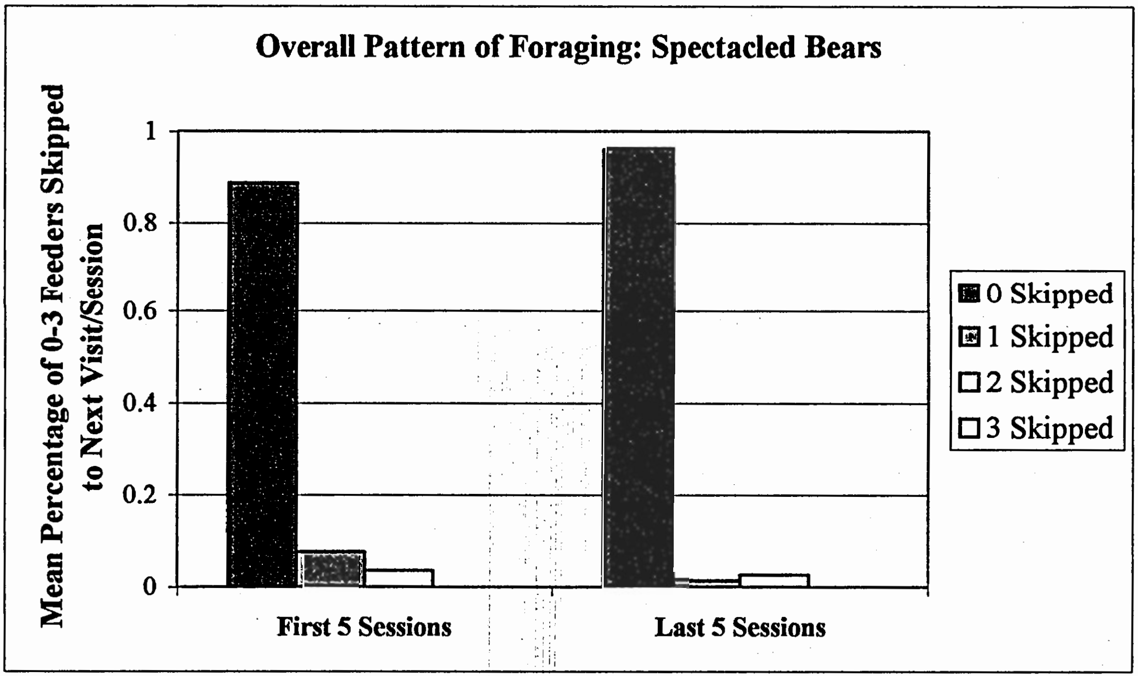

Figure 12 The mean proportion of visits in which the spectacled bears bypassed 0, 1, 2, or 3 feeders to visit successive feeders in the first five and last five sessions of the exploratory task.

A randomly traveling forager would be expected to visit 5.252 baited feeders in their first 8 visits. I calculated the mean number of baited feeders visited in the first 8 visits in the first five sessions and last five sessions of the exploratory task for each individual panda (see Figures 13-15), as well as the overall mean of all giant pandas (Figure 16). As can be seen in the figures, all of the giant pandas (with the exception of the SDZ male) visited more baited feeders in their first 8 visits than would be expected. The SDZ male did not visit all of the feeders in each trial in the first 5 sessions of the task. However, he was visiting 8 baited feeders in his first 8 visits by the last five sessions of the exploratory task. In the first five sessions of the exploratory task, the giant pandas visited a mean of 7.31 baited feeders which was significantly more than would be expected had they been foraging randomly [$t(5) = 12.74$, $p < 0.001$]. The mean number of visits to baited feeders in the last five sessions was 7.97, which was also significantly more than would be expected by chance [$t(6) = 95.18$, $p < .001$]. A paired sample t test indicated that the mean number of visits to baited feeders in the first 8 visits increased significantly from the first five sessions to the last five sessions [$t(5) = -4.33$, $p = 0.007$], indicating that the giant pandas learned to forage more efficiently over time.

The spectacled bears also visited more baited feeders in the first 8 visits than would be expected had they been foraging randomly. Figure 17 depicts the mean number of baited feeders visited in the first 8 visits in the first five sessions and last five sessions of the exploratory task for both spectacled bears, and Figure 18 depicts the overall mean of the spectacled bears. In the first five sessions, the spectacled bears visited a mean of 7.63 baited feeders in their first 8 visits. Sessions in which fewer than 8 visits were made were excluded from analysis. A Kolmogorov-Smirnov test indicated that this was significantly different from the 5.252 expected by a randomly traveling forager [D_{max} = 0.99, $p < 0.001$]. Their performance in the last five sessions improved to a mean of 8.0 visits to baited feeders, which was significantly better than would be expected had they been foraging randomly [D_{max} = 0.99, $p < 0.001$]. A Wilcoxon Signed-rank test indicated that there was no significant difference in the mean number of visits to baited feeders in the first 8 visits between the first five sessions and the last five sessions [$Z = 1.34$, $p = 0.18$]. The performance of the spectacled bears was not significantly different from that of the giant pandas, in either the first five sessions [$U = 3.5$, $p = 0.40$] or the last five sessions [$U = 6.0$, $p = 0.59$].

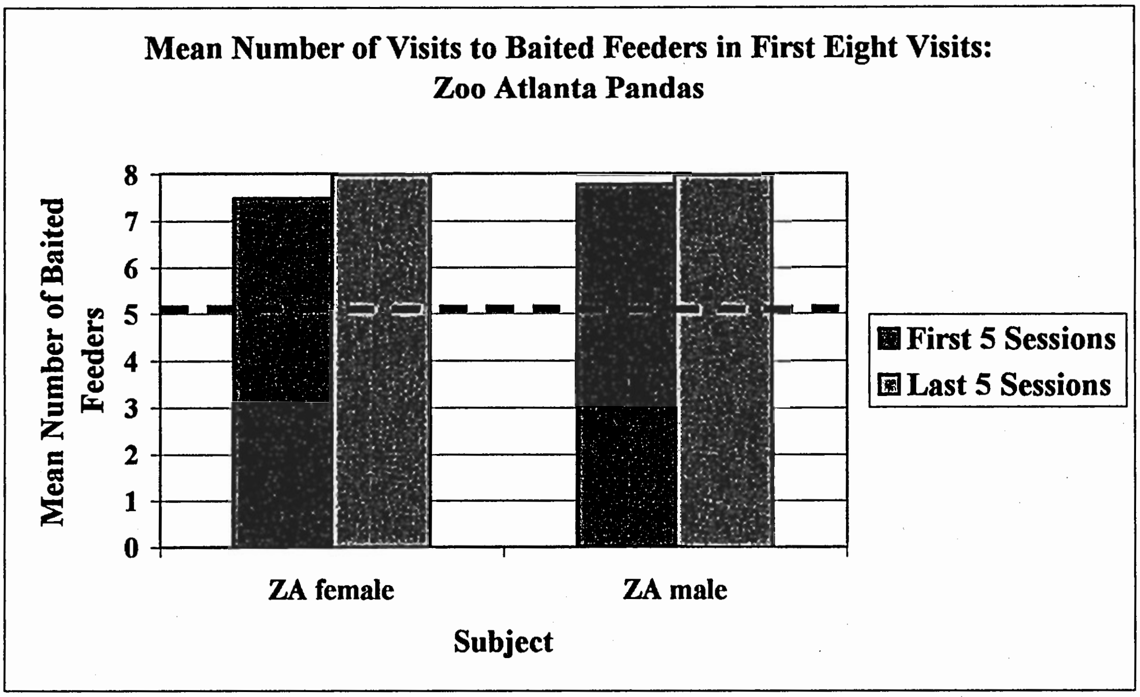

Figure 13 Mean number of baited feeders visited by the Zoo Atlanta pandas in the first 8 visits in the first five sessions and last five sessions of the exploratory task. The dashed line represents chance performance for a randomly traveling forager.

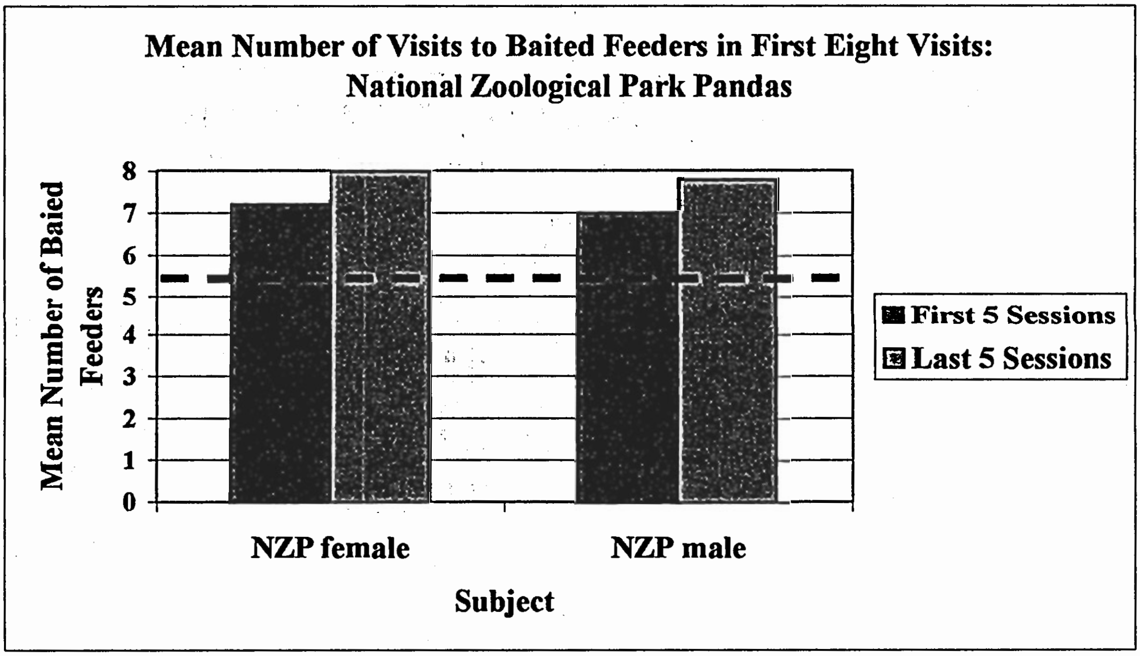

Figure 14 Mean number of baited feeders visited by the National Zoological Park pandas in the first 8 visits in the first five sessions and last five sessions of the exploratory task. The dashed line represents chance performance for a randomly traveling forager.

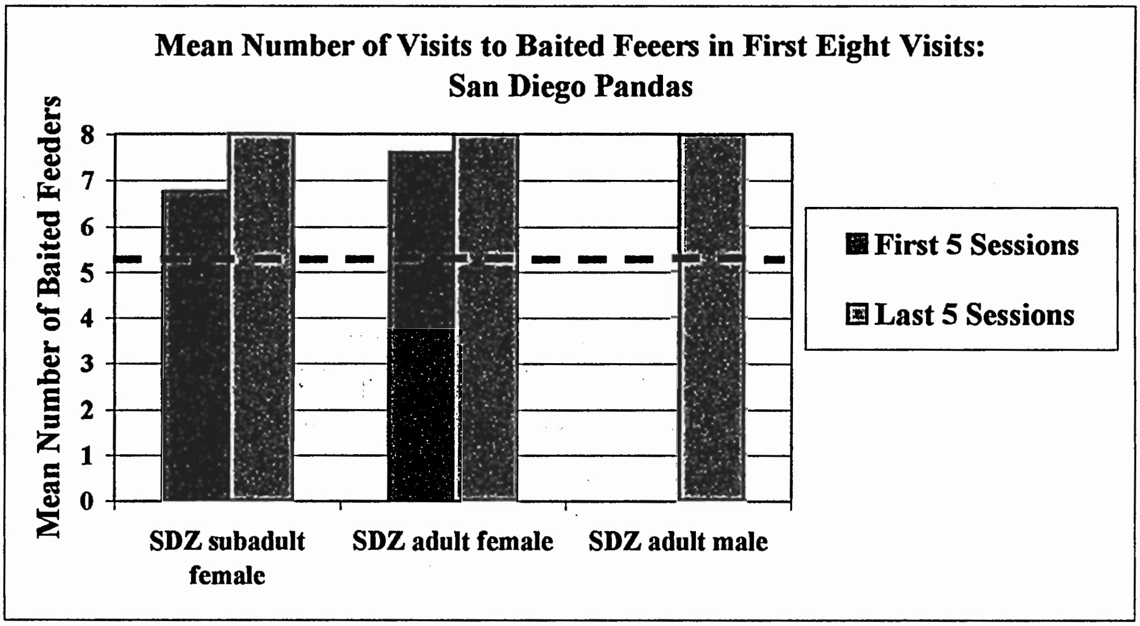

Figure 15 Mean number of baited feeders visited by the San Diego Zoo pandas in the first 8 visits in the first five sessions and last five sessions of the exploratory task. The dashed line represents chance performance for a randomly traveling forager.

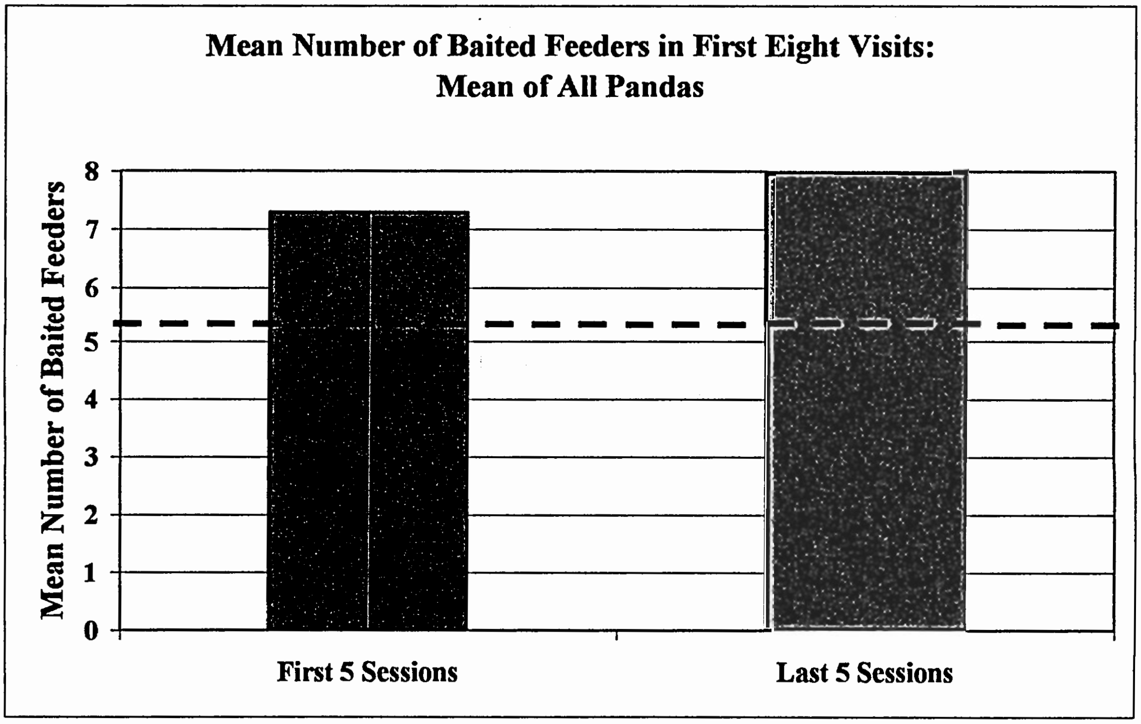

Figure 16 Mean number of baited feeders visited by all pandas in the first 8 visits in the first five sessions and last five sessions of the exploratory task. The dashed line represents chance performance for a randomly traveling forager.

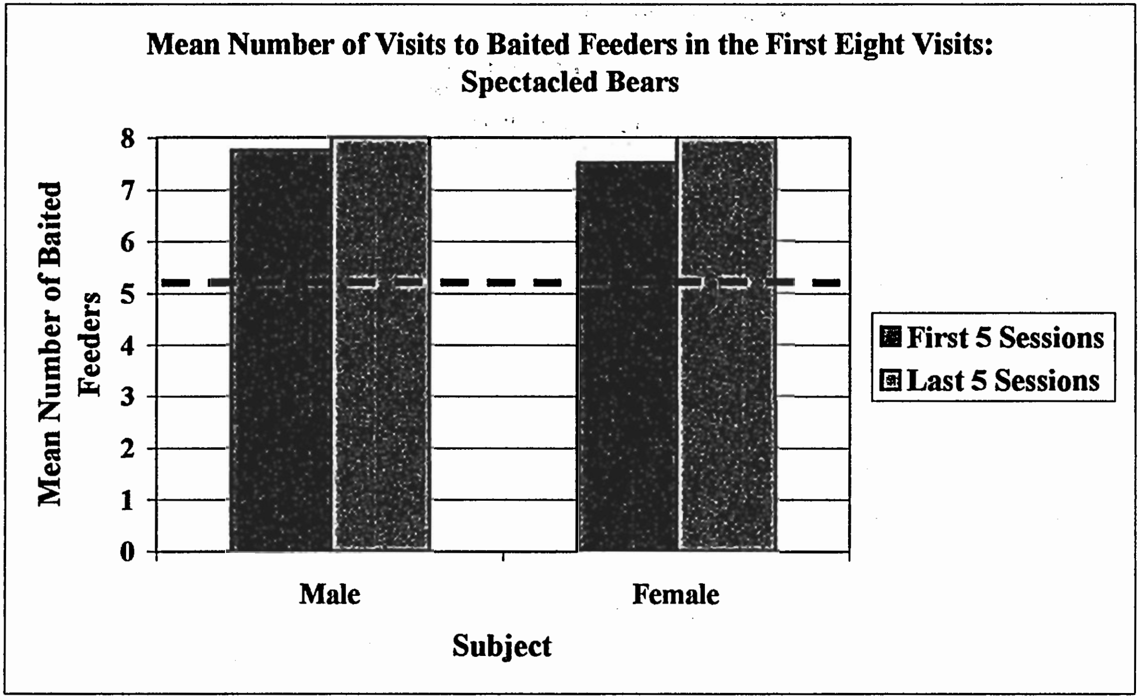

Figure 17 Mean number of baited feeders visited by the spectacled bears in the first 8 visits in the first five sessions and last five sessions of the exploratory task. The dashed line represents chance performance for a randomly traveling forager.

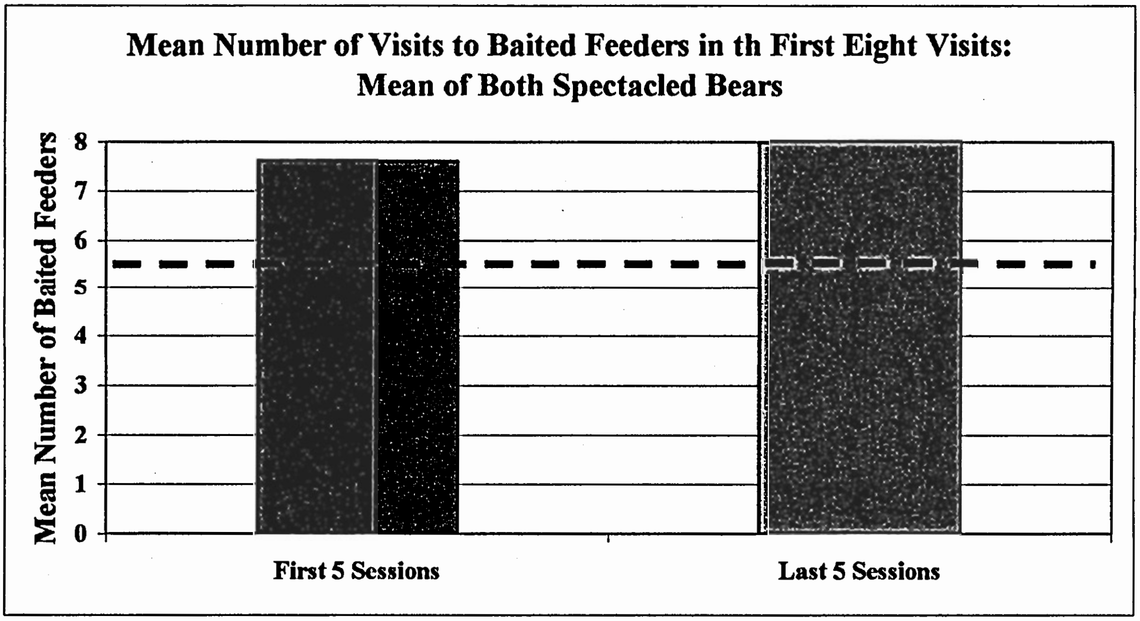

Figure 18 Mean number of baited feeders visited by the spectacled bears overall in the first 8 visits in the first five sessions and last five sessions of the exploratory task. The dashed line represents chance performance for a randomly traveling forager.

The giant pandas only needed to visit 8 feeders to obtain all of the food in a session. Any more visits than 8 were unnecessary. Figures 19-21 present the total number of feeders visited in each sessions by the giant pandas at each of the three institutions. Figure 22 presents the overall mean number feeders visited in each session by all giant pandas. In the first five sessions of the exploratory task, the giant pandas visited a mean of 11.53 feeders, which was statistically greater than the 8 visits necessary to obtain all of the food [$t(6) = 5.38$, $p = 0.003$]. In the last 5 sessions, the giant pandas visited a mean of 9.43 feeders [$t(6) = 3.46$, $p = 0.013$], which was also statistically greater than necessary to deplete all feeders. The mean number of visits to feeders decreased significantly across sessions [$R = 0.445$, $p < 0.001$] (see Figure 22). As can be seen in Figure 19, the ZA giant pandas visited only 8 feeders in each of the last 5 sessions. None of the giant pandas at either NZP or SDZ performed as accurately or consistently in the last five trials. The giant pandas at the National Zoo visited a mean of 10.5 feeders in the last 5 sessions, and the giant pandas at SDZ visited a mean of 9.67 feeders. A Kruskal-Wallis one way analysis of variance indicated that the observed difference across institutions was not, however, statistically significant [$H = 5.14$, $p = 0.08$].

Figure 23 depicts the total number of feeders visited in each trial by each of the spectacled bears. In the first days of the study, the female did not visit all 8 feeders in a trial. Therefore, she was not depleting all of the food. However, by the 9th day of testing she was visiting all 8 feeders fairly regularly. In contrast with the giant pandas, the number of feeders visited in a session by the spectacled bears increased over time (see Figure 24). The spectacled bears visited a mean of 6.7 feeders in the first five sessions, which was not significantly less than the 8 necessary as measured by a one-sample

Kolmogorov-Smirnov test [$D_{max} = 0.58$, $p = 0.35$]. Their performance improved to a mean of 8.2 visits per session, which was also not significantly different from the 8 necessary to obtain all food [$D_{max} = 0.50$, $p = 0.50$]. The change in the number of feeders visited from the first to the last sessions was significant [$R = 0.38$, $p = 0.03$]. A Mann-Whitney U test indicated that there were no species differences in performance. The mean number of visits made by the giant pandas in the first five sessions ($X = 11.53$) was not significantly greater than the mean number of visits made by the spectacled bears in the first five sessions ($X = 6.7$) [$U = 6.5$, $p = 0.87$]. The mean number of visits made by the giant pandas in the last five sessions ($X = 9.43$) was also not significantly different from that of the spectacled bears in the last five sessions ($X = 8.2$) [$U = 3.0$, $p = 0.11$].

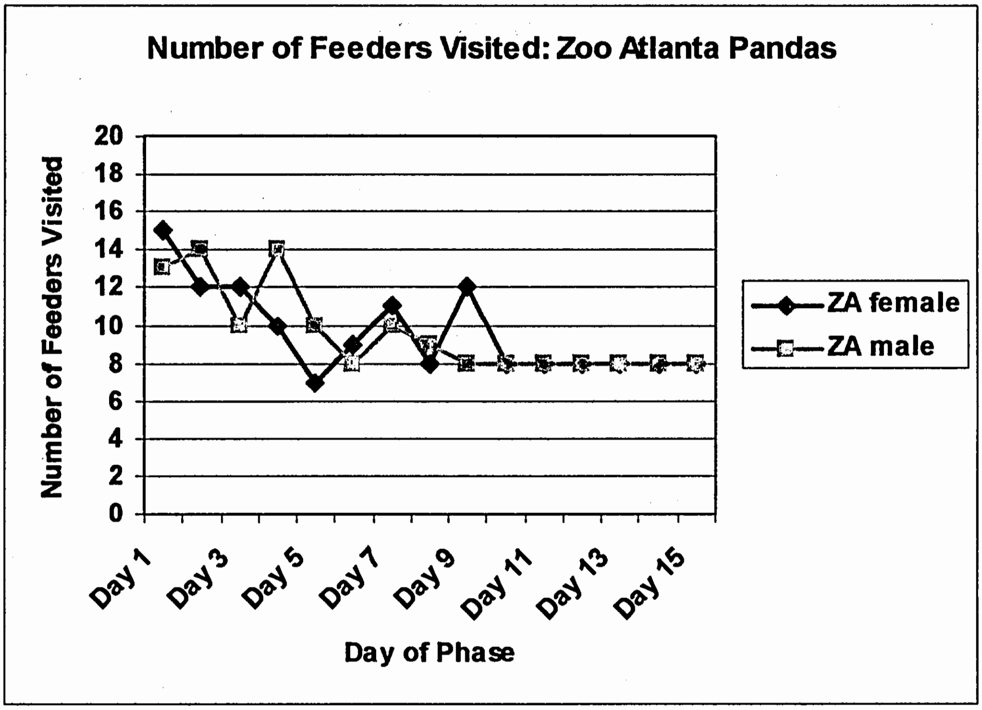

Figure 19 Total number of feeders visited in each session by the Zoo Atlanta pandas.

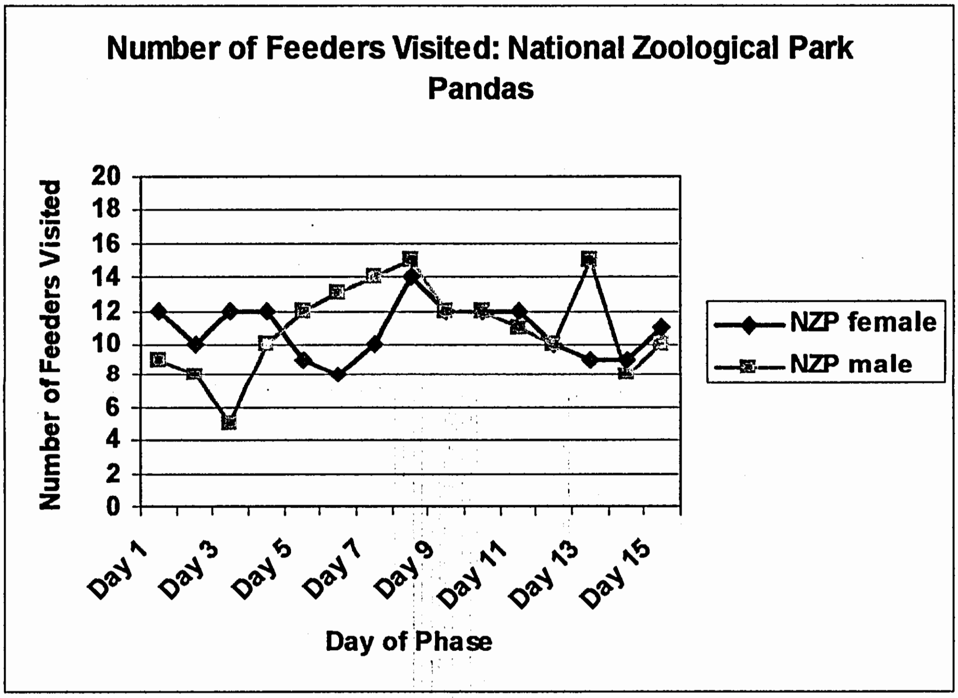

Figure 20 Total number of feeders visited in each session by the National Zoological Park pandas.

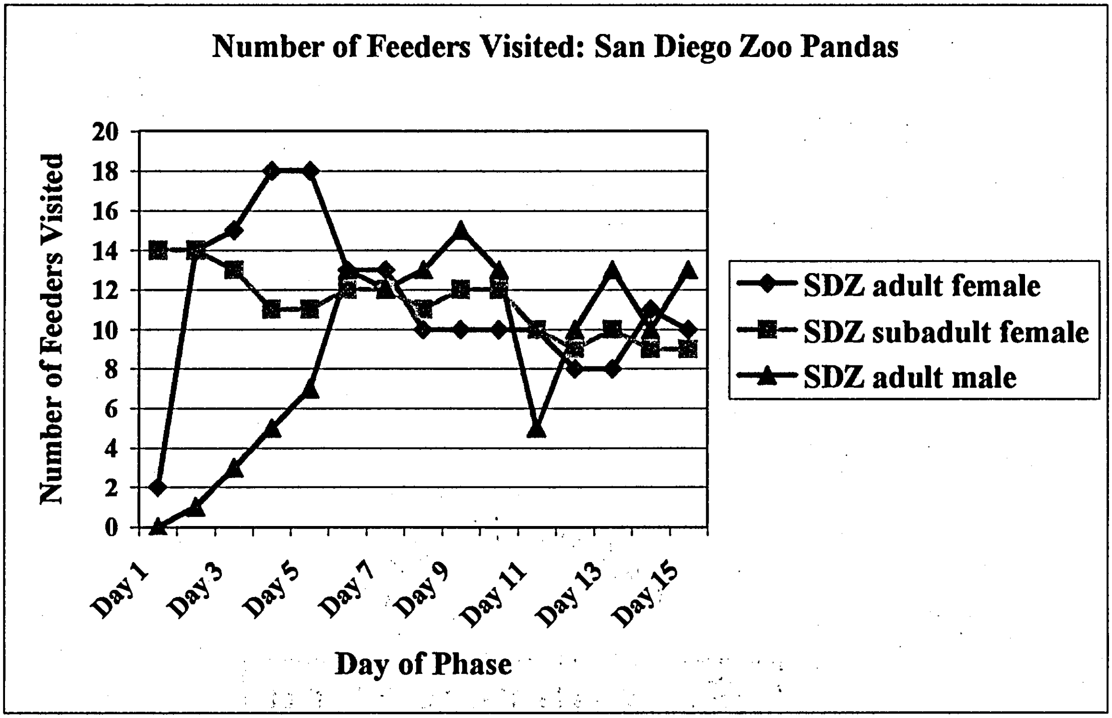

Figure 21 Total number of feeders visited in each session by the San Diego Zoo pandas.

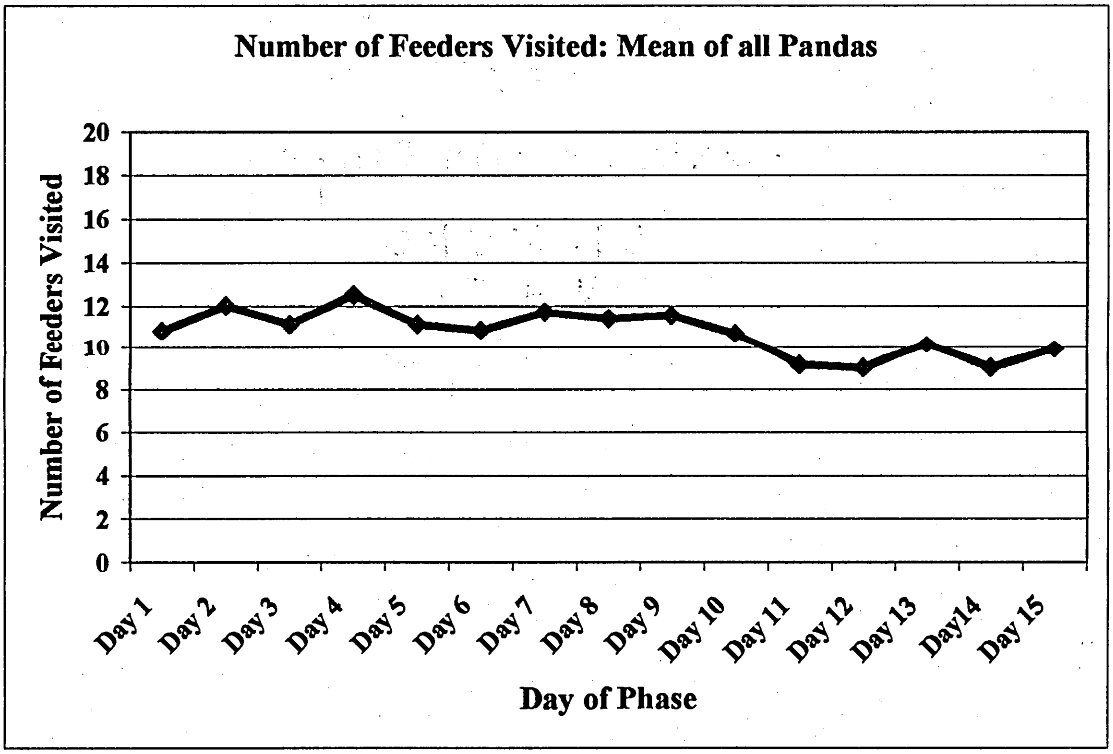

Figure 22 Mean number of feeders visited in each session by the all pandas.

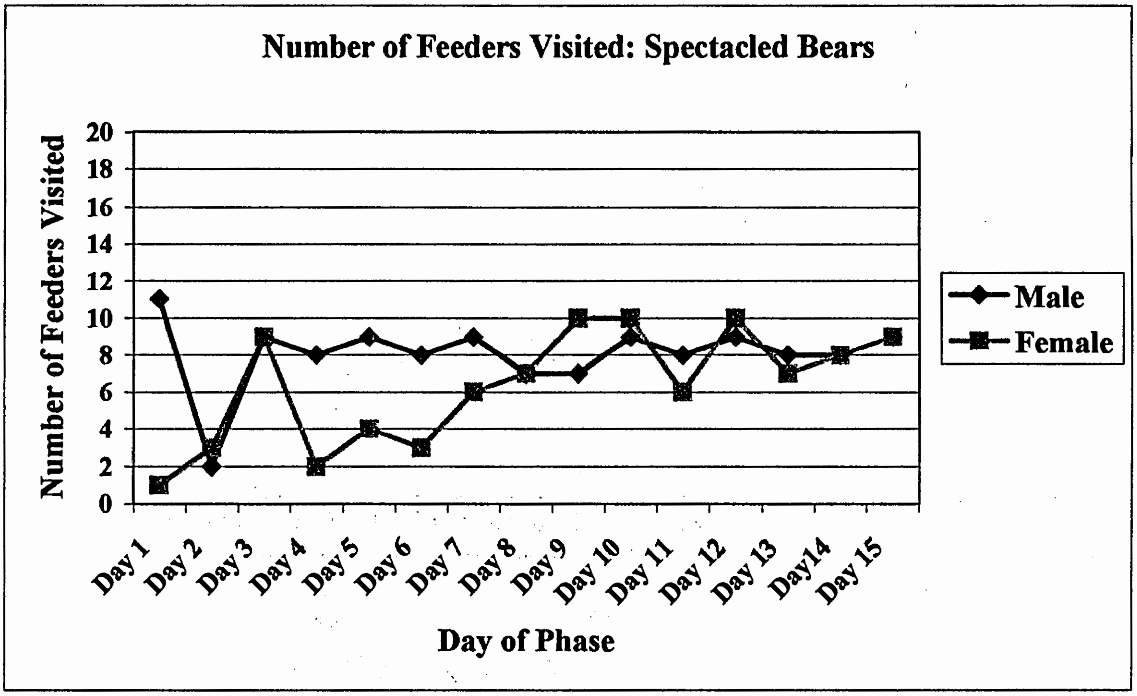

Figure 23 Total number of feeders visited in each session by the spectacled bears.

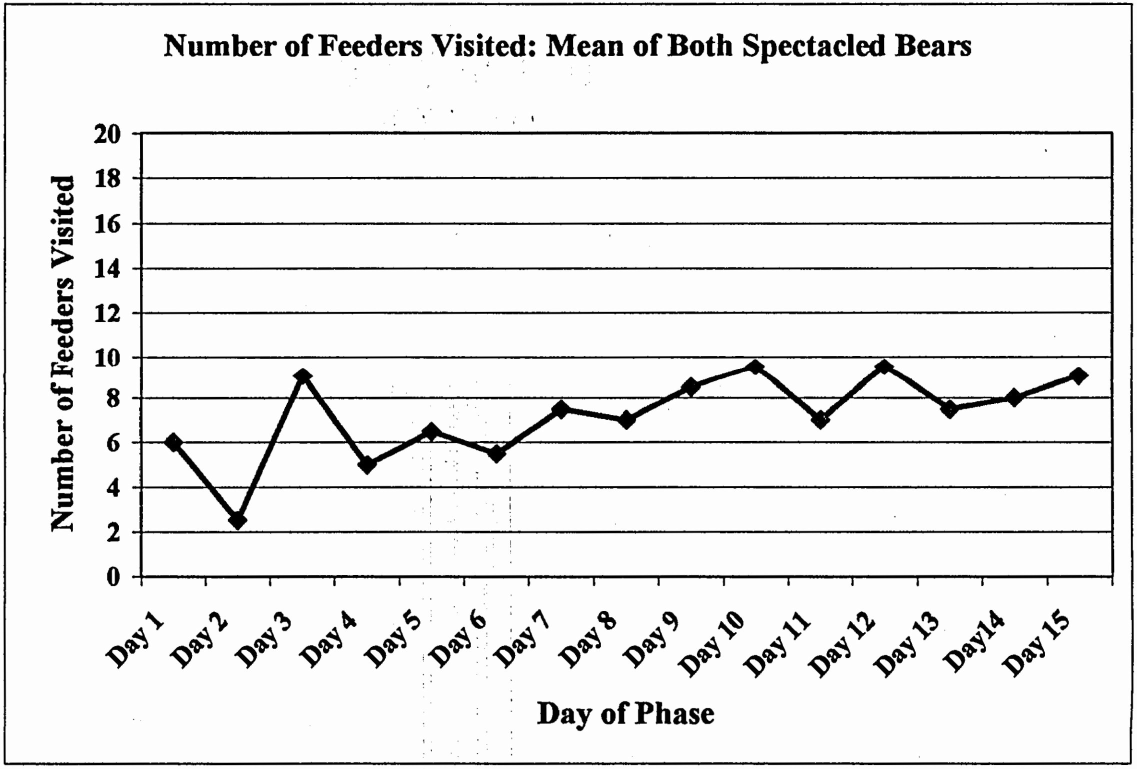

Figure 24 Mean number of feeders visited in each session by the spectacled bears.

I was also interested in whether the bears would avoid feeders they had already depleted within a trial. Figures 25-27 present the mean number of revisits to feeders during each session for each of the giant pandas at the three institutions. Figure 28 presents the mean of all subjects. The number of revisits per session decreased significantly across trials from a mean of 4.4 in the first session to 1.86 in the last session [R = 0.42, p < .001]. The total number of revisits ranged from 22 (ZA male) to 56 (SDA adult female) across the 15 sessions. As can be seen in Figure 25, the ZA giant pandas achieved perfect performance in the last 6 sessions, never returning to feeders they had already visited. Figure 29 presents the total number of revisits to feeders during a session for the each of the spectacled bears, and Figure 30 presents the mean of both spectacled bears. The spectacled bears revisited a mean of only 1.10 feeders in the first five sessions and 0.6 feeders in the last five sessions. The observed decrease in revisits by the spectacled bears across sessions was not significant [R = 0.19, p = 0.32]. The rate of revisits by the spectacled bears was lower than that observed in the giant pandas. However, a Mann Whitney U test indicated that the difference between the giant pandas (X = 3.97) and the spectacled bears (X = 1.1) in the mean number of feeders revisited in the first five sessions was significant [U = 0.0, p = 0.046]. The difference between the mean number of revisits in the last five sessions by the spectacled bears was not significantly different from that of the giant pandas [U = 4.0, p = 0.37].

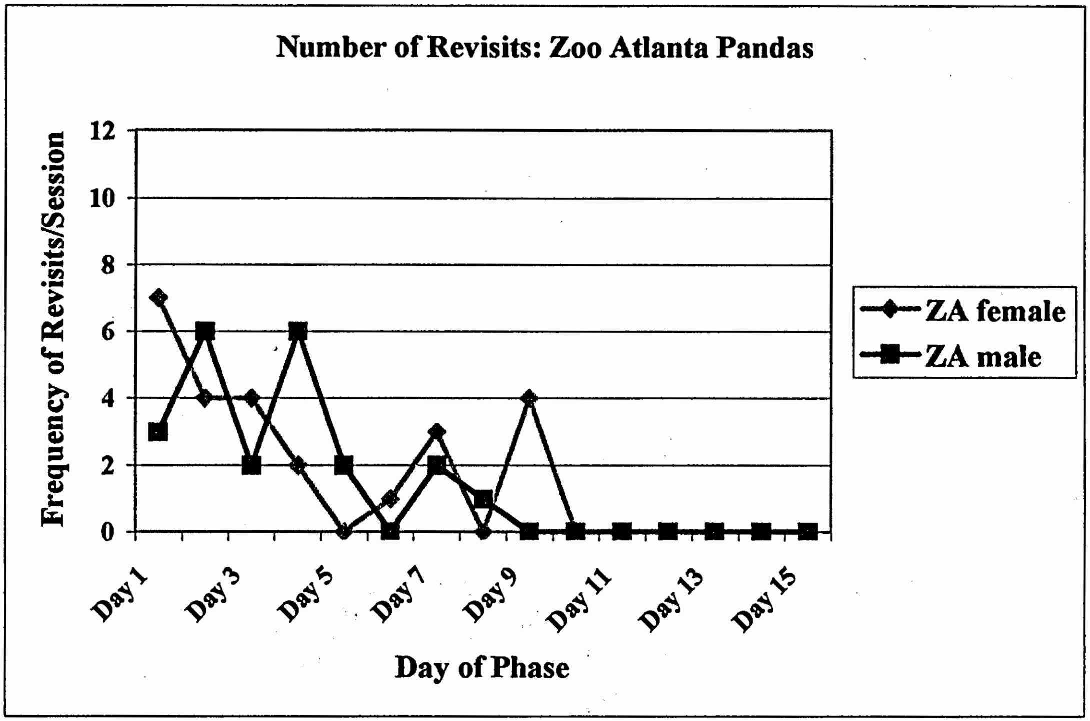

Figure 25 The total number of visits to previously visited feeders in each session by the Zoo Atlanta pandas.

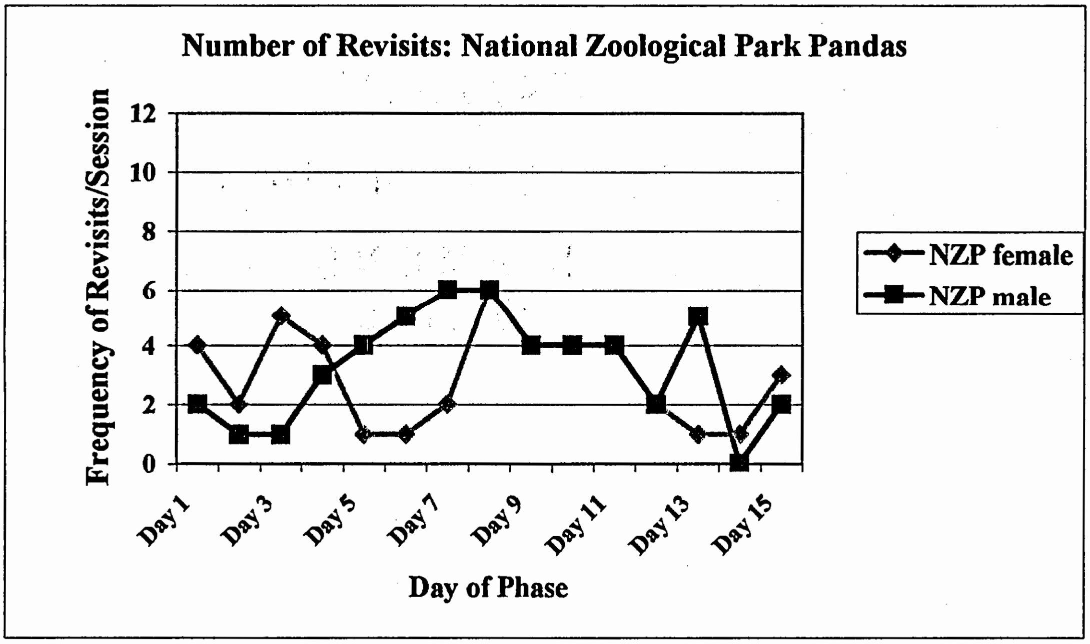

Figure 26 The total number of visits to previously visited feeders in each session by the National Zoological Park pandas.

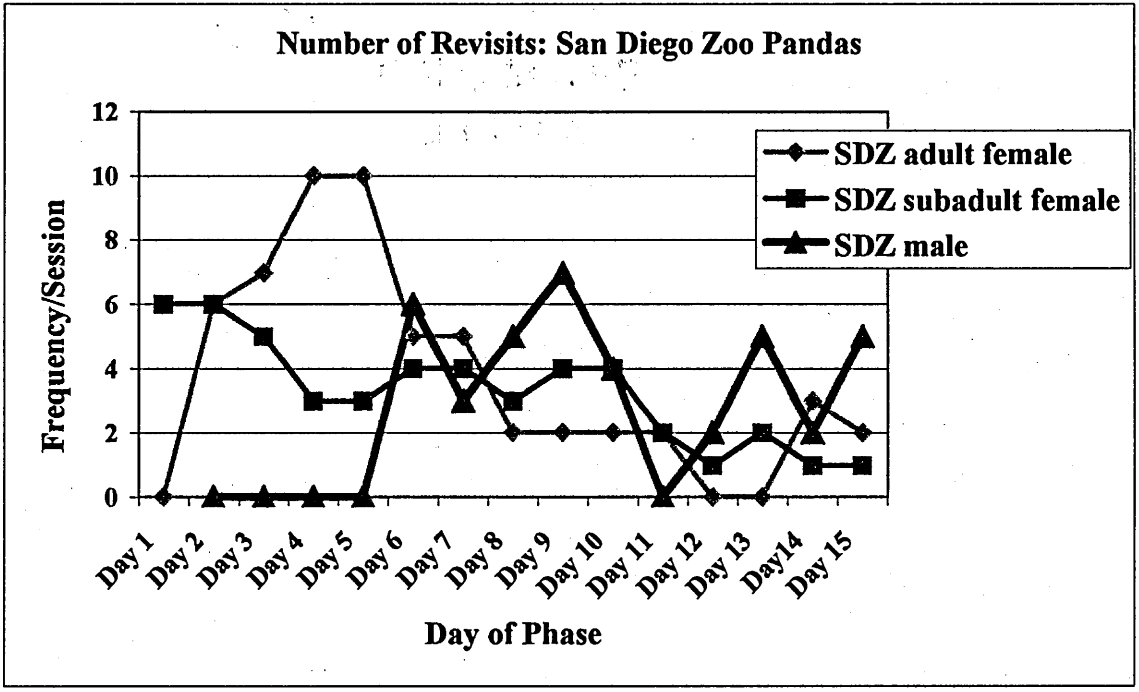

Figure 27 The total number of visits to previously visited feeders in each session by the San Diego Zoo pandas.

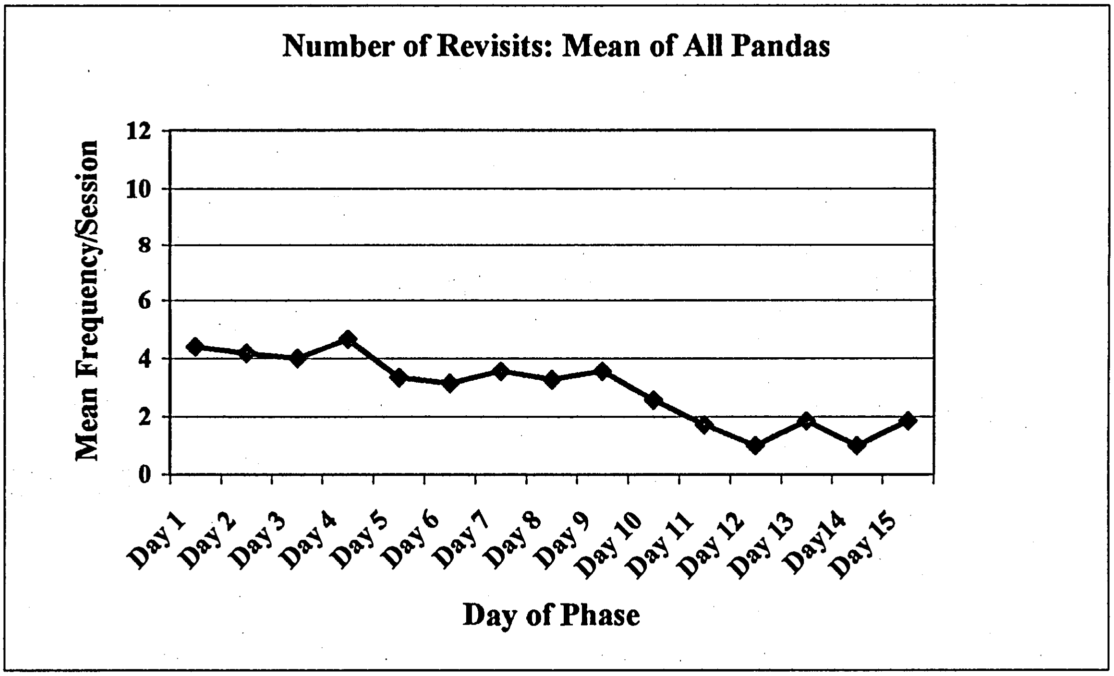

Figure 28 The mean number of visits to previously visited feeders in each session by all pandas.

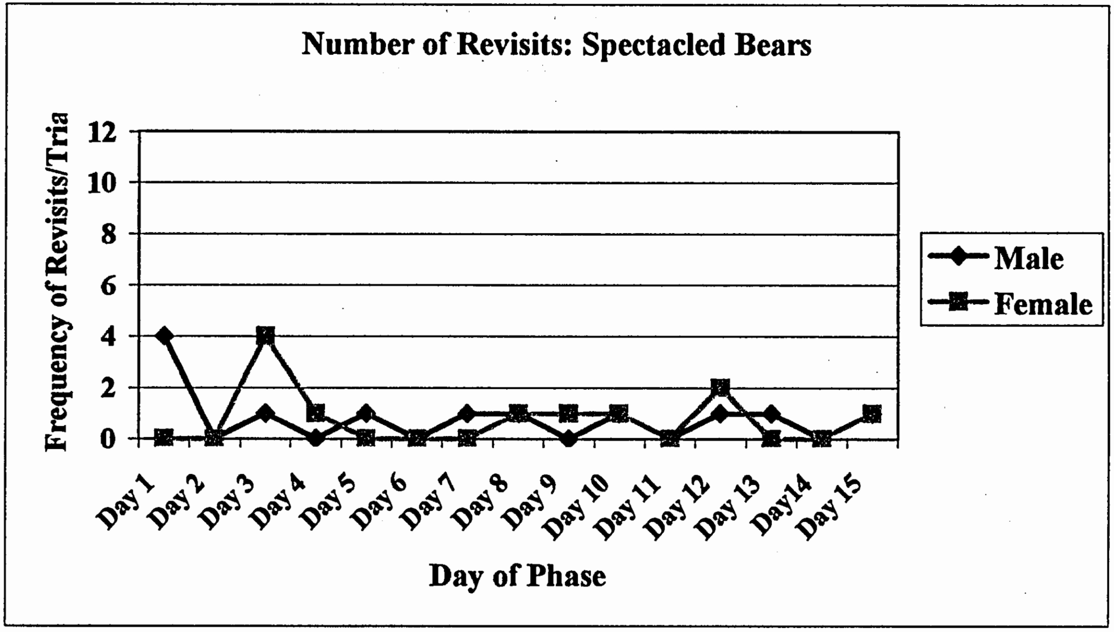

Figure 29 The total number of visits to previously visited feeders in each session by the spectacled bears.

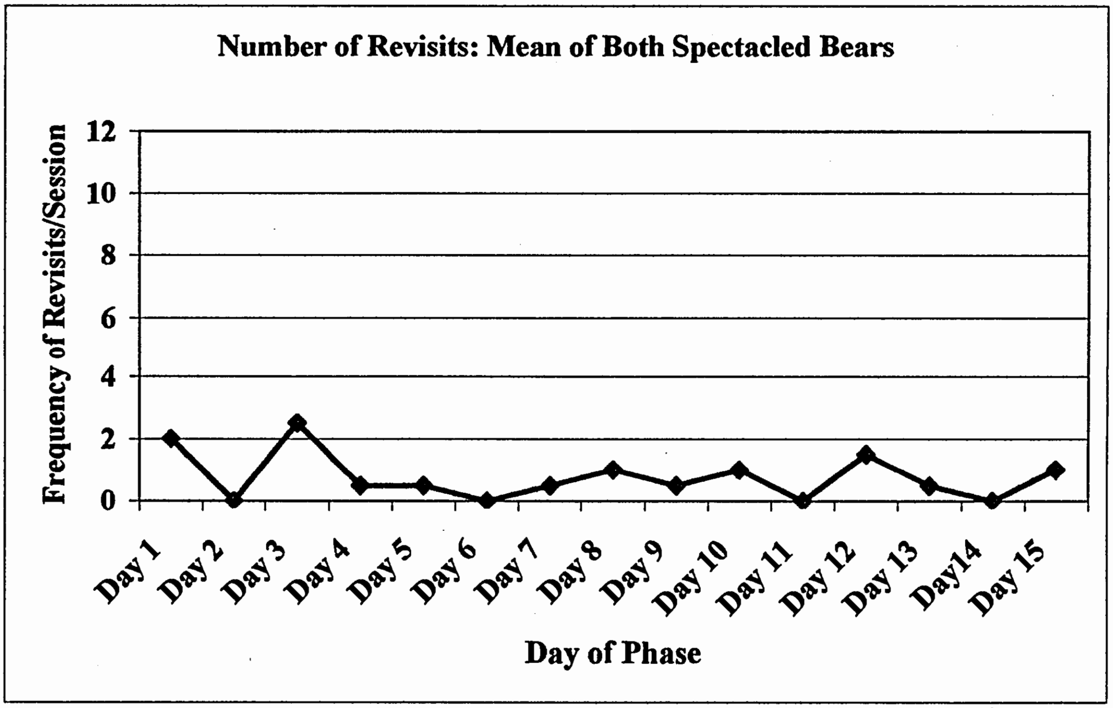

Figure 30 The total number of visits to previously visited feeders in each session by the spectacled bears.

6.1.4 Discussion

The giant pandas and the spectacled bears quickly learned to open the lids of the feeders to obtain food with no training. There was a significant decrease in the length of time it took the giant pandas and spectacled bears to visit all feeders during a trial, suggesting that they became more proficient at the task with experience. The giant pandas developed strong individual preferences for direction of travel between feeders (clockwise or counterclockwise) and the position of the feeder from which to start (feeder in position 1 or feeder in position 8). The spectacled bears did not develop as strong a bias in responding, however, their behavior was still fairly predictable.

Both species of bear used a very efficient least-distance strategy of foraging, even in the first five test sessions, visiting significantly more adjacent feeders between visits in the first five and last five test sessions than would be expected by chance. For the giant pandas, visits to adjacent feeders were more frequent in the last five sessions of the task than they were in the first five sessions. This suggests that their efficiency in travel improved with experience with the testing situation. The spectacled bears were no less efficient in the first five sessions in their method of travel than they were in the first five sessions. Though the spectacled bears visited more adjacent feeders in the first five sessions of Foraging Task 1 than the giant pandas, there were no significant differences between the species in the mean number of visits to adjacent feeders in either the first five sessions or the last five sessions.

It was expected by that the bears would have visited a mean of 5.252 baited feeders in their first eight visits if they had adopted a random foraging pattern. Both the giant pandas and the spectacled bears visited more baited feeders in their first eight visits than would be expected had they been foraging randomly in the first five and last five test sessions. The giant pandas showed evidence of improvement with experience with the test situation. They visited significantly more baited feeders in their first eight visits in the last five test sessions than they did in the first five test sessions. The spectacled bears also showed evidence of improvement in the number of baited feeders visited in their first eight visits, however, the difference between the first five test sessions and last five test sessions was not statistically significant. There were no significant species differences in the number of visits to baited feeders in either the first five or the last five test sessions.

Because the food did not replenish after being depleted, the bears needed to visit only eight feeders to obtain all available food in each trial. Visits to more than eight feeders would be inefficient, and visits to less than eight feeders would indicate that not all of the food had been exploited. The giant pandas, but not the spectacled bears, visited significantly more feeders than the eight necessary in both the first five and last five test sessions. However, there was a significant decrease in the total number of feeders visited by the giant pandas across the test trials. The spectacled bears, on the other hand, did not visit significantly more or less than the eight feeders necessary to obtain all of the food in either the first or last five test sessions. Finally, the spectacled bears revisited previously depleted feeders less often than the giant pandas in both the first five and last five test sessions. However, the difference was statistically significant only for the first five test sessions.

The results of Foraging Task 1 offer only partial support for the hypothesis that there would be differences in learning and errors between the giant pandas and the spectacled bears. Unlike the giant pandas, the spectacled bears did not develop strong individual biases for direction of travel or for the first feeder visited during a trial, suggesting that their responding was more flexible than that of the giant pandas. It might be predicted that a more rigid pattern of responding as performed by the giant pandas would serve to decrease the number of revisits in a trial. For instance, an animal that starts preferentially with one particular feeder and travels in same direction in each trial would be more likely to be able to learn environmental cues that would signal when to stop opening feeders. However, the spectacled bears revisited significantly fewer feeders in the first five test sessions than the giant pandas in this foraging task. The ability to avoid revisiting previously depleted feeders has been referred to as working memory for the task (Honig, 1978). The finding that the spectacled bears revisited significantly fewer previously depleted feeders in the first five test sessions of Foraging Task 1 suggests that they may have initially had better working memory skills than the giant pandas. However, the giant pandas learned with experience to avoid previously depleted feeders as evidenced by improved performance across trials. There was no significant difference between the species in their number of revisits in the last five test sessions. It is difficult to interpret these results. There were large individual differences in the number of revisits made by the giant pandas; therefore, the species difference observed may not necessarily reflect true species differences in learning or working memory for the task. Rather it may reflect the fact that only two spectacled bears were tested in this study.

6.2 Foraging Tasks 2 and 3: Spatial Learning and Reversal Task

6.2.1 Methods

In this foraging task, the bears were tested to determine their ability to use spatial discriminative stimuli alone to locate viable food sites. In the first trial of Foraging Task 2, four of the eight feeders were randomly chosen to be baited with food. Placement of the baited feeders remained constant in each of the remaining trials of the task. One trial was conducted each day for 15 consecutive days or until the subject reached a criterion level of performance. The maximum number of sessions in each experiment was set at 30 days. Criterion for termination of Foraging Tasks 2-5 was met if the subjects reached a performance level of at least 3 correct choices of the first 4 choices per session in at least four of five consecutive sessions. All feeders were thoroughly cleaned between sessions to eliminate any olfactory discriminative stimuli that could be left by the bears on the feeders during foraging. Of interest in this task was the ability of the bears to learn to visit the baited or correct feeders and ignore unbaited feeders. This task is often described as a win-stay foraging task. In this type of task, efficient foraging requires the animal to learn to visit only those sites which were baited in the preceding trial. This strategy is appropriate when prey or food is either clumped in nature such that one item is associated with other items in that particular location or when it replenishes quickly after exploitation (Olton, Handelmann, & Walker, 1981).

The purpose of the reversal task was to rule out the use of visual or olfactory discriminative stimuli to locate food in the previous task. The four feeders that were empty across trials in Foraging Task 2 were baited in Foraging Task 3. If the bears travel directly to sites that were baited in the spatial task, it can be assumed that they were not using visual or olfactory discriminative stimuli to locate food. However, if the first few choices of the bears are to baited sites then it cannot be concluded that they were using spatial memory alone to locate food. The spatial location of all baited feeders remained constant for the remaining trials in the foraging task. One session was conducted each day for 15 days or until the performance criterion was met. All feeders were cleaned between sessions to minimize or eliminate any olfactory discriminative stimuli that could be left on the feeders by the bears during foraging.

6.2.2 Data Analysis

In Foraging Tasks 2 and 3, the dependent variable was the number of visits to baited feeders of the first four visits. In the spatial task, feeders 1, 4, 5 and 7 were baited with food. A randomly traveling forager would be expected to visit a mean of 1.655 baited feeders in the first four choices across trials, assuming that each site is equally likely to be chosen. The mean number of visits to baited feeders of first four visits in each block was compared to that expected by chance using one-sample t tests for the panda data and one-sample Komolgorov-Smirnov tests for the spectacled bear data. The mean number of visits to baited feeders in the first four visits was calculated for the first five trials and last five trials of the foraging tasks. To determine if one species learned a task more quickly than another, the number of trials required to reach criterion were compared between species using a Mann-Whitney U test.

6.2.3 Results

Figures 31-33 present the mean number of visits to baited feeders (correct visits) of the first four visits in the first and last five sessions of the spatial and reversal tasks by the giant pandas at each of the three institutions. Figure 34 presents the mean of all giant pandas. As can be seen, even in the first five sessions of the spatial memory task the giant pandas performed significantly better than would be expected if foraging randomly, visiting a mean of 2.03 baited feeders in their first four visits [t(6) = 4.62, p = 0.004]. However, as observed in the exploratory task, the giant pandas were not traveling randomly. Rather, they were using an adjacency strategy, traveling either clockwise from the feeder in position 1 or counterclockwise from the feeder in position 8 and visiting adjacent feeders. Based on this pattern of foraging, it would be expected that the giant pandas would visit 2 correct feeders of their first 4 visits. For example, if a panda started at the feeder in position 1 and traveled clockwise to feeders 2, 3 and 4, he or she would make two visits to baited feeders (feeders 1 and 4) and two visits to empty feeders (feeders 2 and 3) in the first four visits. A one-sample t test showed that the giant pandas did not make significantly more correct choices than the expected 2 in the first block of 5 trials (X = 2.03) [t(6) = 0.35, p = 0.74].

Figure 35 presents the mean number of visits to baited feeders (correct visits) of the first four visits in the first and last five sessions of the spatial and reversal tasks by the spectacled bears. Unlike the giant pandas, the number of baited feeders visited in their first 4 visits in the first 5 sessions of the spatial task was not different from that expected by a random forager (X = 2.3) [D_{max} = 0.71, p = 0.17]. Their pattern of movement between feeders was similar to that observed in the exploratory task. Based on this pattern of foraging, it would be expected that the spectacled bears would visit 2 correct feeders in their first 4 visits. A one-sample Komolgorov-Smirnov test showed that the spectacled bears did not make significantly more correct choices than the expected 2 in the first block of 5 trials [D_{max} = 0.58, p = 0.35].

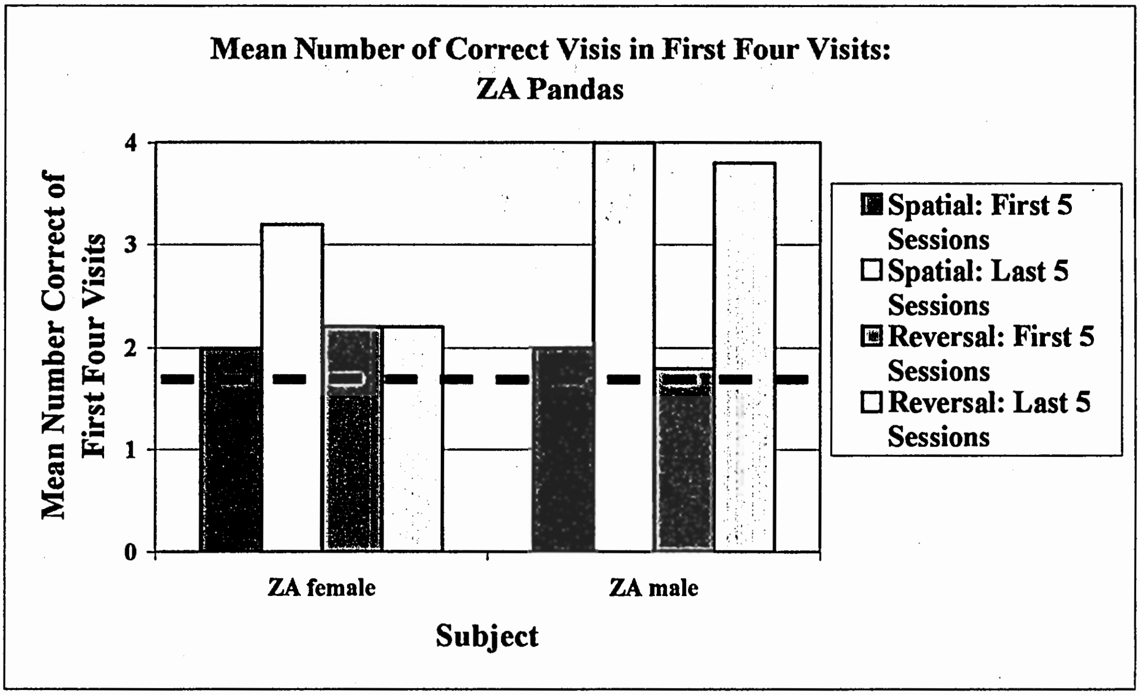

Figure 31 Mean number of visits to baited feeders (correct visits) of the first four visits in the first and last five sessions of the spatial and reversal tasks by the Zoo Atlanta pandas. The dashed line represents chance performance.

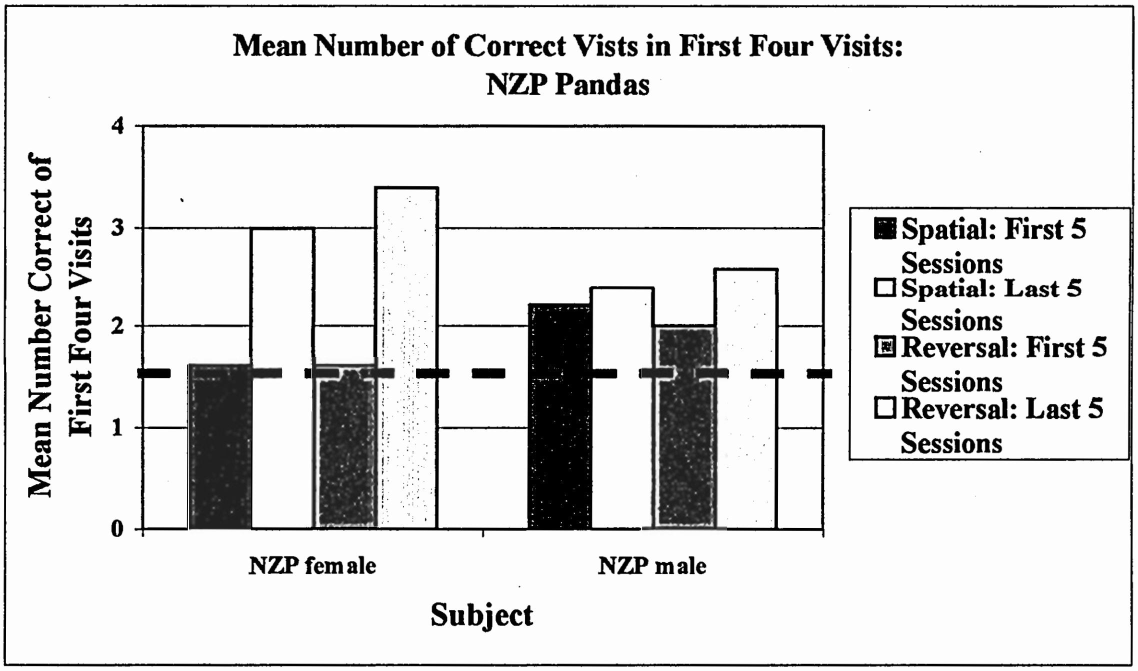

Figure 32 Mean number of visits to baited feeders (correct feeders) of the first four visits in the first five and last five sessions of the spatial and reversal tasks by the National Zoological Park pandas. The dashed line represents chance performance.

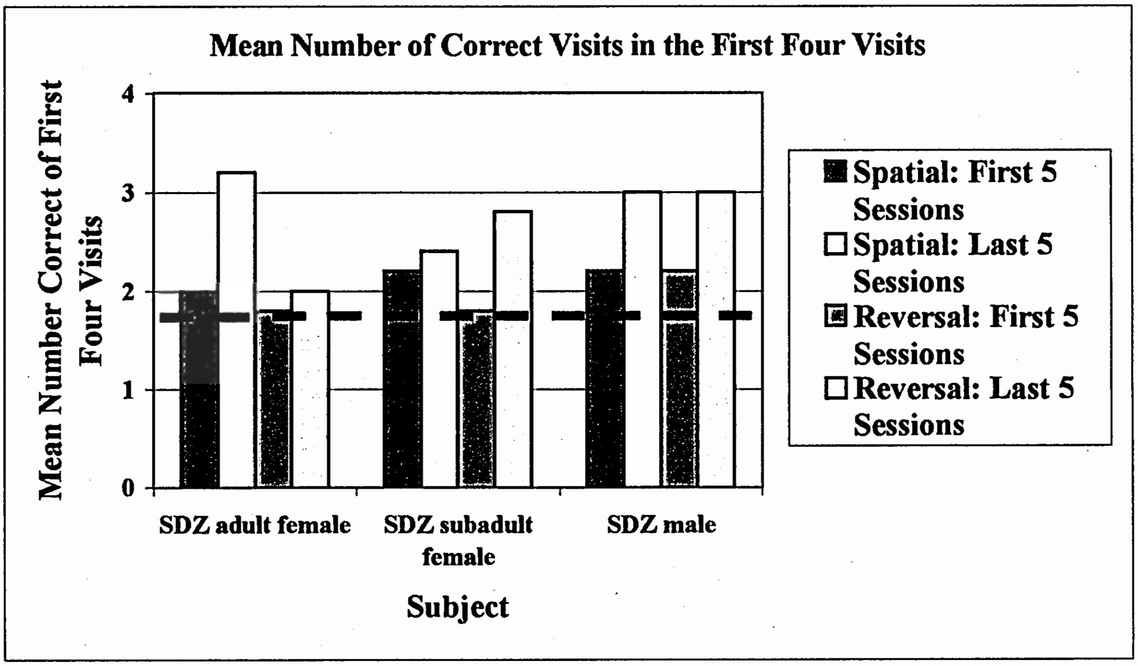

Figure 33 Mean number of visits to baited feeders (correct feeders) of the first four visits in the first and last five sessions of the spatial and reversal tasks by the San Diego Zoo pandas. The dashed line represents chance performance.

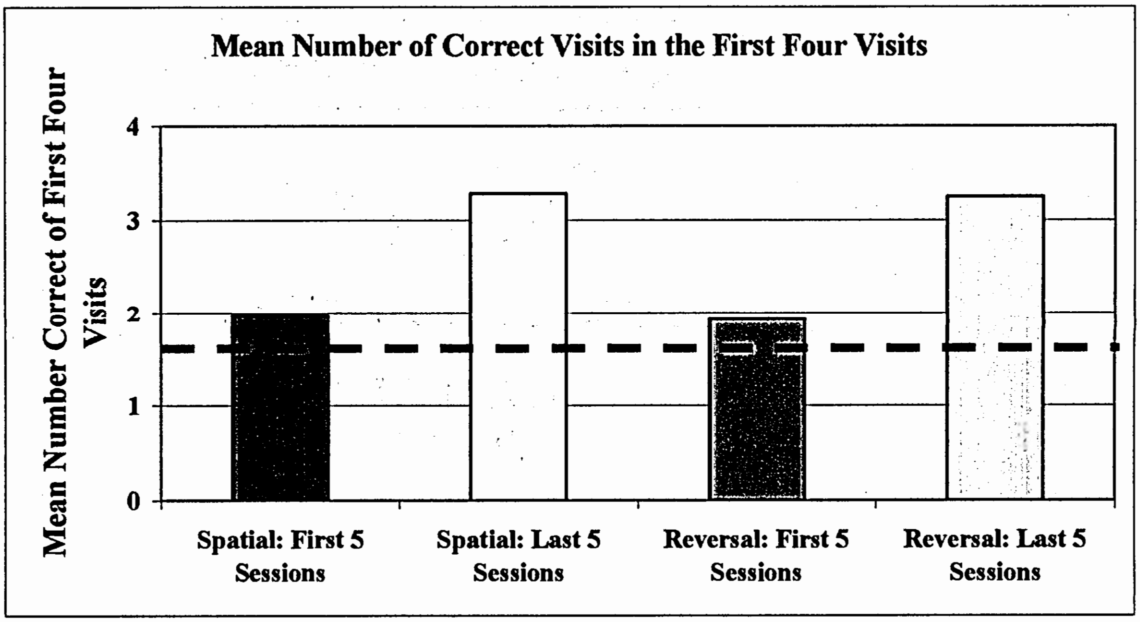

Figure 34 Mean number of visits to baited feeders (correct feeders) of the first four visits in the first and last five sessions of the spatial and reversal tasks by all pandas. The dashed line represents chance performance.

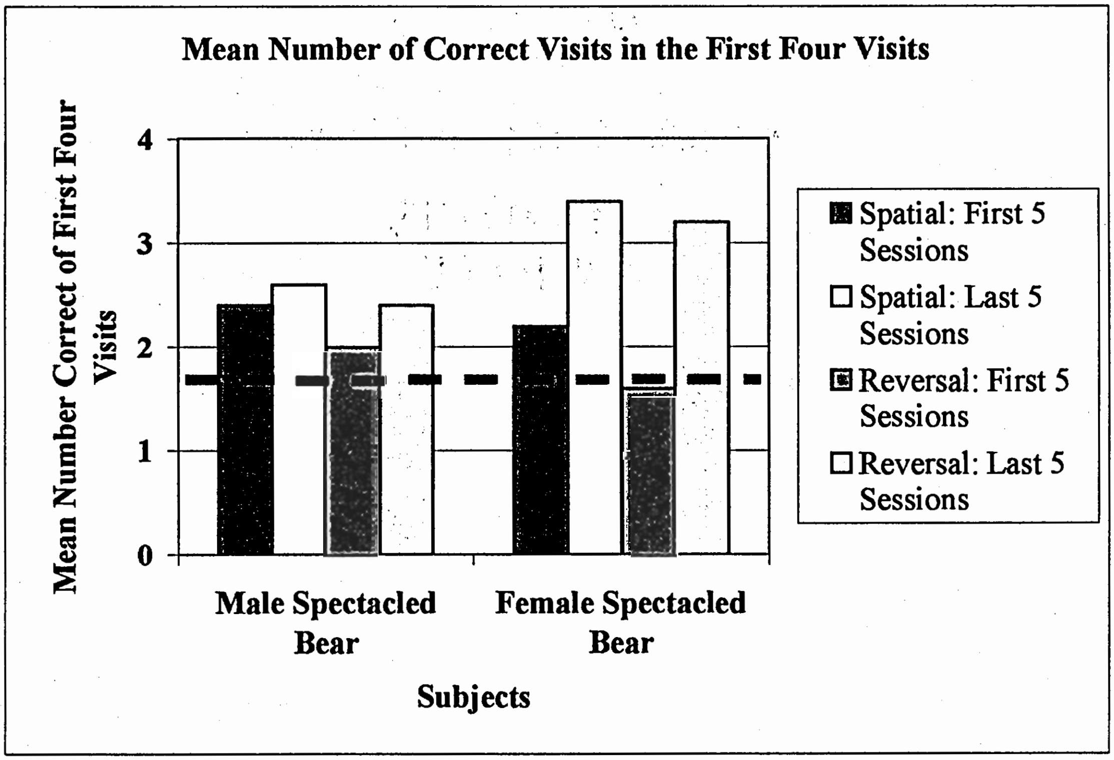

Figure 35 Mean number of visits to baited feeders (correct feeders) of the first four visits in the first and last five sessions of the spatial and reversal tasks by the spectacled bears. The dashed line represents chance performance.

Table 2 provides the number of trials each of the bears required to meet criterion performance in both the spatial and reversal tasks. As can be seen, five of the seven giant pandas and one of the spectacled bears reached criterion performance (3 or more visits to baited feeders of the first four visits in at least four of five consecutive trials) within 30 trials of the spatial task. Both ZA giant pandas reached criterion performance, making 3 or more correct choices of their first four choices in five consecutive trials, before the first 15 sessions had been completed. The male reached criterion performance in 11 trials, visiting a mean of 3.8 correct feeders in his first four choices in trials 6-10. The female reached criterion performance in 13 trials, visiting a mean of 3.2 correct feeders in her first four choices in trials 9-13. Trials for these two giant pandas were terminated after 15 sessions. Of the two NZP giant pandas, only the NZP female reached criterion performance within 30 trials, visiting a mean of 3.0 feeders in her first four choices in trials 14-18. The male did not reach criterion performance within the 30 trials, visiting a mean of 2.4 feeders in his first 4 visits in trials 26-30. Two of the three SDZ giant pandas reached criterion performance within 30 trials. The adult female reached criterion performance in 30 trials, visiting a mean of 3.2 baited feeders in her first 4 visits in trials 26-30. The adult male reached criterion performance in 24 trials, visiting a mean of 3.0 feeders in his first 4 visits in trials 20-24. The subadult female, did not show evidence of learning the task, however, data collection was terminated after only 21 trials for reasons that are unclear.

The female spectacled bear reached criterion performance within the 30 trials. As can be seen in Figure 35, the female spectacled bear visited a mean of 3.4 baited feeders in her first 4 visits in trials 8-13 of the spatial task. The male spectacled bear never showed evidence of having learned the task, visiting a mean of 2.6 baited feeders in his first 4 visits in trials 26-30. Unfortunately, because the male spectacled bear never reached criterion the behavior of the female spectacled bear could not be analyzed statistically. Her behavior, though, is similar to that of the giant pandas that reached criterion. Her average of 3.4 visits to baited feeders in the first 4 visits was more than the average of the giant pandas that reached criterion. Therefore, her behavior is presumably different from that which would be expected by either a randomly foraging animal or one using a least-distance strategy.

Table 2 Number of trials required by each panda to reach criterion performance in both the spatial and reversal tasks. *The SDZ male was run for 4 trials beyond the 30 maximum because of poor performance in 4 of the previous trials.

		Number of Trials to Reach Criterion	
Subject	Species	Spatial	Reversal
ZA Female	Panda	13	Did Not Reach
ZA Male	Panda	10	22
NZP Female	Panda	18	28
NZP Male	Panda	Did Not Reach	Did Not Reach
SDZ Adult Female	Panda	30	Did Not Reach
SDZ Subadult Female	Panda	Did Not Reach	30
SDZ Male	Panda	24	34*
NZP Female	Spectacled Bear	13	12
NZP Male	Spectacled Bear	Did Not Reach	Did Not Reach

Those giant pandas that reached criterion performance within 30 trials visited a mean of 3.28 baited feeders in their first 4 visits during the last five trials of the spatial task. This was significantly more than the 1.655 feeders expected had they been foraging randomly [$D_{max} = 0.911$, $p < 0.001$], and was also significantly more than the 2 expected had they been using an adjacency pattern of foraging [$D_{max} = 0.84$, $p < 0.001$]. As can be seen in Figure 31, the ZA male visited 4 baited feeders in each of his first four visits in each of the last 5 sessions of the spatial task. This level of performance was not matched by any of the other giant pandas.

It is possible that the five giant pandas and female spectacled bear were using either olfactory or visual discriminative stimuli, rather than spatial discriminative stimuli alone to locate feeders baited with food. Therefore, a reversal was conducted after criterion performance had been reached such that feeders 2, 3, 6 and 8 were baited instead of feeders 1, 4, 5, and 7. As can be seen in Figures 31-33, the reversal disrupted performance for those bears that reached criterion performance in the spatial task. A Wilcoxon Signed-Rank test indicated that the mean number of correct visits of the first 4 visits by the giant pandas decreased significantly from 3.28 in the last 5 trials of the spatial task to 1.92 in the first five trials of the reversal task ($X = 1.92$) [$Z = -2.02$, $p = 0.04$]. Their performance in the first five trials of the reversal task was not significantly different than their performance in the first five trials of the spatial task ($X = 1.96$) [$Z = -0.58$, $p = 0.56$]. In the first 5 sessions of the reversal task, the giant pandas who reached criterion performance did not visit more baited feeders than would be expected had they been foraging randomly [$D_{max} = 0.48$, $p = 0.14$] or than would be expected had they been using an adjacency strategy [$D_{max} = 0.42$, $p = 0.26$]. Similarly, the number of baited feeders visited by the female spectacled bear decreased from 3.4 feeders in the last five trials of the spatial task to 1.6 feeders in the first five trials of the reversal task. Statistical analyses could not be conducted to determine if this decrease was significant, however, her decrease in performance was more pronounced than that observed in the giant pandas. The mean number of baited feeders visited in the first 4 visits of the first 5 trials of the reversal task was also less than that observed in the first 5 trials of the spatial task ($X = 2.2$), suggesting a disruption in the traveling pattern used in the first 5 trials of the spatial task.

Four of the seven giant pandas and one of the spectacled bears reached criterion performance within 30 trials of the reversal phase (see Table 2). The ZA male, who reached criterion performance within 10 trials of spatial task, reached criterion performance in the reversal task in 22 trials. The NZP female reached criterion performance in 28 trials, as compared with 18 trials in the spatial task. The SDZ subadult female who did not reach criterion performance in the spatial task, reached criterion performance in the reversal task in 30 trials. And the SDZ male, who reached criterion performance in the spatial task in 24 trials, reached criterion performance in the reversal task in 34 trials. He was allowed to complete 4 extra trials in the task because of disinterest in the task in other sessions. For these four giant pandas, one-sample Komolgorov-Smirnov tests indicated that the mean number of visits to baited feeders in the first four visits in their last 5 trials of the reversal task ($X = 3.25$) was significantly greater than would be expected had they been foraging randomly ($X = 1.655$) [$D_{max} = 0.87$, $p = 0.001$] and that expected using an adjacency foraging strategy ($X = 2$) [$D_{max} = 0.79$, $p = 0.004$]. For all of the giant pandas that reached criterion both in the spatial task and reversal task, learning of the reversal task took more trials (X = 17.3) than learning of the spatial task (X = 28).

The female spectacled bear reached criterion performance in the reversal task within 12 days. This was similar to the 13 trials it took her to reach criterion performance in the spatial task. In the last five trials of the reversal task, the female spectacled bear visited a mean of 3.2 baited feeders in her first 4 visits. Because the sample size is limited, it is not possible to statistically determine if the mean number of visits to baited feeders in the last 5 trials of the reversal task differed from that of either the first 5 trials of the reversal task or last five trials of the spatial task. However, the means of the last five trials of the reversal task (X = 3.2) is similar to that observed in the last five trials of the spatial task (X = 3.4), and greater than that observed in the first 5 trials of the reversal task (X = 1.6). The male spectacled bear never reached criterion performance, visiting a mean of 2.4 baited feeders in his first 4 visits in the last 5 sessions of the reversal task. Effects of order of testing could not be statistically analyzed because only 5 of the seven giant pandas showed evidence of learning, leaving one of the institutions (NZP) with only one subject.

In each trial of the spatial task, the giant pandas only needed to visit 4 feeders to obtain all of the hidden food. Figures 36-42 present the number of visits to baited feeders in the first four visits and the total number of feeders visited by each of the giant pandas in each session of the spatial and reversal tasks. At the beginning of the study, the giant pandas were visiting all eight of the feeders to find food. In the first block of 5 trials, they visited a mean of 8.23 feeders in each trial. A one-sample t test indicated that this was significantly more than the 4 visits necessary to deplete the feeders [t(6) = 11.01, p <

0.001], but not significantly more than eight feeders [t(6) = 0.60, p = 0.57]. As the giant pandas gained more experience with the task, they began visiting fewer feeders in each session. As can be seen in Figure 36, it can be seen that the ZA male visited four baited feeders in the last 5 sessions of the spatial task and only those four feeders. He did not check any of the other feeders. This level of performance was not matched by any of the other giant pandas. In the last five trials of the spatial task, most of the giant pandas were still visiting more feeders (X = 5.77) than the 4 necessary to obtain all of the food [t(6) = 3.76, p = 0.01]. However, this was significantly less than would be expected if they had simply been visiting all 8 feeders [t(6) = -4.73, p = 0.003]. Those giant pandas that reached criterion performance within 30 trials of the spatial task did not visit significantly more feeders in the last five trials of the spatial task than the 4 necessary to deplete all of the feeders (X = 5.32) [t(5) = 2.47, p = 0.07]. They learned across trials to predominantly visit only those feeders that were baited in a session.

The male and female spectacled bear visited a mean of 3.6 and 5.8 feeders in the first five trials of the spatial task respectively. The mean of the two giant pandas was not significantly less than the four feeders necessary to obtain all of the food (X = 4.7) [D_{max} = 0.46, p < 0.001]. It was significantly fewer than would be expected had they been traveling to all 8 feeders [D_{max} = 0.99, p = 0.63]. This resulted not from the fact that the spectacled bears showed evidence of knowing where the food was in the first five trials, but because the male spectacled bear visited only 1, 2, and 3 feeders in the first 3 trials of the spatial task. His responding improved in the last five trials of the spatial task to a mean of 5.8 feeders visited. The female, however, visited fewer feeders (X = 3.7). Statistical tests could not be conducted on the last 5 trials of the spatial task because the male spectacled bear showed no evidence of learning either the spatial or reversal task.

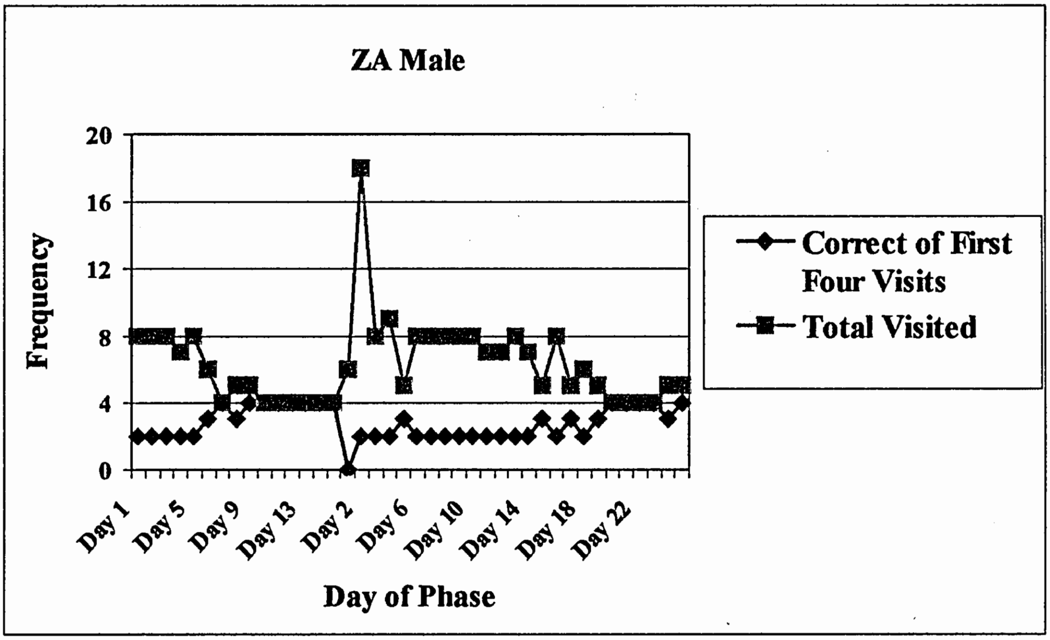

Figure 36 Number of visits to baited feeders in the first four visits and total number of feeders visited by the male Zoo Atlanta panda in each session of the spatial and reversal tasks.

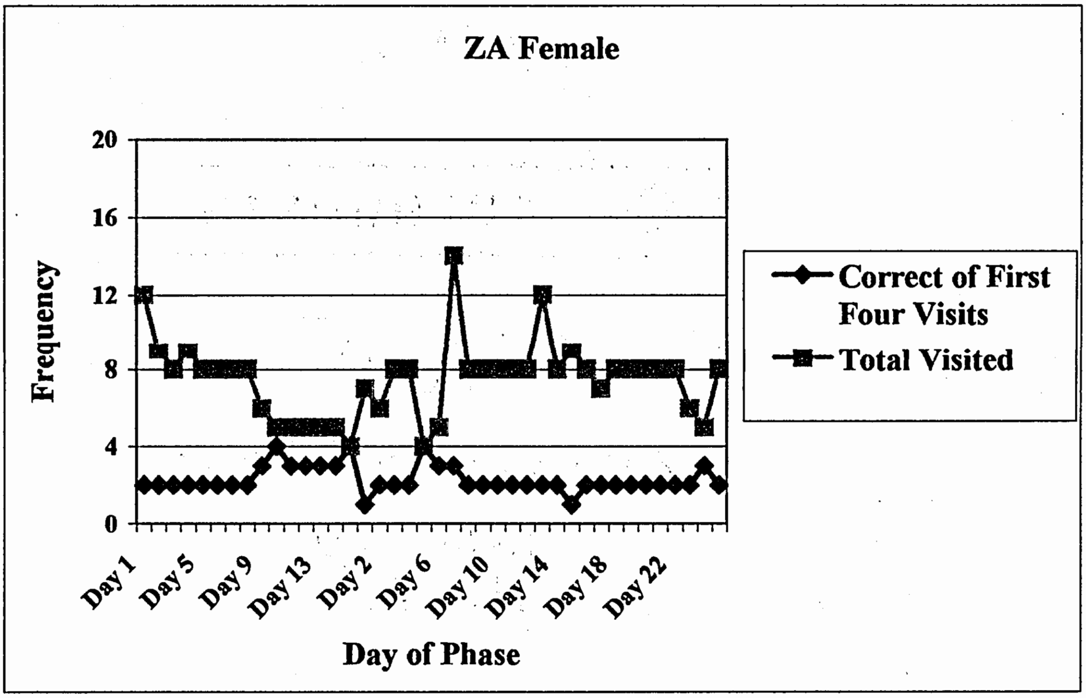

Figure 37 Number of visits to baited feeders in the first four visits and total number of feeders visited by the female Zoo Atlanta panda in each session of the spatial and reversal tasks.

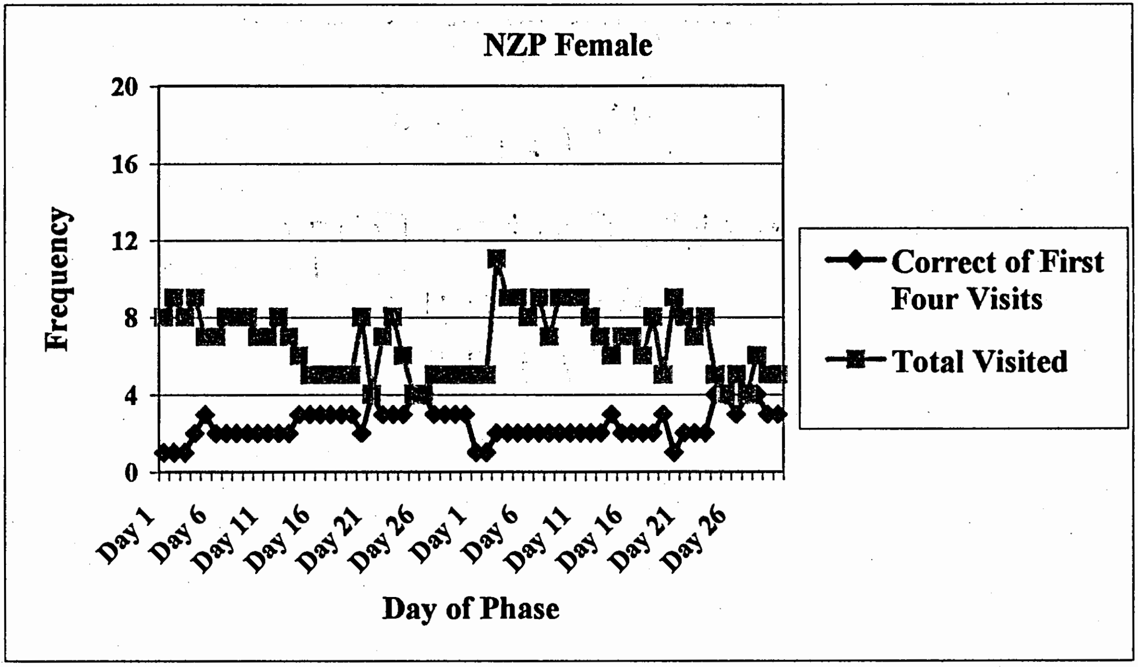

Figure 38 Number of visits to baited feeders in the first four visits and total number of feeders visited by the female National Zoological Park panda in each session of the spatial and reversal tasks.

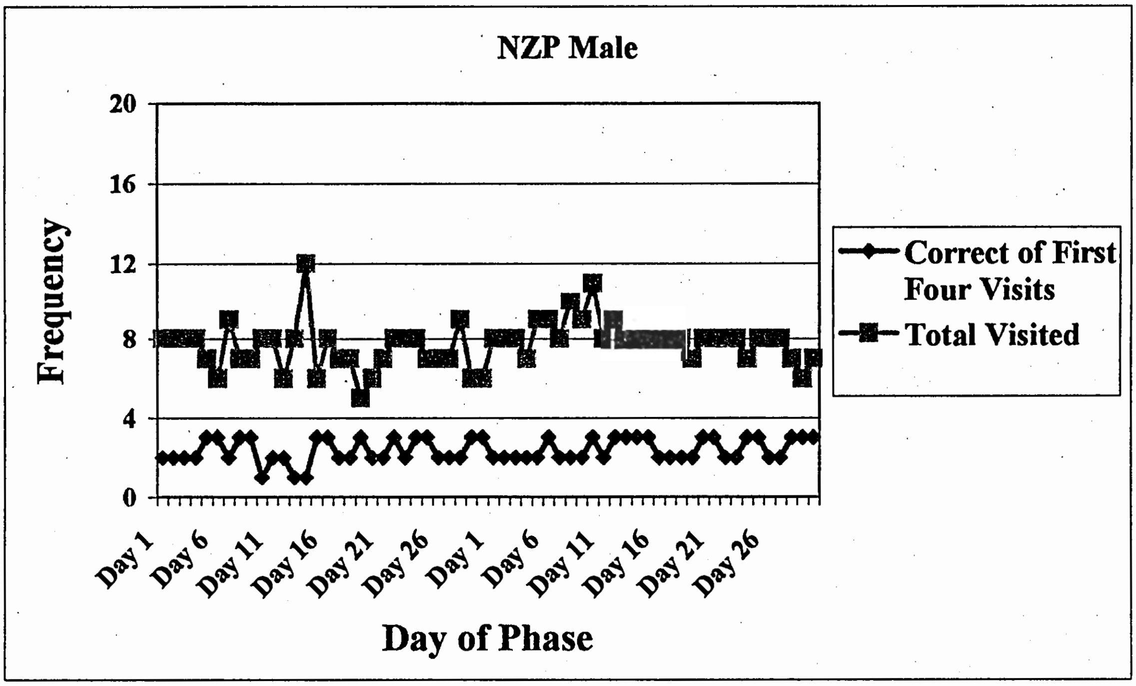

Figure 39 Number of visits to baited feeders in the first four visits and total number of feeders visited by the male National Zoological Park panda in each session of the spatial and reversal tasks.

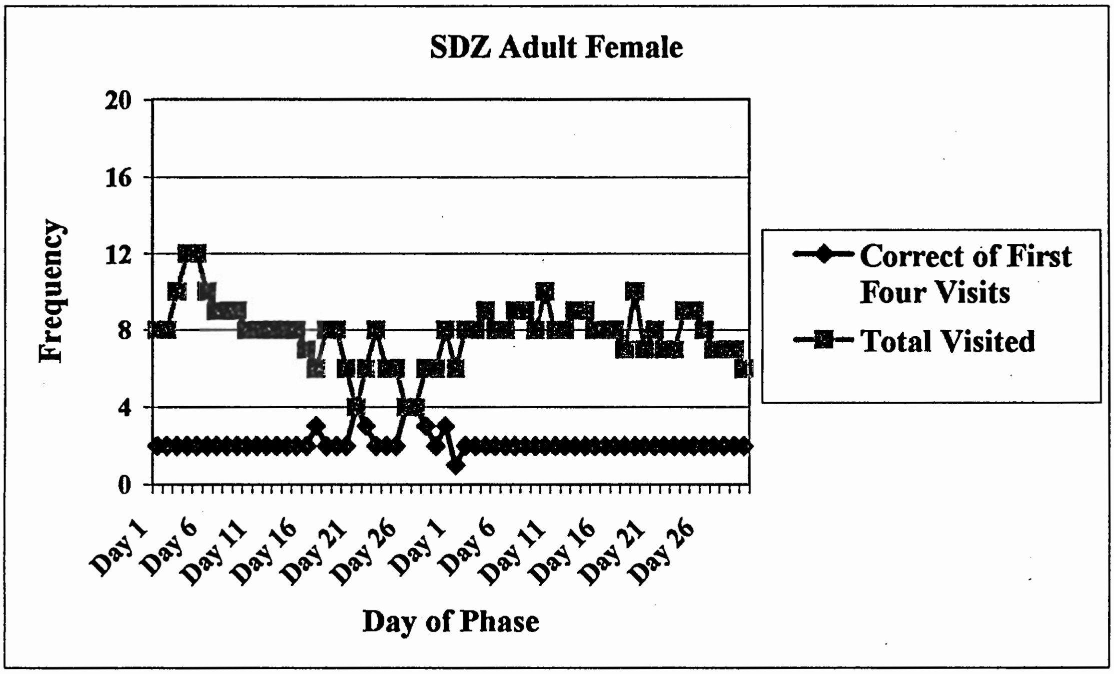

Figure 40 Number of visits to baited feeders in the first four visits and total number of feeders visited by the adult female panda at the San Diego Zoo in each session of the spatial and reversal tasks.

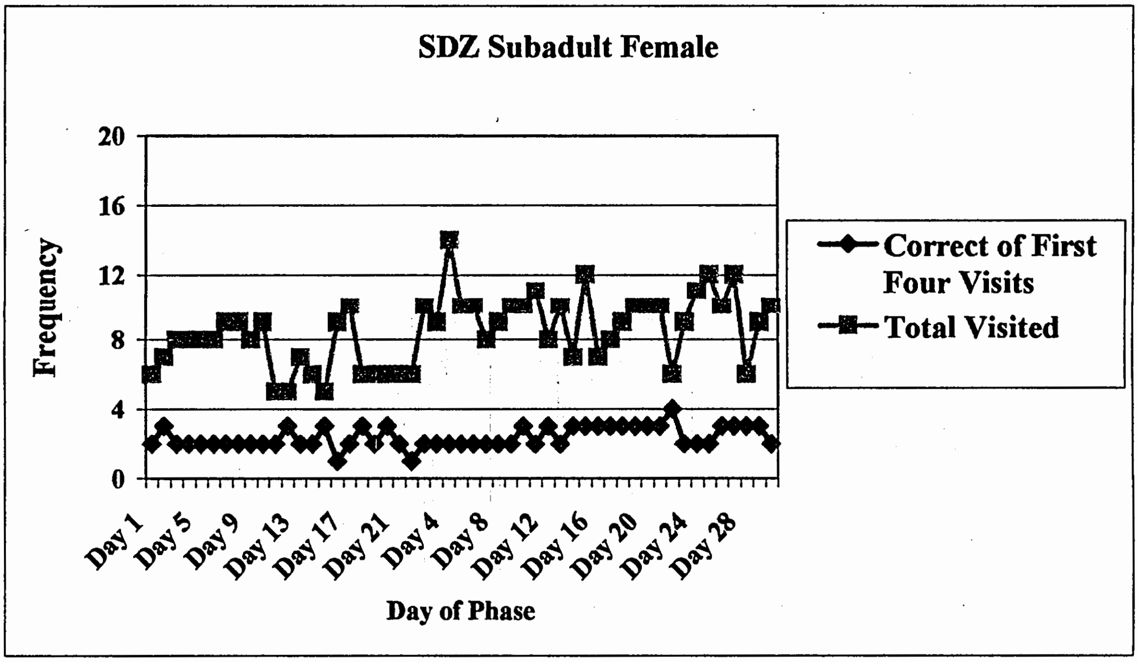

Figure 41 Number of visits to baited feeders in the first four visits and total number of feeders visited by the subadult female panda at the San Diego Zoo in each session of the spatial and reversal tasks.

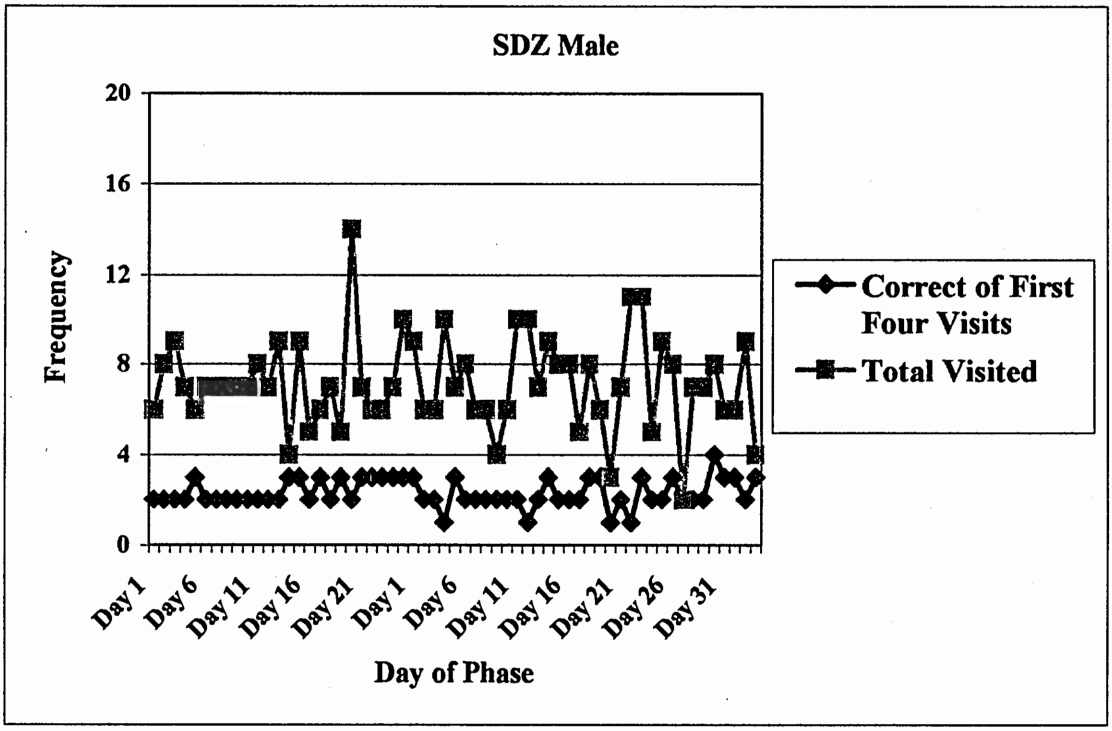

Figure 42 Number of visits to baited feeders in the first four visits and total number of feeders visited by the male panda at the San Diego Zoo in each session of the spatial and reversal tasks.

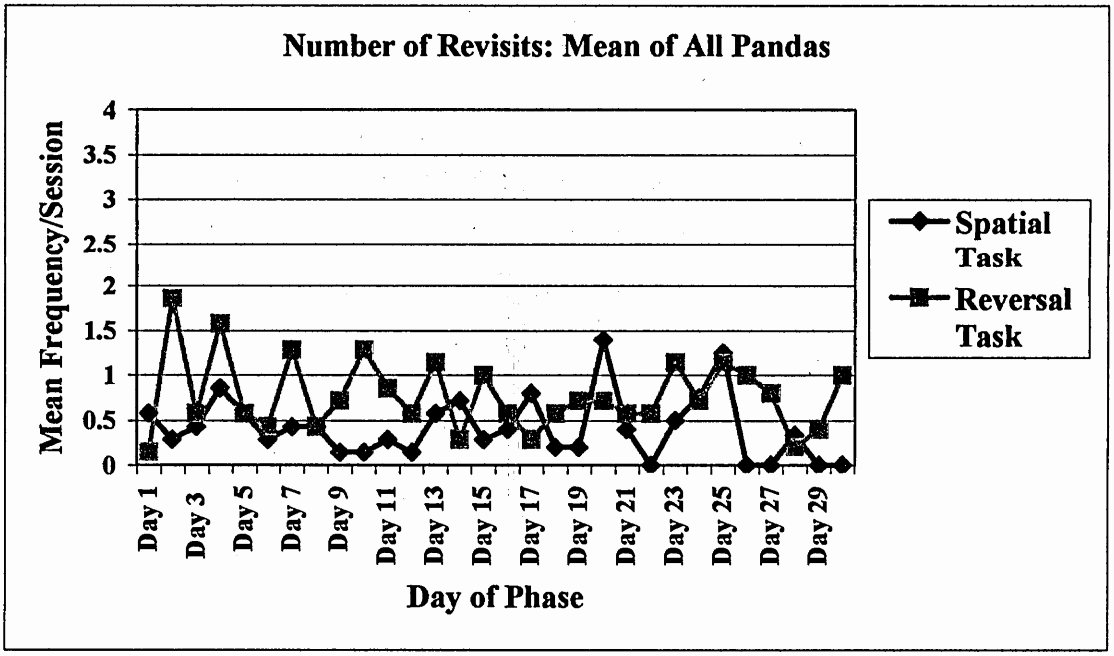

Figure 43 Mean number of revisits in the spatial task and reversal tasks by all pandas.

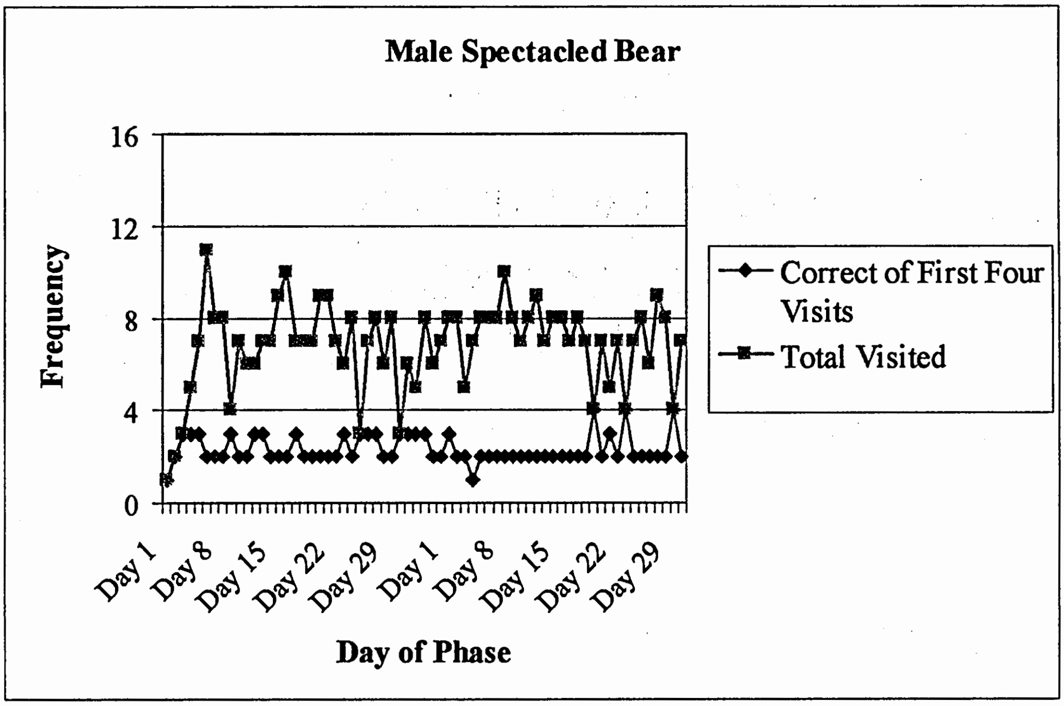

Figure 44 Number of visits to baited feeders in the first four visits and total number of feeders visited by the adult male spectacled bear at the National Zoo in each session of the spatial and reversal tasks.

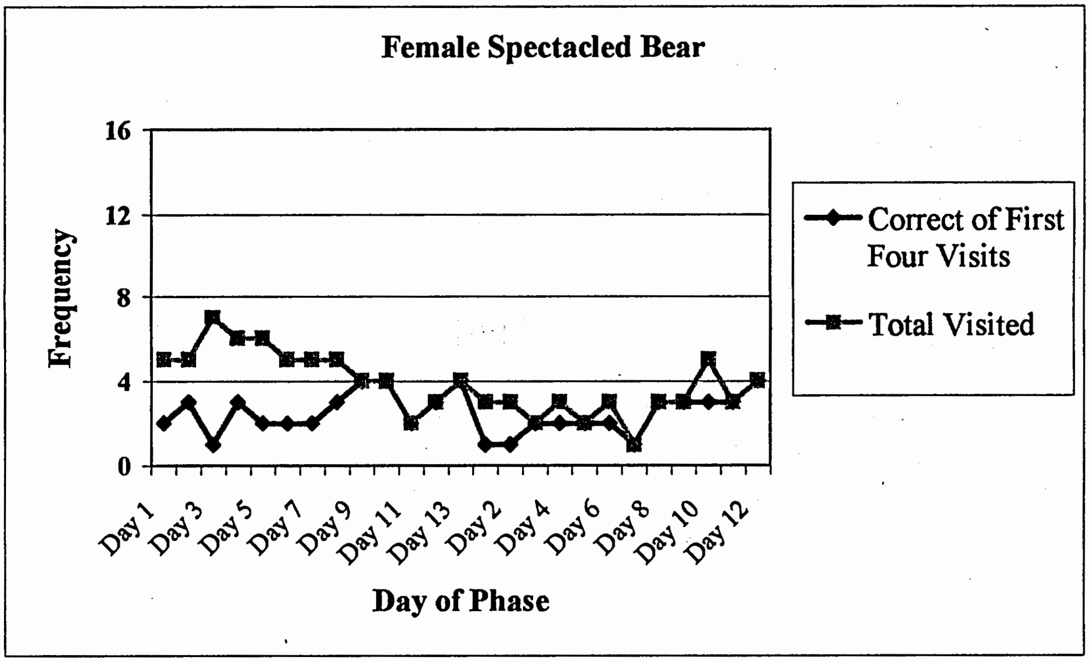

Figure 45 Number of visits to baited feeders in the first four visits and total number of feeders visited by the female spectacled bear at the National Zoo in each session of the spatial and reversal tasks.

As was the case for the spatial task, the giant pandas only needed to visit 4 feeders in each trial to obtain all of the hidden food in the reversal task. In the first 5 sessions, the giant pandas visited significantly more feeders ($X = 8.11$) than the four necessary to deplete all feeders [$t(6) = 8.11$, $p < 0.001$]. They did not visit significantly more than 8 feeders [$t(6) = 0.28$, $p = 0.79$], indicating that they were traveling directly to all eight feeders looking for food. In the last 5 trials of the session, the giant pandas were still visiting more feeders than necessary ($X = 6.63$) to obtain all of the food, and their behavior was not significantly different from that of a panda traveling to all eight feeders in a trial [$t(6) = -2.23$, $p = 0.07$]. In the first five trials of the reversal task, the mean number of visits increased to 7.8 for those whose performance reached criterion, which was significantly greater than 4 [$t(6) = 7.8$, $p = 0.001$] but not significantly greater than a visit to all 8 feeders [$t(6) = -0.48$, $p = 0.66$]. However, for those giant pandas who reached criterion performance within the 30 trials of the reversal task, one-sample Komolgorov-Smirnov tests indicated that they were visiting significantly more feeders in the last five trials of the reversal task than the 4 necessary to obtain food ($X = 6.33$) [$D_{max} = 0.66$, $p = 0.03$], but less than the 8 eight feeders they would visit were they simply traveling to all feeders [$D_{max} = 0.70$, $p = 0.02$].

In the reversal task the male spectacled bear visited a mean of 7.2 feeders in the first 5 trials and 6.8 feeders in the last 5 trials. The female spectacled bear visited a mean of only 2.6 baited feeders in the first 5 trials of the reversal task, indicating again that performance was disrupted by the reversal. The mean number of visits in the first 5 trials of the reversal task was not significantly different than either 4 visits [$D_{max} = 0.50$, $p = 0.50$] or 8 visits [$D_{max} = 0.79$, $p = 0.09$]. In the last 5 trials of the reversal task she visited a mean of 3.2 feeders. Statistical tests could not be conducted on the last 5 trials of the reversal task because the male spectacled bear showed no evidence of learning either the spatial or reversal task.

Overall, the giant pandas revisited (returned to previously visited feeders) very few feeders per session of both the spatial and reversal tasks. Figure 43 presents the overall mean number of revisits in the spatial and reversal tasks across all giant pandas, and Table 3 presents the mean number of revisits in the first five and last five sessions of the spatial and reversal task for each of the individual giant pandas and spectacled bears. In the spatial task, the total number of revisits across sessions of the spatial task ranged widely across the giant pandas. For example, the ZA male did not revisit any feeders during the spatial task, whereas the SDZ subadult female revisited 23 feeders. Moreover, the NZP male revisited 9 feeders during the entire course of the reversal task, whereas the SDZ subadult female revisited 76 feeders. There was no significant difference between the mean number of feeders revisited in the first five sessions (X = 2.71) and last five sessions (X = 2.14) of the spatial task [t(6) = 0.28, p = 0.79]. The increase in the number of revisits from the last five sessions of the spatial task and the first five sessions of the reversal task (X = 4.71) was not significant [t(6) = -1.43, p = 0.20]. Finally, there was no significant difference between the mean number of feeders revisited in the first five sessions and last five sessions (X = 2.71) of the reversal [t(6) = 1.14, p = 0.30].

The spectacled bears revisited fewer feeders overall than the giant pandas in the spatial and reversal tasks. However, they did not perform better than the best panda in either the first and last 5 trials of the spatial task or the first and last 5 trials of the reversal.

Table 3. Mean number of revisits in the first five and last five sessions of the spatial and reversal task for each of the bears.

		Spatial		Reversal	
Subject	Species	First 5 Sessions	Last 5 Sessions	First 5 Sessions	Last 5 Sessions
ZA Female	Panda	6	0	0	0
ZA Male	Panda	0	0	11	0
NZP Female	Panda	2	1	5	0
NZP Male	Panda	0	1	1	0
SDZ Adult Female	Panda	10	1	1	0
SDZ Subadult Female	Panda	1	5	11	14
SDZ Male	Panda	1	7	4	5
NZP Female	Spectacled Bear	1	0	0	0
NZP Male	Spectacled Bear	1	1	1	1

6.2.4 Discussion

In Foraging Tasks 2 and 3, there were no local cues associated directly with the food source that could be used as beacons. To forage efficiently, the bears were required to learn the relationship between global cues in the environment and the location of baited feeders. Four of the eight feeders were baited with food. It would be expected that a randomly traveling forager would visit a mean of 1.655 baited feeders in their first four visits to feeders. In the first five test sessions of the spatial task, all seven giant pandas and both spectacled bears visited significantly more baited feeders in their first four visits than would be expected by chance. However, because of the biases in direction and feeder from which to start traveling the bears were using a least-distance foraging strategy rather than a random foraging strategy. After correcting for this least-distance strategy, there was no significant difference between the number of baited feeders expected to be visited in the first four visits and the number observed.

Five of the seven giant pandas and one of the spectacled bears showed evidence of being capable of using global spatial cues alone to locate food. Each of these bears learned to travel directly to the four baited feeders in their first four visits within 30 trials. There were large individual differences in the number of trials needed by each bear to reach criterion. Those bears that did reach criterion performance visited significantly more baited feeders in their first four visits in the last five test sessions than would be expected had they been either traveling randomly or using a least-distance strategy. Memory for the location of food between trials is often referred to as reference memory or long term memory (Honig, 1978). However, it was possible that the bears were using some other means of localizing baited feeders.

For those giant pandas and spectacled bear that learned to travel directly to the positions of the four feeders that had been baited with food during a trial, a change in the stimulus, specifically the location of the baited feeders, resulted in a change in behavior. This indicated that these giant pandas had learned spatial location of the baited feeders on the basis of global cues in the environment. On the first day of the reversal task the bears that had learned the spatial task continued to visit feeders that had been baited in the previous task. The number of baited feeders visited in the first five test sessions of the reversal task was not significantly different from that observed in the first five test sessions of the spatial task. The bears were visiting more baited feeders in their first four visits than would be expected had they been foraging randomly. Using a least-distance strategy allowed them to still exploit more baited food sites than a random forager. Four of the seven giant pandas and one of the spectacled bears reached criterion performance in the reversal task within 30 test sessions. They visited significantly more baited feeders in their first four visits in the last five test sessions of the reversal task than would be expected had they been traveling randomly or using a least-distance foraging strategy.

The giant pandas and spectacled bears visited all eight feeders in the first five test sessions of the spatial and reversal tasks to determine the availability of food. This is referred to as sampling in the optimal foraging literature (Stephens & Krebs, 1986). Those that learned to travel to directly to the baited feeders in the spatial and reversal task visited significantly less than all eight feeders. In fact, they did not visit significantly more feeders than the four necessary to obtain all of the food. This indicates that, rather than visit the four baited feeders first in a test session and then check the empty feeders to determine if they had been baited, the bears that showed evidence of learning the spatial task stopped opening feeders after the last baited feeder had been exploited.

In the spatial task, the giant pandas and spectacled bears made relatively few visits to previously depleted feeders, particularly in the last five sessions. There were large individual differences between the giant pandas in the number of revisits in the spatial and reversal task. The spectacled bears visited fewer feeders than the giant pandas across all sessions of the spatial and reversal tasks, however, neither spectacled bear performed better than the panda that visited the fewest number of previously baited feeders in the first and last test sessions of the spatial and reversal tasks. One interesting finding was that three of the seven giant pandas revisited more feeders in the first five sessions of the reversal task than they had in either the first five or last five sessions of the spatial learning task. Mellgren and Brown (1988) observed an abrupt increase in the number of revisits made by rats in an open-field foraging situation when food was not found where it was expected. Interestingly, the SDZ subadult female, who did not reach criterion in the spatial memory task, responded to the reversal task with a sharp increase in the number of revisits in the reversal task. It is possible that she had learned the position of the baited feeders, despite the fact that her behavior indicated the contrary.

Because only one of the spectacled bears reached criterion performance on the spatial and reversal tasks, it was not possible to compare rate of learning and rate of mistakes between that individual and the giant pandas on those tasks. However, there were no striking differences in performance between the two species either in number of trials needed to reach criterion performance on the spatial task or in revisits to previously baited feeders. The female spectacled bear did reach criterion performance on the reversal task a full ten trials sooner than the fastest learning giant panda, indicating her relative adaptability to change.

6.3 Foraging Task 4: Visual Discriminative Stimulus Task

6.3.1 Methods

This task was designed to test the ability of the bears to use visual discriminative stimuli alone to locate viable food sources. Four feeders were pseudo-randomly baited at the beginning of each session of the study. Therefore, the location of the four baited feeders was different in each session. To prevent place learning by chance, the stipulation for random baiting was that the same feeder could not be baited over three consecutive trials. The four baited feeders were distinguishable from the unbaited feeders by a difference in the appearance of the feeder itself. Specifically, the baited feeders had white lids and the unbaited feeders had black lids. To forage efficiently, the bears had to learn the association between the appearance of the feeders and the presence of food. Black and white were chosen because it is unknown if bears are able to see in color. One trial was conducted each day for 15 days or until the performance criterion (3 correct of first four visits in at least 4 of 5 consecutive sessions) is met. All feeders were cleaned between sessions to minimize or eliminate any olfactory discriminative stimuli that could be left on the feeders and used as scent trials by the bears during foraging.

6.3.2 Data Analysis

In the visual task, four of the eight feeders were baited randomly in each trial. A randomly foraging animal would be expected to visit a mean of 1.655 baited feeders in the first four visits, assuming that each site is equally likely to be chosen. The mean number of visits to baited feeders of the first four visits was calculated across three blocks of trials for each of the subjects: Trials 1-5, Trials 13-17, and Trials 26-30. One-sample t tests were used to compare the mean number of visits to baited feeders of the first four visits made by the giant pandas in each block of trials with that expected by chance. One-sample Komolgorov-Smirnov tests were used to compare the mean number of visits to baited feeders of the first four visits made by the spectacled bears in each block of trials with that expected by chance. To determine if one species learned a task more quickly than another, the number of trials required to reach criterion were compared between species using a Mann-Whitney U test.

6.3.3 Results

As was observed in the spatial and reversal tasks, the giant pandas foraged more efficiently in all trials of the visual task than would be expected had they been foraging randomly. Figures 46-48 present the mean number of visits to baited feeders in the first four visits by each of the giant pandas in the first, middle, and last five sessions of the visual task. Figure 49 presents the overall mean of all giant pandas. In each of the three blocks of trials, the giant pandas visited significantly more baited feeders than would be expected had they been foraging randomly. In the first block of 5 trials, the giant pandas visited a mean of 2.03 baited feeders in their first four visits [$t(6) = 2.95$, $p = 0.03$]. In the middle block of 5 trials, the giant pandas visited a mean of 2.11 feeders in the first four visits [$t(6) = 3.35$, $p = 0.02$]. And in the last block of 5 trials, the giant pandas visited a mean of 2.17 baited feeders in their first four visits [$t(6) = 2.83$, $p = 0.03$]. However, as observed in the exploratory task, the giant pandas and the spectacled bears were not traveling randomly. To determine the number of baited feeders each panda was expected to have visited using an adjacency strategy, each session had to be examined individually. For example, assume that the feeders in positions 1, 2, 3, and 7 have been randomly chosen to have the olfactory scent and be baited with food. A panda that preferentially chooses the feeder in position 1 first and then travels in a clockwise direction will be likely to make 3 correct choices in their first four visits, simply because their first four visits will be to feeders 1, 2, 3, and 4. On the other hand, a panda that preferentially chooses the feeder in position 8 and travels in a counterclockwise direction will be likely to make 1 correct choice in their first four visits because their first four visits will be to feeders 8, 7, 6 and 5. Therefore, I adjusted the expected number of visits to correct feeders on the basis of the foraging pattern established by each panda in the exploratory foraging task, taking into account the position of the first visited feeder and overall direction of travel during the trial.

Based on their actual individual foraging patterns in each trial, the giant pandas were expected to visit a mean of 1.97 baited feeders in the first four visits in the first block of 5 trials. This expected value was not significantly different from the observed value (X = 2.03) [t(6) = 0.46, p = 0.66]. In the middle block of 5 trials, the expected number of visits to baited feeders was 2.03, which also was not significantly different from the observed value (X= 2.11) [t(6) = 0.61, p = 0.56]. Finally, the expected number of visits to baited feeders in the last block of 5 trials was 2.09 which was not significantly different from that observed in the giant pandas (X = 2.17) [t(6) = 0.45, p = 0.67]. There was no improvement across trials. The mean number of visits to baited feeders in the first four visits in the first 5 trials (X = 1.97) was not significantly different from the mean number of visits to baited feeders in the first four visits in the last five trials (X = 2.14) [t(6) = -1.3, p = 0.30]. There also did not seem to be an effect of order of testing on performance in the visual task. Kruskal-Wallis tests indicated that the mean number of visits to baited feeders in the first four visits did not differ significantly between the giant pandas at each of the three institutions in either the first block of 5 trials [$H = 1.67$, $p = 0.44$], the second block of 5 trials [$H = 0.49$, $p = 0.78$], or the third block of 5 trials [$H = 0.18$, $p = 0.92$]. The non-random foraging pattern of the giant pandas allowed them to be more efficient foragers than would be expected if they had used a random pattern of foraging. However, none of the giant pandas appeared to have learned the association between the visual discriminative stimulus and the presence of food.

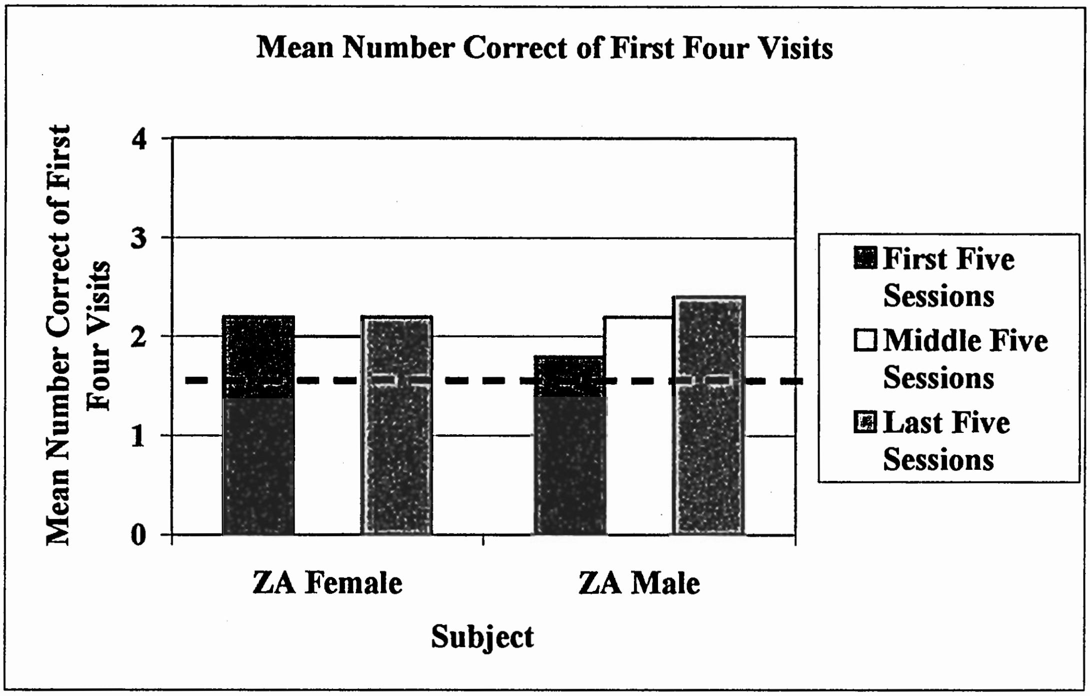

Figure 46 Mean number of visits to baited (correct) feeders in the first four visits by the Zoo Atlanta pandas in the first, middle and last five sessions of the visual task. The dashed line represents chance performance.

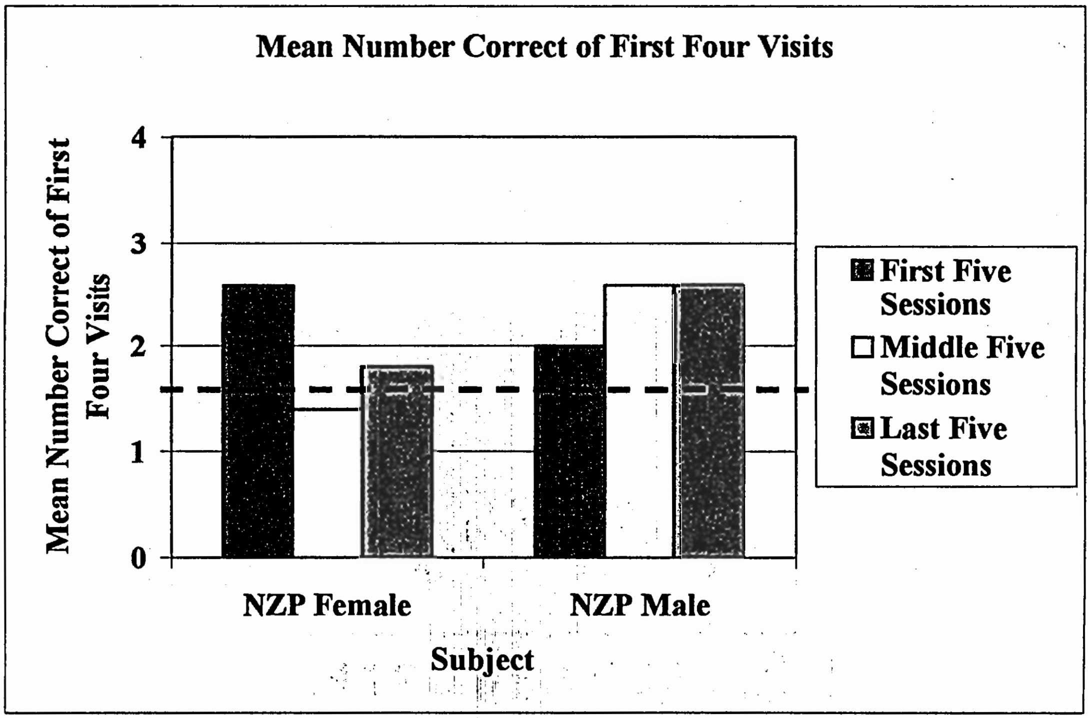

Figure 47 Mean number of visits to baited (correct) feeders in the first four visits by the National Zoological Park pandas in the first, middle and last five sessions of the visual task. The dashed line represents chance performance.

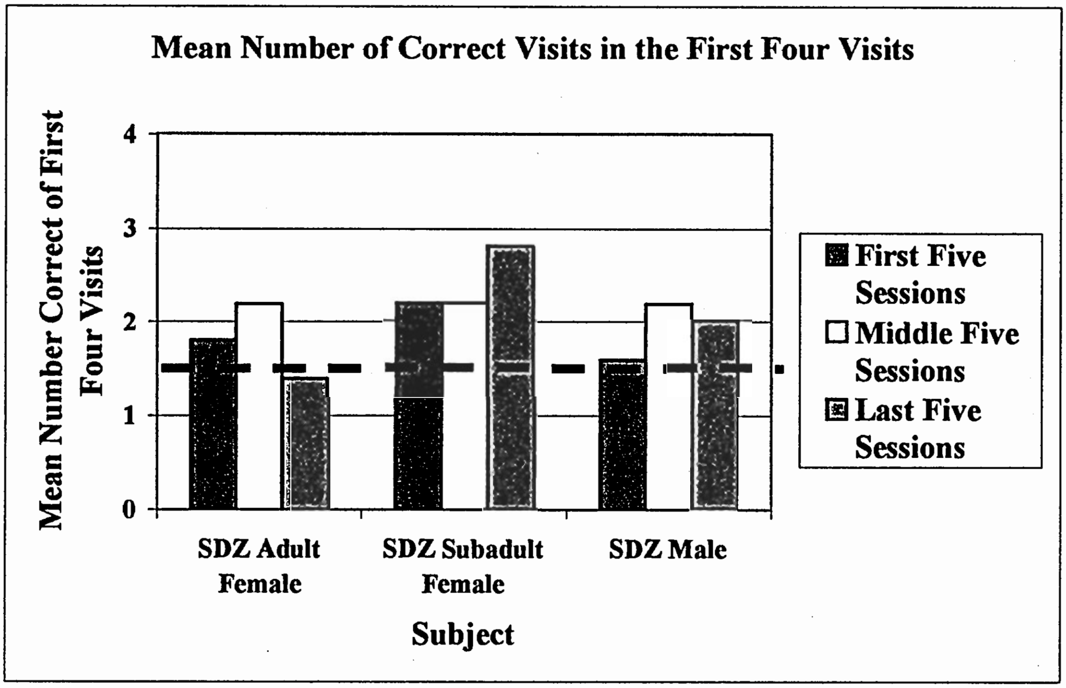

Figure 48 Mean number of visits to baited feeders (correct) in the first four visits by the San Diego Zoo pandas in the first, middle and last five sessions of the visual task. The dashed line represents chance performance.

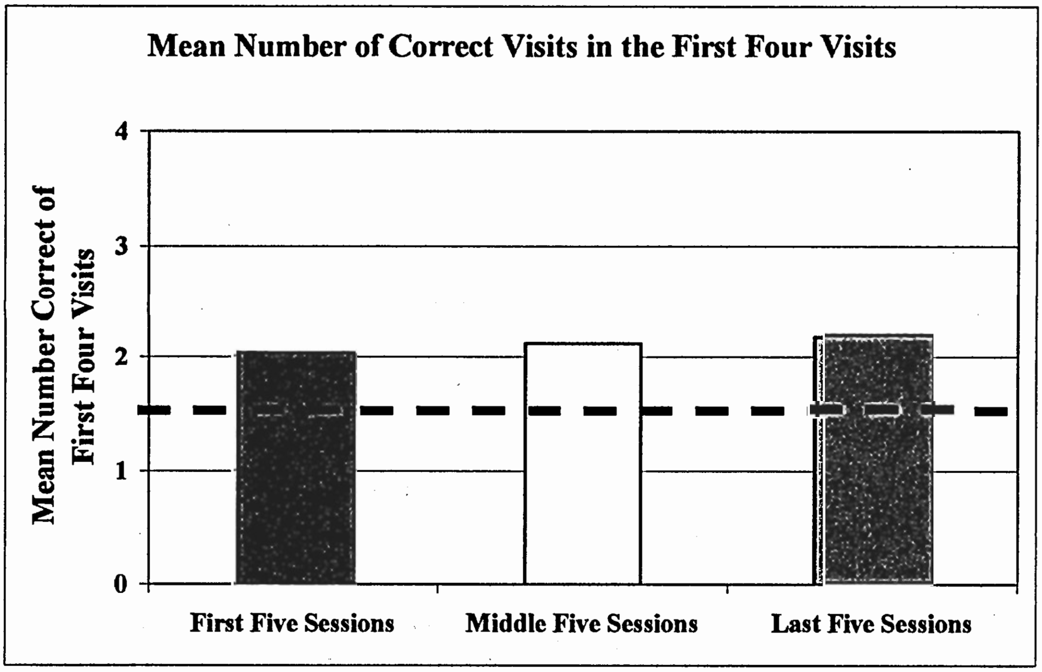

Figure 49 Mean number of visits to baited feeders (correct) in the first four visits by all pandas in the first, middle and last five sessions of the visual task. The dashed line represents chance performance.

Figures 50-56 present the number of visits to baited feeders in the four visits and the total number of feeders visited by each of the giant pandas at each of the three institutions. The giant pandas visited many more feeders than the 4 visits necessary to obtain all of the food, visiting a mean of 9.49 feeders during each trial in the first block of 5 trials [$t(6) = 25.21$, $p < 0.001$], a mean of 8.31 feeders in the second block of 5 trials [$t(6) = 14.44$, $p = < 0.001$], and a mean of 7.89 feeders in the last block of 5 trials [$t(6) = 21.69$, $p = < 0.001$]. The mean number of visits in each trial was significantly greater than 8 in the first block of 5 trials [$t(6) = 6.83$, $p < 0.001$]. In the second block of 5 trials [$t(6) = 1.05$, $p = 0.33$], and the last block of 5 trials [$t(6) = -0.64$, $p = 0.55$], the giant pandas visited each of the eight feeders in a session.

Figure 57 presents the mean number of revisits averaged across the giant pandas in each session of the visual task. The giant pandas revisited (visited previously depleted feeders) a mean of 18.14 feeders across the 30 trials of the visual task. The number of revisits ranged widely from as few as 10 in 30 trials by one panda (SDZ adult female) to 54 in 30 trials by another panda (male, San Diego Zoo).

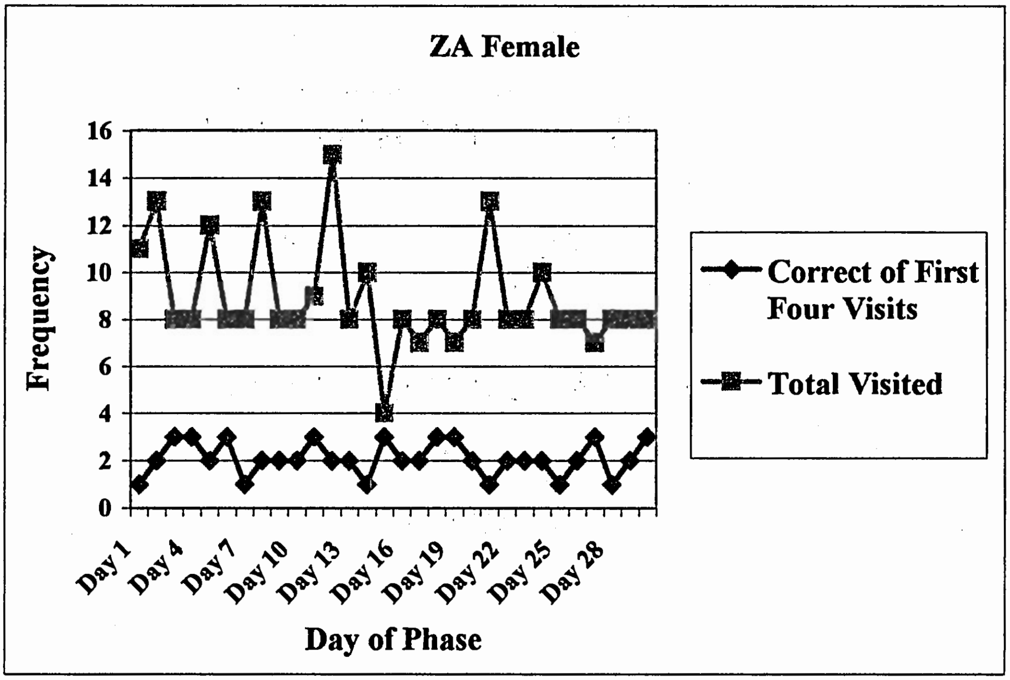

Figure 50 Number of visits to baited feeders in the first four visits and total number of feeders visited by the male panda at Zoo Atlanta in each session of the visual task.

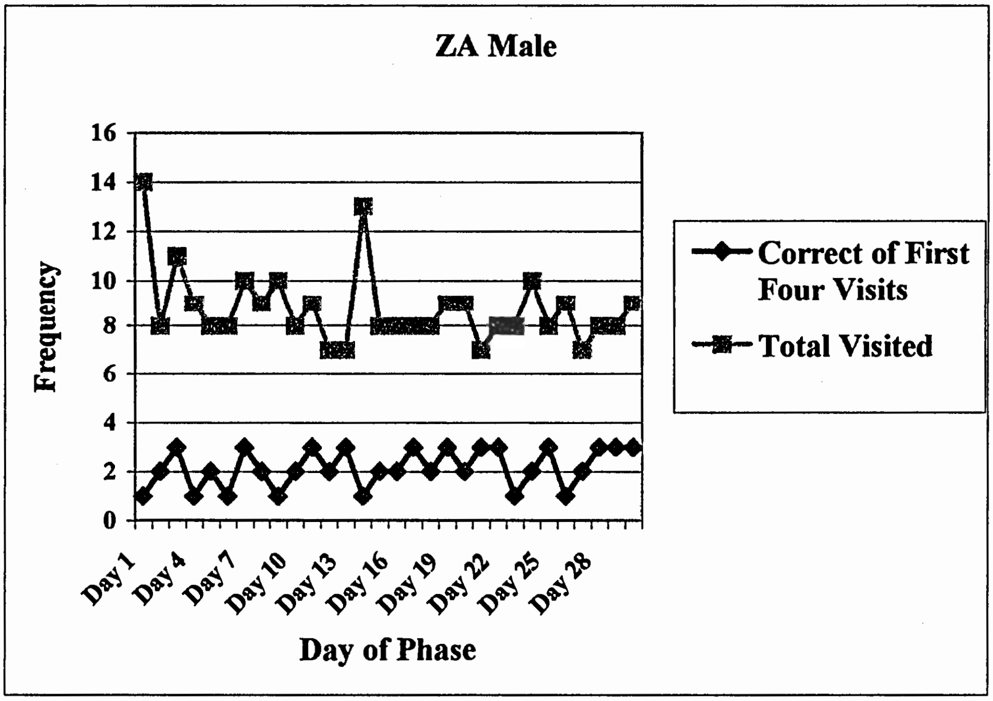

Figure 51 Number of visits to baited feeders in the first four visits and total number of feeders visited by the female panda at Zoo Atlanta in each session of the visual task.

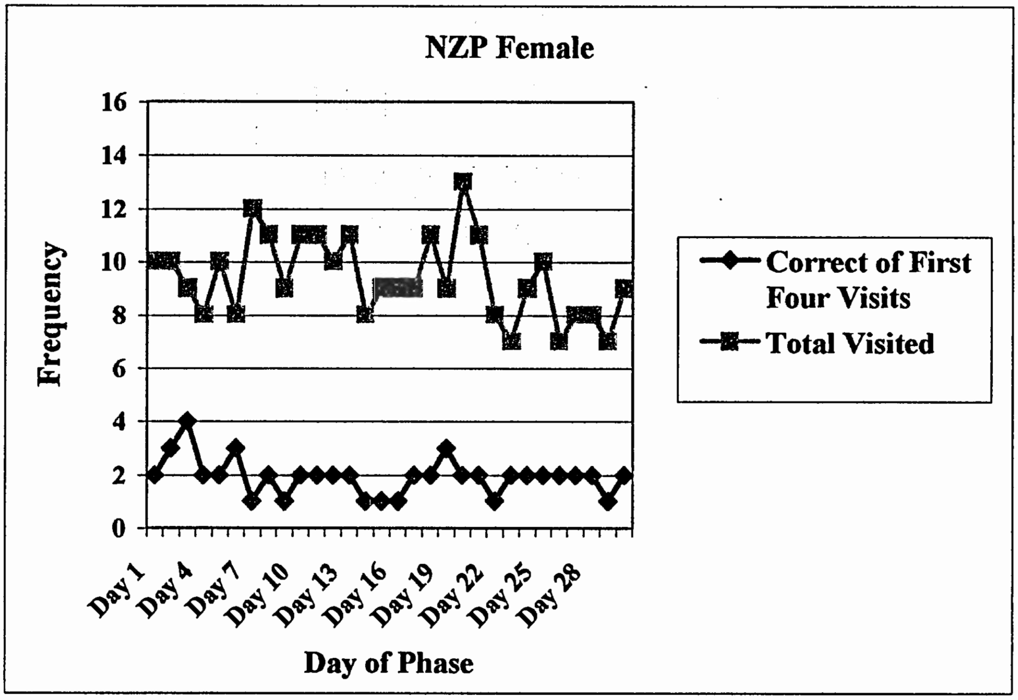

Figure 52 Number of visits to baited feeders in the first four visits and total number of feeders visited by the female panda at the National Zoological Park in each session of the visual task.

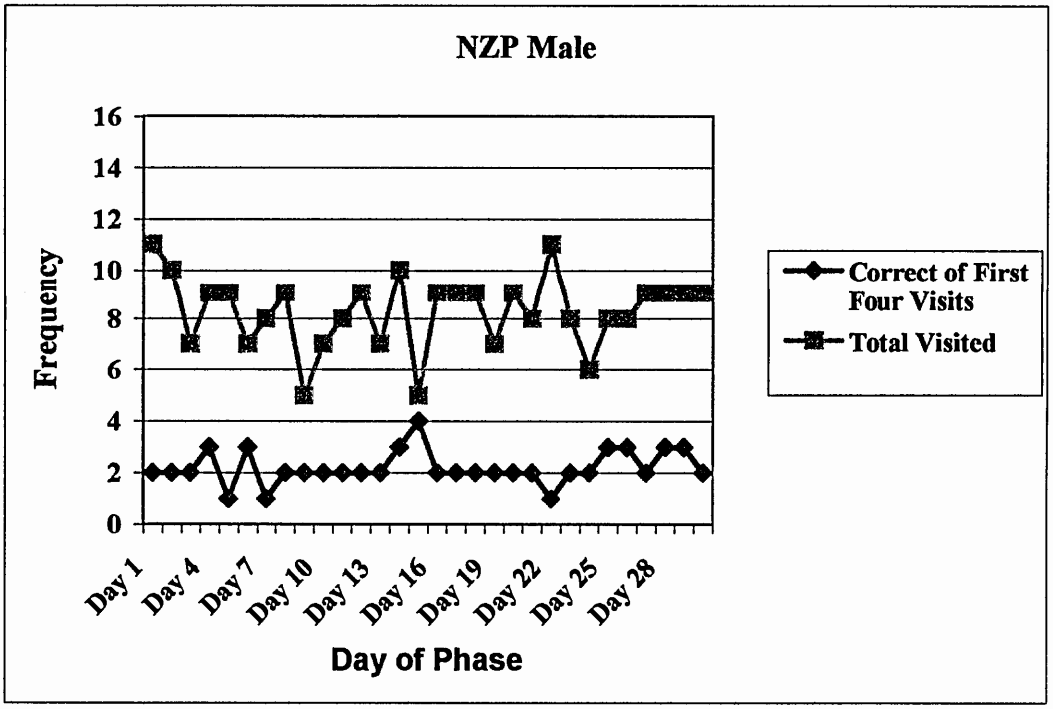

Figure 53 Number of visits to baited feeders in the first four visits and total number of feeders visited by the male panda at the National Zoological Park in each session of the visual task.

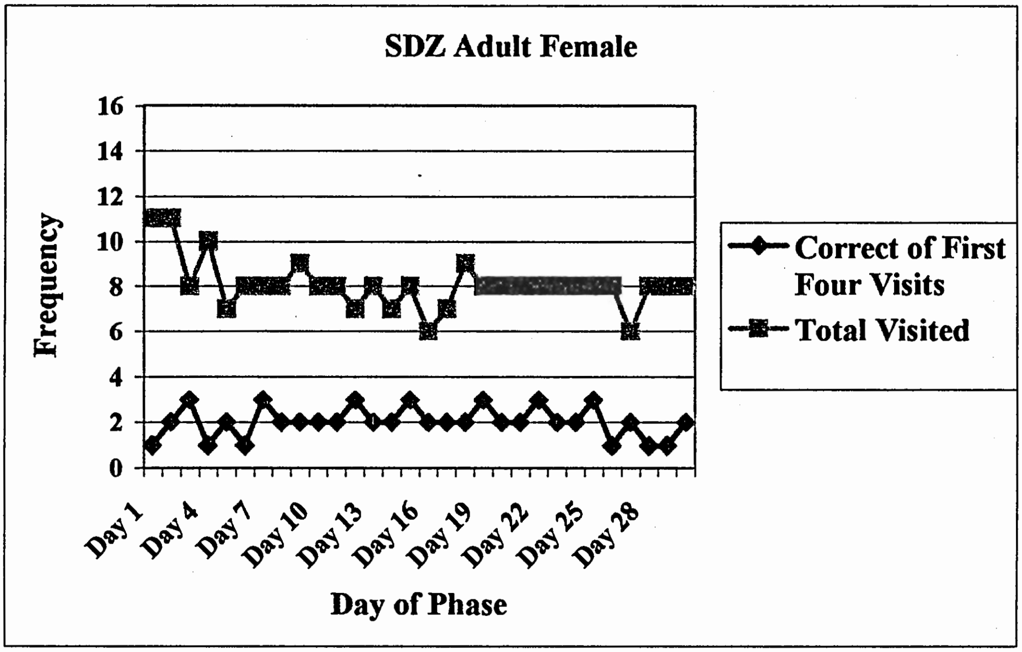

Figure 54 Number of visits to baited feeders in the first four visits and total number of feeders visited by the female panda at the San Diego Zoo in each session of the visual task.

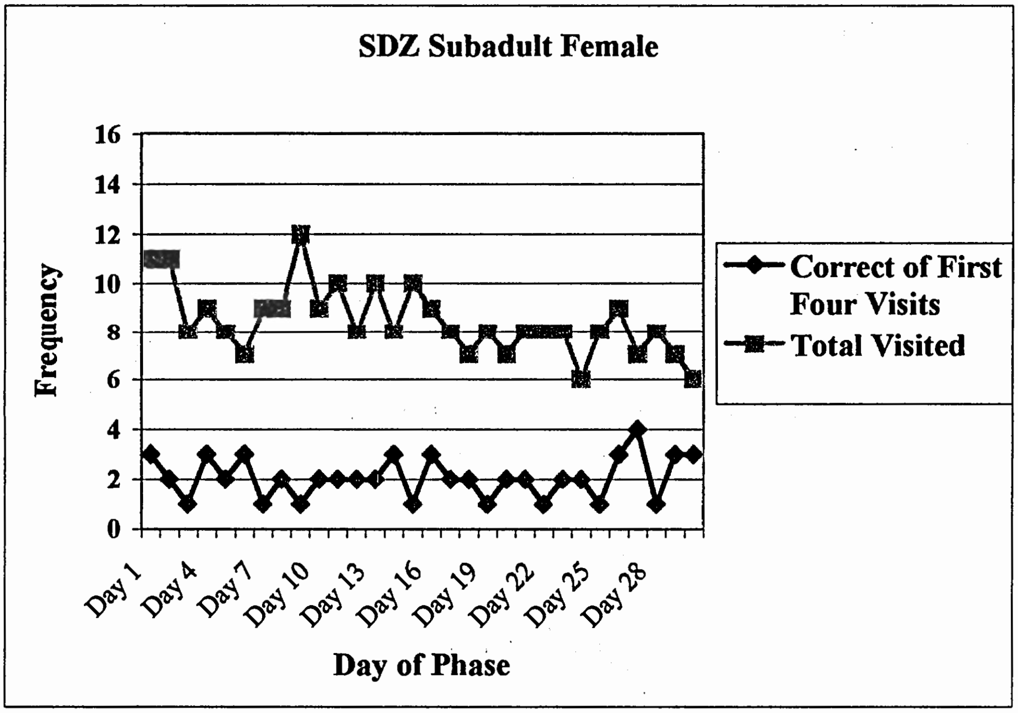

Figure 55 Number of visits to baited feeders in the first four visits and total number of feeders visited by the subadult female panda at the San Diego Zoo in each session of the visual task.

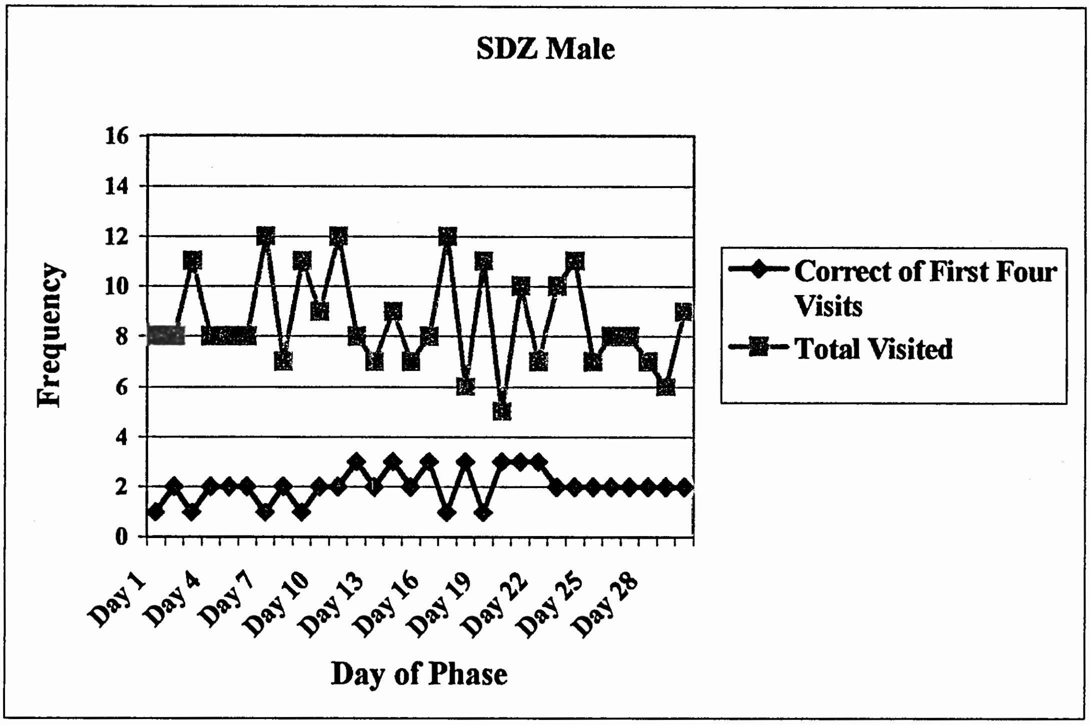

Figure 56 Number of visits to baited feeders in the first four visits and total number of feeders visited by the female panda at the National Zoological Park in each session of the visual task.

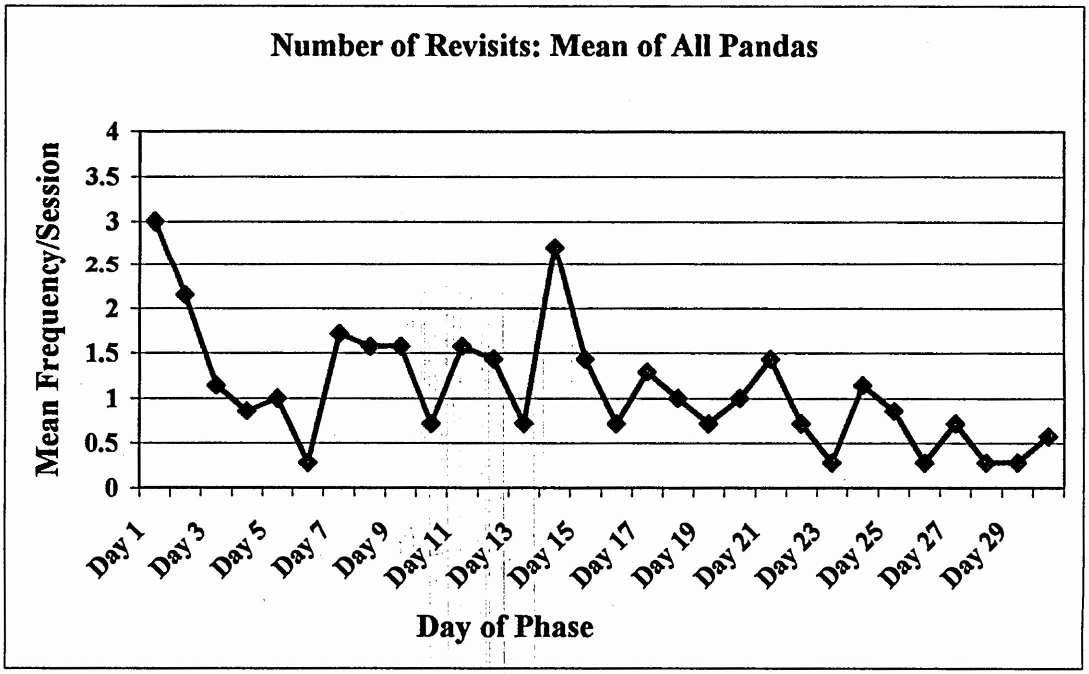

Figure 57 Total number of visits to previously visited feeders in each session by all pandas in the visual task.

In contrast with the giant pandas, the spectacled bears did not forage differently than would be expected by a randomly traveling forager in the first 5 trials of the visual task. Figure 58 presents the mean number of visits to baited feeders in the first four visits by the spectacled bears in the first, middle, and last five sessions of the visual task. A one-sample Komolgorov-Smirnov test indicated that there was no significant difference between the mean number of baited feeders visited in the first four visits (X = 1.8) and that expected by chance in Trials 1-5 (X = 1.655) [D_{max} = 0.48, p = 0.58]. However, both of the spectacled bears reached criterion performance (3 or more correct choices of the first four choices in at least four of five consecutive trials) within 30 trials. The male reached criterion performance within 16 trials, and the female reached criterion performance within 22 trials. Performance increased in the last 5 trials to a mean of 3.3 baited feeders in the first 4 visits, which was significantly better than would be expected by a randomly traveling forager [D_{max} = 0.94, p = 0.007].

The spectacled bears were using a least-distance strategy in their foraging. Therefore, I adjusted the expected number of visits to correct feeders on the basis of the foraging pattern established by each spectacled bear in the exploratory foraging task, taking into account the position of the first visited feeder and the overall direction of travel during the trial. Based on their actual foraging pattern in each trial, the spectacled bears were expected to visit a mean of 1.8 baited feeders in their first four visits in the first block of 5 trials. A Komolgorov-Smirnov test indicated that the spectacled bears did not visit significantly more baited feeders (X = 1.8) than was expected of them in the first five trials (X = 1.8) [D_{max} = 0.42, p = 0.77]. They did, however, perform significantly better in the last five trials during which they met criterion performance (X = 3.3) than was expected using an adjacency strategy (X = 2.1) [$D_{max} = 0.86$, $p = 0.04$].

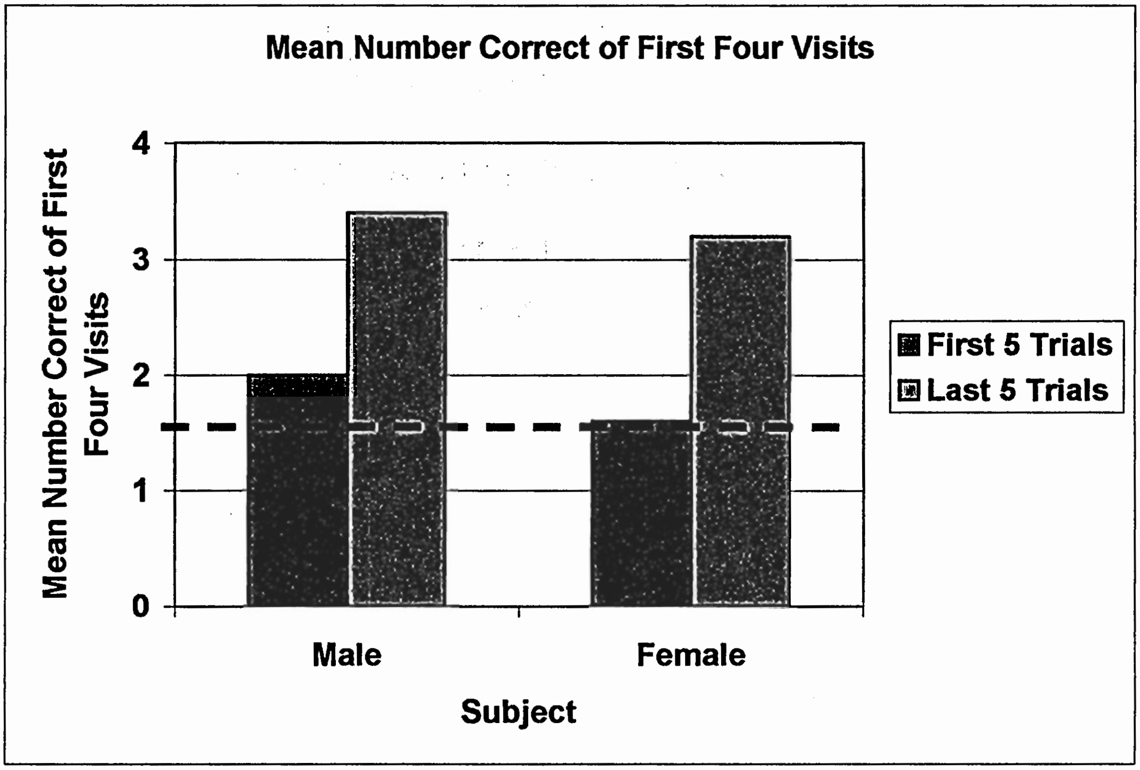

Figure 58 Mean number of visits to baited feeders (correct) in the first four visits by the spectacled bears in the first 5 trials and last 5 trials of the visual task. The dashed line indicates chance performance by a random forager.

To determine if the behavior of the spectacled bears was under control of a discriminative stimulus other than the visual discriminative stimulus, I wanted to conduct a reversal trial similar to that done following the spatial task. However, the study had to be suspended for 7 days following trial 22 so that medical exams could be conducted on a male spectacled bear that was not included in the study. There was a concern that a postponement of the study could affect their learned behavior. Therefore, despite the fact that both bears had reached criterion performance, I continued the visual task for 15 days after the break before conducting the reversal. In the first five trials following the break in testing, the mean number of visits to baited feeders in the first four visits ($X = 3.1$) was significantly more than would be expected had they been foraging randomly ($X = 1.655$) [$D_{max} = 0.91$, $p = 0.02$]. However, it was not significantly different from that expected by a forager using an adjacency strategy ($X = 2.25$) [$D_{max} = 0.77$, $p = 0.10$]. Performance did not improve in trials 11-15. The spectacled bears visited more baited feeders in their first 4 visits in these trials than would be expected had they been foraging randomly ($X = 2.8$) [$D_{max} = 0.87$, $p = 0.03$], but they were still not performing better than would be expected by using a least-distance strategy (expected $X = 2.3$) [$D_{max} = 0.69$, $p = 0.19$].

For management purposes, this phase of the study was completed before criterion conditions had been met. Despite the fact that the behavior of the spectacled bears was not under the control of the visual discriminative stimulus, I reversed the task, baiting the feeders with the black lids instead of the feeders with the white lids. The male spectacled bear only visited one baited feeder in his first four visits, even though he was expected to visit 2 baited feeders using a least-distance foraging strategy. During this reversal trial, he only depleted food from 2 of the baited feeders despite the fact that he had depleted all four feeders of the food in the previous trials. Therefore, performance seems to have been disrupted by the switch of the food to the feeders with the black lids. The female visited 2 baited feeders in her first four visits, which was what was expected if she were using a least-distance strategy. It is unknown why the break in testing disrupted performance so significantly.

To deplete all of the feeders in the visual task, the spectacled bears only needed to visit 4 of the 8 feeders. Figures 59 and 60 present the mean number of visits to baited feeders in the first four visits as well as the total number of feeders visited by the spectacled bears in each session of the visual task. In the first 5 trials of the visual task they visited a mean of 7.7 feeders in each trial. A Komolgorov-Smirnov one sample test indicated that this was significantly more than the 4 visits necessary to deplete the feeders [$D_{max} = 1.0$, $p < 0.001$]. They were not visiting significantly fewer than 8 feeders [$D_{max} = 0.50$, $p = 0.50$], indicating that they were visiting all 8 feeders in their efforts to find food. However, in the last five trials in which each spectacled bear reached criterion performance they visited a mean of only 4.6 feeders during a trial. This was not significantly different from that necessary to deplete all food during a session [$D_{max} = 0.655$, $p = 0.24$], but was significantly less than would be expected had they been visiting all 8 of the feeders [$D_{max} = 0.999$, $p < 0.001$]. As can be seen in Figures 59-60, there were several trials in which the spectacled bears visited only those four feeders that had the visual discriminative stimulus.

The spectacled bears revisited a mean of 5.5 feeders across the trials of the visual task. All 6 of the male's revisits were to feeders that had been baited during the trial. Three of the female's revisits were to feeders that had been baited during the trial. To compare the behavior of the giant pandas and the spectacled bears, I calculated the frequency of revisits across the first 20 trials of the visual task for both the spectacled bears and the giant pandas. The giant pandas revisited a mean of 26.6 feeders across the first 20 trials. A Mann-Whitney U test indicated that the spectacled bears revisited significantly fewer feeders in their task than the giant pandas [$U = 0.0$, $p = 0.04$].

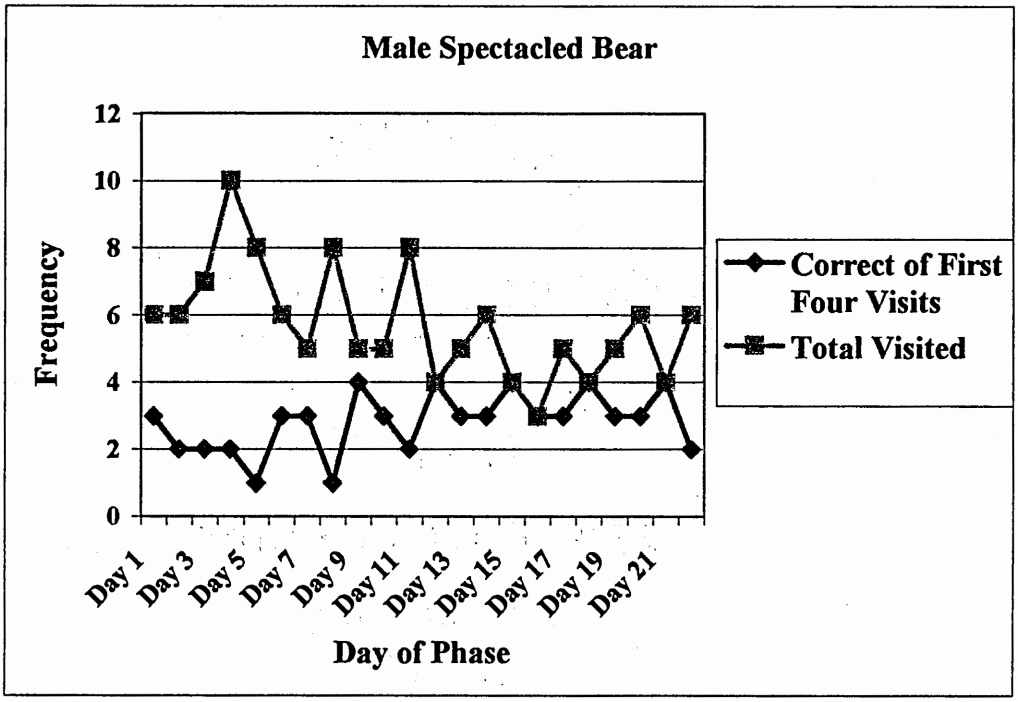

Figure 59 Number of visits to baited feeders in the first four visits and total number of feeders visited by the male spectacled bear in each session of the visual task.

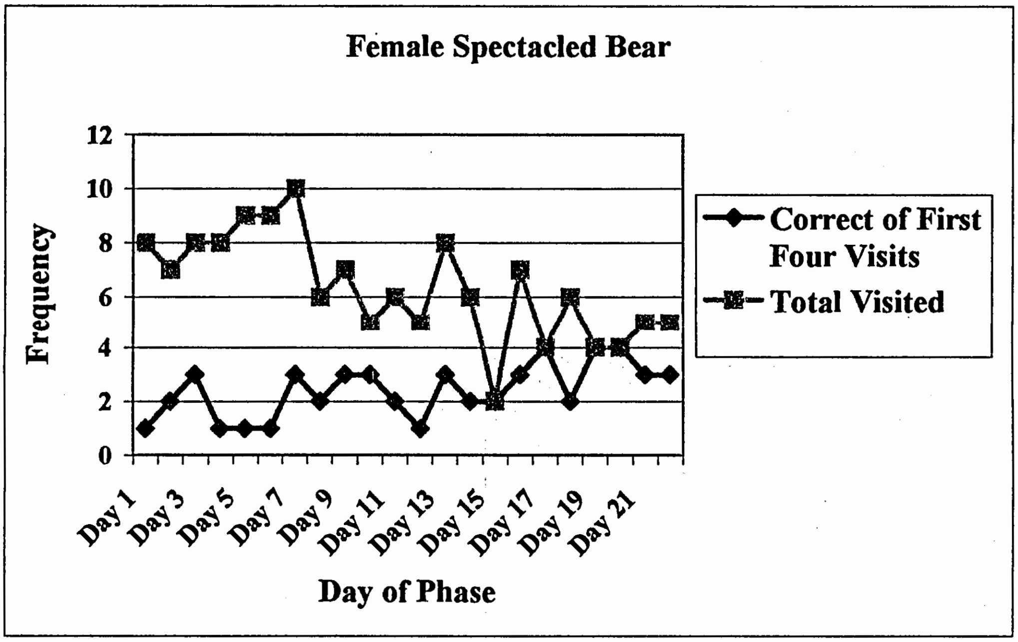

Figure 60 Number of visits to baited feeders in the first four visits and total number of feeders visited by the female spectacled bear in each session of the visual task.

6.3.4 Discussion

In Foraging Task 4, four of the eight feeders were baited in each trial. Baited feeders were signaled by the presence of a white lid, and unbaited feeders were signaled by the presence of a black lid. The location of the baited feeders was randomly determined at the beginning of a trial so that spatial cues could not be used to identify the baited feeders. Only the visual cue (color of lid) could be used as a discriminative stimulus. The data were averaged across three blocks of five trials for the giant pandas. As observed in the exploratory, spatial and reversal tasks, the giant pandas visited more baited feeders in their first four visits than would be expected had they been foraging randomly in the first block of five trials. They also visited significantly more baited feeders in their first four visits in the middle and last block of five trials. However, the number of baited feeders visited in the first four visits in each block of trials was not significantly different from that expected from a forager using a least-distance strategy. There was no improvement across trials in the number of baited feeders visited in the first four visits, indicating that none of the giant pandas learned the association between the visual signal and the presence of food. They visited significantly more than the four feeders necessary to deplete all of the food in each of the three blocks of trials. They simply traveled to all eight feeders looking for food.

Unlike the giant pandas, the spectacled bears did not visit more baited feeders in their first four visits than would be expected had they been foraging randomly in the first five trials of Foraging Task 4. However, the number of baited feeders visited in the first four visits was also not significantly different from that expected had they been using a least-distance strategy. This indicates that their behavior was somewhere in between in these trials. Both spectacled bears learned to travel directly to the baited feeders within 30 test sessions. The male reached criterion performance within 16 trials, and the female reached criterion performance within 22 trials. Both bears visited more baited feeders in their first four visits than would be expected by either random foraging or foraging using a least-distance strategy. In addition, they were not visiting more feeders during the last five test sessions than the four necessary to obtain all of the food. Unfortunately, an unexpected week-long break in testing disrupted performance. After the break the spectacled bears were no longer foraging more efficiently than would be expected. However, a reversal was still conducted in which the baited feeders were signaled by the black lids and the unbaited feeders were signaled by the white lids. This reversal seemed to disrupt the performance of the male but not the female, suggesting that he was not using other cues such as the smell of the feeder to travel directly to the baited feeders.

The visual stimulus gained stimulus control over the behavior of both of the spectacled bears, but none of the giant pandas. In the wild, the diet of spectacled bears includes many visually distinct food items such as fruit and bromeliads. Furthermore, the spectacled bear diet includes embedded food items that require extractive foraging. Visual cues such as fruit color or leaf shape or tree size emanating from the source of the embedded food item could be used as beacons to localize viable food sources. The results of this foraging task support the hypothesis that there would be species differences in performance based on foraging ecology, such that the more frugivorous spectacled bears would learn the visual task more quickly and make fewer errors than the more folivorous giant pandas.

6.4 Foraging Task 5: Olfactory Discriminative Stimulus Task

6.4.1 Methods

The purpose of this task was to determine if the bears could use olfactory discriminative stimuli alone to locate viable food sites. This task was similar to that of Foraging Task 4; however, baited food sites were distinguishable only by a scent associated with the feeder. Four of the eight feeders were randomly chosen and baited with food before the start of each trial. One drop of lemon oil (McCormicks™ lemon extract) was added to and rubbed across the lid of each of the feeders. Lemon oil was chosen because it is known to be a smell that attracts the giant pandas. Prior to testing, it was determined that the spectacled bears were also capable of smelling the oil by presenting the scent to them on a neutral substrate and observing their behavior for prolonged sniffing. Efficient foraging required the bears to learn the association between the scent and the presence of food. One session was conducted each day for 15 days or until the performance criterion was met. All feeders were cleaned between sessions to minimize any eliminate or olfactory discriminative stimuli that could be left on the feeders by the bears during foraging, as well as remove the lemon oil from the feeders between trials.

6.4.2 Data Analysis

As in the visual task, four of the eight feeders were baited randomly in each trial of the olfactory task. A randomly foraging animal would be expected to visit a mean of 1.655 baited feeders in its first four visits. The mean number of visits to baited feeders of the first four visits was calculated across three blocks of trials for each of the subjects: Trials 1-5, Trials 13-17, and Trials 26-30. One-sample t tests were used to compare the mean number of visits to baited feeders of the first four visits made by the giant pandas in each block of trials with that expected by chance. To obtain all of the food in the task, the bears only needed to visit 4 feeders. One sample t-tests were also used to compare the total number of feeders visited in each trial by the giant pandas with either 4 feeders or 8 feeders. a Kruskal-Wallis one way analysis of variance was used to examine the possibility of differences in performance between the giant pandas at the three institutions. One-sample Komolgorov-Smirnov tests were used to compare the mean number of visits to baited feeders of the first four visits made by the spectacled bears in each block of trials with that expected by chance and to compare the mean number of feeders visited per trial with 4 or 8. A Mann-Whitney U test was used to determine if the spectacled bears revisited significantly fewer feeders in the olfactory task than the giant pandas

6.4.3 Results

Figures 57-59 present the mean number of visits to baited feeders in the first four visits by the giant pandas at each of the three institutions. Figure 60 shows the mean across all giant pandas. In each of the three blocks of trials, the giant pandas visited significantly more baited feeders in their first four visits than would be expected had they been traveling randomly between feeders. In the first block of 5 trials, the giant pandas visited a mean of 1.97 baited feeders in their first four visits [$t(6) = -15.14$; $p < 0.001$). In the middle block of 5 trials, the giant pandas visited a mean of 2.23 baited feeders in their first four visits [$t(6) = -13.22$; $p < 0.001$]. In the last block of 5 trials, the giant pandas visited a mean of 2.14 baited feeders in their first four visits [$t(6) = -10.49$; $p < 0.001$]. However, as observed in the visual task, their pattern of movement was not random in any of the trials. Therefore, the expected number of correct visits in a trial was adjusted on the basis of their preferred pattern of movement.

Based on their actual foraging pattern in each trial, the giant pandas were expected to visit a mean of 1.91 baited feeders in the first four visits in the first block of 5 trials. This was not significantly different from the observed value (X = 1.97) [t(6) = 0.46, p = 0.66]. In the middle block of 5 trials, the expected number of visits to baited feeders was 2.06, which also was not significantly different from the observed value (X = 2.22) [t(6) = 1.26, p = 0.26]. Finally, the expected number of visits to baited feeders in the last block of 5 trials was 2.14 which was not significantly different from that observed in the giant pandas (X = 2.14) [t(6) = 0.02, p = 0.99]. The mean number of visits to baited feeders in the first four visits in the first 5 trials was not significantly different than the mean number of visits to baited feeders in the first four visits in the last five trials [t(6) = -1.13, p = 0.30]. There did not seem to be an effect of order of testing on performance. Kruskal-Wallis tests indicated that the mean number of visits to baited feeders in the first four visits did not differ significantly between the giant pandas at each of the three institutions in either the first block of 5 trials [H = 2.34, p = 0.31], the middle block of 5 trials [H = 0.76, p = 0.69], or the last block of 5 trials [H = 3.46, p = 0.18].

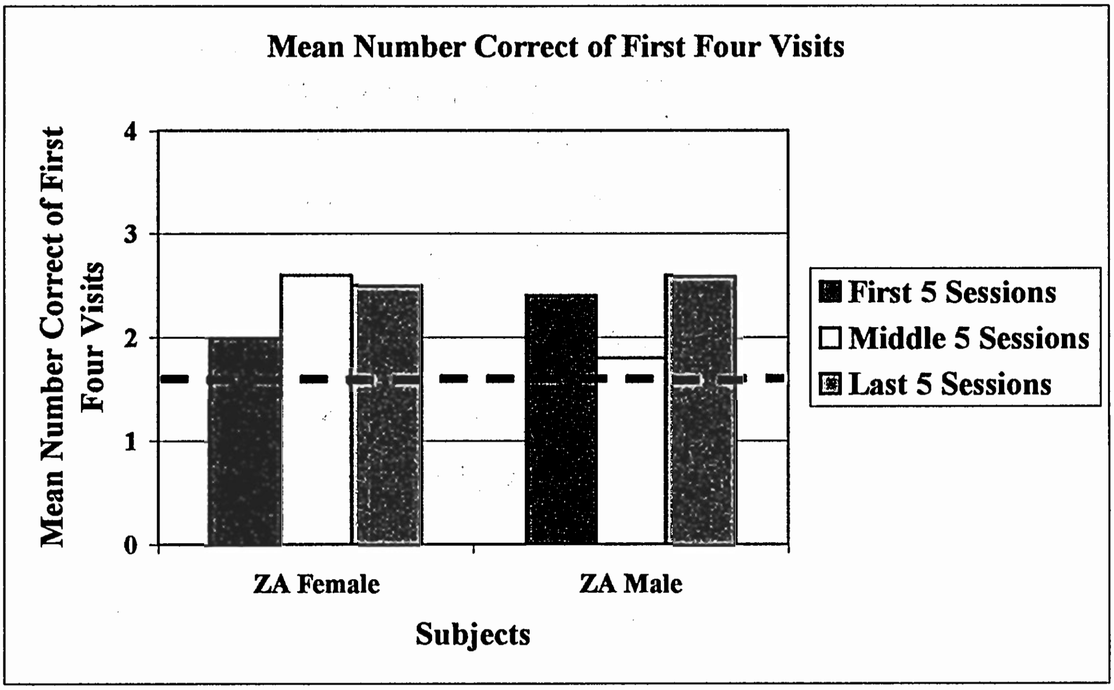

Figure 61 Mean number of visits to baited feeders (correct) in the first four visits by the Zoo Atlanta pandas in the first, middle and last five sessions of the olfactory task. The dashed line represents chance performance by a random forager.

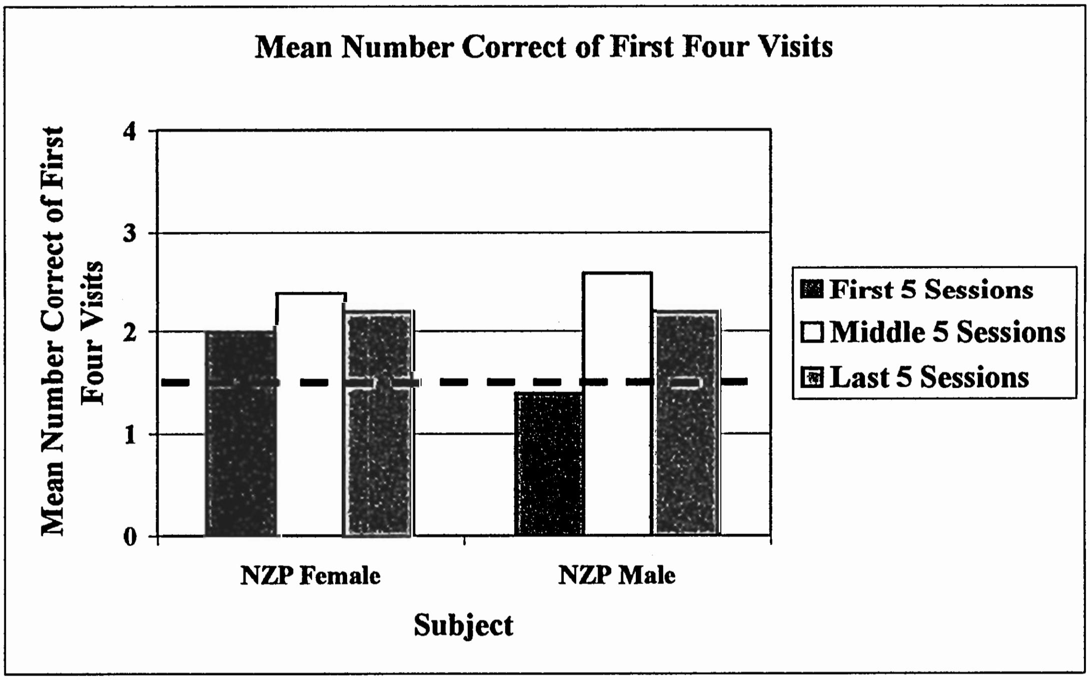

Figure 62 Mean number of visits to baited feeders (correct) in the first four visits by the National Zoological Park pandas in the first, middle and last five sessions of the olfactory task. The dashed line represents chance performance by a random forager.

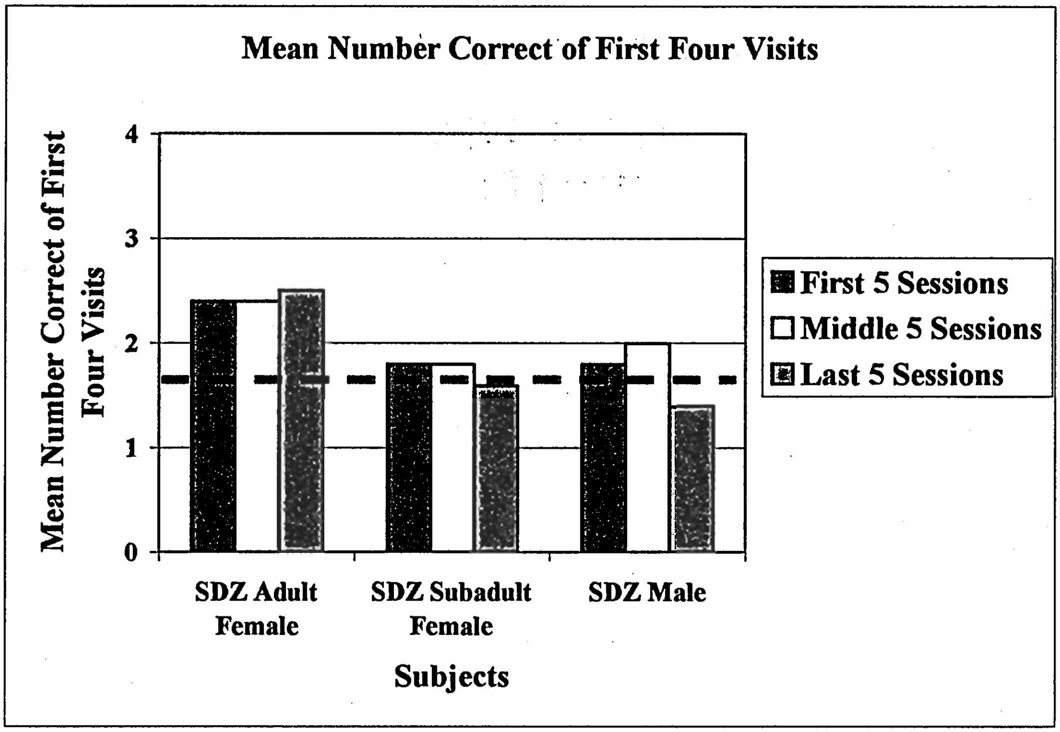

Figure 63 Mean number of visits to baited feeders (correct) in the first four visits by the San Diego Zoo pandas in the first, middle and last five sessions of the olfactory task.

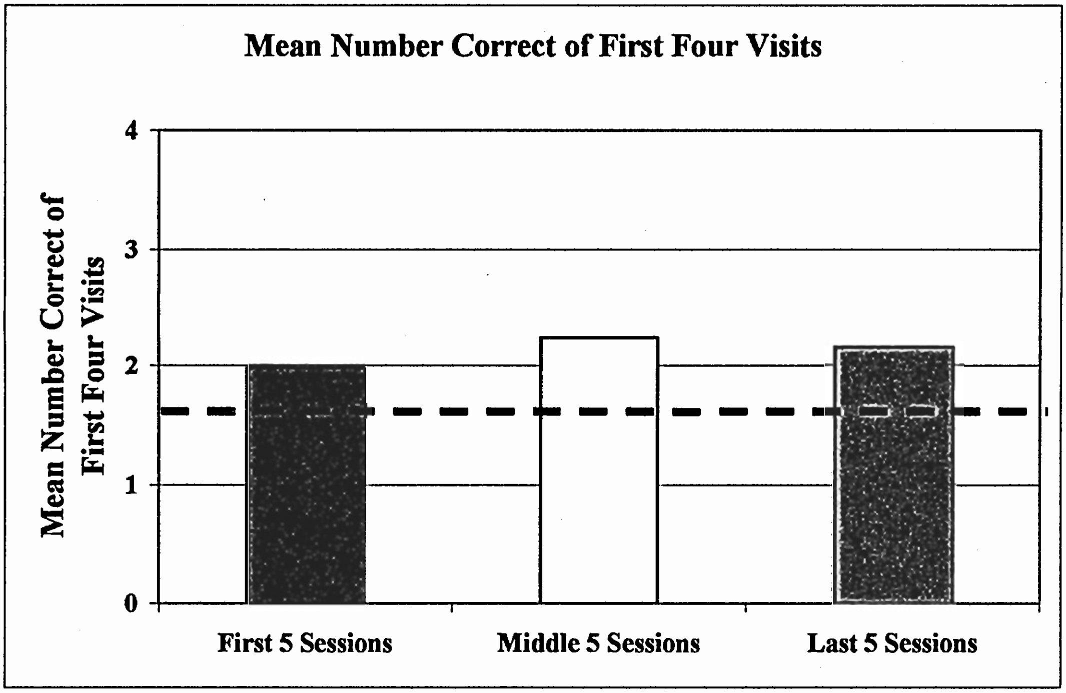

Figure 64 Mean number of visits to baited feeders (correct) in the first four visits by all pandas in the first, middle and last five sessions of the olfactory task.

As observed in the visual task, the non-random foraging pattern of the giant pandas allowed them to be more efficient foragers than would be expected if they used a random pattern of foraging. However, none of the giant pandas appeared to have learned the association between the olfactory discriminative stimulus and the presence of food. In fact as can be seen for each of the individual giant pandas (see Figures 65-71), the giant pandas visited many more feeders than the 4 necessary to obtain all of the food, visiting a mean of 8.54 feeders during a trial in the first block of 5 trials [$t(6) = 10.03$, $p < 0.001$], a mean of 10.1 feeders in the middle block of 5 trials [$t(6) = 7.09$, $p < 0.001$], and a mean of 9.69 feeders in the last block of 5 trials [$t(6) = 14.04$, $p < 0.001$]. The mean number of visits in each trial was not significantly greater than 8 in either the first block of 5 trials [$t(6) = 1.20$, $p = 0.28$] or the middle block of 5 trials [$t(6) = 2.41$, $p = 0.05$], suggesting that the giant pandas were searching all feeders in their attempt to find food in these sessions. They visited significantly more feeders than 8 in the last block of 5 trials [$t(6) = 4.16$, $p = 0.006$]. The giant pandas revisited a mean total of 50.6 feeders in the 30 trials (1.7 feeders per trial). Figure 72 shows the number of revisits to previously visited feeders by all giant pandas in each session of the olfactory task. The number of revisits ranged widely from as few as 12 revisits in 30 trials by the ZA female to as many as 124 in 30 trials by the SDZ male. The giant pandas were not more likely to revisit feeders that had been baited in a session ($X = 54.3\%$) than feeders that had not been baited in a session [$t(6) = 1.27$, $p = 0.25$].

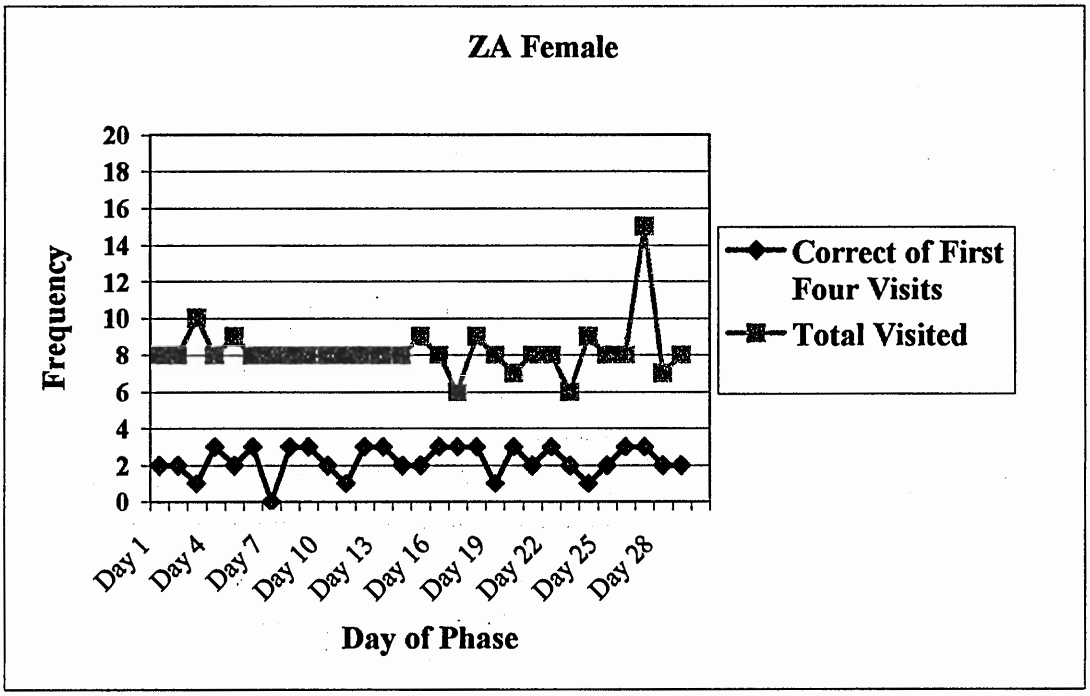

Figure 65 Number of visits to baited feeders in the first four visits and total number of feeders visited by the female panda at Zoo Atlanta in each session of the olfactory task.

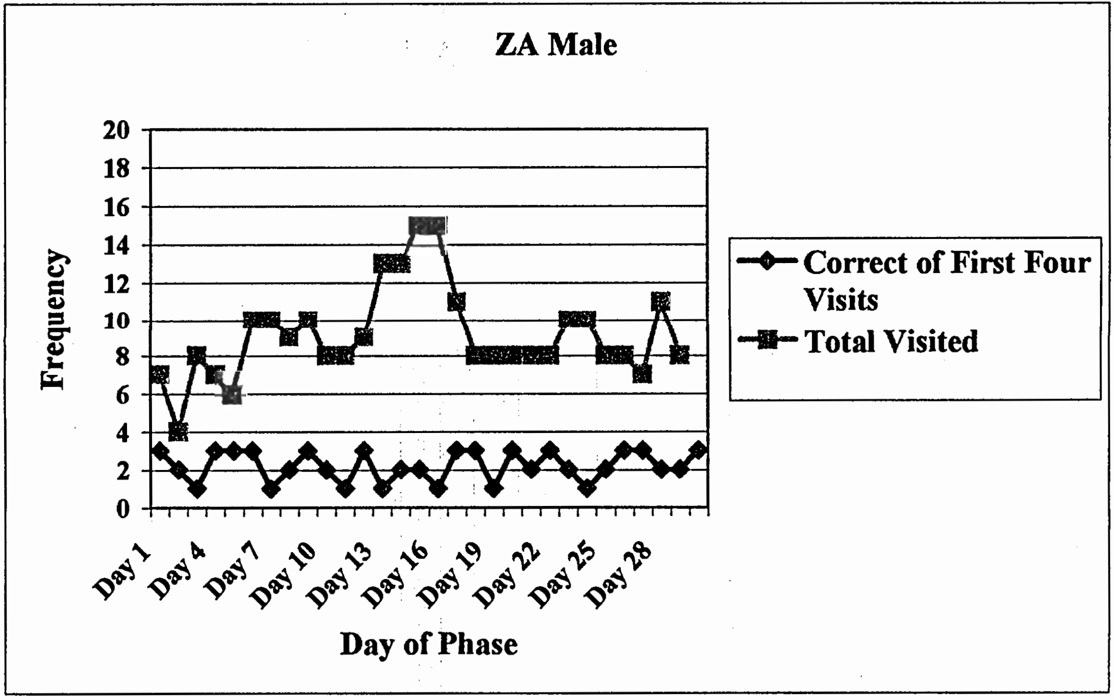

Figure 66 Number of visits to baited feeders in the first four visits and total number of feeders visited by the male panda at Zoo Atlanta in each session of the olfactory task.

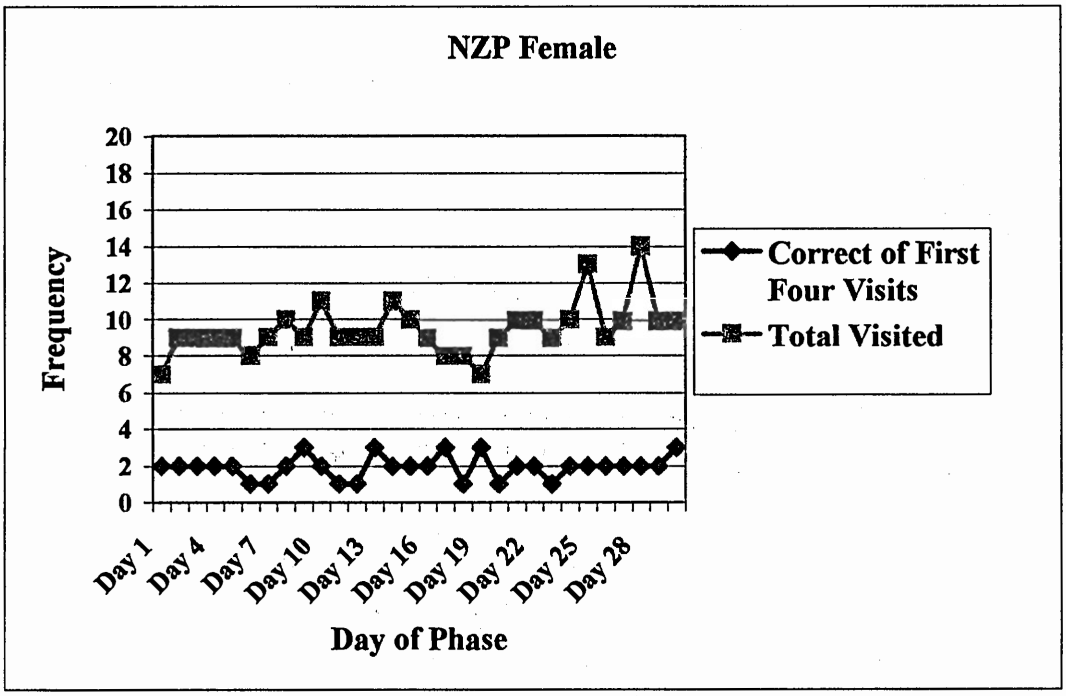

Figure 67 Number of visits to baited feeders in the first four visits and total number of feeders visited by the female panda at the National Zoological Park in each session of the olfactory task.

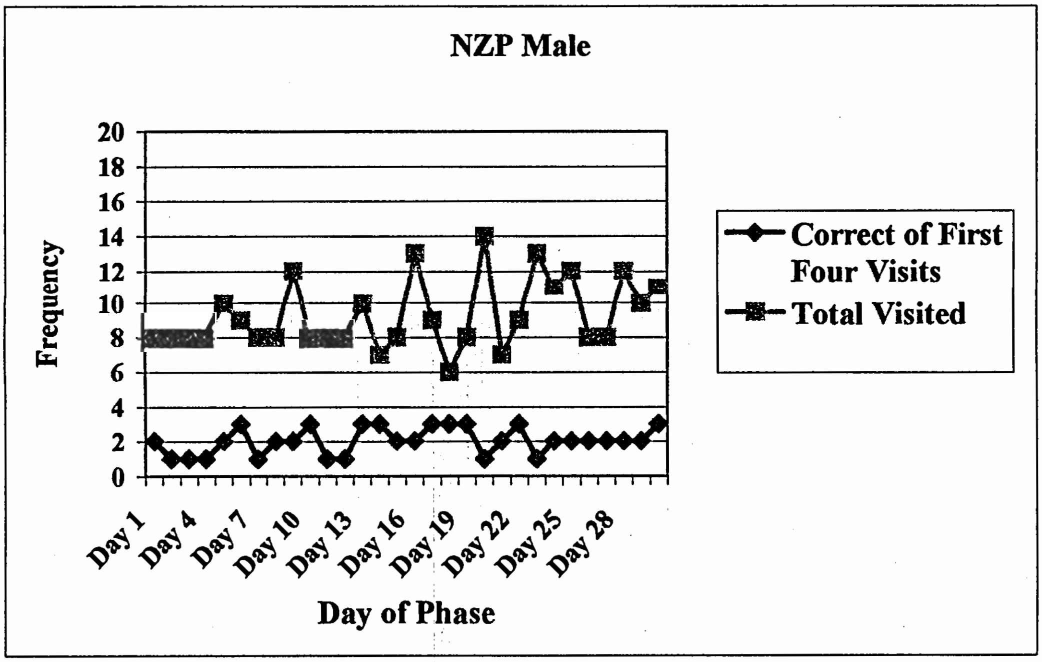

Figure 68 Number of visits to baited feeders in the first four visits and total number of feeders visited by the adult female panda at the San Diego Zoo in each session of the olfactory task.

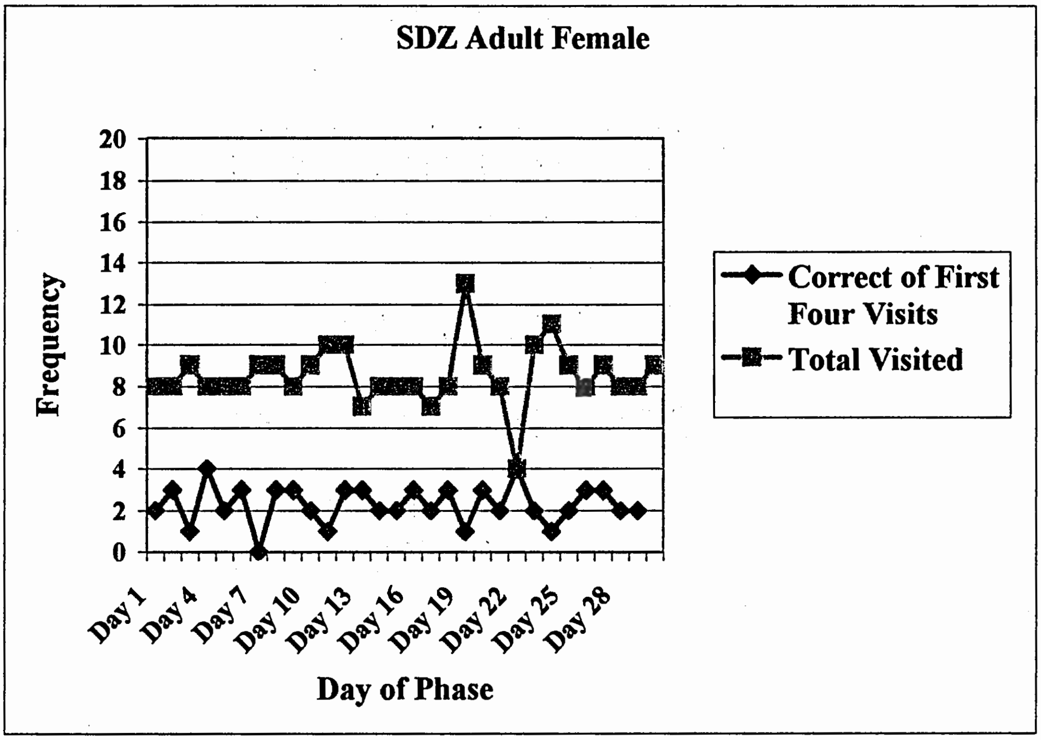

Figure 69 Number of visits to baited feeders in the first four visits and total number of feeders visited by the adult female panda at the San Diego Zoo in each session of the olfactory task.

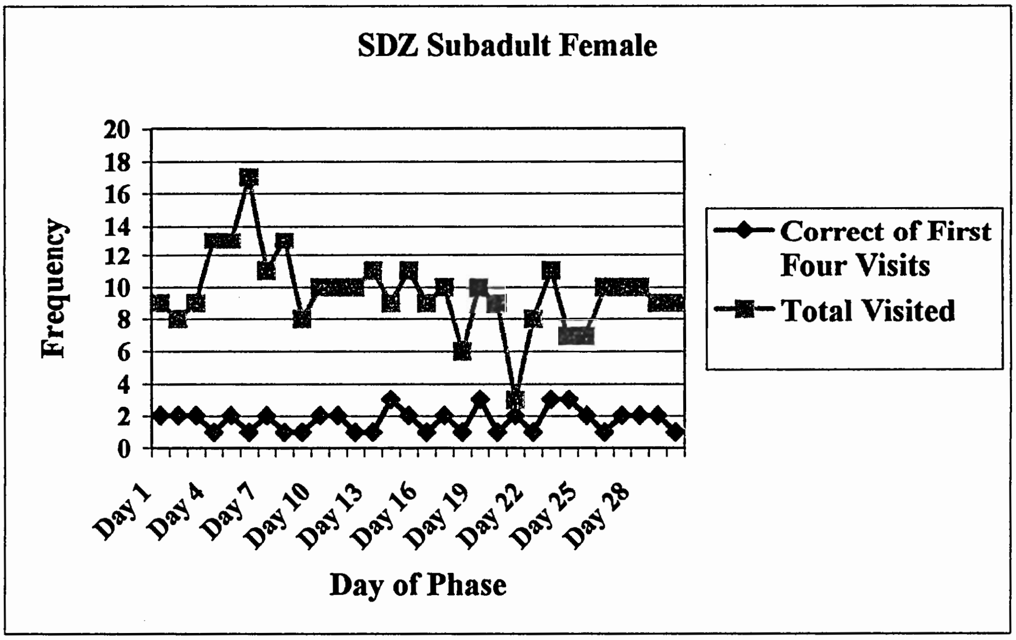

Figure 70 Number of visits to baited feeders in the first four visits and total number of feeders visited by the subadult female panda at the San Diego Zoo in each session of the olfactory task.

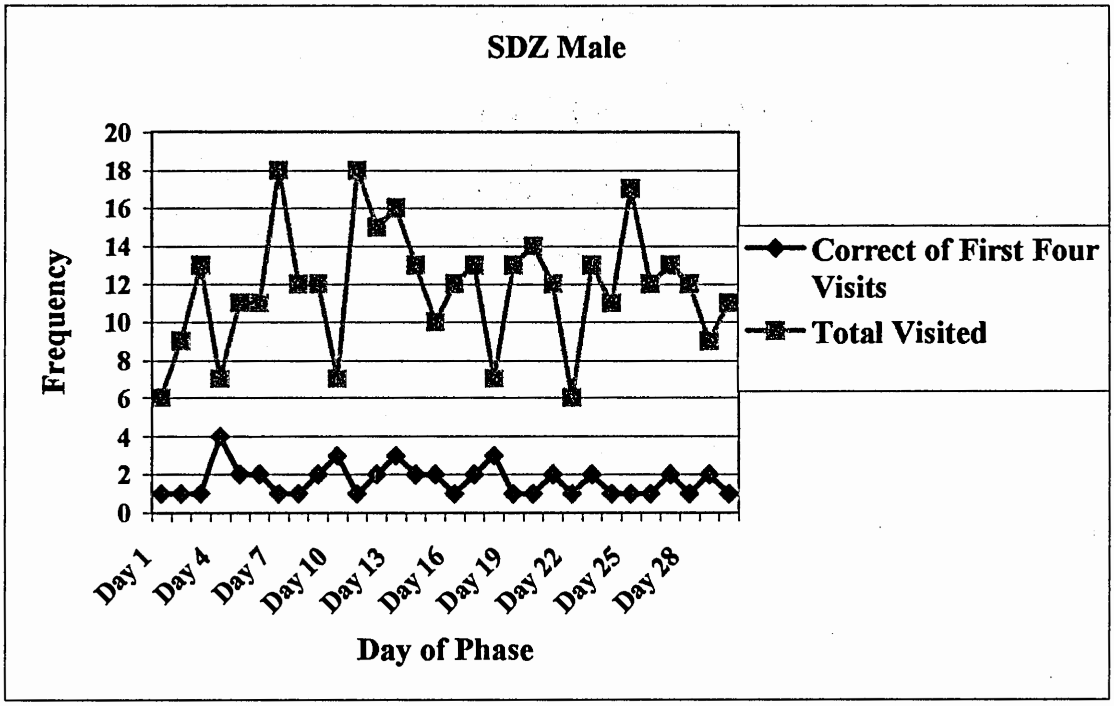

Figure 71 Number of visits to baited feeders in the first four visits and total number of feeders visited by the male panda at the San Diego Zoo in each session of the olfactory task.

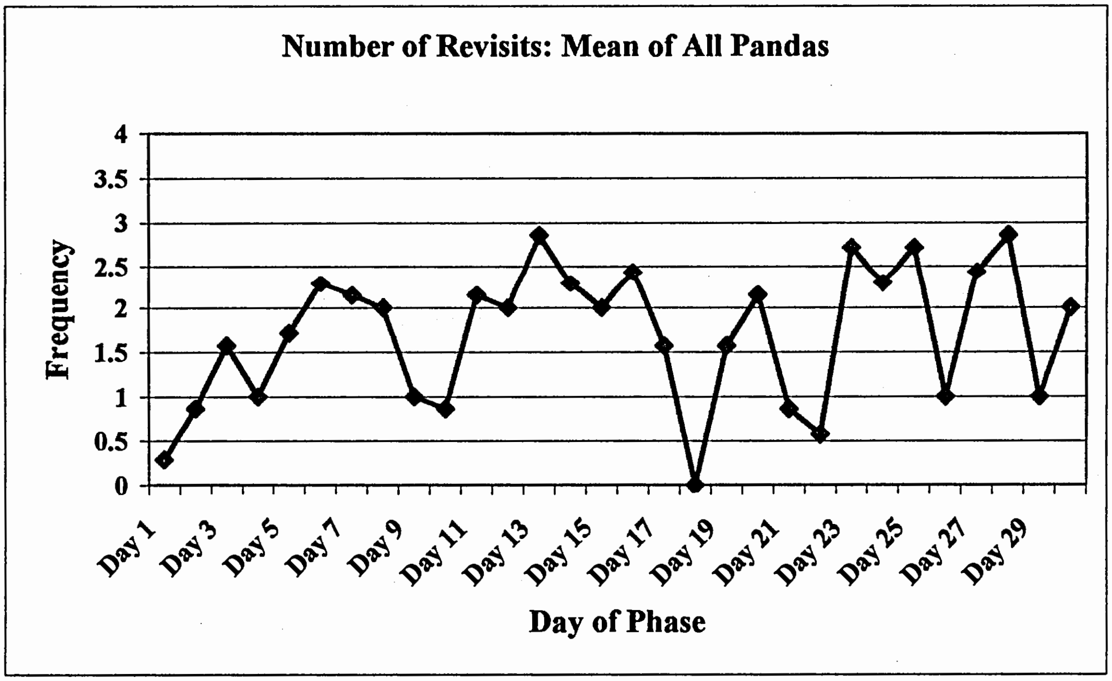

Figure 72 Number of visits to previously visited feeders by all pandas in each session of the olfactory task.

The behavior of the spectacled bears also did not seem to be under the control of the olfactory cue. Figure 73 presents the mean number of visits to baited feeders in the first four visits by the male and female spectacled bear. In the first five sessions, the spectacled bears visited a mean of 2.6 baited feeders in their first four visits. This was not significantly different from the 1.655 baited feeders that would be expected of a random forager [$D_{max} = 0.77$, $p = 0.10$]. It was also not significantly different from the mean of 2.5 visits to baited feeders in the first four visits that was expected based on the adjacency strategy they had used in the exploratory task [$D_{max} = 0.46$, $p = 0.65$]. There was no improvement in performance in the middle five sessions (Trials 13-17). The spectacled bears were still visiting a mean of 2.2 baited feeders in their first four visits, which was not significantly different from the 1.655 expected of either a randomly traveling forager [$D_{max} = 0.56$, $p = 0.39$] or from that expected based on an adjacency foraging strategy [$D_{max} = 0.35$, $p = 0.93$]. Finally, in the last five sessions of the task the spectacled bears visited a mean of 2.2 baited feeders in their first four visits, which was not significantly different than would be expected from a randomly traveling forager [$D_{max} = 0.64$, $p = 0.27$]. It was also not significantly different than would be expected from a forager using an adjacency strategy with preferred starting points ($X = 1.9$) [$D_{max} = 0.54$, $p = 0.42$].

In each trial, the spectacled bears only needed to visit 4 feeders to obtain all of the food in the yard. Figures 74 and 75 present the total number of visits in a session and the total number of visits to baited feeders in the first four visits. It is clear from these figures that the spectacled bears never learned to travel directly to feeders with the olfactory cue. In the first five sessions of the olfactory task, they only visited a mean of

4.2 feeders in each trial, which was significantly fewer than eight feeders [$D_{max} = 0.99$, p , 0.001], but not significantly different from the four feeders necessary to obtain all of the food [$D_{max} = 0.34$, $p = 0.93$]. However, the feeders they visited were not necessarily baited feeders and in some trials there was still food left in the feeders at the end of the trial, indicating that their foraging was not optimal in these sessions. It is possible that the break in testing between consecutive foraging tasks disrupted their behavior. In the middle five sessions, the spectacled bears were visiting a mean of 7.4 feeders in each trial, which was significantly more than the 4 necessary to obtain all of the food from the feeders [$D_{max} = 0.99$, $p < 0.001$] but not significantly different from a visit to all 8 feeders [$D_{max} = 0.45$, $p = 0.70$]. In the last five sessions the spectacled bears were still visiting significantly more feeders in a session than the four necessary to obtain all of the food [$D_{max} = 0.99$, $p < 0.001$] but not significantly different from visiting all 8 feeders [$D_{max} = 0.50$, $p = 0.50$].

There was a significant difference between the total number of revisits by giant pandas and spectacled across all trials of the olfactory task. The giant pandas revisited a mean of 50.6 feeders during the olfactory task, whereas the spectacled bears revisited a mean of only 3.5 feeders [$H = 0.0$, $p = 0.04$]. Therefore, the spectacled bears were making fewer errors than the giant pandas before the end of a trial.

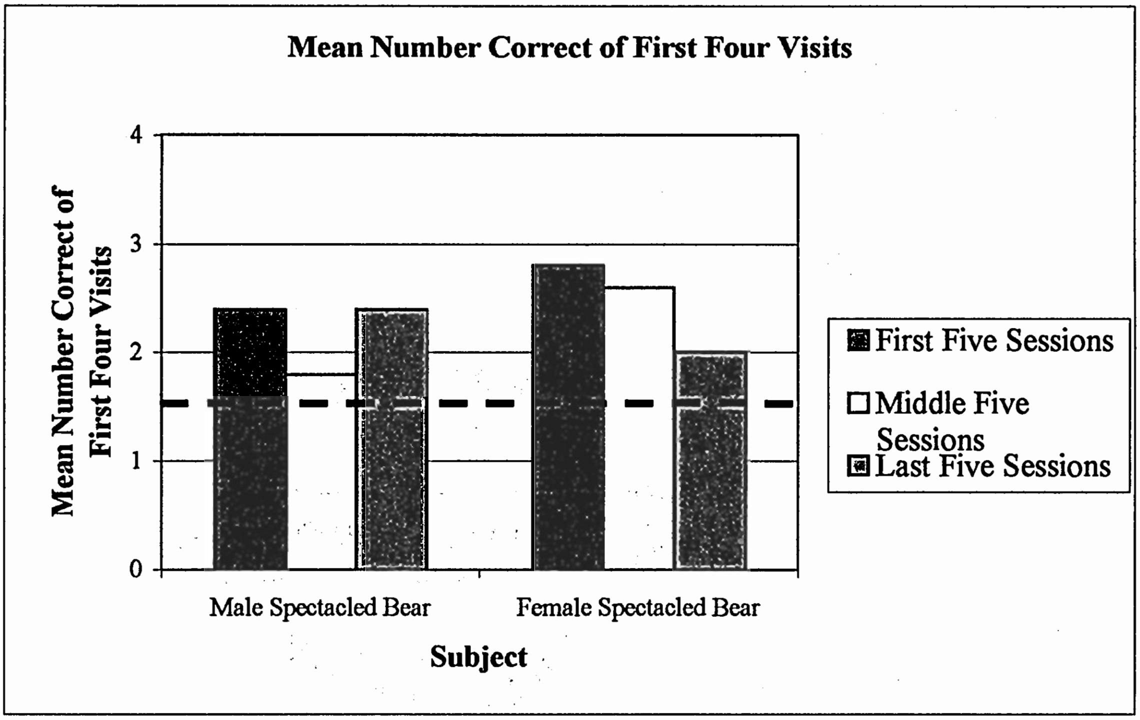

Figure 73 Mean number of visits to baited feeders (correct) in the first four visits by the spectacled bears in the first, middle and last five sessions of the olfactory task. The dashed line represents chance performance by a random forager.

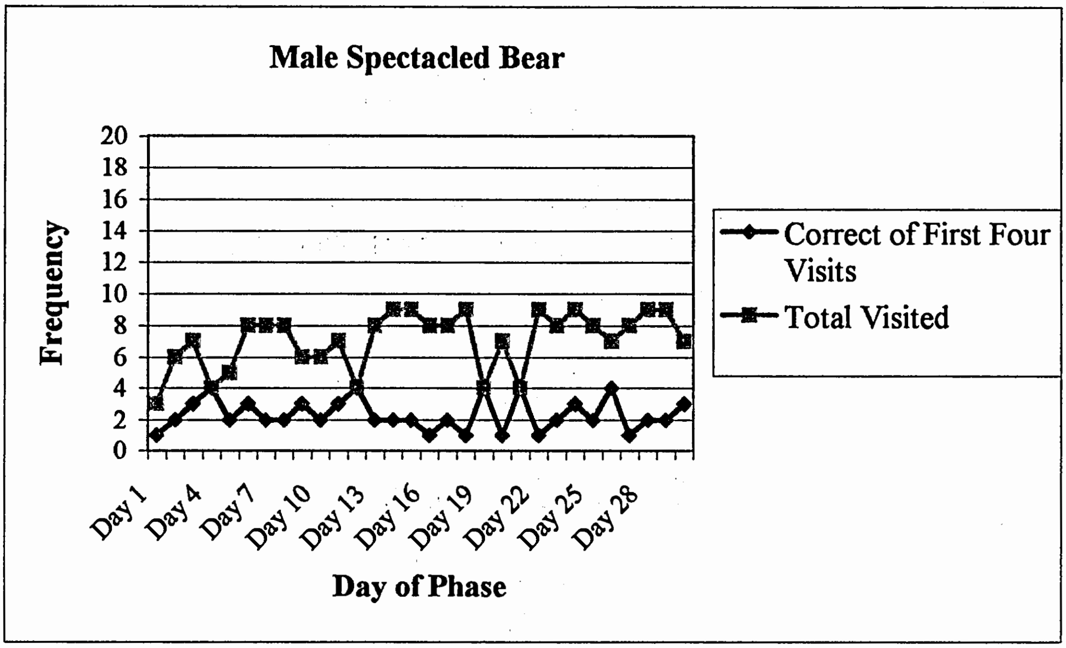

Figure 74 Number of visits to baited feeders in the first four visits and total number of feeders visited by the male spectacled bear in each session of the olfactory task.

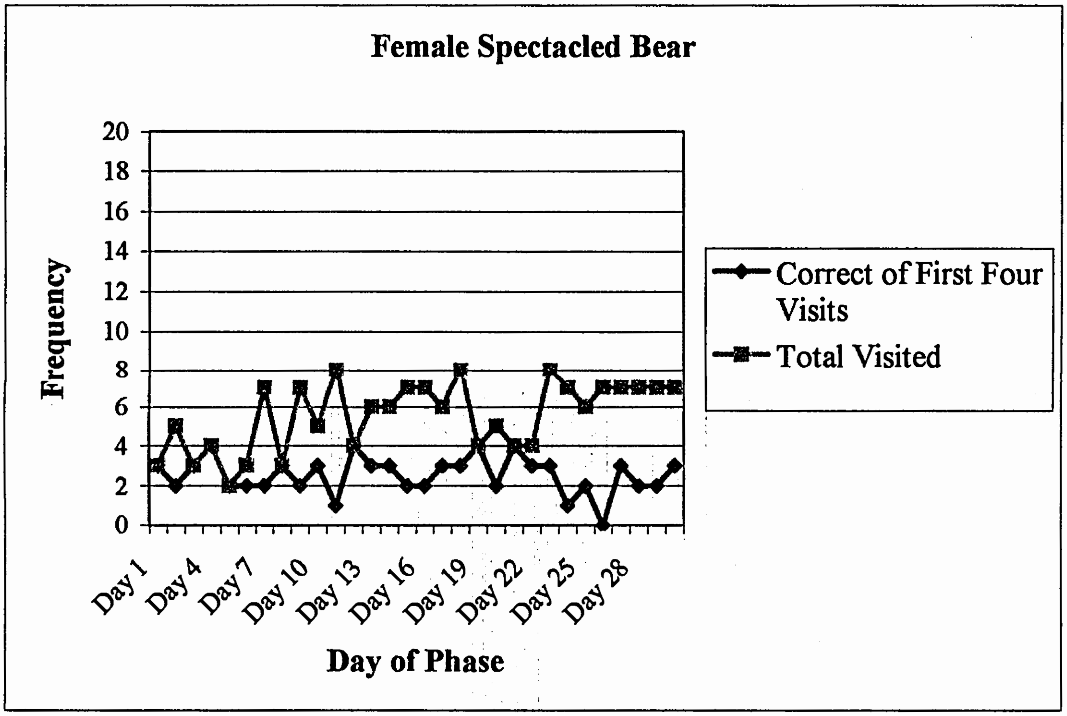

Figure 75 Number of visits to baited feeders in the first four visits and total number of feeders visited by the female spectacled bear in each session of the olfactory task.

6.4.4 Discussion

The behavior of neither the giant pandas nor the spectacled bears came under the control of the olfactory stimulus. The giant pandas visited significantly more baited feeders in their first four visits than would have been expected had they used a random pattern of foraging in each of the three blocks of trials. However, they used an adjacency strategy. Their accuracy in choosing baited feeders was not significantly different than would be expected based the adjacency strategy used throughout the study. The behavior of the spectacled bears did not differ from that which would be expected from a randomly traveling forager. They also did not visit significantly more baited feeders than would be expected by chance given the adjacent strategy of foraging used during the study. In most blocks of trials, the giant pandas and spectacled bears visited significantly more feeders than the four necessary to obtain all reinforcement. However, they did not visit significantly fewer than eight feeders, indicating that they were simply visiting each feeder during a trial.

6.5 Foraging Task 6: Spatial vs. Visual vs. Olfactory Discriminative Stimuli

6.5.1 Methods

This foraging task was designed to determine which of the three stimuli discriminative stimuli tested in the preceding tasks, if any, the bears preferentially use when foraging. Two randomly chosen feeders were baited and signaled in a search trial by spatial, visual, and olfactory discriminative stimuli. All stimuli were identical to those used in the previous foraging tasks. After a 10-minute period, the bears were removed from the test area and the feeders were thoroughly cleaned to remove the olfactory discriminative stimuli. The bears were then presented with a re-search trial in which two of the feeders were signaled by visual discriminative stimuli and two by olfactory discriminative stimuli. The location of the signaled feeders was pseudo-randomly chosen with the stipulation that they could not be located in the same spatial position as baited feeders in the search trial. Therefore, in the research trial two of the feeders had a visual cue (white lids), two had the olfactory cue (lemon oil), and two were in the same location as the baited feeders in the preceding search trial. None of the feeders in the re-search trial was baited with food, forcing the subjects to make more than one choice in their attempts to find food. The order of the choices made by the subjects was recorded and used to determine if visual, olfactory, or spatial discriminative stimuli are more important in foraging. For instance, if the first visit by a subject was to a feeder signaled by a visual discriminative stimulus it would indicate that visual discriminative stimuli are a more important source of information, whereas a first visit to a feeder signaled by a spatial or olfactory discriminative stimulus indicated that spatial or olfactory discriminative stimuli are more important.

It was important that the bears did not come to predict that all of the feeders in the re-search trial were empty. Therefore, some of the search trials were followed by another search trial rather than a re-search trial (search/search session). To train the giant pandas to enter and leave the test situation twice in one session, the first 10 search trials were followed by another search trial. After trial 10, the number of search/search sessions between search/re-search sessions were either 1, 2, 3 or 4. This number was randomly chosen after each search/re-search session. Data were recorded on general behavior and each visit to a feeder. One session was conducted each day until 15 search/re-search sessions had been conducted. All feeders were cleaned between sessions to minimize or eliminate any olfactory discriminative stimuli that could be left on the feeders by the bears during foraging.

Because of circumstances beyond my control (weather related delays in testing, staffing issues, volunteer issues), the data from the spectacled bears is not currently available and will not be presented in this document. They will be tested on this same foraging task at a later date for comparison with the giant pandas.

6.5.2 Data Analysis

In Foraging Task 6, two of the feeders were signaled by a visual discriminative stimulus, two were signaled by an olfactory discriminative stimulus, two were in the same spatial position as the previously baited feeders, and two were not signaled by discriminative stimuli in the re-search phase. If the giant pandas had no preference for choosing a feeder on the basis of one discriminative stimulus or another in the re-search phase of the test sessions, it would be expected that the feeders with each type of discriminative stimulus would be equally likely to be the first and second feeders visited in a re-search trial. Therefore, based on chance it would be expected that visits to feeders would be equally distributed with no regard to the type of information with which each is associated. Data collected in the re-search phase of the test trials in Foraging Task 6 were analyzed by examining the frequency with which the feeders with the visual, olfactory, or spatial discriminative stimuli were encountered in the either the first or second visit during foraging. A Friedman one way analysis of variance was used to determine if there were differences in the number of times a feeder with each discriminative stimulus was chosen first or second during foraging. Post-hoc analyses were conducted using Wilcoxon signed rank tests to determine if there were significant differences between the frequency with which the individual discriminative stimuli were chosen in the first or second visits. Finally, the feeders in the re-search phase of the test trials were not baited to encourage the giant pandas to visit all of the feeders. Therefore, the total number of feeders visited in each re-search trial of the test sessions was compared to 8, the total number of feeders available for visitation, using one-sample t-tests.

The filler trials were also important for examining the ability of the giant pandas to use a win-stay strategy. One-sample t-tests were used to determine if the giant pandas were using a random or least-distance foraging strategy. If the giant pandas were using a random pattern foraging they would be expected to visit a mean of 0.49 baited feeders in the first two visits during the search and re-search trials. The number of baited feeders expected to be visited in the first two visits if they were using an adjacency strategy of foraging was calculated from the direction of travel and preference for starting feeder in the exploratory task. Two of the giant pandas foraged randomly throughout the search and re-search trials of the filler tasks. The other five visited more baited feeders in their first two visits than would have been expected had they been foraging randomly using a random or least-distance pattern of foraging. These two groups were categorized as the low performance group and the high performance group respectively. The behavior of the giant pandas in both groups was compared to that expected had they been foraging randomly or using an adjacency strategy using one sample Komolgorov-Smirnov tests. The groups were compared to each other using Kruskal Wallis tests. All results were considered to be significant at p values less than 0.05.

6.5.3 Results

In the importance of discriminative stimuli task, there were two types of trials, "test" sessions and "filler" sessions. In the test sessions, a search trial (2 of the 8 feeders had all three discriminative stimuli and were baited with food) was followed by a re-search trial (visual and olfactory discriminative stimuli moved to 2 randomly chosen feeders and all feeders were left unbaited). These trials differed from the filler trials in which search trials were followed by a re-search trial with conditions identical to those experienced in the search trial. The filler sessions were designed both as training sessions and to prevent the giant pandas from learning that searching behavior in the re-search trials would not be rewarded. Of interest was the order in which the giant pandas visited the feeders and the number of feeders visited during a trial. There were 15 test trials and 46 filler trials.

In the test trials, I calculated the frequency with which the giant pandas visited feeders with visual discriminative stimuli, olfactory discriminative stimuli, spatial discriminative stimuli or no discriminative stimuli in their first two visits to feeders during the re-search phase. The data is shown in Figures 76-78 for individual giant pandas. Neither the NZP female (Figure 77) nor the SDZ male (Figure 78) appeared to be using one discriminative stimulus more often than the others in their first two choices, therefore their data was not included in the overall mean. As can be seen in Figure 79, for those giant pandas that showed evidence of discriminative responding, 74.4% of the first two visits were to feeders signaled by the visual cue, 14.5% were to feeders in the same spatial location as those that had been baited in the preceding search phase, 7.0% were to feeders signaled by the olfactory cue, and 4.1% were to feeders that had no associated cue. A Friedman one-way analysis of variance indicated that there was a main effect of type of information on the frequency with which the giant pandas visited certain feeders in their first 2 choices [$\chi2 = 11.94$, $p = 0.008$]. Post-hoc analyses using Wilcoxon signed rank tests indicated that the giant pandas were more likely to visit feeders with white lids than feeders that were in the same position as those baited in the preceding search trial [$Z = -2.02$, $p = 0.04$], feeders signaled by an olfactory discriminative stimulus [$Z = -2.03$, $p = 0.04$] or feeders that had no discriminative stimulus [$Z = -2.02$, $p = 0.04$]. However, they were not significantly more likely to visit feeders in the same spatial location as that of the baited feeders in the search trial in their first two visits or feeders signaled by the olfactory cue [$Z = -1.10$, $p = 0.27$]. They were more likely to visit feeders in the same spatial location as those baited in the search trial in their first two visits than the feeders with no signal [$Z = -2.02$, 0.04], but were not more likely to visit feeders signaled by the olfactory cue than visit feeders with no cue [$Z = -1.46$, 0.14].

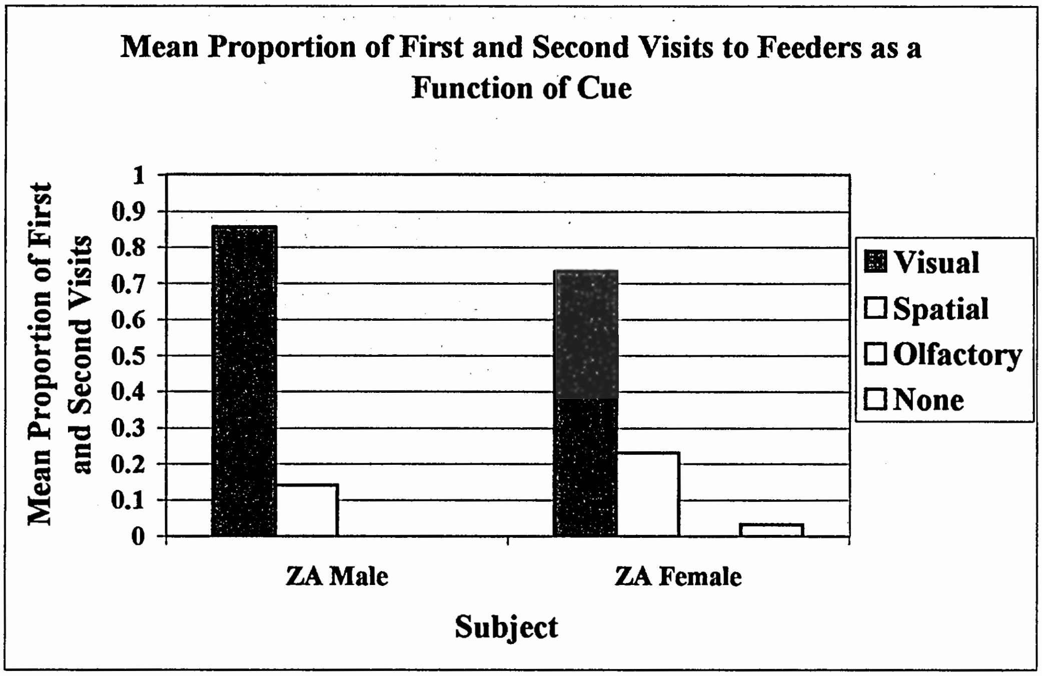

Figure 76 The frequency with which the ZA pandas visited feeders with visual, olfactory, spatial cues, or no cues in their first two visits to feeders during the re-search trials of test sessions.

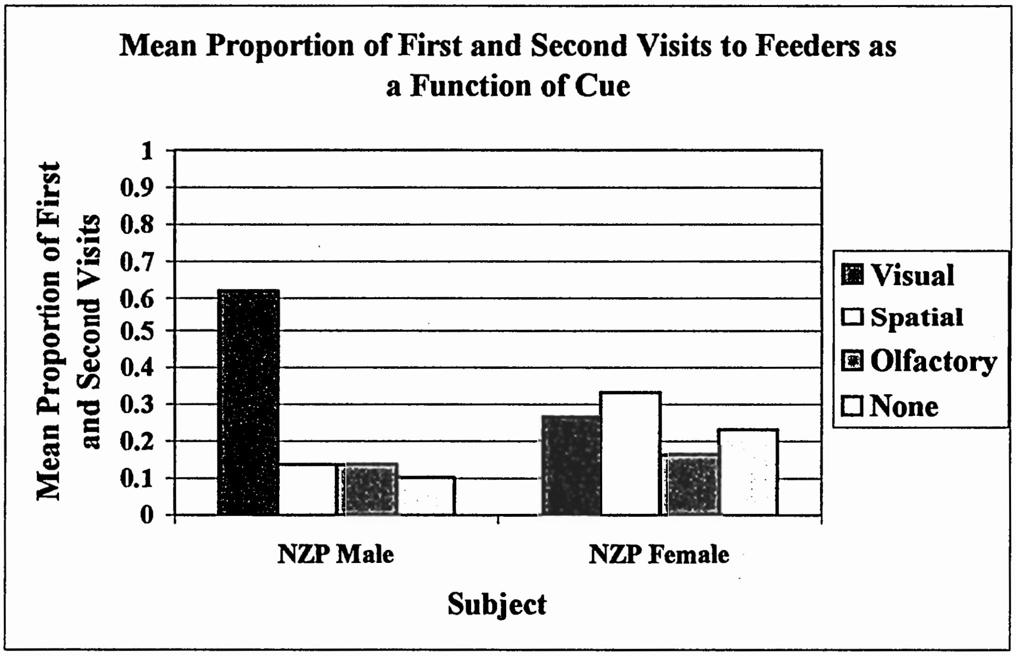

Figure 77 The frequency with which the NZP pandas visited feeders with visual, olfactory, spatial cues, or no cues in their first two visits to feeders during the re-search trials of test sessions.

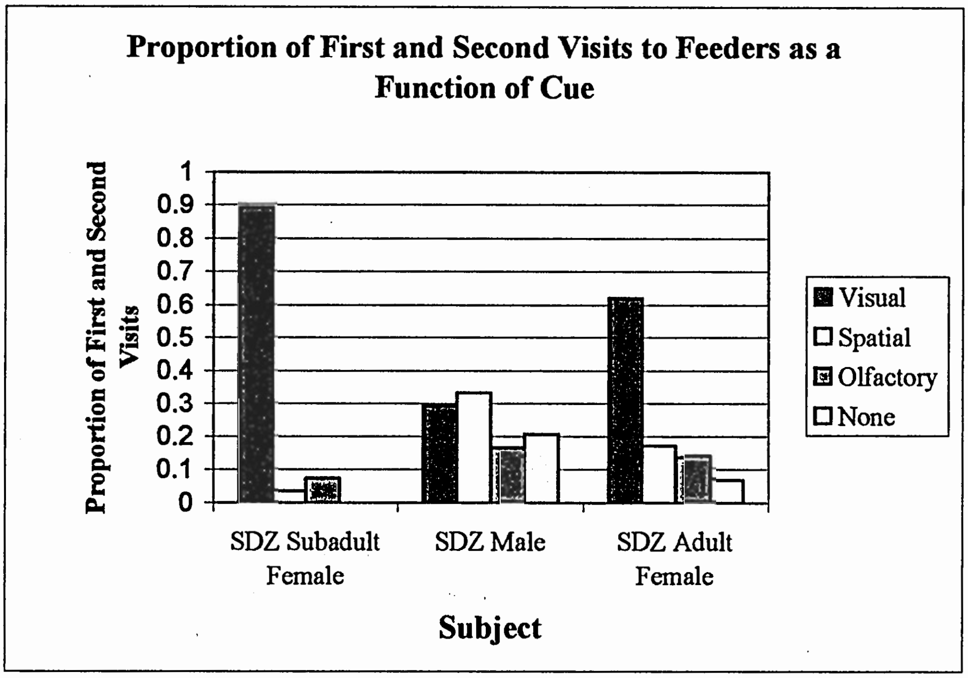

Figure 78 The frequency with which the SDZ giant pandas visited feeders with visual, olfactory, spatial cues or no cues in their first two visits to feeders during the re-search trials of test sessions.

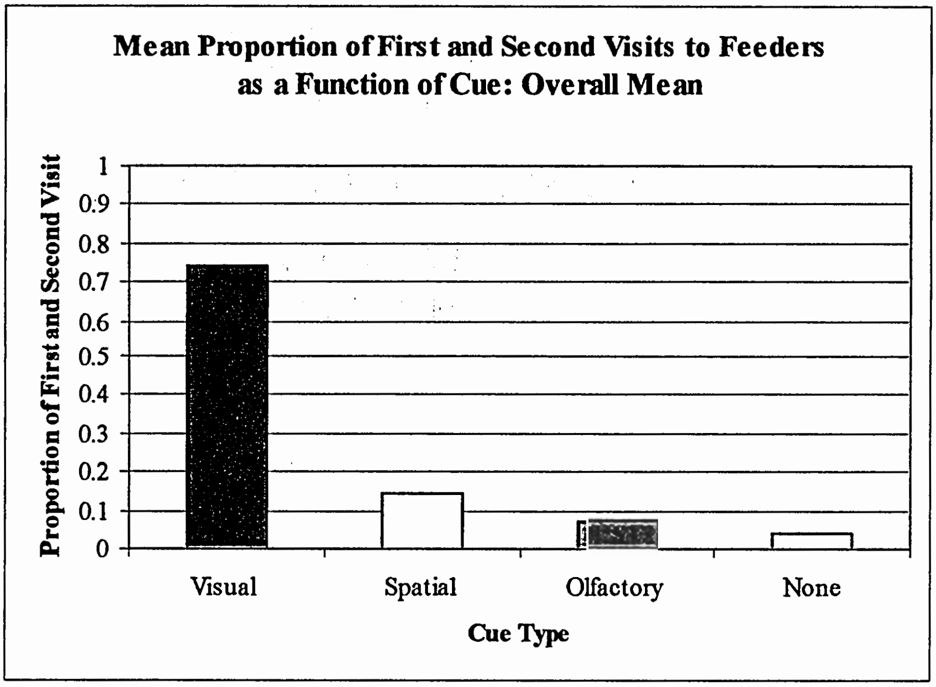

Figure 79 The frequency with which the giant pandas visited feeders with visual, olfactory, spatial cues or no cues in their first two visits to feeders during the re-search trials of test sessions (excluding SDZ male and NZP female).

To encourage the giant pandas to search all of the feeders for food, the feeders were not baited in the re-search trials of the test sessions. However, the giant pandas visited significantly fewer than all 8 of the feeders in both the first five sessions (X = 4.26) [t(6) = -5.40, p = 0.002] and the last five sessions of the re-search trials (X = 3.12) [t(6)) = -10.92, p < 0.001]. Searching in the last five sessions of the re-search was limited to only 2 or 3 feeders by most giant pandas. The behavior of the giant pandas was not significantly different from either 2 [t(6) = 2.51, p = 0.05] or 3 visits [t(6) = 0.27, p = 0.80]. This data is depicted in Figure 80.

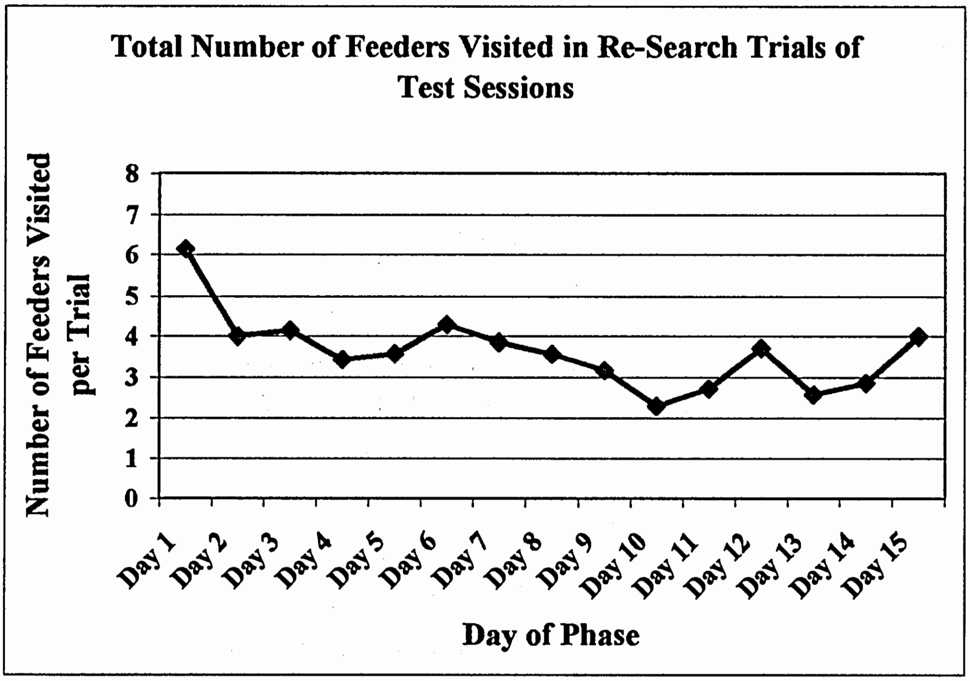

Figure 80 Total number of feeders visited (mean of all pandas) in the re-search trials of the test sessions.

The filler sessions were intended to prevent behavior in the re-search trials of the test sessions from reaching extinction. They were similar to win-stay tasks used in other studies and are, therefore, interesting in and of themselves. In the filler sessions, a randomly traveling forager would be expected to visit 0.47 baited feeders in their first 2 visits during both the search trials and the re-search trials. To forage efficiently, the giant pandas should develop a win-stay strategy. That is, in the re-search trial they should return to the feeders that had been baited in the preceding search trial. Figures 81-87 show the mean number of visits to baited feeders (correct visits) of the first two visits by each of the giant pandas at the three institutions in the search and re-search trials of the filler sessions, and Figure 88 shows the mean of all giant pandas. In the re-search trials of the first 5 filler sessions of the importance of discriminative stimuli task, the giant pandas visited a mean of 1.02 baited feeders in their first 2 visits. This was significantly better than would be expected had they been foraging randomly [t(6) = 4.82, p = 0.003]. The number of visits to baited feeders in the first two visits was also significantly more than expected had the giant pandas been using an adjacency strategy similar to that used in the other phases of the study (X = 0.49) [t(6) = 4.63, p = 0.004]. The giant pandas visited significantly more baited feeders in their first two visits in the last five sessions (X = 1.54) than would be predicted on the basis of either random travel (X = 0.47) [t(6) = 6.41, p = 0.001] or an adjacency strategy (X = 0.69) [t(6) = 5.09, p = 0.002].

In the search trials of the first 5 sessions the giant pandas were not visiting more baited feeders in their first 2 visits (X = 0.57) than would be expected had they been foraging randomly (X = 0.47) [t(6) = 1.27, p = 0.25]. They also were not visiting more baited feeders in their first 2 visits than would be expected had they been using an adjacency strategy based on direction of travel in previous tasks (X = 0.69) [t(6) = 1.01, p = 0.35]. In the last 5 search trials of the filler sessions, the giant pandas were visiting significantly more baited feeders (X = 1.46) than would be expected had they been traveling either randomly among the feeders (X = 0.47) [t(6) = 4.46, p = 0.004] or using an adjacency strategy (X = 0.69) [t(6) = 3.47, p = 0.01]. This indicates that at least some of the giant pandas had learned to travel directly to baited feeders in the search trials of the filler sessions using either the visual or olfactory discriminative stimulus. As determined by the test sessions, they were using the visual discriminative stimulus.

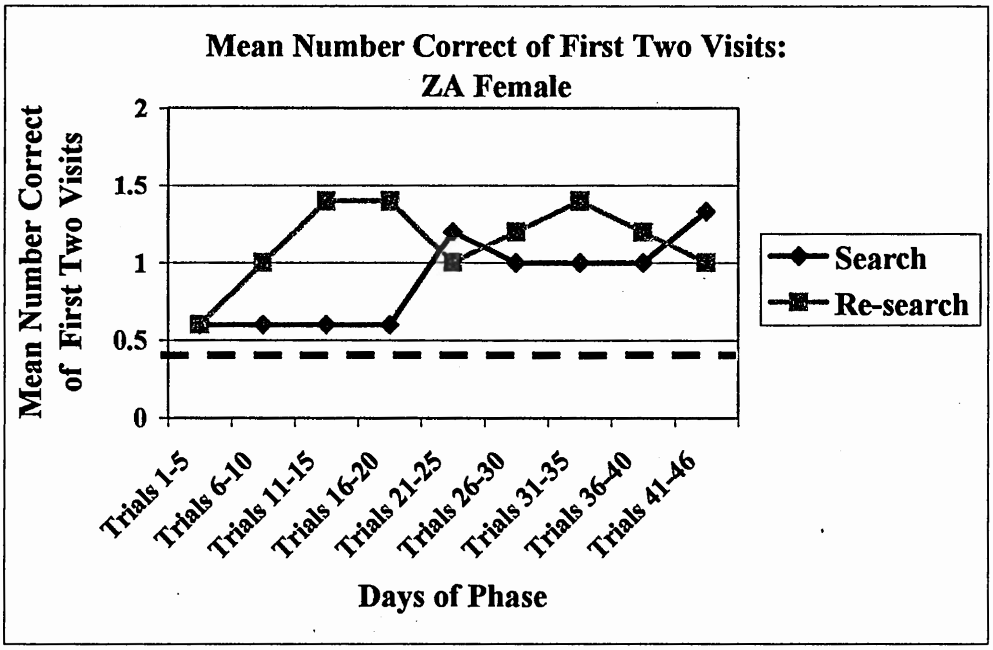

Figure 81 Mean number of visits to baited feeders (correct visits) of the first two visits by the ZA female in the search and re-search trials of the filler sessions. The dashed line represents chance performance.

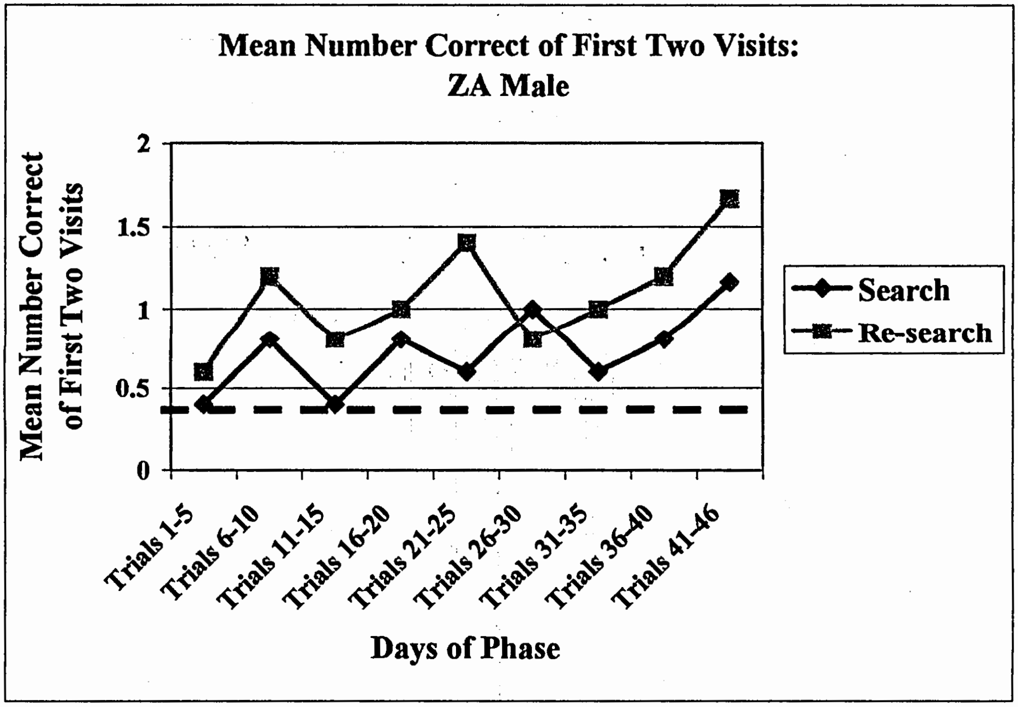

Figure 82 Mean number of visits to baited feeders (correct visits) of the first two visits by the ZA male in the search and re-search trials of the filler sessions. The dashed line represents chance performance.

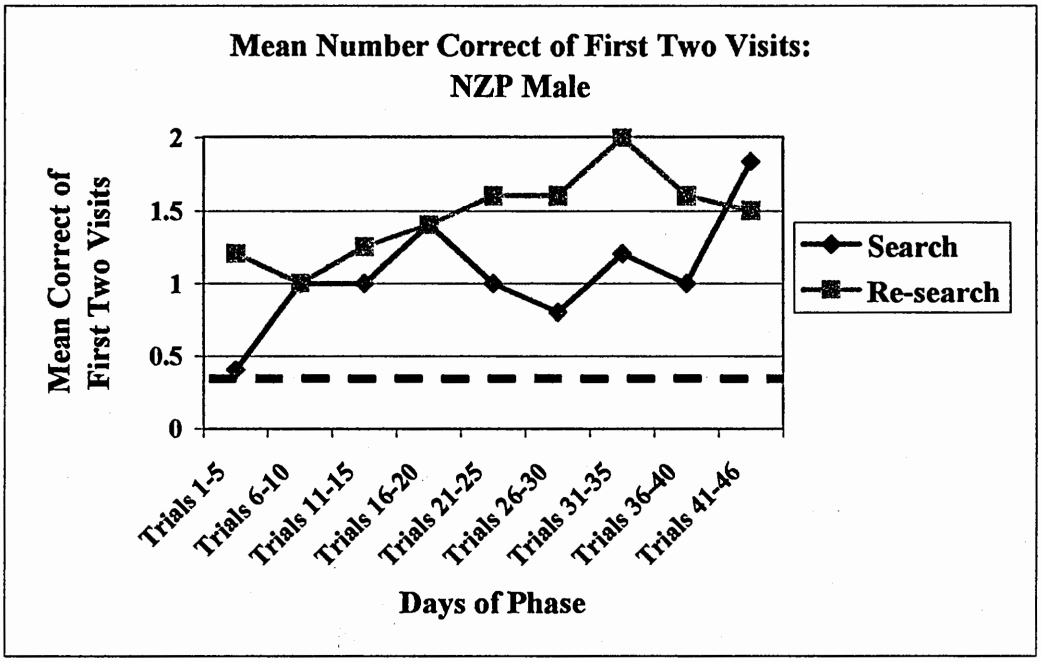

Figure 83 Mean number of visits to baited feeders (correct visits) of the first two visits by the NZP male in the search and re-search trials of the filler sessions. The dashed line represents chance performance.

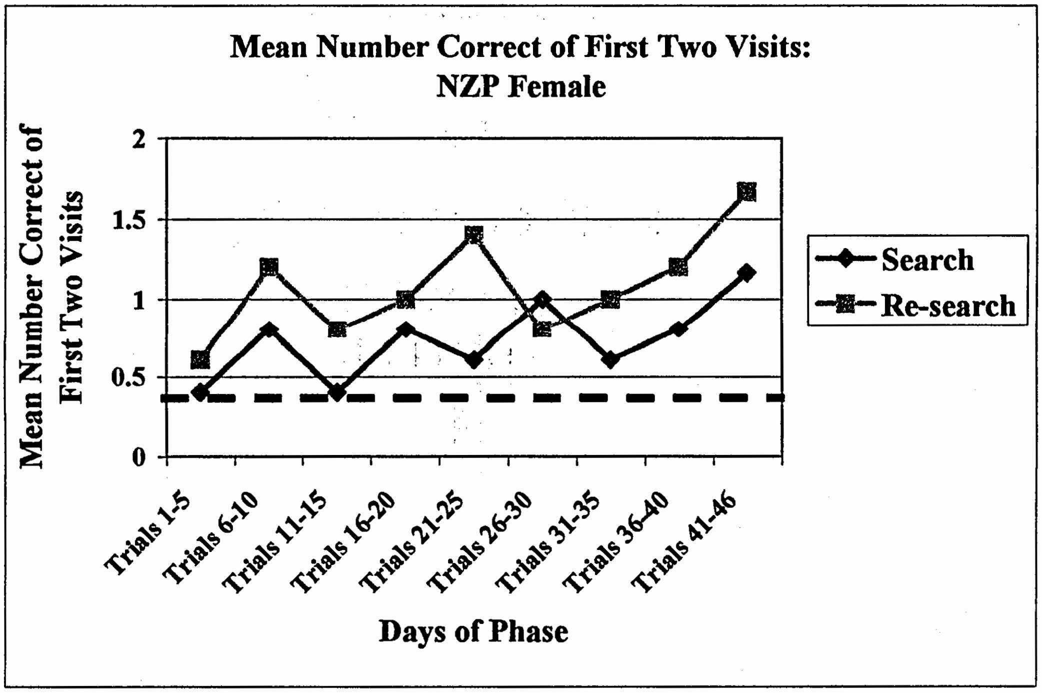

Figure 84 Mean number of visits to baited feeders (correct visits) of the first two visits by the NZP female in the search and re-search trials of the filler sessions. The dashed line represents chance performance.

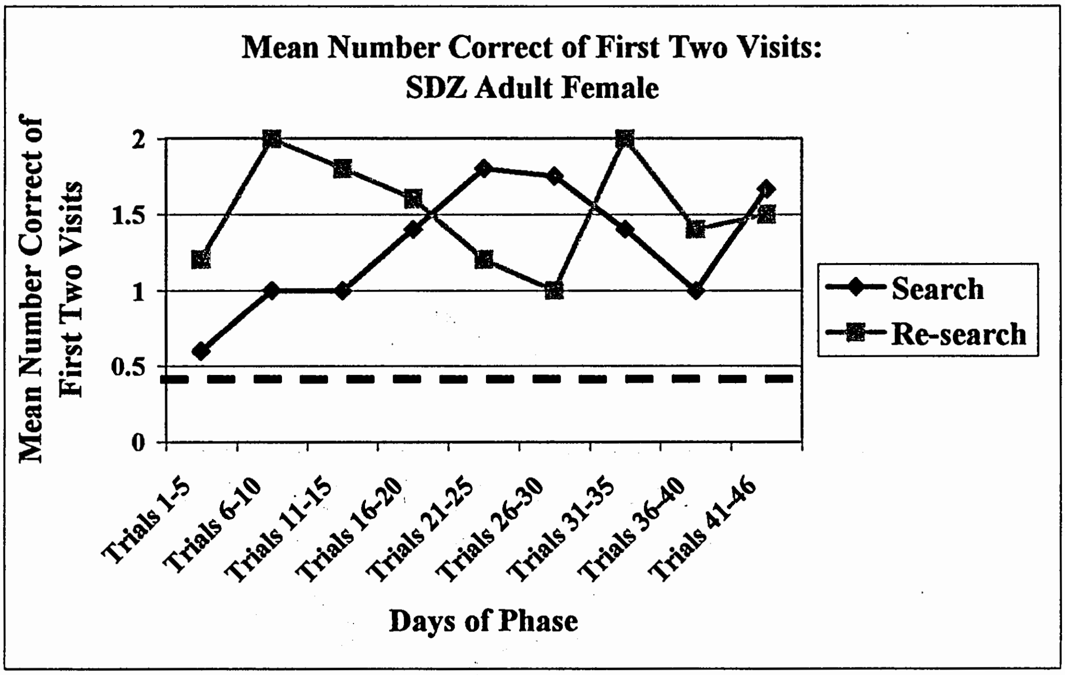

Figure 85 Mean number of visits to baited feeders (correct visits) of the first two visits by the SDZ adult female in the search and re-search trials of the filler sessions. The dashed line represents chance performance.

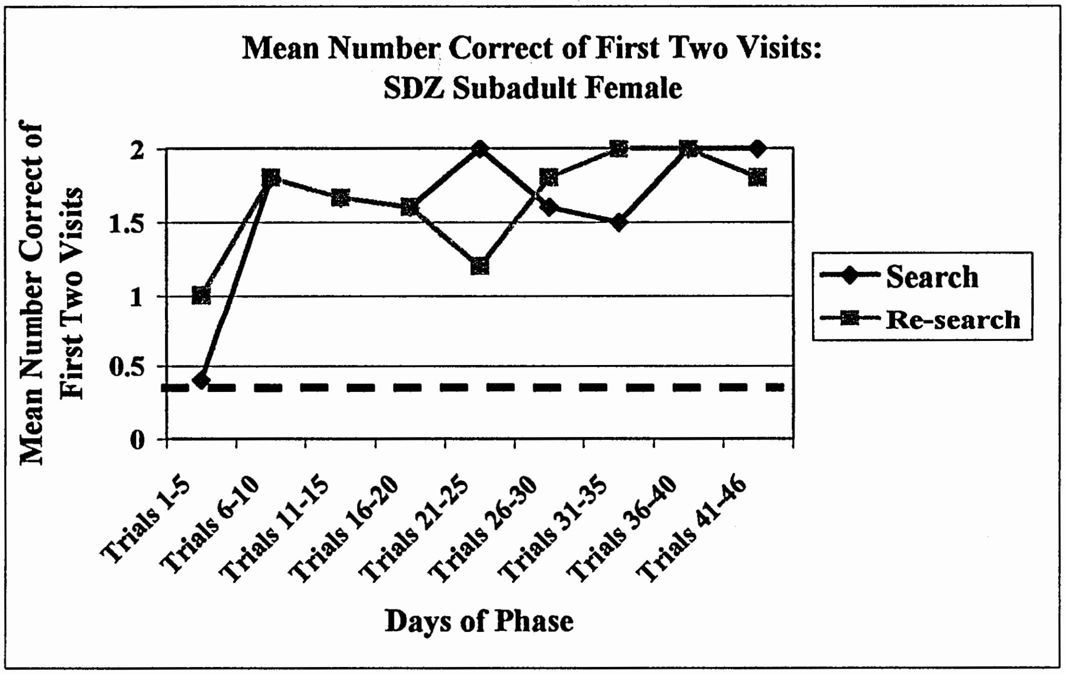

Figure 86 Mean number of visits to baited feeders (correct visits) of the first two visits by the SDZ subadult female in the search and re-search trials of the filler sessions. The dashed line represents chance performance.

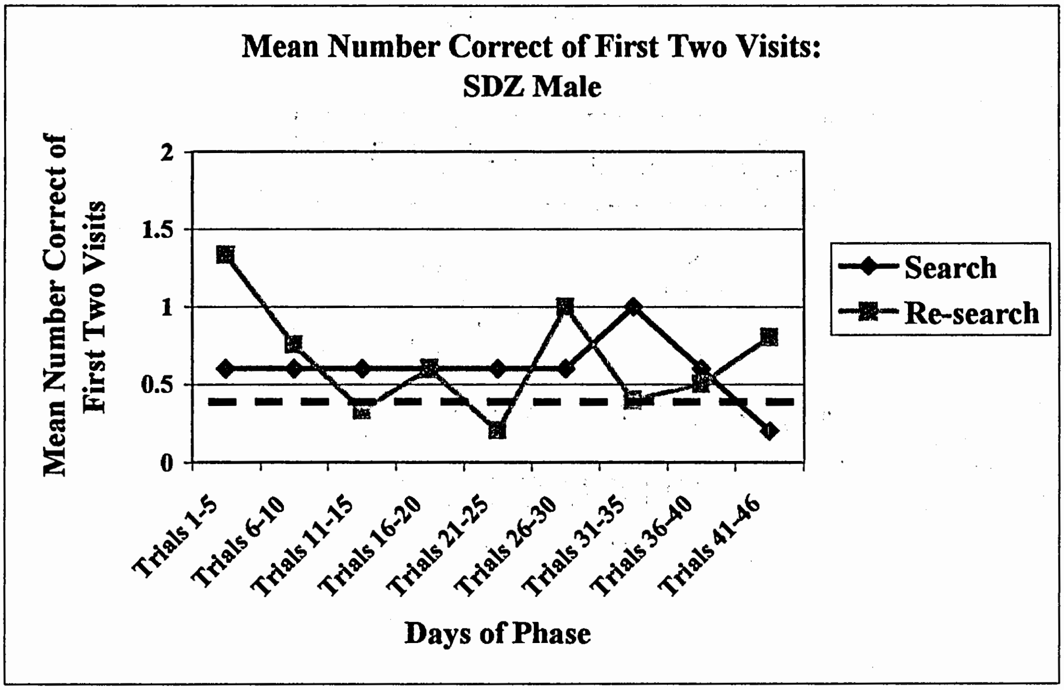

Figure 87 Mean number of visits to baited feeders (correct visits) of the first two visits by the SDZ male in the search and re-search trials of the filler sessions. The dashed line represents chance performance.

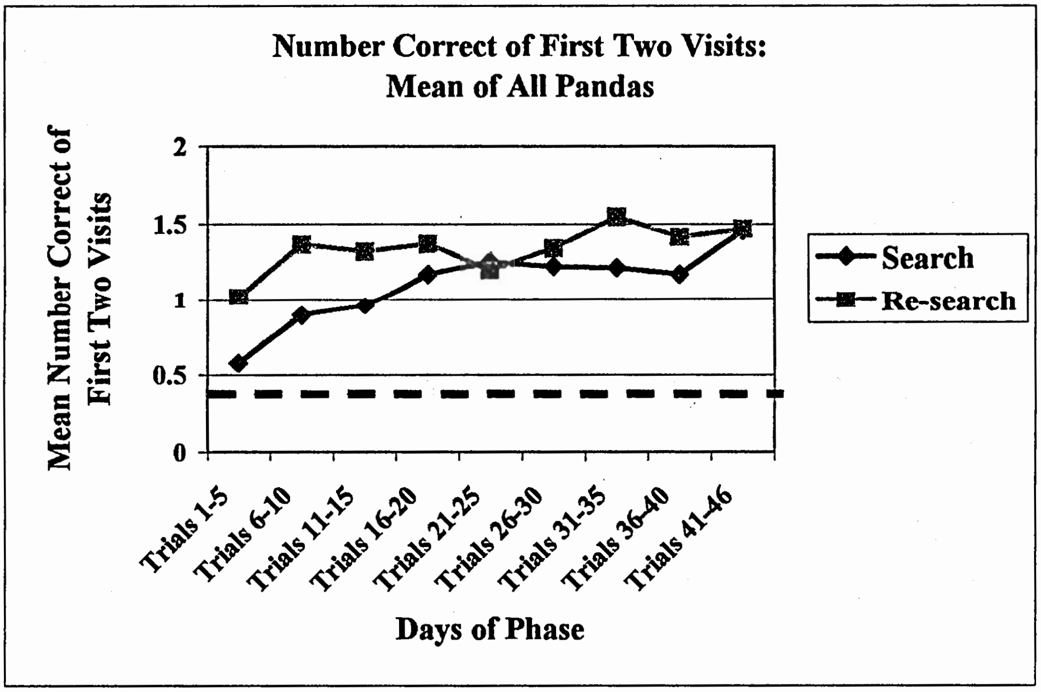

Figure 88 Mean number of visits to baited feeders (correct visits) of the first two visits by the SDZ male in the search and re-search trials of the filler sessions. The dashed line represents chance performance.

As can be seen in Table 3, five of the seven giant pandas became very accurate in their foraging in the re-search trials of the filler sessions, choosing 2 baited feeders in their first two visits in at least 4 of 5 sessions. Both the male and the female panda at NZP reached this level of performance in 31 and 43 sessions respectively. The adult female and subadult female at SDZ reached this level of performance within 7 and 9 sessions respectively. The male at ZA visited 2 baited feeders in his first two visits in at least 4 of 5 sessions by the 10th session. Neither the SDZ male nor the ZA female reached this level of performance across any of the 62 filler sessions. The five giant pandas that reached a high level of performance will be referred to in the rest of this section as the "high performance" group and the other two giant pandas will be referred to as the "low" performance group.

Four of the 7 giant pandas reached a criterion performance level in the search trials of the filler sessions, traveling directly to 2 baited feeders in their first 2 visits in at least 4 of 5 sessions. By the 10th search trial of the filler sessions, the subadult female at SDZ was visiting 2 baited feeders in her first 2 visits in at least 4 of 5 consecutive sessions. The adult male at ZA reached this level of performance in 18 trials, the adult female at SDZ reached this level in 25 trials, and the adult male at NZP reached this level in 45 trials.

Table 3 Number of trials required by each panda to reach criterion performance in the search trials and re-search trials of the filler sessions of the compound stimulus task.

		Number of Trials to Reach Criterion	
Subject	Group	Search Trials	Re-Search Trials
ZA Female	Low Performance	Did Not Reach	Did Not Reach
ZA Male	High Performance	18	10
NZP Female	High Performance	Did Not Reach	43
NZP Male	High Performance	45	31
SDZ Adult Female	High Performance	25	7
SDZ Subadult Female	High Performance	10	9
SDZ Male	Low performance	Did Not Reach	Did Not Reach

The giant pandas in the high performance group visited a mean of 1.04 baited feeders in their first 2 visits in the re-search trials of the first five filler sessions. This was significantly more visits to baited feeders in the first 2 visits than would be expected by both by a randomly traveling forager (0.47) [$D_{max} = 0.70$, $p = 0.02$] and a forager using an adjacency strategy ($X = 0.44$) [$D_{max} = 0.71$, $p = 0.02$]. In the last five re-search trials of the filler sessions, giant pandas in the high performance group visited a mean of 1.8 baited feeders in their first 2 visits, which was also significantly greater than both that expected by a randomly foraging animal [$D_{max} = 0.91$, $p < 0.001$] and that expected had they been using an adjacency strategy ($X = 0.44$) [$D_{max} = 0.92$, $p < 0.001$]. The giant pandas in the high performance group visited a mean of 1.8 baited feeders in their first 2 visits in the last 5 re-search trials, which was significantly greater than the number of baited feeders visited in their first 2 visits in the first 5 re-search trials ($X = 1.04$) [$Z = 2.06$, $p = 0.04$].

The giant pandas in the low performance group visited a mean of 0.97 baited feeders in their first 2 visits in the first 5 re-search trials and a mean of 0.9 baited feeders in the last 5 re-search trials. The number of visits to baited feeders in the first 2 visits in the re-search trials of those first 5 sessions was not significantly different than that expected by a randomly foraging animal [$D_{max} = 0.55$, $p = 0.22$] or that expected had they been using an adjacency strategy ($X = 0.60$) [$D_{max} = 0.53$, $p = 0.27$]. The number of visits to baited feeders in the first 2 visits in the re-search trials of the last 5 sessions was also not significantly different from that expected by a randomly foraging animal [$D_{max} = 0.63$, $p = 0.11$] or that expected had they been using an adjacency strategy ($X = 0.70$) [$D_{max} = 0.55$, $p = 0.22$]. There was no significant difference in the number of visits to baited feeders in the first 2 visits between the first 5 and last 5 re-search trials [$Z = -0.45$, $p = 0.66$]. A Kruskal-Wallis test indicated that the performance of those in the high performance group did not differ significantly from those in the low performance group in the re-search trials in the first 5 sessions of the task [$H = 5.5$, $p = 0.84$]. However, performance did differ significantly between the groups in the last five trials [$H = 0.0$, $p = 0.02$].

In the search trials of the last 5 sessions of the filler task, the high performance giant pandas visited a mean of 1.8 baited feeders in their first 2 visits, which was better than would be expected had they been foraging randomly [$D_{max} = 0.91$, $p < 0.001$] and better than expected had they been using an adjacency strategy [$D_{max} = 0.89$, $p < 0.001$]. All of the individuals that developed a high accuracy of performance in the search trials were also in the high performance group identified in the re-search trials. With the exception of the subadult female from SDZ, the giant pandas in this high performance group reached the high level of performance in the re-search trials before they reached a high level of performance in the search trials. This suggests that the initial learning of either the olfactory or the visual discriminative stimulus took place during the re-search trials and then transferred to later search trials. As the results from the test trials indicate, it was the visual discriminative stimulus that they learned to associate with the presence of food.

In the filler sessions of foraging task 6, the giant pandas only needed to visit 2 feeders to obtain all of the food in each session. Figures 89-95 present the mean number of visits to feeders in the search and re-search trials of the filler sessions, and Figure 96 presents the mean of all giant pandas. In the first 5 search trials of the filler sessions, the giant pandas visited a mean of 7.29 feeders during each session. This was significantly more than the 2 visits necessary to obtain all of the food [$t(6) = 9.29$, $p < 0.001$], and not significantly less than the 8 expected had they searched exhaustively for food [$t(6) = -1.26$, $p = 0.26$]. A Kruskal-Wallis test indicated that there was no significant difference between the number of feeders visited in the re-search trials of the first 5 filler sessions by the high performance ($X = 6.6$) and low performance groups ($X = 8.3$) [$H = 10.5$, $p = 0.11$]. However, in the last 5 search trials of the filler sessions the giant pandas visited a mean of 3.66 feeders, which was not significantly different from the 2 visits necessary to obtain the food [$t(6) = 1.65$, $p = 0.15$]. This was less than the 8 visits that would suggest exhaustive searching [$t(6) = -4.33$, $p = 0.005$]. The difference in the mean number of feeders visited in the search trials of the last five filler sessions between the giant pandas in the high performance group ($X = 2.3$) and low performance group ($X = 5.47$) approached significance [$H = 11.5$, $p = 0.05$].

The giant pandas visited significantly fewer feeders than the 8 expected had they searched exhaustively for food in the first five re-search trials of the filler sessions ($X = 5.43$) [$t(6) = -2.58$, $p = 0.04$]. However, it was significantly more feeders than the 2 expected had they gone directly to feeders that were baited in the search trial and stopped searching [$t(6) = 3.44$, $p = 0.01$]. The giant pandas visited significantly fewer feeders in the first 5 re-search trials than the first 5 search trials in the filler sessions [$t(6) = 3.03$, $p = 0.02$], further indicating that they were using a win-stay strategy in the re-search trials. There was no significant difference between the number of feeders visited in the re-search trials of the first 5 filler sessions by the high performance ($X = 6.2$) and low performance groups ($X = 3.5$) [$U = 5.0$, $p = 1.0$]. In the re-search trials of the last 5 filler sessions of the compound stimulus task, the giant pandas visited a mean of 2.91 feeders, which was significantly fewer than the 8 expected had they searched exhaustively for food [$t(6) = -15.73$, $p < 0.001$], but still more feeders than the 2 feeders expected had they gone directly to feeders that had been baited in the preceding search trials and stopped searching [$t(6) = 2.83$, $p = 0.03$]. There was no difference in performance between the search trials and re-search trials of the last five filler sessions [$t(6) = 0.93$, $p = 0.39$], indicating that the giant pandas had learned to visit fewer feeders in the search trials. There was no significant difference between the mean number of feeders visited in the last 5 re-search trials by the high performance ($X = 2.8$) and low performance groups ($X = 3.1$) [$U = 5.0$, $p = 1.0$].

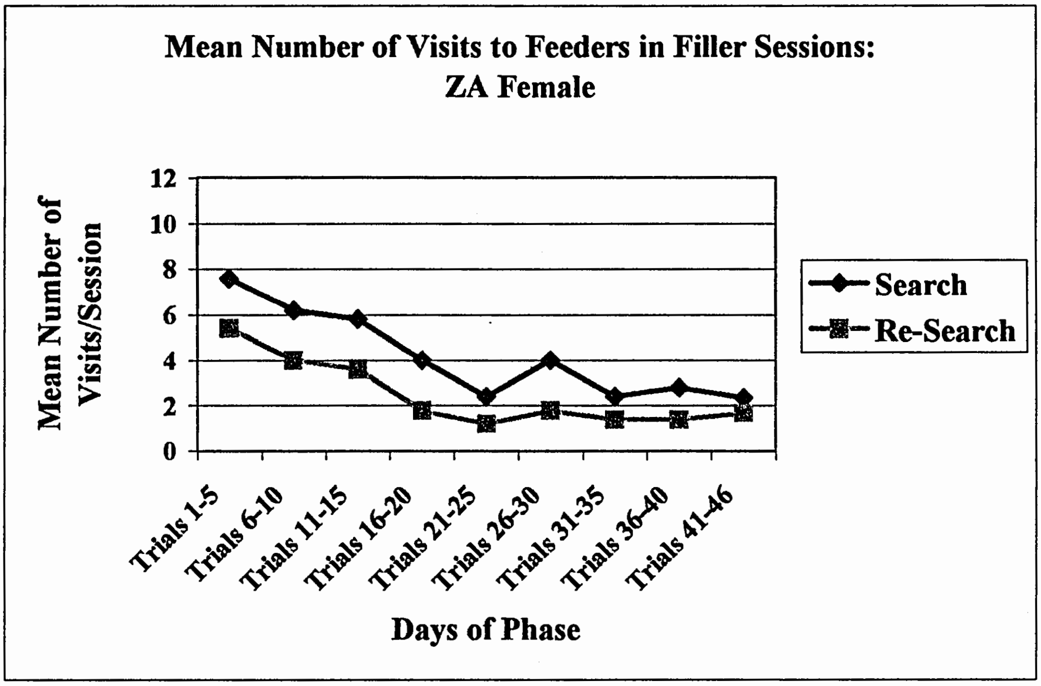

Figure 89 Mean number of visits to feeders by the ZA female in the search and re-search trials of the filler sessions.

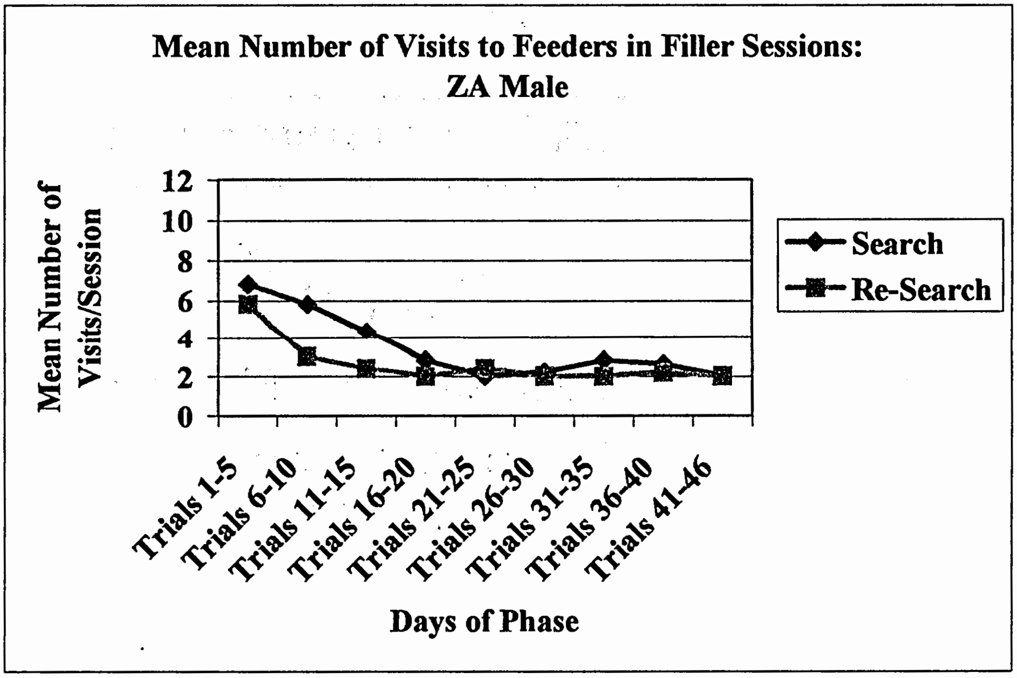

Figure 90 Mean number of visits to feeders by the ZA male in the search and re-search trials of the filler sessions.

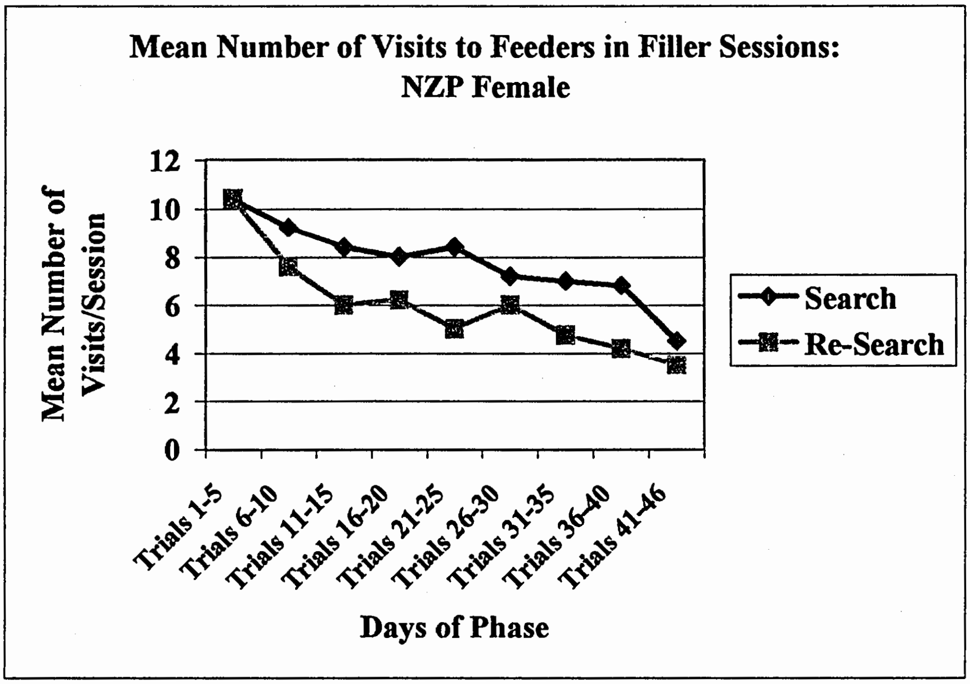

Figure 91 Mean number of visits to feeders by the NZP female in the search and re-search trials of the filler sessions.

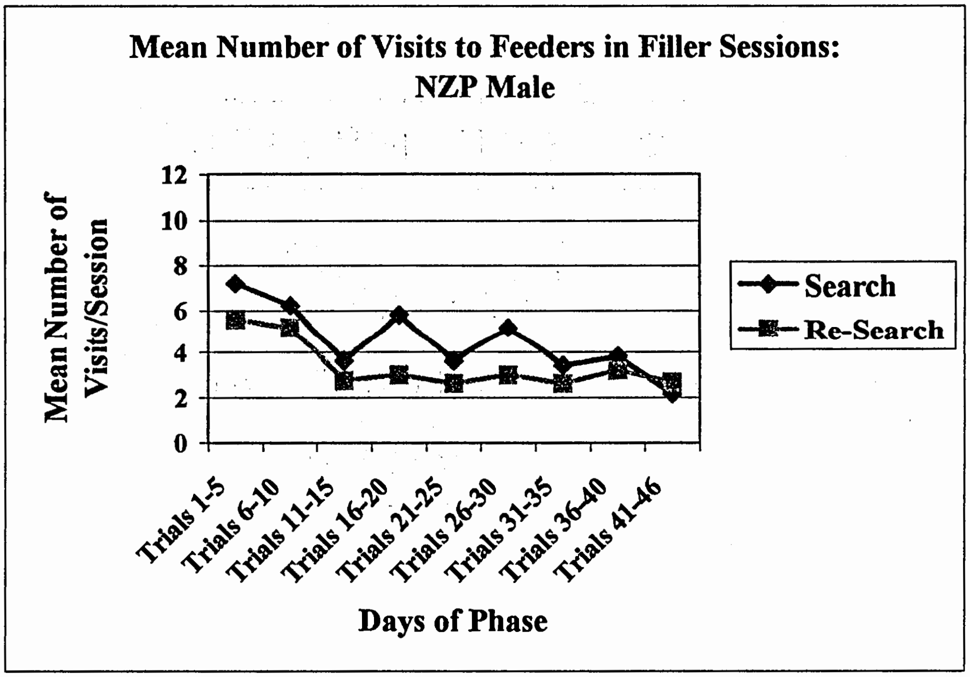

Figure 92 Mean number of visits to feeders by the NZP male in the search and re-search trials of the filler sessions.

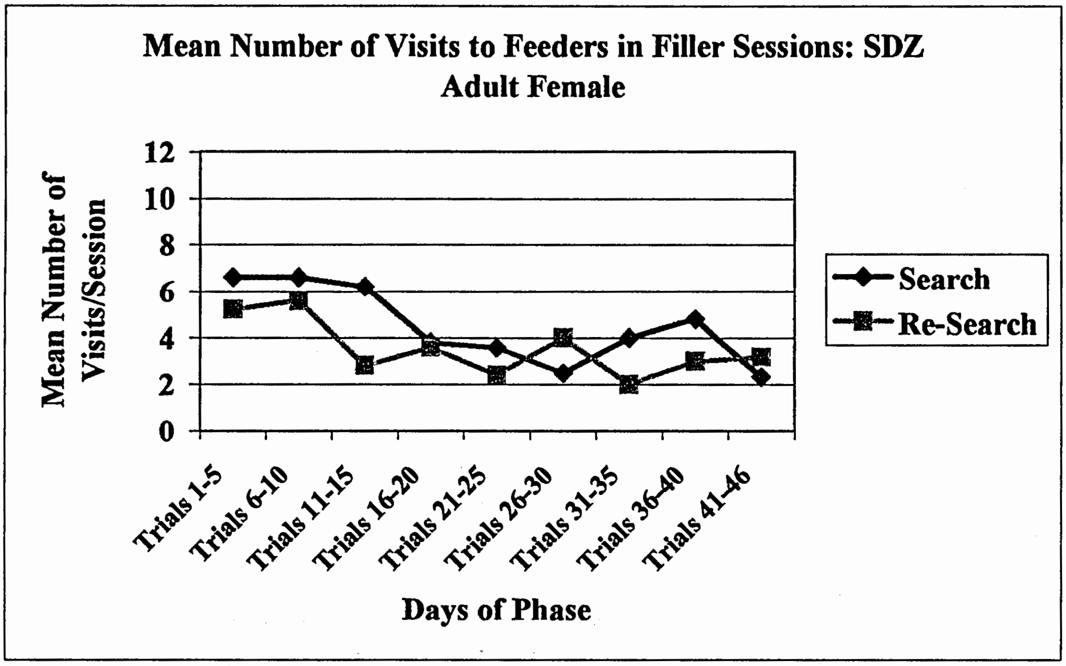

Figure 93 Mean number of visits to feeders by the SDZ adult female in the search and re-search trials of the filler sessions.

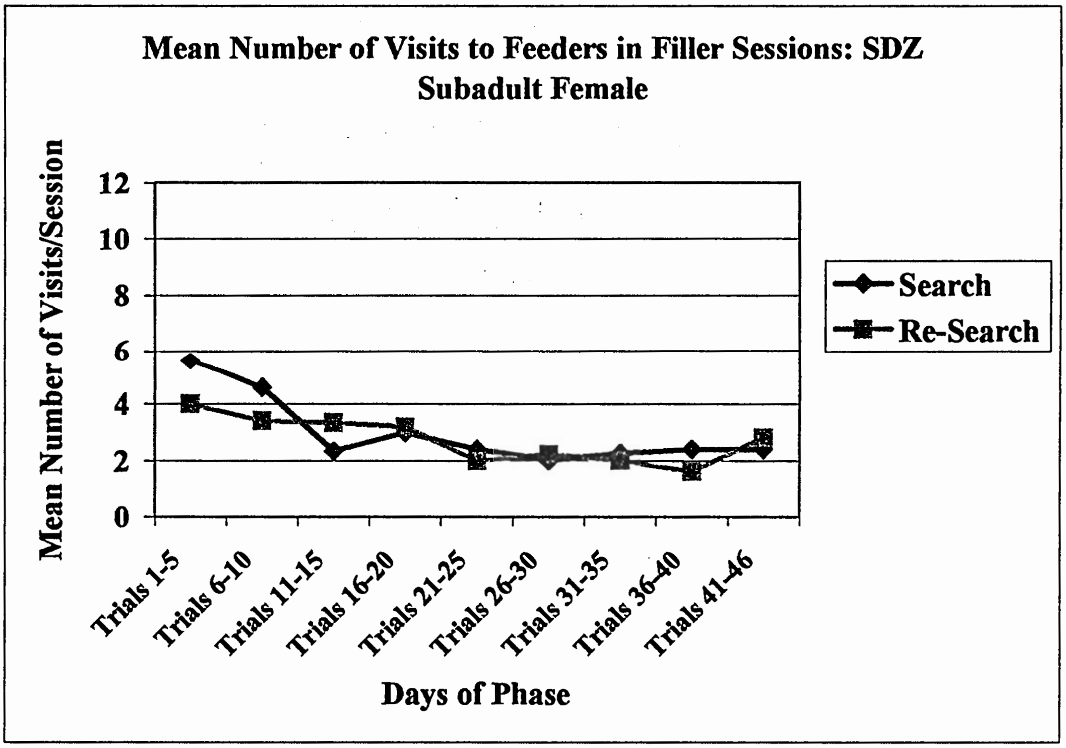

Figure 94 Mean number of visits to feeders by the SDZ subadult female in the search and re-search trials of the filler sessions.

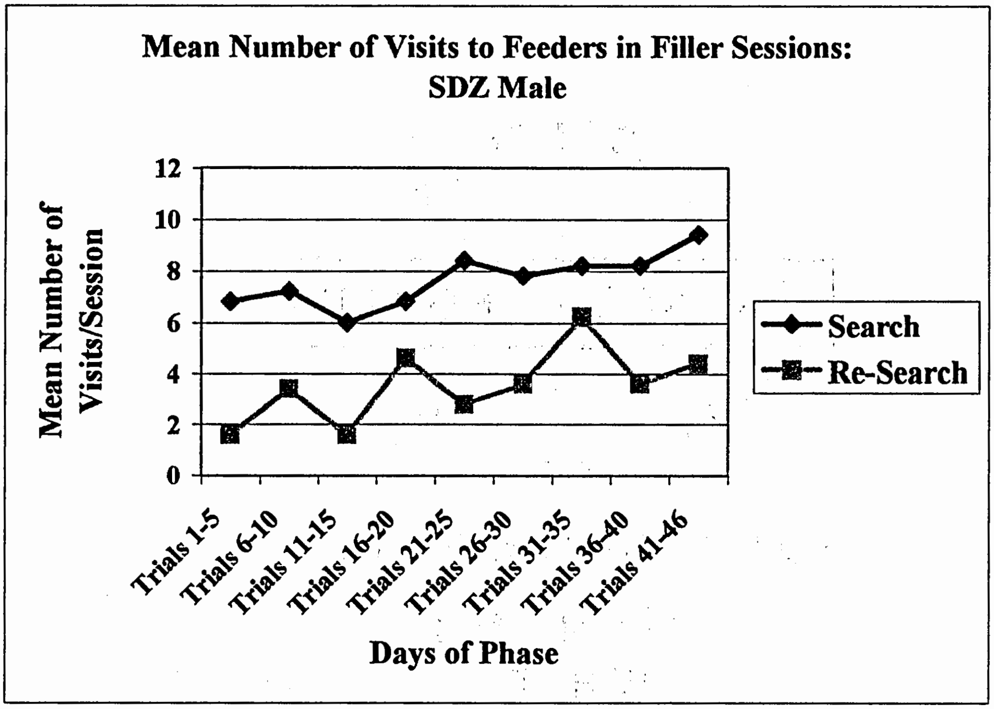

Figure 95 Mean number of visits to feeders by the SDZ male in the search and re-search trials of the filler sessions.

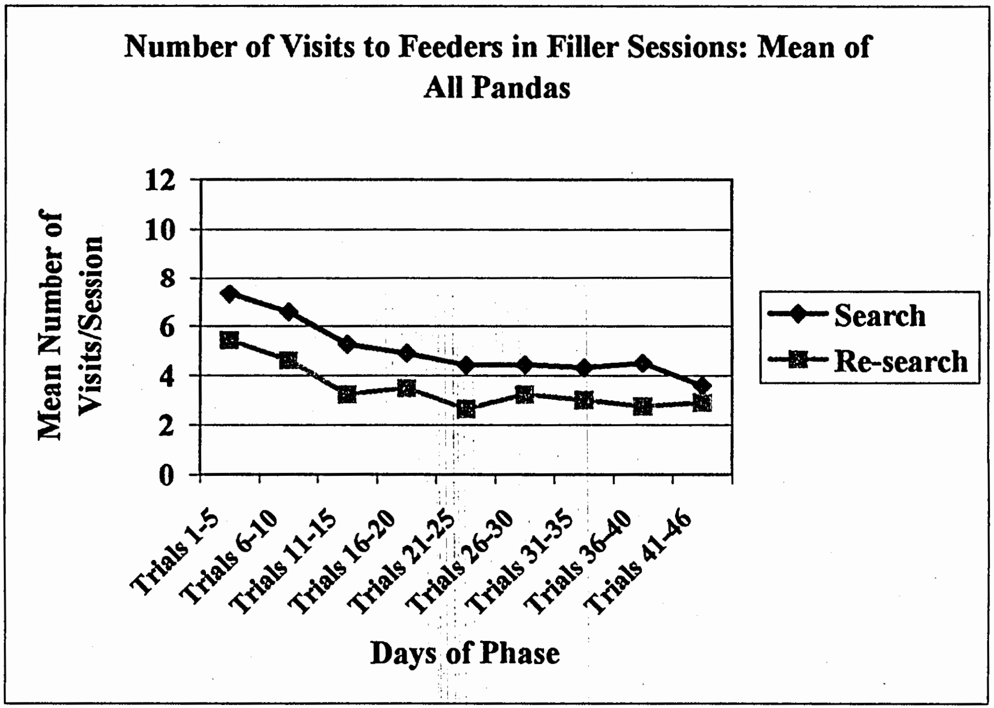

Figure 96 Mean number of visits to feeders by all pandas in the search and re-search trials of the filler sessions.

6.5.4 Discussion

In the test trials of Foraging Task 6, five of the seven giant pandas preferentially used visual cues for localizing food. They were significantly more likely to visit feeders signaled with the visual cue in their first two visits than they were to visit feeders in the same spatial location as the baited feeders in the previous trial or to visit feeders signaled by the olfactory cue. The difference in the likelihood of visiting feeders in same spatial location as the baited feeders in the search trial and visiting feeders signaled by the olfactory cues in the re-search trial of the filler sessions was significant, indicating that spatial cues were more important than olfactory cues. The olfactory cues were relatively unimportant, as indicated by the fact that the giant pandas were no more likely to visit feeders signaled by the olfactory cue than they were to visit unsignaled feeders. These results were surprising given that the visual cue failed to gain stimulus control over the behavior of the giant pandas in Foraging Task 4. Two of the giant pandas, the NZP female and the SDZ male, failed to show a clear a preference for one type of cue or another.

In the re-search trials of the test sessions, none of the feeders were baited with food. The purpose of leaving the feeders empty was to encourage the giant pandas to search all of the feeders so that a hierarchy of cue use could be established. The mean number of feeders visited in a trial was only 4.26; however, most of the giant pandas visited no more than 2 or 3 per trial. This indicates that they were traveling directly to feeders that they expected to be baited with food and failed to sample the other feeders for changes in food availability.

The filler trials were originally conducted for the purposes of training the giant pandas to shift for the test trials and to prevent them from learning that the re-search trial never contained food. However, the results from these trials were interesting in and of themselves. In both the search and re-trials of the filler sessions, a randomly traveling forager would be expected to visit a mean of 0.47 baited feeders in their first two visits. In the search trials of the first five filler sessions, when all three cues were simultaneously available, the giant pandas did not visit more baited feeders in their first two visits than would be expected had they been foraging randomly or using an adjacency strategy. However, they did visit more baited feeders in their first two visits than would be expected had they been foraging randomly or using an adjacency strategy in the re-search trials of the first five filler sessions. This suggests that, even in the early re-search trials, the giant pandas had learned a win-stay strategy of foraging by either remembering the location of the baited feeders after the 10 minute delay between trials or that they were using one of local cues.

Five of the seven giant pandas reached criterion performance, visiting 2 baited feeders in their first two visits in 4 of 5 test sessions, in the re-search trials of the last five test sessions. There were large individual differences in the number of sessions these giant pandas needed to reach criterion performance, ranging from 7 to 43. In the search trials of the filler sessions, two feeders were randomly chosen to be baited with food in each trial. Had the giant pandas been foraging based on the spatial location of the food sites, they would have been unable to accurately predict the location of the two baited feeders. However, if they had learned the association between the visual or olfactory discriminative stimulus and the presence of food, they would have started traveling directly to the baited feeders in the search trials. In the last five search trials of the filler sessions, the giant pandas were visiting more baited feeders in their first two visits than would have been expected had they been using a random pattern of foraging or an adjacency strategy based on their preferred pattern of movement. Four of the seven pandas reached criterion performance within the 62 filler sessions. The number of trials necessary to reach criterion performance ranged from 10 to 45. It was clear from these results that either the visual or olfactory cue or both cues had gained stimulus control over behavior in the search trials. It is interesting to note that, with the exception of the SDZ subadult female, the giant pandas reached criterion performance in the re-search trials before they reached criterion performance in the search trials. This suggests that the initial learning of the association between the visual discriminative stimulus and the presence of food may have been formed in the re-search trials and then transferred to the search trials.

The giant pandas only needed to visit two feeders to obtain all of the food in both the search trials and re-search trials of the filler sessions. They visited all eight feeders in the first five search trials of the filler sessions. However, they visited fewer than eight feeders in the last five search trials of the filler sessions. They also visited fewer than eight feeders in both the first five and last five re-search trials. The giant pandas visited significantly more than the two feeders necessary to obtain all of the food in each block of trials, indicating that they rarely traveled directly to the two baited feeders and stopped foraging. This high level of performance accuracy was seen only in the SDZ subadult female and the ZA male.

CHAPTER 7

DISCUSSION OF RESULTS AND IMPLICATIONS OF COGNITIVE RESEARCH IN ZOOS

7.1 General Discussion

Animals are under strong selective pressure to minimize the costs and maximize the benefits of their behavior, be that foraging behavior, social behavior, or anti-predator behavior. The factors involved in optimal or efficient behavior have most thoroughly been examined with respect to foraging. Efficient foraging requires attention to choice of prey, handling time, encounter rate, and staying time within a patch (i.e., the amount of time a forager should remain in a patch before moving to another patch), and search methods for prey. Optimal foraging theory has not sufficiently dealt with the initial search for food sources or optimal patterns of movement to locate a new source of food (Pyke, 1984). Nevertheless, it might be predicted from this theory that local or distal cues can gain control of foraging behavior and improve efficiency by decreasing search time for resources in the future.

It has long been recognized that there may be constraints, either physiological or environmental, which prohibit or adversely affect the ability of an organism to forage optimally (Pyke, Pulliam & Charnov, 1977; Stephens & Krebs, 1986). Specifically, there may be differences in the ability of discriminative stimuli to gain control of foraging behavior of distantly related or closely related species based on the evolutionary history of the animal and the reinforcement contingencies of the animal's natural habitat. I hypothesized that there would be differences in learning between giant pandas and the spectacled bears given that they occupy very different foraging niches in the wild. Giant pandas are folivorous (Schaller, et al., 1985), subsisting almost entirely on bamboo. Spectacled bears, on the other hand, are frugivorous, foraging on a wide range of fruits, nuts, and other patchily distributed foods such as the hearts of bromeliads (Peyton, 1980).

Seven giant pandas and two spectacled bears were tested in five experiments designed to examine their ability to forage efficiently when all feeders of eight were baited (Foraging Task 1), their ability to locate food in the absence of local discriminative stimuli when four of eight feeders were baited (Foraging Tasks 2 and 3) and their ability to use visual and olfactory cues alone as discriminative stimuli signaling the presence of food in particular feeders (Foraging Tasks 4 and 5). The giant pandas were also tested in a task designed to examine the relative importance of visual, olfactory and spatial stimuli in foraging (Foraging Task 6). The results of this study provide partial support for hypothesized species differences in learning.

In the exploratory task, both the giant pandas and the spectacled bears were very efficient foragers. All bears learned to decrease the time necessary to exploit all of the feeders. Despite differences in testing locations, there were no significant species differences in the time it took the bears to obtain all of the food from the feeders. All bears developed biases for direction of travel and for the feeder with which to start foraging. However, the response preference was most pronounced and predictable in the giant pandas. The bears used an adjacency strategy of foraging, visiting more adjacent feeders than would be predicted by chance or random foraging. In fact, the male giant panda at Zoo Atlanta visited only adjacent feeders in both the first five and last five sessions of the foraging task. There were no species differences in the propensity for traveling to adjacent feeders.

In the exploratory foraging task, a randomly traveling forager was predicted to visit a mean of 5.252 baited feeders in their first eight visits. All of the bears visited more baited feeders in their first eight visits than would have been predicted by on the basis of chance alone. The giant pandas and spectacled bears visited a mean of 7.31 and 7.63 baited feeders respectively. The difference between the species was not significant. Their behavior was comparable to that observed in other species tested using traditional radial-arm mazes. For example, rats tested in a traditional radial arm maze visited a mean of 7.6 baited arms in their first eight visits (Bond, Cook & Lamb, 1981; Olton & Samuelson, 1976), pigeons visited a mean of 6.28 (Bond, Cook, & Lamb, 1981) and 7.1 baited arms (Roberts & van Veldhuizen, 1985), and cattle visited a mean of 7.78 baited arms (Bailey, Rittenhouse, Hart & Richards, 1989). Although the positioning of the feeders in this study was designed to simulate that used in radial-arm maze studies, direct comparison between the performance by the bears in this task and performance by other species in traditional radial arm mazes is difficult at best. In a traditional radial arm maze, the subject is forced to return to a central location among the array arms between visits to successive food sites. Independent movement between food sites is not allowed. In this study, the giant pandas and spectacled bears could move freely between food sites. Free movement between sites may not provide as much experimental control as can be obtained using the traditional arm maze, but it allows for foraging behavior that most closely resembles that which would be possible in nature.

Few studies have been conducted using an open-field paradigm similar to that used in this study. However, two studies allow direct cross-species comparisons with the bears and suggest that the performance of the bears was more accurate than that of pigeons (*Columba livia*) and common marmosets (*Callithrix jacchus jacchus*). Spetch and Edwards (1986) examined spatial working memory in pigeons in an open room with eight ground feeders. In separate experiments, the feeders were placed in either a circular arrangement or a linear arrangement with the feeders placed near or far from each other. The circular arrangement used with the pigeons most closely resembled the arrangement used in this experiment with the bears. The six pigeons in the Spetch and Edwards study visited a mean of 7.28 baited feeders in their first eight choices. Using a similar methodology, Macdonald, Pang and Gibeault (1994) tested the foraging skills of four monkeys by presenting them with eight baited feeders and found that the monkeys visited a mean of 6.81 baited feeders in their first eight visits. I compared the mean number of correct visits made by inexperienced pigeons in their first eight choices with that of the giant pandas and spectacled bears in the last 10 sessions of the study using a Mann-Whitney U test. Sessions in which all eight baited feeders were not visited were excluded from analysis. The pigeons visited significantly fewer baited feeders in their first eight choices (X = 7.28) than both the seven giant pandas (X = 7.84) [U = 1.5, p = 0.005] and the two spectacled bears (X = 7.82) [U = 0.0, p = 0.046] in my study. The giant pandas also performed significantly better than the common marmosets tested by MacDonald and colleagues, visiting 6.81 baited feeders in their first eight visits which was significantly fewer than the 7.68 baited feeders visited by the giant pandas [U = 0.0, p = 0.008].

One explanation for the superior performance of the giant pandas and spectacled bears could be the pattern of movement adopted during foraging. According to Olton and Samuelson (1976), the simplest and most efficient strategy for visiting feeders is to choose adjacent food sites. Both species of bear in this study traveled in a very systematic manner. For most of the giant pandas, the starting point and direction of travel were consistent across the last five sessions of the exploratory task. For example, the behavior of four of the seven giant pandas became relatively fixed across trials such that they started with the same feeder and traveled in the same direction when making their first eight visits in each of the last five sessions. Deviation from this pattern of responding mostly took place in the first five trials of the task, suggesting that the bears learned to improve their adjacency strategy across trials. All of the giant pandas visited only adjacent feeders in their first eight visits in each of the last five sessions of the exploratory task. The spectacled bears also tended to use an adjacency strategy, however, their biases were not as pronounced as those developed by the giant pandas. For instance, the male spectacled bear started foraging with the feeder in position 1 in 4 of the last 5 sessions, but his direction of travel was not consistent. The female spectacled bear behaved similarly to the male ZA panda in that she started with the feeder in either position 1 or 8. Typically, when she started with the feeder in position 1 she traveled in a counterclockwise direction and when she started with the feeder in position 8 she traveled in a clockwise direction.

The adjacency strategy and response bias of the giant pandas and spectacled bears differed from that reported by other species tested in traditional and open-field radial arm maze studies. In studies using traditional radial arm mazes, rats do not seem to use a particular pattern of movement that is discernable to experimenters when traveling between feeders and do not use an adjacency strategy (Olton & Samuelson, 1976; but see Foreman & Ermakova, 1998). Pigeons tested in a traditional radial arm maze were reported to have a tendency to turn right or left after returning to the center platform, however, they did not consistently travel to adjacent feeders in the same way as the giant pandas and spectacled bears (Bond, Cook & Lamb, 1981). Moreover, large mammals tested in a modified version of the traditional radial arm maze also do not appear to develop a fixed pattern of responding. Bailey, Rittenhouse, Hart and Richards (1989) tested crossbred heifers (Hereford x Holstein) and steers (Angus x Hereford and Barzona x Hereford) using a radial arm maze apparatus similar to that originally used with rats but modified to accommodate large animals. They found that the cattle performed as efficiently as rats and pigeons, choosing a mean of 7.78 baited arms in their first eight choices. However, heifers did not always choose adjacent arms more often than other arms suggesting that they were not using a simple turning strategy to avoid revisiting previously depleted arms. The steers, on the other hand, did choose adjacent arms more often than other arms, but there was a high level of variability between trials.

It could be argued that the difference in behavior results from the fact that the species tested in the traditional arm maze were confined to the arms and cannot travel freely between food sites. However, the same lack of biases in responding has been observed for species tested in open field mazes similar to that used in the present study. For example, the monkeys in the study conducted by MacDonald, Pang and Gibeault (1994) did not seem to use a consistent search pattern in foraging that was obvious to the experimenters. Similarly, only one of the 4 pigeons in the study conducted by Spetch and

Edwards (1986) developed a consistent pattern of foraging across trials similar to that used by the giant pandas. This particular bird started foraging from the feeder in either position 4 or 5 and always traveled in a clockwise direction visiting only adjacent feeders. The behavior of the other three pigeons was not as predictable and they often traveled to non-adjacent feeders between visits.

In the first experimental study of spatial ability in hummingbirds, Healy and Hurly (1995) reported that hummingbirds also do not form a sequential search pattern when tested in an open field of artificial flowers. The foraging behavior of free-ranging rufous hummingbirds (*Selasphorus rufus*) was examined using an apparatus similar to a radial arm maze in an open field. Eight artificial flowers containing a sucrose solution were arranged in a circular array. Of interest in this study was the pattern of travel between the flowers, and the ability of the hummingbirds to avoid previously depleted sites. The results of the study showed that the hummingbirds were capable of avoiding flowers they had already depleted after intervals ranging from a few minutes to a few hours. However, unlike the bears in the present study they appeared to use a random search method rather than simply moving from one flower to the nearest adjacent flower even though it would have been the most efficient strategy. This further implicates the use of spatial memory for the task.

Very few studies report other species using a strategy similar to that of the giant pandas and spectacled bears to obtain hidden food, and even those studies report differences in response pattern from those observed in the present study. Menzel (1973) reported that each of six wild-born chimpanzees (*Pan troglodytes*) used an adjacency strategy in their search for hidden objects in an outdoor enclosure. However, unlike the giant pandas and spectacled bears, the chimpanzees rarely started foraging at the same location or traveled in the same direction in consecutive trials. In win-stay and win-shift tasks yellow-nosed monkeys (*Cercopithecus ascanius whitesidei*) developed a preference for the feeder from which to start looking for food and direction of travel during the search phase, allowing them to minimize the distance between search sites (MacDonald & Wilkie, 1990). However, in an exploratory task similar to that conducted with the giant pandas and spectacled bears in the present study, they showed no fixed pattern of visits to different sites, did not preferentially visit adjacent food sites and the order of retrieval of food items was never repeated between trials.

The ability to avoid revisiting depleted feeders within a trial is often interpreted as evidence of working memory for places visited (Olton et al., 1981). Most authors contend that the seemingly random nature of the movement of the species coupled with the tendency of subjects to avoid visiting previously depleted sites is indicative of working memory (Healy & Hurly, 1995; MacDonald, Pang & Gibeault, 1994; Olton & Samuelson, 1976; Spetch & Edwards, 1986). An adjacency strategy such as that adopted by the bears in the present study is not only efficient in terms of time and energy used during travel, but it also decreases the chance of revisiting a feeder that has already been visited without the need for working memory. Accurate behavior is only dependent on the ability to remember the last arm visited in each choice (Foreman & Ermakova, 1998). Therefore, because of the pattern of behavior and an adjacency strategy used by the giant pandas and spectacled bears, caution should be taken when interpreting the ability of the bears to avoid revisiting feeders in the first eight visits in terms of working memory. It is possible that they were using a simple rule of thumb, such as "start at preferred site and travel to adjacent feeders until reaching an empty feeder", rather than spatial working memory to end their search and avoid revisiting sites they had already depleted. This type of foraging strategy would not require working memory. The proclivity for the giant pandas to start with a particular feeder and travel either clockwise or counterclockwise until all eight feeders were visited may have accounted for their ability to avoid revisiting feeders within the first eight choices. It is unclear why the species tested in other studies using a similar paradigm did not develop a more efficient adjacency strategy. Several factors are known to affect the use of an adjacency strategy of foraging, including distance between food sites, species of animal and prevalence or saliency of environmental cues (Foreman & Ermakova, 1998). It is possible that differences in any one of these factors are responsible for differences observed across studies. It is also possible that the working memory of other species tested in similar tasks is more well-developed than that of the giant pandas and spectacled bears, allowing them to remember the location of the depleted sites regardless of travel pattern. Future research should be conducted to further examine the conditions under which bears may use a foraging strategy other than an adjacency strategy.

Despite their response strategy, there is some evidence that the bears in the present study were using working memory during the task. For example, in the exploratory task the pandas visited significantly more feeders than the eight necessary to deplete all feeders in both the first five and last five sessions of the study. Unlike other studies in which the subjects are often removed from the apparatus following a particular number of visits to the arms (MacDonald & Wilkie, 1990; Olton & Samuelson, 1976; Spetch & Edwards, 1986), the bears in this study were free to continue visiting feeders as long as they wanted. In the last five sessions of the study the giant pandas were visiting eight baited feeders in their first eight choices. Since no revisits were occurring in the first eight choices of the last five sessions, all of the revisits in these sessions occurred after the initial eight visits. One might expect that if working memory was not involved in the behavior of the giant pandas the bears would simply continue on their preferred path in a circle until they began encountering empty feeders. It would, therefore, be expected that the majority of the revisits would be to the feeders first visited on the path. However, approximately half of the visits to previously depleted feeders were not to feeders adjacent to the last feeder visited. This suggests that revisits may have been treated independently of first visits. Menzel (1973) attributed the ability of the chimpanzees in his study to avoid returning to depleted food sites as either memory for places to be visited that was erased with each visit or to memory for places they had been during a trial. Improvement in working memory for feeders visited across sessions of the task may, therefore, be a likely explanation for the decrease in the number of revisits observed in this study.

Although all of the bears developed an adjacency strategy, visiting adjacent feeders more often than non-adjacent they did not appear to be following a particular fixed stereotypic route. Their pattern of movement in each session was not identical to the next for the majority of the bears. Only one of the giant pandas used a pattern that was entirely predictable across the last five sessions of the study. The ZA female panda always started her search with the feeder in position 1 and traveled clockwise until she reached the feeder in position 8. None of the other bears developed such a fixed pattern of travel. This type of behavior would imply that she developed a route. I did not measure the actual number of steps between feeders that would allow a determination of the rigidity of the response pattern. Furthermore, the bears did not simply travel to adjacent feeders until they came to an empty feeder, which could be used as a signal to stop searching. This suggests that they were not following a simple rule of thumb to stop searching.

The giant pandas at Zoo Atlanta became very efficient in the last five sessions of the exploratory task, visiting eight baited feeders in their first eight visits and visiting only those eight baited feeders during a session. None of the other giant pandas or the spectacled bears reached this level of performance. Though the difference in the number of revisits across institutions was not statistically significant, the highly accurate performance of the ZA giant pandas compared to that of the other bears warrants attention. At the time of testing, the ZA giant pandas were being switched from their diet in Chengdu to their diet at Zoo Atlanta. They were being hand-fed their entire daily ration of biscuits in an effort to ensure that each of the giant pandas was receiving and eating the amount recommended by the nutritionist. The giant pandas at the other institutions were scatter-fed their daily ration of biscuits before and throughout the course of the study. Scatter-feeding is often used as a form of enrichment to encourage extended foraging and exploratory behavior (Shepherdson, 1998). One consequence of this feeding regimen is that, because the pieces of food are often hard to find when thrown under grass and brush, animals may be rewarded for returning to locations already visited. Therefore, it is possible that a history of scatter-feeding negatively affected the ability of the giant pandas at the National Zoo and the San Diego Zoo to learn to avoid revisiting previously visited feeders. The spectacled bears did not visit significantly more than the eight feeders necessary in the first or last five sessions of the exploratory task, and they revisited fewer feeders than the giant pandas in both the first five and last five sessions of the task. It would be interesting to further examine the influence that feeding practices might have on tests of learning.

The results from the exploratory task suggest that, like other species tested, giant pandas and spectacled bears may be predisposed to avoiding repeating choices in their initial search for food (i.e., in their first eight visits). This may be advantageous for animals whose resources do not replenish quickly after they are exploited. For example, flowers vary in their ability to replenish nectar following depletion by a nectarivore. Hummingbirds avoid revisiting flowers until enough time has passed between visits for the nectar to be replenished (Healy & Hurly, 1995). The diets of both giant pandas and spectacled bears would also not be expected to replenish quickly. Therefore, return visits should not occur within a few minutes or hours. Return visits should only occur after sufficient time has passed to allow the regrowth of resources, which may be days or weeks following depletion.

Evidence for the ability of giant pandas and spectacled bears to use distal spatial cues alone to localize viable resources comes from the results of the spatial and reversal tasks. It would be expected that a randomly traveling forager would visit 1.655 baited feeders in their first four visits by chance alone. Even in the first five sessions of the spatial task, the bears were visiting more baited feeders in their first four visits than would be expected had they been foraging randomly. Their adjacency pattern of movement allowed them to forage more efficiently than would be expected by chance, despite the fact that they did not know the location of the baited feeders. However, six of the bears began visiting more baited feeders in their first four visits than expected from their adjacency strategy within 30 trials. They were not using local visual or olfactory cues to travel directly to baited sites, as evidenced by the fact that a reversal of the position of the baited feeders disrupted performance. Furthermore, most of the bears reached criterion performance on the spatial task more quickly than they reached criterion performance in the reversal task, suggesting that the learning of one set of contingencies can interfere with the subsequent learning of a new set of contingencies. This suggests that once an association is learned, it is difficult for the bears to adjust to sudden environmental changes.

Honig (1978) referred to the retention of invariant information from one day or one trial to the next as reference memory. This contrasts with working memory which refers to memory for information learned within a trial. Information learned within a trial should be forgotten between trials. However, for performance to improve across trials in tasks with differentially baited feeders, information should be remembered across trials. Most studies that have used the traditional radial arm maze have focused on working memory; however, some studies have used the apparatus to examine reference memory. Foreman and Ermakova (1998) reviewed the literature and found that, when four of eight arms are baited on a radial arm maze, rats require approximately 30 days to reach a performance criterion similar to the one set in the present study. Rats were also reported to be capable of learning a reversal of the task in approximately four days. Five of the bears reached criterion performance in the spatial task in fewer than 30 trials. Three did so in fewer than 15. However, only five of the nine bears tested successfully learned the reversal task. The female spectacled bear reached criterion performance within 12 trials, but none of the giant pandas reached criterion performance until at least the 22nd trial. Therefore, the bears did not as easily adjust to environmental change as rats tested under similar conditions.

It is not surprising that at least one of the spectacled bears tested in this study exhibited an ability to use spatial stimuli alone to locate food sources, considering the distribution of the food resources in their habitat. However, the giant pandas may not have been predicted to perform as well on the spatial task. The question is, why might giant pandas exhibit spatial memory when locating food? Given the abundance of bamboo in their environment (Schaller et al., 1985; Wei et al., 2000) and the fact that bamboo patches grow close together in proximity (Schaller et al., 1985), it might seem surprising that most of the giant pandas in my study were able to return daily to baited food sites using spatial memory and that there were no striking species differences in performance between they and the spectacled bears. Bamboo does not replenish itself quickly when depleted. For example, a patch would not be expected to regenerate over the course of a night as simulated in this study (Schaller et al., 1985). There are several possible reasons why spatial memory may be an asset for giant pandas. First, current giant panda habitats may not necessarily reflect those in which giant pandas originally evolved. The range of the giant panda has become severely restricted over the past 100 years (Schaller et al., 1985). The distribution of bamboo in those environments may have favored the evolution of spatial memory. Second, spatial memory may not be necessary for locating food in their current environments at all. However, it may have developed for the efficient localization of other resources such as water or den sites or even receptive females. There is some evidence from studies conducted with thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) that spatial memory is not only an asset for foraging but also in mate-searching (Schawagmeyer, 1994). Specifically, male ground squirrels can decrease their search time for sexually receptive females and avoid sites with reduced mating opportunities using spatial memory. Those individuals with better spatial memory would presumably be more competitive and have the opportunity to mate with more females than males less adept at spatial memory tasks. Third, giant pandas may use spatial memory in their current habitats to selectively forage for preferred species, parts (stems, leaves, shoots) or ages of bamboo (new, 2 year, or old). These preferences are known to change seasonally throughout the year (Schaller et al., 1985; Reid and Hu, 1991; Wei et al., 2000). It is possible that giant pandas use spatial memory to remember the location of preferred patches of bamboo, thereby increasing foraging efficiency throughout the year. This has been shown to be true in other herbivores.

Recently, researchers have begun to examine spatial learning in domesticated animals, particularly cattle and sheep. Just as one might ask why giant pandas would have the need for spatial memory when foraging on bamboo, one might also ask why grazers would have the need for spatial memory when foraging at pasture. According to Bailey, Rittenhouse, Hart and Richards (1989) and Edwards, Newman, Parsons, and Krebs (1997), grazing animals at pasture show preferences for foraging in patches of vegetation that are high in both quality and quantity. They exploit their environment in such a way that suggests that they might be able to remember the location of these resources, which would allow them to return to preferred sites and avoid non-preferred sites later in foraging. To test the spatial abilities of grazers, researchers have used a variety of methods, some of which claim to have found results similar to studies conducted with rats and pigeons.

Several elegantly designed investigations of spatial memory in sheep have been conducted in open field testing environments similar to the testing environment used in the present study. Edwards, Newman, Parsons, & Krebs (1996) designed their study with the purpose of identifying how sheep selectively exploit patches differing in quality. Unlike other spatial memory experiments, this study had three different levels of complexity. Bowls placed in a pasture served as patches. The bowls were deep enough to prevent the sheep from seeing food until they approached the patch. In three separate conditions, either one of eight, two of sixteen or four of thirty-two patches were baited with food. Eleven trials were conducted over the course of six to eight days. For the first six trials, the location of the baited patches remained constant. However, on the seventh trial the experimenters either randomly baited other food patches or left all of the food patches empty. Animals using either visual or olfactory discriminative stimuli would be predicted to travel directly to the newly baited feeders following a random switch of baited feeders. When the bowls were empty they would be predicted to search randomly or not at all. During trials 8-11, the feeders that were not baited in the first six trials were baited for those subjects in the shift group, whereas the feeders that were baited in trials 1-6 were baited throughout the remainder of the study for those in the group in which there was no food in trial 7. The results weighed heavily in favor of spatial memory as the means by which sheep locate food at pasture. All sheep searched randomly for the baited food site during the first trial of the study. However, they visited fewer sites than would be expected by chance in the second session suggesting that they had learned the location of viable food sources after a single exposure. Sheep in both the switch and no food groups immediately traveled to patches that had contained food in the previous trials suggesting that they were not using either visual or olfactory discriminative stimuli to locate viable food patches. There was no difference in rate of learning between sheep exposed to eight, sixteen, or thirty-two patches. At the end of this first experiment, the sheep were tested for their ability to locate the baited feeder after either 24 or 72 hours. The sheep accurately located the patch containing food after both intervals. It was hypothesized that the ability to remember the location of a preferred food site for as many as three days may allow sheep to return directly to food sites once those sites have had the chance to replenish.

According to Bailey, Rittenhouse, Hart, Swift and Richards (1989) and Edwards, Newman, Parsons, and Krebs (1997), detailed studies of pastures have revealed that they are not as homogenous as once believed. Grazing animals spend the majority of their time foraging in areas of pastures that contain high quality and high quantity concentrations of preferred grasses. They exploit their environment in a way that suggests that they might be able to remember the location of these resources, allowing them to return to preferred sites and avoid non-preferred sites later in foraging. In both open-field and laboratory experimental tests, spatial memory has been found to be used by large herbivores such as sheep, cattle, and deer in locating preferred food patches when grazing (Gillingham & Bunnell, 1989; Bailey et al., 1989; Edwards et al., 1997; Dumont & Petit, 1998). Though grasses at pasture do not replenish quickly after being depleted by a grazer, a foraging animal may not fully deplete a patch in one visit which would make return visits worthwhile. Spatial memory has been found to be long-lived in both sheep (3 days) and cattle (15 days) (Edwards et al., 1996), suggesting that they may be capable of returning to previously depleted patches following an interval long enough for re-growth of the plant. It would be interesting to conduct further research with the giant pandas and spectacled to determine how long their memory for the location of viable food sources lasts.

The results of the spatial and reversal foraging tasks provided clear evidence that bears can use distal cues to orient toward viable food sources. However, they do not provide any information on the nature of the spatial learning. As stated in the introduction, the bears could be using route based learning, landmark learning or a cognitive map formed through experience with the environment. Though the bears all developed somewhat preferred travel paths during each of the tasks, individuals rarely traveled in exactly the same pattern or took the same amount of time to travel between trials. This sheds doubt on the possibility that they had simply learned and memorized a specific route to improve foraging efficiency. Many species are known to use either specific landmarks or the overall shape of the testing area to localize baited feeders. Presumably, the closer a discriminative stimulus is to the location of the reward, the more easily the association between the stimuli will be made (Honig, 1987). However, this is not always the case in spatial memory. For instance, one somewhat surprising aspect of rat spatial learning is that they learn to use only the overall metric shape of an area to find a hidden food source, even when salient (at least to the experimenter) environmental discriminative stimuli are readily available. If an open-field testing area has a rectangular shape rats will learn to locate food in a hidden goal by searching from a particular fixed distance from the nearest corner of the area. A random rotation of the area results in errors in location of the hidden food regardless of the fact that visual discriminative stimuli and olfactory discriminative stimuli could be used as landmarks and beacons for locating the food (Cheng & Spetch, 1998; Gallistel, 1990). However, other research has shown that rats are able to use both landmarks and global geometry simultaneously to improve performance (Greene & Cook, 1997). If discriminative stimuli or landmarks are placed within the testing arena in a location that is more proximal to the food goal, rats learn to locate the hidden goal much more quickly than when discriminative stimuli are more distally located (Cook & Tauro, 1999). Therefore, it seems that the use of visual discriminative stimuli and room geometry is dependent on the spatial characteristics of the discriminative stimuli. As would be predicted, the closer a landmark is to the goal, the better the performance of the rat (Hogarth, Roberts, Roberts, & Abroms, 2000). Close proximity turns the landmark into a beacon that rats readily come to associate with the presence of food.

Subsequent studies using a similar testing environment found that pigeons are able to use both global and local features of the environment when learning the location of a baited food site (Spetch & Edwards, 1989). For example, Spetch and Honig (1988) found that the spatial arrangement of landmarks between trials affected working memory within trials. Pigeons were allowed to visit 8 baited feeders. Working memory was evaluated by examining their ability to avoid previously depleted food sites. It is possible that in a working memory task a landmark gains control over foraging behavior within that trial. That is, the relative location of the landmark could be forgotten between trials. However, the results showed that when landmarks are altered between trials, from one day to the next, pigeons perform more poorly than if the landmarks are left in a constant position. Therefore, the position of the landmarks between trials is learned and used to avoid revisiting previously depleted sites within trials.

Similar to the results of research conducted with rats (Cheng & Spetch, 1998; Gallistel, 1990), studies have shown that food-storing birds learn the spatial configuration of landmarks rather than either the visual properties of the landmarks or local discriminative stimuli that might be associated with the cache site. Local discriminative stimuli and landmarks can be displaced, removed, or covered up as the season progresses making them relatively useless for long-term cache recovery. Though food-storing birds tend to overlook potential visual associations that could be used as beacons to signal the presence of or distinguish between cache sites, the proximity of visual discriminative stimuli to a hidden food goal is important for accurate relocation of cache sites (Lechelt & Spetch, 1997; Spetch, 1995). European jays, for example, have been found to preferentially use landmarks that are both tall (20 cm high) and close in proximity (15-30 cm) to the goal. This is presumably related to the fact that it is easier to hone in on a location based on landmarks that are nearer to the goal. Furthermore, tall landmarks are less likely to become obscured during winter by fallen leaves and snow (Bennett, 1993). Prominent landmarks near to the goal in an unfamiliar arena can cause overshadowing of other source information surrounding the goal (Gould-Beierle & Kamil, 1999). The testing environments of the giant pandas and spectacled bears provided a variety of landmarks that could have been used to guide orientation.

Cognitive mapping is considered to be the most complex form of animal navigational abilities because, according to Tolman (1948), it does not depend on simple stimulus-response behavior. "It is only when animals reorganize their past experiences which have been stored in a map-like format, that we can see the operation of the complex intelligence process" (Ellen, 1987, p. 34). However, this does not mean that only higher organisms are capable of formulating and using cognitive maps. Based on an extensive review of spatial cognition, Gallistel (1990) came to the conclusion that cognitive mapping is ubiquitous across the animal kingdom. According to Gallistel (1989,1990), when animals move they do so with reference to a cognitive map of their environment, and this map is often used even when the goal functions as a beacon. Gallistel argues that beacons are only important in the last moment of search after the animal is near the position of the goal. "The hypothesis is that the orientation of animals toward the goals they seek to approach or avoid is not governed by the intrinsic characteristics of those goals but rather by their geometric position, as represented on the animals' cognitive map" (Gallistel, 1990, p. 153). He cites examples from studies conducted with a diverse range of animals including hoverflies, honeybees, fish, food storing birds, and chimpanzees to support his claims. The results of these studies are impressive and seem to suggest that even lower invertebrates are capable of advanced cognitive mapping.

It is not possible to determine if the bears in the present study had developed a cognitive map of their environment that could be used to accurately localize viable food sources. Recent evidence casts doubt on the validity of the conclusions of past research on cognitive mapping (Bennett, 1996). The ability to use novel short-cuts in a testing situation, a hallmark of the use of cognitive mapping, is usually determined by removing an animal from a path of movement and placing them in another location. If the animal can still find its way to the goal without first going back to the area from which it was moved, then it is considered to have taken a novel short-cut. It has recently been asserted by Bennett (1996) that the majority of these studies have been flawed. First, most researchers studying cognitive mapping in animals fail to ensure that the supposedly "novel" short-cuts the animals take are truly novel. This is particularly true with studies that are conducted in the field. Second, most researchers fail to eliminate the possibility that the animals are using some form of route-based navigation. Finally, most studies fail to provide testing situations in which the landmarks associated with the goal are not visible from the new angle. According to Bennett (1996), in all claims of cognitive mapping by animals he reviewed there were no cases in which all simpler alternatives could be eliminated. Because of the failure of experimenters to adequately control for alternative explanations, he advises that the term cognitive map be avoided. In addition, an attempt by one experimenter to control for the use some of these simpler alternatives failed to find evidence for cognitive mapping abilities in rats (Benhamou, 1997). Much of the behavior that was attributed to "insight" in studies of cognitive mapping can be explained by simpler means (Reid & Staddon, 1998). It might be argued that most spatial memory processes are actually nothing more than associative learning processes (Willson & Wilkie, 1993). That is, spatial memory should not be discussed as if it were something separate from associative learning as the title of this dissertation implies.

Only one of the two spectacled bears showed evidence of learning the spatial memory task, making the comparison between her and the giant pandas difficult. However, there did not seem to be striking differences between her performance on the task and the performance of the giant pandas. There is no evidence from the literature to suggest that the fundamental way that animals use landmarks or the overall shape of the testing environment is different across related species or those with different foraging ecologies. For instance, both food-storing black-capped chickadees and nonfood-storing pigeons have been found to use the perpendicular distance of an edge in relation to a landmark to locate a hidden food site (Cheng & Sherry, 1992). Furthermore, despite the differences that have been found between these species in spatial memory, Cheng and Sherry found no significant differences in behavior between in their use of landmarks to identify spatial locations. These results have been corroborated by studies of food-storing and non-storing birds which found no differences between species in the manner in which they use landmarks to locate hidden food (Gould-Beierle & Kamil, 1998). Future studies should examine the factors affecting the localization of viable food sources by giant pandas and spectacled bears such as quality of landmarks, proximity of landmarks in relation to the food source, and size and shape of testing area.

It is possible that species differences in the spatial and reversal tasks were not found in the present study because the tasks may have been relatively simple. Some baseline capacity for spatial memory is presumably necessary for guidance in most species. For instance, even German cockroach larvae (*Blatella germanica*) have been observed to use develop an orienting strategy towards food sources with the aid of landmarks (Durier & Rivault, 2000). On a simple spatial memory task, it might be expected that most species would be capable of performing with some degree of accuracty. Gross species differences may only be obvious as the tasks examining spatial memory become more difficult. Platt and colleagues (1996) found that, whereas Wied's marmosets (*Callithrix kuhli*) performed more accurately on a spatial delayed matching-to-sample task and learned a color memory task more quickly than golden lion tamarins

(*Leontopithecus rosalia*) at short delays, the tamarins outperformed the marmosets at long delays. This difference in performance as difficulty of the task increased was in accordance with hypotheses based on the foraging ecology of the two species.

In this study, the visual and olfactory cues failed to acquire stimulus control over the behavior of the giant pandas. In both of these tasks, the giant pandas visited all eight feeders in each of the trials using an adjacency foraging strategy. The visual cue, but not the olfactory cue, acquired stimulus control over the behavior of the spectacled bears. There are several reasons why stimulus control might not be established in a test situation (for review, see Domjan & Burkhard, 1993). One is sensory capacity. Different species have different sensory capabilities, and stimuli cannot gain control over behavior if they cannot be perceived by the organism. It could be argued that the giant pandas were unable to distinguish between the black and white visual cue in Foraging Task 4. However, the results from Foraging Task 6 ruled this out as a possible explanation for the failure of the visual cue to acquire stimulus control over behavior. The majority of the giant pandas learned the association between the white lid of feeders and the presence of food. If the white lid could become a discriminative stimulus signaling food availability in one task, there is no reason to expect that they could not detect the differences between the feeders in the previous task. It is, however, possible that the bears were unable to detect the odor. McCormick's™ lemon extract was used as the positive discriminative stimulus, and the lack of scent was used as the negative discriminative stimulus. This explanation is unlikely for several reasons. Prior to the study, the giant pandas at Zoo Atlanta had been exposed to this scent. It was used to draw the attention of the giant pandas to certain areas of their enclosure. Likewise, lemon extract had been used successfully as an enrichment product with the giant pandas at the San Diego Zoo. Another possible explanation is that the lemon extract, which is mostly composed of alcohol, dissipated or evaporated between application and the start of a trial. However, several of the giant pandas in the study were reported to have engaged in scent anointing behavior in the first few days of exposure to the feeders signaled by the lemon extract. For instance, in some trials the giant pandas spent time rolling and rubbing themselves on the feeders with the scent. Moreover, both giant pandas at the National Zoological Park engaged in scent anointing behavior with other objects during the first two trials of the olfactory task, suggesting that their senses were potentially heightened following exposure to the olfactory cue used in the study. It is unlikely, therefore, that they were unable to smell the scent of the lemon extract or that the scent had dissipated in all of the trials between the time of application and the time of the trial. Bears have very keen senses of smell. The olfactory scent was strong to the experimenters and should have been easy to detect by the bears. It is possible that the salience of the cue was inconsistent between trials, making it a relatively poor predictor of food availability.

Another reason for why a stimulus may fail to gain control over behavior is experience with the stimulus (Domjan & Burkhard, 1993). If an organism is sensory deprived or has little experience in making discriminations between stimuli, it will be difficult for them to distinguish similarities and differences between those stimuli in the future. Sensory deprivation is not a likely explanation for the failure of the visual cues to gain control over behavior in the giant pandas or for the olfactory cues to gain control over behavior in both species. Though many captive environments are not as complex and rich in sensory stimuli as the natural environment, both species were housed in naturalistic enclosures and had considerable exposure to environmental enrichment. Furthermore, they presumably have had the opportunity to learn discriminations between particular environmental circumstances and food in the course of routine husbandry and training. However, experience with the olfactory stimulus may have adversely affected its ability to become a discriminative stimulus. For instance, prior exposure to the lemon extract for the Zoo Atlanta and San Diego Zoo giant pandas may have weakened its ability to serve as a discriminative stimulus in the present study. As far as I know, this stimulus was never used in conjunction with food reinforcement.

Repeated exposure to a particular stimulus in the absence of reinforcement has been shown to significantly impair the subsequent establishment of control by that stimulus when it is presented later as a positive discriminative stimulus (Domjan & Burkhard, 1993). This is referred to as latent inhibition. This may explain the inability of the lemon extract to gain stimulus control over behavior in this study. However, the giant pandas at the National Zoological Park had not been previously exposed to lemon extract prior to the present study, and they also did not show evidence of stimulus control by the olfactory discriminative stimulus. For these giant pandas, there may have been an order effect which impaired their ability to perform well when presented with the olfactory task. They were presented with Foraging Task 5 after Foraging Tasks 4 and 2 and 3. To my knowledge, the spectacled bears had no prior experience with the olfactory stimulus and they also did not show evidence of learning the task.

Assuming that the olfactory cue was detected by the giant pandas in each trial and that the salience of the scent was consistent, the results of this experiment were unexpected, especially considering the very sophisticated olfactory capabilities of not only giant pandas and spectacled bears (Schaller et al., 1985; Swaisgood et al., 1999) but of bears in general (Brown, 1993). However, olfaction has been found to be unimportant in other radial arm maze studies with other species considered to have well-developed olfactory systems. Specifically, numerous studies have shown that rats do not use intramaze olfactory cues when locating food in a radial arm maze, even if the olfactory cues are their own scent markings or feces (Foreman & Ermakova, 1998). However, other studies have shown that animals are capable of using olfactory cues to track the presence of food, particularly if those cues emanate directly from the food source. For instance, squirrel monkeys readily learn to use an olfactory cue such as banana odor or peanut odor as a positive discriminative stimulus signaling the presence of food (Laska & Hudson, 1993).

The olfactory cues used in these studies and the present study were arbitrary or extrinsic to the food used as the reinforcer. Moreover, it was not a scent normally associated with any food item that would be in the diet of giant panda or spectacled bear in the wild. It is possible that an intrinsic odor (one normally associated with the food item itself) or an odor normally associated with food items present in their diet (e.g., apple extract or juice, sweet potato juice, pear extract or juice, etc.) may have been a better stimulus to use in this study. Giant pandas seem to use their sense of smell to determine the palatability of bamboo both in the wild and in captivity. They are often seen breaking and then smelling stalks of bamboo before consumption (Schaller et al., 1985). However, there may be no extrinsic olfactory cues that reliably allow giant pandas to predict the availability of bamboo. There could, however, be many visual and spatial extrinsic cues associated with preferred patches of bamboo. This may include environmental cues that signal the patch such as a body of water, a slope of a hill, trees under which the bamboo grows well, the size of trees under which bamboo grows, etc. Future studies should examine the ability of giant pandas and spectacled bears to use intrinsic and extrinsic cues as discriminative stimuli signaling the presence of food. Naturally occurring odors may be more salient cues than artificial odors.

In contrast to the performance of the giant pandas, both of the spectacled bears learned that the visual cue was a discriminative stimulus signaling the presence of food in Foraging Task 4. Other species have been shown to be capable of using visual cues to locate viable food sites when the spatial location of the baited feeders is randomly determined at the beginning of each trial. The first experimental study of bears conducted by Bacon and Burghardt (1974) found that American black bears were able to accurately choose the baited feeder of two feeders on the basis of the color of the feeder. In another two-choice test, cuttlefish were found to be able to accurately orient and move toward one side of their aquarium in response to a light that served as a discriminative stimulus for the presence of food. Macdonald (1992) determined that wild grey squirrels were capable of discriminating between salty and sweet biscuits on the basis of artificial coloring of the biscuits. This type of discrimination is similar to that observed in traditional taste conditioning experiments. Furthermore, Drea and Wallen (1995) found that rhesus monkeys (*Macaca mulatta*) were also able to learn a two-discrimination test in which a baited feeding apparatus was signaled by one color and a non-baited feeding apparatus was signaled by another color. Each of these studies involved discriminating between two possible colors or choices. Other studies using more complex environmental conditions and conditions have also found that some species are able to use visual cues to locate food.

Hogarth, Roberts, Roberts and Abrams (2000) found that rats were capable of learning to associate a randomly moving beacon (a white arm cover) with the presence of food at the end of the arms of a traditional radial arm maze within ten trials. Platt, Brannon, Briese, & French (1996) found that both golden lion tamarins and Wied's marmosets were capable of using a visual cue alone to locate baited feeders in a delayed matching-to-sample task, though their performance on this type of task was not as accurate as their performance on a similar delayed matching-to-sample task. In a large outdoor enclosure, long-tailed macaques (*Macaca fascicularis*) were observed spontaneously travel to locations with visual beacons or features similar to those that had been associated with the presence of food in previous trials. Similar untrained learning has been found in other studies.

Edwards, Newman, Parsons, and Krebs (1997) tested the ability of sheep to associate visual discriminative stimuli with food quality by pairing visually distinct discriminative stimuli with preferred and non-preferred food items. Twenty-four food sites placed along the walls in a pasture, each paired with either white clover or ryegrass, were baited with either preferred food or non-preferred food. There were three conditions, one in which white clover was paired with the preferred food and ryegrass was paired with the non-preferred food, another with the opposite pairing, and a third in which white clover and ryegrass were randomly paired with preferred and non-preferred foods. In all conditions, the white clover and ryegrass that served as discriminative stimuli could not be consumed by the sheep. Sheep were given 10 trials in as many days.

Spatial memory was prevented by randomly choosing the location for the discriminative stimulus/food pairing before each trial. Correct choices were considered to be visits to preferred food patches. The results showed that sheep can, in fact, learn to use visual discriminative stimuli as beacons to locate preferred food sites. On the first trial the sheep foraged randomly, visiting both preferred and non-preferred food patches in equal proportion. However, by the end of the testing period sheep in the consistently cued conditions improved their performance such that the majority of their first 12 visits (approximately 90%) were to preferred food sites. These results indicate that sheep can learn to associate the quality of a food patch with visual discriminative stimuli that are not directly associated with the food in those patches and that are not learned through direct sampling. This could increase foraging efficiency in a spatially and temporally complex environment.

Lopez, Gomez, Rodriguez, Broglio, Vargas, and Salas (2001) designed a series of experiments to determine whether turtles (*Pseudemys scripta*) were capable of using distal visual discriminative stimuli and local visual discriminative stimuli to locate a hidden food goal. In this study, one of four feeders was baited in a pool of water. Thirty turtles were randomly assigned to either the place procedure group, the discriminative stimulus procedure group or to the control group. For the place procedure group, the location of the baited feeder remained constant across trials. For the discriminative stimulus procedure group, the location of the baited feeder was chosen randomly at the beginning of trial. However, the baited feeder was signaled by the presence of a removable visual discriminative stimulus. Finally, the location of the baited feeder was randomly chosen and completely unsignaled for the control group. Both the place and discriminative stimulus procedure groups were further tested for their ability to locate the hidden food goal when all of the extramaze room discriminative stimuli were concealed, half were concealed, the discriminative stimuli were transposed, and when the start location was altered. The results showed that, whereas the performance of the control animals remained random throughout the study, both the place group and discriminative stimulus group improved in their ability to locate the hidden food goal. The turtles in the discriminative stimulus task improved more quickly and reached a higher level of performance than those in the place task.

The difference between the giant pandas and the spectacled bears in their performance on the visual task may reflect differences in the sensory capabilities of each species. For instance, the vision of the giant pandas may not be as acute as that of the spectacled bears. No research has been conducted to determine differences in vision across species of bears; however, there is no reason to believe that two species within the same taxonomic family would have gross differences in general visual capacity (Ted Grand, personal communication). Foraging Task 6 indicated that the giant pandas were capable of distinguishing between the black and white lids of the feeders. Therefore, a difference in sensory capabilities is not a strong argument for the observed differences in learning between the species. A more legitimate explanation may be that the results observed in this study are reflective of preparedness for the task. That is, because of their foraging ecology and evolutionary history spectacled bears may be predisposed to learn a visual association task more readily than giant pandas. Research has shown that some species are better able to process and retain information in short-term memory better when it is presented in one sense mode than another. For example, pigeons (Kraemer &

Roberts, 1984) and monkeys (Colombo & D'Amato, 1986) perform better on visual delayed matching to sample tasks than they do on auditory delayed matching-to-sample tasks. Rats (Cohen, Galgan, & Fuerst, 1986) and dolphins (Herman, 1975; Herman & Gordon 1974) on the other hand perform better on auditory delayed matching-to-sample tasks. This type of within-species difference in the ability to learn stimuli presented in different modes has been referred to as modal asymmetry (D'Amato & Colombo, 1985).

Modality asymmetries are presumed to be the result of natural selection favoring ease of learning of stimuli relevant to behavior in the environment. They are not believed to be based on deficits in perception of one stimulus or another. For instance, though dolphins typically have difficulty responding on visual matching-to-sample tasks, they have no actual visual deficits. For instance, once it was established that they could readily learn to match auditory information, Forestell and Hermann (1988) conducted an experiment in which visual stimuli were paired with auditory stimuli during training. This resulted in the dolphin's learning of not only the auditory-visual identity matching but also the visual-visual identity matching. Therefore, the difficulty was in the ease of learning a visual cue rather than ease of perceiving a visual cue. Rather, the difficulty is in the ease with which certain associations can be learned.

From an evolutionary standpoint, the ability of visual cues to gain control over behavior may be more important for frugivores such as spectacled bears than for folivores like giant pandas. Very few studies have examined species differences in the ease with animals with different foraging ecologies learn visual tasks (Fragaszy, 1981; Platt, Brannon, Briese, & French, 1996), however, Finlay and Sengelaub (1981) hypothesized that species occupying different environmental and dietary niches might differ in the way they are able to use vision in naturalistic behaviors such as exploration and foraging. Specifically, animals that live in an environment in which the availability of food sources changes with season may be able to find new food sources more efficiently through associative learning. For frugivores, there are many intrinsic and extrinsic visual cues that could be discriminative stimuli signaling either the presence or quality of a food source. Spectacled bears are known to eat the fruit of several species of tree and bushes (Mondolfi, 1989). As fruit ripens it sometimes changes color, therefore, the color of the food could become a discriminative stimulus for the palatability of the food item. It has been suggested that color vision in non-human primates may be important for allowing an animal to discriminate among visually distinct food items differing in palatability or toxicity (Lucas, Darvell, Lee, Yuen, & Choong, 1997; Savage, Dronzek, & Snowdon, 1987). In fact, macaques (*Macaca fascicularis*) in the wild consume leaves that are dark to light green more often than those that are more yellow or red, presumably because yellow leaves are more mature making them more fibrous and less nutritious (Lucas, Darvell, Lee, Yuen, & Choong, 1997).

Spectacled bears eat many food items that are embedded such as the unopened petioles of palms, the hearts of bromeliads, and seeds encased in shells or coverings (Mondolfi, 1989). Food-caching species have been observed to use seedlings that emerge from their caches as beacons to locate other buried seeds within the same cache (Pyare & Longland, 2000). The visual characteristics of the outer coverings of these embedded food sources could become discriminative stimuli that signal the presence of food. Therefore, natural selection may have favored the ability to readily learn associations between a variety of visual cues and the presence of food. The bamboo diet of giant pandas poses a slightly different problem. Different species of bamboo are visually distinct from each other, but only generally in terms of leaf and culm size. Unlike the leaves of some plants, the leaves of bamboo do not change in color with age. Distinctions between species are generally based on differences in culm or stem size and leaf size. It is possible that giant pandas would have been capable of learning a different type of visual cue such as size of the lid of the feeder or shape of the lid of the feeder rather than color. Menzel (1996) found that macaques (*Macaca fasciluris*) learned to associate visual stimuli, specifically the shape of objects, with the presence of food in an open field foraging task.

The purpose of the final experiment was to examine how the bears would respond in the presence of multiple discriminative stimuli. Despite having failed to learn the association between the visual cue and the presence of food in Foraging Task 4, the giant pandas preferentially relied on the visual cue in Foraging Task 6. This finding indicates that the lack of learning observed Foraging Task 4 could not have resulted from an inability of the giant pandas to perceive the difference between the white and black discriminative stimuli. It also sheds doubt on the possibility that the visual cues associated with the lid of the feeders were less salient than the spatial cues that were associated with location of the feeders. The methodology used in this experiment was fundamentally different from that used in the other foraging tasks. Rather than having one search trial in each test session, there were either two sequential, identical search trials or one search followed by one re-search trial in which the contingencies had been changed. This design allows the experimenter to rank order choices of feeders. However, it is difficult to know if the observed preference for one cue over the other is indicative of a true cue preference or of a win-shift foraging strategy. For example, the re-search trial of the test sessions followed approximately 10 minutes after the search trial. It is possible that the giant pandas visited the visual cue first, because they were avoiding revisiting previously depleted feeders. If this situation were the case, the giant pandas were exhibiting within-bout foraging behavior, possibly treating the second trial as one in the same bout or patch. In the wild, bamboo would not regenerate very quickly after consumption. Therefore, a win-shift strategy would be the most appropriate. In contrast, there was a 24 hour delay between trials between the search trials of the spatial and reversal task.

Bailey, Rittenhouse, Hart and Richards (1989) tested cattle in a radial arm maze and imposed delays of 0.5, 1, 2, 4, 8 and 12 hours between the fourth and fifth arm choices. The cattle maintained efficient foraging, avoiding previously depleted arms, at all delays up to eight hours. After eight hours, performance sharply decreased. The authors pointed out that most foraging bouts of cattle do not last longer than eight hours. Therefore, delays longer than eight hours may be treated as separate foraging bouts. The giant pandas may have considered the trial on the next day to be a new bout and altered their behavior as such. Whereas this argument is intriguing, it is flawed because the giant pandas learned to return to feeders that had been baited in the preceding search trial of the filler sessions. Most species that have been tested under similar paradigms have found either preferential responding to spatial cues or no preference for a particular cue at all when several competing cues are dissociated from one another.

One of the earliest studies that examined this was conducted by Tinkelpaugh (1932). Chimpanzees, rhesus monkeys, human adults and human children were tested in a series of delayed reaction trials in which food was hidden in one of a pair of receptacles in view of the subject/participant, who was required to locate the hidden food after differential delay. When the experimenters surreptitiously changed the position of the baited feeders, the ability of the subjects to accurately locate the baited containers decreased, despite the fact that the containers were visually distinct. Differences in the containers could have easily been used as discriminative stimuli or beacons signaling the presence of food. Tinkelpaugh determined that animals respond on the basis of many different cues, but that of these, positional cues were the dominant. More recent studies of primate behavior have shown that other primates, specifically wild capuchin monkeys (*Cebus capucinus*), also rely preferentially on spatial information to locate viable sources of food, even when olfactory and visual discriminative stimuli are available (Garber & Paciulli, 1997).

Several studies have shown that birds rely preferentially on spatial information when spatial cues are in conflict with other cues. Homing pigeons (*Columba livia*), for example, are well-known for their ability to return to nest sites after long distances and long delays. Research has shown that they return to the correct location of nest sites even when the visual characteristics of those nest sites have been switched with those of another nest site (Strasser & Bingman, 1996). Food-storing birds are also well-known for their ability to return to a specific site and food-storing parids have been observed to respond preferentially to spatial discriminative stimuli in one-trial associative memory tasks when both spatial and non-spatial discriminative stimuli are simultaneously available (Krebs, Clayton, Healy, Cristol, Patel, & Jolliffe, 1996). For example, Brodbeck (1994) compared the performance of food storing black-capped chickadees

(*Parus atricapillus*) and non-storing dark eyed juncos (*Junco hyemalis*) on a series of tasks in which they were allowed to find food in one of four visually unique feeders arranged in a particular spatial configuration. By allowing the birds to find food in a visually and spatially distinct feeder and then switching either the visual or spatial aspect, both in terms of location of one particular feeder within the array and the location of the entire array in the testing room, it was possible for the experimenter to examine which aspects of the testing situation were controlling behavior. The results showed that even when the feeder that contained the hidden reward was visually distinct from all of the other feeders, the food-storing birds did not use this as a beacon. Rather, they returned to the spatial location where they had previously found food. Furthermore, it was found that the location of the feeder in relation to the whole room (global information) exerted more control over the behavior than the location of the feeder within the array. In contrast, dark eyed juncos did not show a preference for one type of information or discriminative stimulus over another. Similar results were found in an operant delayed-matching-to-sample task (Brodbeck & Shettleworth, 1995).

Like food-storing birds, rufous hummingbirds (*Selasphorus rufus*) appear to be more sensitive to the relative spatial location of a feeder than to an associated visual discriminative stimulus. In a study conducted by Brown and Gass (1993), hummingbirds were allowed to visit six feeders, one of which was associated with a visual discriminative stimulus, a colored light illuminated 2.5 cm above the baited feeder. The spatial location of this feeder and discriminative stimulus remained constant. Once the hummingbirds had learned to exclusively visit the correct feeder, the visual discriminative stimulus was switched to a different feeder. The birds visited the same spatial location as the previously correct feeder rather than to the new feeder signaled by the visual discriminative stimulus, indicating that spatial location was more important in learning. To demonstrate that the birds were actually capable of seeing the discriminative stimulus, the researchers conducted a second study in which the spatial location of the visually signaled baited feeder changed unpredictably from day to day. To choose the correct feeder, the birds had to learn the association between the visual discriminative stimulus and the presence of food. All birds in the study were able to directly approach and visit the correct feeder on the basis of the visual discriminative stimulus alone. It was hypothesized that the preferential use of spatial location over visual discriminative stimuli is related to the fact that most flowers on an individual plant have petals that are visually indistinct, making relative spatial location more important for these birds in the wild.

In another study of hummingbirds, Healy and Hurly (1998) found that hummingbirds learned the spatial location of a baited feeder more quickly if it was visually distinct than if the feeders were identical. However, despite the fact that the visual discriminative stimuli apparently made the task simpler to learn, they were not used by the birds to return to the baited feeder. When the position of the feeders was moved, the birds returned to the correct spatial location rather than the correct visually distinct feeder. Healy and Hurly were also interested in whether the birds were locating baited flowers based on the relative spatial position of the feeder to the other feeders in the array or on the relative spatial position of the feeder to distal discriminative stimuli in the environment. Hummingbirds were trained to respond to the center feeder of a cross-shaped array. In a re-search trial the entire array was shifted. When the flowers were spaced far apart during training, the birds returned to the center feeder within the array. However, when the feeders were spaced far apart during training, the birds returned to the feeder that was now in the same spatial location as the center feeder had been during training. These results show that hummingbirds are capable of using both local and distal discriminative stimuli depending on the situation. Perhaps the most interesting finding was that, not only do the birds fail to use visual discriminative stimuli associated with the feeder to locate the feeder, they also do not even use the presence of the feeder itself. When a baited feeder was moved from its original location, the hummingbirds go directly the original spatial location even though they should be able to see that the feeder itself is no longer there.

Sheep also rely on spatial location to localize viable food sources, even when visual cues are available. Edwards and his colleagues (1996) examined the ability of the sheep to use visual discriminative stimuli to locate food. One of eight patches was baited for six days. Subjects were divided into two groups, one in which a visual discriminative stimulus of white clover was placed in front of the food bowl and the other in which no discriminative stimulus was available. Measures were taken to prevent the sheep from removing and/or eating the visual cue. The results showed that sheep in both conditions searched randomly for the baited bowl in the first trial. Whereas both groups improved to above chance levels in the second trial, the group with the visual discriminative stimulus found the baited feeder more rapidly than the group that did not have a visual discriminative stimulus. When the location of the baited food site was switched randomly in the fifth trial, all sheep traveled directly to the patch that had contained food in the previous trial, even though the visual discriminative stimulus for the cued group had also switched to the new location. These results suggest that, whereas visual discriminative stimuli may be helpful to sheep in their search for food, spatial memory is more important.

Studies conducted under more highly controlled laboratory conditions have also shown that memory for spatial location may be better than memory for the visual properties of a stimulus. Wilkie, Jacobs, and Takai (1985) conducted three experiments using a delayed-matching-to-sample paradigm. Pigeons were tested for their ability to match a sample stimulus with a test stimulus on the basis of either color of the sample or location of the sample (right or left keys of an operant test chamber) after either a constant or variable delay period. All three experiments found that the pigeons performed more accurately when responding to the location of the sample stimulus was reinforced than when responding to the sample color was reinforced, indicating that the properties associated with location overshadowed the visual properties of the stimulus. Likewise, Shettleworth and Westwood (2002) found that food-storing black-capped chickadees more accurately remember sample stimuli when correct responding is based on the location of the stimulus than on the color of the stimulus in delayed-matching-to-sample paradigms. Interestingly, nonstoring dark-eyed juncos showed no difference in performance between the two stimulus properties.

Few studies have shown preferential responding for visual cues, as observed in the giant pandas in Foraging Task 6. In their study of gray squirrels (*Sciurus carolinensis*), McQuade, Williams, and Eichenbaum (1986) found that these food-storers place more importance on visual cues than olfactory or spatial cues in tasks simulating cache recovery. Twelve artificial caches (Petri dishes with lids) were signaled by olfactory cues (phenyl ethyl alcohol and geraniol) and visual cues (blue or yellow tape over the cover of a Petri dish). One of the scents and one of the visual cues served as a negative discriminative stimulus (the dish never contained food) and the other served as the positive discriminative stimulus (the dish always contained food). The baited caches were always located in a predictable spatial location. In test trials, the olfactory and visual discriminative stimuli were reversed such that the cue that served as the negative discriminative stimulus became the positive discriminative stimulus and vice versa. The results showed that reversals of the positive and negative visual discriminative stimuli disrupted performance more that reversals of either spatial or olfactory stimuli. Furthermore, spatial reversals disrupted performance more so than reversals of olfactory cues. McQuade and colleagues interpreted their findings in terms of selective pressures for foraging in the wild, hypothesizing that extrinsic olfactory cues may not be important and visual cues may be the most salient for squirrel foraging in the wild.

Daehler, Bukatko, Benson, and Myers (1976) conducted a study with human children and found that there might be a developmental aspect of reliance on visual and spatial cues. Children ages 18, 24, 30 and 36 months were presented with four experimental conditions. In the first condition, hidden food was predictable on the basis of location. In the second condition, the presence of food was associated with both location cues and the size of the container. In the third condition, the presence of food was associated with location, size and color of the containers. In all conditions, the addition of visual cues enhanced memory for the location of the hidden food. In a fourth condition, the visual cues and location cues were disassociated from each other. Only the 36-month-old children responded preferentially to the visual cue, indicating a reliance on the visual cues for locating food. The authors suggest that these results reflect differences in cognitive development. Therefore, it may be predicted that animals would be more likely to track spatial location than visual cues.

The differences in preferences for using spatial cues or local cues between studies may be methodological. In each of the studies that report preferential reliance on spatial information for the localization of viable food sources, only one of a group of feeders was baited with food and signaled by local and spatial cues. It has been suggested that it is easier to remember the location of one baited feeder when it is presented with many other feeders (Einon & Pacteau, 1987; Lavenex & Schenk, 1995). On the other hand, when more than one feeder is baited, as was the case in the present study and in the experiment conducted with grey squirrels by McQuade and colleagues (1986), it may be easier to use a beacon to find baited food sites. Pigeons that were trained on a radial arm maze task in which differentially baited arms were signaled by color cues exhibited decreases in accuracy when the cues were disassociated from the location (Roberts & Van Veldhuizen, 1985). These results contrast those of other studies conducted with pigeons when only one feeder was baited during a trial. This suggests that different research designs may elicit different response strategies. However, Garber and Dolins (1996) and Garber and Paciulli (1997) found that, even when four of eight or five of thirteen food sites were baited, both wild moustached tamarins (*Sanguinus mystax*) and wild capuchin monkeys (*Cebus capucinus*) relied preferentially on spatial cues associated with baited food sites when visual beacons were dissociated from location. Future research should be conducted to examine the factors affecting reliance on specific cues. Preferential cue use may change even in the same species when tested under different environmental circumstances.

Researchers interested in food-storing birds have hypothesized that global spatial cues are better predictors of cache location than visual local cues because global cues are more salient (Sherry & Duff, 1996). Caches are often created many months before exploitation, during which time local cues can become displaced or masked by environmental factors. For example, food-storers are known to be capable of successfully recovering caches even after local cues have been covered with heavy snow. Because of the drastic environmental changes that can occur between the time a cache is made and the time it is exploited, local discriminative stimuli would be unreliable. It has been suggested that visual cues are less important for hummingbirds than spatial location for locating food because their territories contain many individual flowers of the same species (Hurly & Healy, 1996; Hurly & Healy, 2002). These individual flowers are visually indistinct, therefore, spatial location is the best predictor for locating flowers that have not been visited. The food resources and habitat of giant pandas are quite different from that of food-storing birds or hummingbirds. Bamboo grows several feet in height. Giant pandas eat the leaves and stem that grow above the ground, therefore, a heavy snow is not likely to greatly impact visibility. Visual cues used for foraging such as leaf and stem size could be used to reliably orient toward preferred food sites.

It is possible that, as observed in studies of modal asymmetry in other species, the pairing of the visual stimulus with the spatial stimulus enhanced learning of that stimulus. In Foraging Task 4, the spatial location of the feeders was unpredictable. The visual cue was the only reliable discriminative stimulus signaling the presence of food.

In the first fifteen trials of Foraging Task 6, the visual cue and olfactory cues were consistently paired with predictable spatial cues. Perhaps in the same way that the pairing of the auditory and visual stimuli facilitated learning of the visual stimulus for dolphins (Forestell & Herman, 1988), the association between the spatial cue and the visual cue facilitated learning of the visual cue and increased the saliency and effectiveness of that visual cue as a discriminative stimulus for the giant pandas. In studies with hummingbirds, it has been observed that the presence of a visual cue (color of an artificial flower) facilitates learning of the spatial location of flowers containing nectar (Healy & Hurly, 1998). Furthermore, Brown (1994) found that hummingbirds were able to use a visual cue alone to localize a baited feeders when the location of the visual cues was randomly chosen between trials, however, these birds had extensive preliminary training with the visual cue paired with a feeder whose location did not change. Therefore, it is unclear if the visual cue would have gained control over behavior had they always been presented in random locations.

The giant pandas were no more likely to visit feeders with the olfactory cue in Foraging Task 6 than they were to visit feeders that had no cue at all. If the pairing of the visual cue and spatial cue facilitated learning of the visual cue, it is unclear why learning of the association between the presence of food and the olfactory cue was not also facilitated. One possible explanation could be that the visual cue was more salient than the olfactory cue, and therefore overshadowed the olfactory cue. To determine if the visual cue overshadowed the olfactory cue, the final experiment could be replicated with only the olfactory and spatial stimulus pairing. In the absence of a competing visual cue, they may have shown evidence of learning. Rats, for example, exhibit a preference for using visual cues when both visual and olfactory cues are available for path localization (Maaswinkel & Whishaw, 1999). However, if they are blindfolded they are capable of using olfactory cues to return to their home location.

Croney, Adams, Washington, and Stricklin (2003) recently conducted a study to examine visual, olfactory and spatial cue use in foraging pigs (*Sus scrofa*) that was very similar to Foraging Task 6 of the present study. In one experiment, viable food sources were signaled by a visual cue and their location was predictable across ten trials. After a criterion level of performance was reached, the researchers randomly dissociated the visual cues with the location. They found that the pigs performed at above chance levels, visiting significantly more viable food sources in their first few visits than would be expected had they been foraging randomly. In a second experiment, they followed the same procedures as the first experiment using olfactory cues as discriminative stimuli for food. When olfactory cues were dissociated from spatial cues, the pigs visited baited feeders signaled by the olfactory cues at a level greater than would be expected by chance. Perhaps the spatial cues would also have facilitated learning of the olfactory cue in the present study with the giant pandas in the absence of a more salient visual cue. It is unknown whether the pigs could have formed associations between visual and olfactory cues and the presence of food in the absence of pairing with spatial cues. Had the visual and olfactory cues not been paired with the spatial location for 10 trials before being randomized, the pigs may also not have learned to associate them with the presence of food. It would be interesting to test naïve pigs on tasks similar to Foraging Tasks 4 and 5 of the present study.

The observation that the giant pandas chose to attend to visual cues in the presence of multiple discriminative stimuli may be indicative of preference for that particular type of stimulus. It does not, however, indicate that memory for a visual stimulus is better than that for a spatial stimulus. We do not know if visual memory is better than spatial memory. Tests should be done using a delayed matching-to-sample paradigm in which various delays are imposed between the search and re-search trials in conditions involving spatial matching-to-sample and visual matching-to-sample.

It is important to note that the purpose of these studies was not to determine the intelligence of each species. The purpose of the research was simply to examine the role of associative and spatial learning in foraging. There were large individual differences in performance on several of the tasks. For example, only five of the seven giant pandas and one of the spectacled bears learned the spatial memory task, as measured by the number of visits to baited feeders of the first four visited. Does this mean that the three bears that did not learn the task are less "smart" than the others? The answer is, not necessarily. It is interesting that tasks such as spatial memory tasks require the animal to suppress their tendency to explore the environment and gather information to reach a criterion level of performance. According to Foreman and Ermakova (1998), it might be advisable for animals to periodically visit previously unrewarding food sites so that they can detect any environmental changes that may have occurred. It could be argued that they are the ones whose behavior is most adaptive in the environment.

Sampling is important because it allows a forager to accurately assess their environment and become aware of environmental change (Mellgren, Misasi, & Brown, 1984). Therefore, sub-optimal foraging behavior may actually be the most adaptive in certain environmental conditions. According to Bernstein (1984), sometimes you have to be stupid to be smart. This was said in reference to the fact that primates often fail to exhibit optimal performance on very simple learning tasks, repeatedly making errors even after being tested for one thousand trials. It might be predicted that when the costs of making errors is low, sampling and "errors" in performance will be high. In the present tasks, the cost of visiting all of the feeders was presumably low. It took the bears very little time to traverse the circle and lift the lids of the feeders. Those that continued sampling all of the feeders, despite regularities in the position of baited feeders, may not have been expending enough energy to significantly increase the costs of foraging. Their continuous sampling prevented them from being adversely affected by changes in the experimental conditions. In fact, one of the giant pandas (NZP male) and the one male spectacled bear that never reached criterion performance on the spatial memory task obtained all four of the biscuits on the first day of the reversal phase. In contrast, of those bears that learned the spatial task four obtained only one of the four biscuits, one obtained two of the four biscuits, and one obtained three of the four biscuits when the location of the baited feeders was reversed. Because, the energy expenditure for the task was presumably low, it could be argued that sampling all of the feeders may actually have resulted in better efficiency and adaptability to the environment.

Not only did sampling decrease for those bears that learned the spatial and reversal tasks, but it also decreased in the spectacled bears in the visual task and in most of the giant pandas in Foraging Task 6. In the re-search trials of the test sessions in this foraging task none of the feeders were baited with food. It was thought that leaving the feeders empty would cause the giant pandas to search through all of the feeders, allowing a hierarchy of cue use to be established based on the order of visitation of the feeders. The giant pandas visited a mean of only 3.12 feeders in the re-search trials of the last five test sessions. The behavior of the giant pandas contrasts that observed by other species in studies that used a similar methodology. For example, hummingbirds were tested in a very similar open-field situation in which artificial flowers were arranged in a circular array and were differentially baited with food to examine their memory for location and visual cues. When none of the flower feeders in an analog of the radial arm maze contained food, the hummingbirds search several flowers before leaving the test area (Hurly & Healy, 1996). Similarly, in a study of the relative important of cues for food-storing and non-storing birds, both black-capped chickadees and dark-eyed juncos were observed to systematically search through all of the feeders presented to them one after another when none were found to contain food (Brodbeck, 1994; Brodbeck & Shettleworth, 1995).

Rarely did the bears travel directly to baited feeders and only the baited feeders, indicating some continued sampling of the environment. However, they still would not have been readily aware of any changes that may have been made by the experimenter to the environment in a given trial. Those giant pandas that sampled fewer feeders in the foraging tasks were slowest to detect environmental changes. In fact, two of the bears failed to receive any reinforcement on the first day of the reversal because they traveled directly to the feeders that had been baited in the preceding trial and failed to sample the other feeders. Scatter-feeding may have negatively impacted the ability of the giant pandas at SDZ and NZP to avoid making the mistake of visiting previously depleted feeders. Had the contingencies changed during the task, it was those giant pandas that would have noticed the difference and adapted their behavior accordingly.

7.2 Suggestions for Future Research

Now that it is known that giant pandas and spectacled bears are capable of using distal cues to localize viable food resources, it would be interesting to further examine the extent to which these cues can be used to increase foraging efficiency. Researchers that study the foraging behavior of frugivores often suggest that not only are they are capable of traveling directly to food sources, but they can also remember both the quality and quantity of food in particular sites. For example, the results of experimental research suggests that Japanese monkeys (*Macaca fuscata*) have long-term memory for the location of specific food items and are capable of matching their search routines to those food items (Menzel, 1991). In other words, their behavior suggests that they have knowledge of not only the availability of food at particular sites but also the quality of the food at those sites. This would increase foraging efficiency for preferred food items. Furthermore, it would be adaptive if animals could remember the location of food sites that predictably are higher in quantity than other food sites. For instance, giant pandas may be able to increase foraging efficiency by being able to remember the location of patches of bamboo that had a greater amount of stalks than other patches. Once in the high quantity patch, they would increase intake and decrease the necessity of travel between patches. There is evidence that some species are capable of remembering more about a patch than its existence alone. Food-storing birds remember not only the location of their caches, but also remember the quality (preferred or non-preferred) (Sherry, 1984a) and quantity of food that was cached in a site (Smith & Sweatman, 1974). They may also remember when they cached food, as evidenced by their ability to learn about the perishability of cached food items (Clayton, Yu, & Dickinson, 2001).

Howery, Bailey, Ruyle, and Renken (2000) found that cattle could also make choices based on the quality food sources in an open field environment. In their experiment, two of sixty-four potential food sites were baited with a high quality food source and two were baited with a low quality food source. The researchers were interested in the ability of cattle to use both spatial memory and visual discriminative stimuli as beacons to locate hidden food. Steers were assigned to one of four conditions: fixed locations with discriminative stimuli, variable locations with discriminative stimuli, fixed location with no discriminative stimuli, and variable location with no discriminative stimuli. In the two cued conditions, the high quality food sites and low quality food sites could be readily distinguished by prominent visual discriminative stimuli placed near the site. In the fixed location conditions, the location of the high and low quality sites remained consistent for one week (six trials) of testing. In the variable location conditions, the locations of the food sources were changed during each trial preventing the use of spatial memory for the task. The results showed that cattle in both the fixed conditions (cued or uncued) found food more quickly and consumed more high quality food than those in the variable conditions. Visual discriminative stimuli in both the fixed and variable conditions increased foraging efficiency by allowing the animals to locate food sites more quickly. Cued animals were also more likely to consume the high quality food first and consumed more food overall during a trial than uncued animals. These results indicate that cattle can locate high quality food by either direct visual discriminative stimuli, or spatial memory when visual discriminative stimuli are unavailable. Whereas visual discriminative stimuli may not have been necessary for the location of viable food sites, they did make foraging more efficient by decreasing search time as was observed in hummingbirds.

Not only do cattle seem to be able to remember where they have been and avoid previously depleted food sites, they also seem to be able to remember the quantity (Bailey, Rittenhouse, Hart, Swift, & Richards, 1989) of food located in each site. Bailey, Rittenhouse, Hart, Swift, and Richards (1989) tested cattle in a parallel arm maze in which cattle entered the testing situation through a gate from which they could then choose to travel down one of five parallel corridors. In each trial, the same feeders were baited with 0.1, 0.2, 0.4, 0.6, or 0.8 kg of grain for seven days. The steers all performed very efficiently, choosing the feeders with 0.4, 0.6, and 0.8 kg in the first three choices 85% of the time. In addition, they returned to the feeders with the richest amounts of food more often than they returned to leaner sources within a trial, avoiding the leaner sources until they were certain that the richer sources had been depleted. Whereas this study suggests that steers are capable of remembering the location of rich sources of food and preferentially visiting those sites, it would have been more convincing had the location of the rich food sources been randomly selected. The experimenters baited the feeders in either ascending or descending order. Therefore, all the steers had to learn was to either turn left or right toward the side with the largest amounts of food and then visit adjacent arms toward the end of the corridor. The ordering of the feeders in this way made it much more likely that, if the steers developed the appropriate right or left bias they would visit the richest feeders in the first three choices. The fact that their performance was above chance indicates that they had learned something about the location of richer food sources, but it may have had less to do with spatial memory and more to do with a simple turning preference. A better test would have been to randomly select the feeders baited with the richest food sources. Learning would require the steers to move less stereotypically through the maze.

Like cattle, it seems that sheep can also learn about the quantity or density of food in a pasture (Dumont & Petit, 1998). Sheep were put to pasture in a field that contained sunken bowls filled with preferred food pellets. Areas of different concentrations were created by placing groupings of either nine or twenty-four bowls in different blocks in the yard. The bowls could not be distinguished until the sheep were in close proximity to them. Over the course of twelve days, the sheep exploited the more dense food sites more often and visited them sooner within the day than the sparse food sites. During the study, steps were taken to ensure that the sheep were not using olfactory or direct visual discriminative stimuli that would help them distinguish food patches. These measures did not affect performance, suggesting that sheep can remember the location of areas that contained a high density of food and return to them when grazing.

In the exploratory task, the bears exhibited a strong tendency to shift after depleting a food site, and learned to avoid revisiting depleted feeders. This behavior is referred to as "win-shift" because the moves or shifts to a different location after being rewarded. Many species have shown similar tendencies to shift in exploratory tasks conducted in radial arm mazes (Foreman & Ermakova, 1998). However, the bears were also able to use a win-stay strategy in the spatial and reversal tasks. Upon finding food in one location, they learned to return to that location. The choice behavior of rats also varies as a function of the number of days food is placed in one location before being shifted to another location (Olton, Walker, Gage & Johnson, 1977). The factors affecting the choice of animal to shift or stay have not been thoroughly explored. It would be interesting, for example, to see if tendency of the bears to shift would weaken if they were unable to completely deplete a food source. Studies have shown that, if a flower is not completely depleted by the foraging hummingbird, they will return to that feeder (Hurly & Healy, 1996). Therefore, they are capable of adjusting their search strategy from a win-shift to a win-stay as appropriate. Similar behavior has been observed in red-winged blackbirds (*Agelaius phoeniceus*) (Beauchamp, Cyr, & Houle, 1987). It would also be interesting to see if species that live in different habitats and exploit different dietary niches would perform differently with respect to tasks that require a win-shift versus a win-stay strategy of responding. There is some evidence that species whose prey or plant material replinshes quickly adopt a win-stay strategy more readily than a win-shift strategy (Burke, Cieplucha, Cass, Russell, & Fry, 2002).

Few species of mammal other than rats and food-caching small mammals have been studied on tests of spatial memory. Those that have been conducted rarely make direct comparisons of species based on a priori predictions of performance. Furthermore, it appears that the definition of spatial memory, as well as the nature of the tasks that are used to measure spatial ability, vary widely among researchers. For example, the ability to shift or stay following reinforcement has been used by researchers as evidence of spatial memory. Whereas, some researchers consider spatial proficiency as the ability to shift, others consider proficiency as the ability to stay, making comparisons between studies difficult. Moreover, some studies have considered proficiency to be the ability to locate a single hidden goal from among eight feeders whereas others consider proficiency to be the ability to locate four hidden goals among eight feeders. It would be beneficial to have a more uniform measure of what it means for an animal to be considered proficient at tasks involving spatial memory. Therefore, not only is there a great deal of research that needs to be conducted on a wide variety of species, but there is also a great deal of research that needs to be conducted to determine which tests are most appropriate for measuring spatial ability and food-searching behavior.

There have been few studies of cognition on animals within the Order Carnivora, particularly in terms of spatial memory ability. Furthermore, there have been no studies of the spatial ability of meat-eating carnivores similar to those conducted with food-storers or herbivores. Of the 169 species of carnivore tested by Gittleman (1986), it was found that relative brain size was correlated with dietary niche such that species categorized as carnivores have larger relative brain sizes than omnivorous and insectivorous carnivores. As observed in other studies, home range size in carnivores is correlated with diet such that carnivores have larger home range sizes than insectivores and folivores/frugivores (Gittleman & Harvey, 1982). For primates, Milton (1988) hypothesized that home range size would be correlated with enhanced cognitive ability. However, this enhanced cognition may not be for spatial learning. Meat-eating carnivores have larger brains than non-meat eating carnivores, presumably because of their greater need for rapid prey detection, pursuit, capture and consumption. For carnivores, home range size is closely tied to the home range size of their prey. Some species of carnivore such as the lion must follow the migratory patterns of large, far-moving prey (Gittleman & Harvey, 1982). Therefore, hypotheses related to home range size and spatial memory ability might be predicted to be supported only by studies of animals that eat widely distributed sessile prey.

It would be interesting to look closely at the carnivore data and make a priori predictions of differences in spatial memory and foraging ability based on distribution and movement of prey. To my knowledge only one study of comparative cognition has been conducted with carnivores (Warren & Warren, 1959). However, this study was conducted using a more traditional generalist approach to cognition rather than an ecological approach. Because of their wide range of diets and the known differences in relative brain size of bears (Gittleman, 1986), comparisons should be made in species other than giant pandas and spectacled bears. Furthermore, in light of the results of this study, it would be interesting to conduct more detailed studies of the brain structures of giant pandas and spectacled bears. Spectacled bears were not included in Gittleman's (1986), however, they might be predicted to have brain/body ratios similar to those of the other more omnivorous bear species. Moreover, specific portions of the brain such as the neocortex should be examined and compared more closely between species. It might be predicted that spectacled bears would have a larger neorcortex than the giant panda because it is known that neocortical size correlates with many aspects of foraging, specifically extractive foraging (Gibson, 1986). Within species comparisons may also be warranted. Among the brown bears (*Ursus arctos*), there are several subspecies that differ in both habitat and feeding ecology (Brown, 1993). The Syrian brown bear eats mostly vegetation whereas the Kamchatka brown bear eats mostly fish. It would be interesting to conduct comparisons in spatial memory in these very closely related animals.

Birds of the family Corvidae and Paridae have been well-studied in research on spatial memory, however, there are many other species of animal that cache their food. There are many species of food-caching rodents that have been observed to use spatial memory in the laboratory such as the yellow pine chipmunk (Vander Wall, 1991), fox squirrels (Jacobs & Shiflett, 1999; Lavenex, Shiflett, Lee, & Jacobs, 1998), gray squirrels (McQuade, Williams, & Eichenbaum, 1986), Merriam's kangaroo rats (Barkley & Jacobs, 1998; Jacobs, 1992), and desert kangaroo rats (Langley, 1994). There are also many other species of birds that are known to cache food, including tropical, carnivorous (Kestrels, owls, shrikes, secretary birds), frugivorous (bowerbirds), and other seed-caching species (acron woodpeckers, tropical corvids) (Stanback, 1991). However, none of these species have been compared to closely related species that are not known to cache food. It would be interesting to conduct research with these species using the same multi-disciplinary approach that has been used to study spatial memory in food-storing birds. Given Milton's hypothesis concerning primary consumers and secondary consumers, it would be interesting to know how a carnivorous cacher and a frugivorous cacher compare not only to each other but also to other closely related carnivorous and frugivorous species that do not cache. In addition, some species of storers can be described as scatter hoarders, creating many caches scattered throughout their home range, whereas other species are considered to be larder hoarders in which food is stored mostly in a small location within their home range (Stanback, 1991). It might be expected that scatter hoarders and larder hoarders would differ when tested on tasks involving spatial memory because scatter hoarders would have to remember a greater number of locations and sets of landmarks.

Like carnivores, reptiles and amphibians are largely understudied in the field of animal cognition. Given the range of feeding and foraging behaviors they are known to exhibit, they may provide valuable species comparisons. Most amphibians can be categorized as either carnivores or omnivores, however, among the reptiles there are representatives of each of the different diet and feeding strategies (Zug, 1993). For example, there are several species of lizards and turtles whose diets are predominantly made up of plant matter ranging from foliage to nectar and fruit. Recent research indicates that there are species-specific differences between the sensory abilities, specifically the ability to discriminate prey using chemical stimuli, of lizards on the basis of their mode of foraging. Active foragers, but not ambush foragers, are able to discriminate prey based on chemical cues from prey (Cooper, 2000). Furthermore, insectivorous lizards and omnivorous lizards respond differently to chemical cues associated with potential prey and plant items such that insectivorous lizards respond more strongly to chemical cues associated with animal prey and omnivorous lizards respond more strongly to chemical cues associated with plant materials (Cooper, Al-Johany, Vitt, && Habegger, 2000). In his discussion of the mechanisms for location and identification of prey in reptiles and amphibians, Zug (1993) discusses vision, chemosensory detection, hearing, and touch. No mention is made of higher level mechanisms such as spatial memory for the location of viable food sources. In fact, only two studies have been published on the spatial learning skills of reptiles. The first study not only tested the performance of lizards on spatial and nonspatial tasks, but it also compared species on the basis of their foraging ecology in the wild. Day, Crews, and Wilczynski (1999) hypothesized that an active forager that consumes clumped, sedentary prey such as *Acanthodactylus boskianus* would perform better on a test of spatial memory than a sit-and-wait forager that collects distributed mobile prey such as *Acanthodactylus scutellatus.* The two species of lizards were tested under three conditions for their ability to locate a heated rock within their environment. In the first experiment, the location of the heated rock was held constant and four extramaze discriminative stimuli were hung like flags over the arena. In the second experiment, intramaze discriminative stimuli were attached within the maze and a single local discriminative stimulus was placed directly behind the heated rock. In the third experiment, the location of the heated rock was changed randomly and was signaled by a red light that served as a beacon. The results showed that the latency to find the heated platform decreased across trials in both species in experiments 1 and 2. However, individuals of both species rarely approached the goal directly on their first visit, even when it was signaled by a local discriminative stimulus. Furthermore, neither species appeared to be using either extramaze or intramaze discriminative stimuli to locate the heated platform, as evidenced by the fact that a disruption of these discriminative stimuli did not influence performance. There were no species differences on any of the tests of spatial learning. The fact that the lizards rarely approached the heated platform on the first visit indicates that they may never have learned the task at all. This led the authors of the study to suggest that spatial memory may not be a navigation strategy used by reptiles.

Another study conducted with turtles found results that contradict those observed with lizards. Lopez and colleagues (2001) found that turtles were capable of using both visual discriminative stimuli and extramaze place cues to locate hidden food. Concealing all extramaze discriminative stimuli and transposing the extramaze discriminative stimuli negatively affected performance for those turtles in the place group, but had no effect on the performance of those turtles in the discriminative stimulus group. However, a partial concealment of the discriminative stimuli had no effect on behavior, which the authors offered as evidence for the use of "a map-like representation of the environmental space that serves as an allocentric frame of reference". Based on the results of this study, the authors hypothesized that spatial learning is a primitive characteristic that may have originally appeared in the common reptilian ancestor of turtles, mammals and birds.

The study of lizards conducted by Day, Crews and Wilczynski (1999) differed from that of Lopez and colleagues (2001) as well as tests of spatial memory in other species in several ways. First, the measure of performance used by Day and colleagues was latency to find the goal as opposed to the number of errors made prior to locating the correct goal. A decrease in latency to locate a goal might simply indicate that less caution was used in traveling through an increasingly less unfamiliar environment. Physically moving more quickly in an environment will result in locating a goal more quickly, regardless of whether spatial memory is involved. Second, while it makes sense to hypothesize that a sit-and-wait predator would have less need for spatial memory skills than an active forager, it is unknown whether actively foraging carnivores are capable of learning traditional tasks that test spatial recall in any species. The study by Lopez and colleagues (2001) is a more appropriate first test of spatial memory in reptiles and is more comparable to studies conducted with other species because the subject of the study was an herbivorous reptile. And finally, Day and colleagues (1999) used a heated rock as the reward rather than food. Even if spatial memory can be used by reptiles to locate food, it may not be necessary for locating sources of heat in the environment. Rather, visual discriminative stimuli such as the amount of light reflected from a surface may be used. Testing for differences in spatial memory based on foraging ecology may not be appropriate using a non-food reward.

The results of the study by Lopez and colleagues (1993) are the first to show that a species of reptile is capable of using both distal and local discriminative stimuli to locate hidden food. However, the authors appeared to treat this study of one species as being representative of all turtles. No mention is made by Lopez and colleagues (1993) of the diet or ecology of the species of turtle tested. *Pseudemys scripta* is a member of the turtle family Emydidae, which includes both terrestrial and aquatic species. Only two genera within this family are herbivorous, *Pseudemys* and *Trachemys* (Zug, 1993). It would be interesting to conduct comparative studies between these species and those in the same family that are classified as being omnivores and carnivores. Studies of turtles are particularly important from an evolutionary standpoint because they are the only living representatives of the order Chelonia believed to have diverged from the same branch as the ancestor of mammals. In addition, there are many species of lizards that are considered to be herbivorous. It would be hasty to conclude that lizards are incapable of using spatial memory in navigation on the basis of results from two carnivorous species. Comparative tests of herbivorous species with diets differing in the amount of foliage and fruit, nectar or seeds would be more comparable to tests of spatial memory conducted with other species of animal.

It became clear in the review of the literature that relatively few studies of spatial memory have been conducted with primates, especially when compared to the volume of research conducted with other species and other types of cognition. Those studies that have been conducted have reported results that were less than remarkable, particularly for species considered to be so cognitively advanced. It is unknown whether this is because of the general lack of research that has been conducted with non-human primates or if non-human primates are simply not more adept at using spatial memory in foraging than other species. Given the close relation between non-human primates and humans (particularly between humans and the great apes), as well as the complexity of the physical and social environments in which most non-human primates live (Tomasello & Call, 1997), it is difficult to imagine that they would not perform as well if not better than other species. There are many closely related primate species that differ in their foraging ecology that could be tested for predicted differences in spatial memory. For example, the howler monkeys and spider monkeys used by Milton (1988) as an example of species that should exhibit differences in cognitive ability based on foraging ecology have never been formally tested or compared in the laboratory. It is unknown if the differences in brain size correspond to differences in behavior.

Another interesting comparison might be one between orangutans and gorillas. Orangutans are highly specialized frugivores, devoting about 53.8% of their feeding time to the consumption of fruit (Rodman, 1977). Orangutan foraging appears to be goal-oriented. They have been observed to travel great distances, often passing up viable food sources on their way to feed in a distant tree containing a larger supply of fruit (Leighton, 1993; Mackinnon, 1977; Rodman, 1988; Wheatley, 1982). Gorillas, on the other hand, are primarily folivorous, spending more of their feeding time eating the leaves, shoots, and stems of plants (Fossey & Harcourt, 1977). According to Milton's (1988) theory, plant material is generally more plentiful and predictable in the forest than fruit. It has also been found that orangutans occupy larger home ranges than gorillas (Clutton-Brock & Harvey, 1977). Therefore, it may be expected that orangutans will have more highly developed spatial skills than gorillas. As stated by Tomasello and Call (1997, p 54), "It would be useful to have a rigorous comparative study in which investigators make a priori predictions about the cognitive mapping skills of different primate species based on their foraging patterns in the wild and then test those predictions against their performance on some standardized set of foraging tasks".

Despite the fact that researchers have hypothesized sex differences in spatial memory on the basis of mating system and levels of dimorphism between the sexes in home range size and foraging strategy, very few species of mammal have been tested. There are many species that would make good subjects for tests of hypotheses concerning sex differences in spatial memory. For example, Silverman and Eals (1992) suggested the potential importance in testing sex differences in spatial ability in a species such as the lion. Lions are polygynous, and males typically disperse. On the basis of this type of social system, it might be predicted that males would outperform females on tests of spatial memory. However, female lions do the majority of the hunting, which would lead to the prediction of female superiority on tests of spatial memory.

Spatial memory is one of the few areas of human cognitive research in which individual differences have been attributed to ecological factors and evolutionary pressures. As previously discussed in this paper, sex differences have been reported in human spatial memory such that men perform better on mental rotation tasks and women perform better on spatial memory tasks (for review see Harris, 1981). This was hypothesized to reflect the division of labor between the sexes in early human society in which the men were predominantly hunters and the women were predominantly gatherers (McBurney, Gaulin, Devineni, & Adams, 1997). Gaulin and Fitzgerald (1986) were the first to hypothesize that males of polygynous species should have spatial memory skills superior to that of females because they have larger home ranges. Their research showed that polygynous male meadow voles not only had larger home ranges, but they also performed better on tests of spatial memory than female meadow voles. These sex differences were not apparent between monogamous male and female pine voles. Based on Gaulin and Fitzgerald's work with voles, Silverman and Eals (1992) hypothesized that the sex differences in spatial ability observed in humans are the result of the division of labor between hunting and gathering during human evolution. The tasks on which males tend to outperform females (mental rotation, sense of direction, way-finding, map reading, maze learning) (Harris, 1981) are also those that would confer an advantage for hunting prey in unfamiliar areas (Silverman & Eals, 1992). On the other hand females who gathered sessile plants that were predictable in both space and time should be better at tasks involving spatial recognition and recall than males.

To test their hypothesis, Silverman and Eals (1992) administered a battery of tests to college students to determine if males and females outperformed each other on tests that tapped into skills necessary for their particular foraging strategy. First, in support of their hypothesis males were found to be superior to females on a test of mental rotation. However, males were not more superior on a task involving object recognition and object recall. Men and women were given one minute to examine an array of stimuli drawn on a piece of paper. In the object recognition test, the participants were then given another sheet of paper containing the same stimuli as well as many additional stimuli. The participants were asked to mark through those stimuli in the new array that were not in the original array of stimuli. In the object location test, the participants were given a second array and asked to indicate which stimuli were located in a different position within the array. Females performed significantly more accurately than males on both tasks. Moreover, female superiority was even more robust when tested in a more naturalistic setting with an actual object array, outperforming males by 60-70%.

It is surprising that few studies have examined sex differences in spatial memory in non-human primates. Sex differences in foraging have been observed in some species of great ape. For example, orangutan males spend more time feeding, have larger day ranges and homes, and have larger daily energetic costs than females (Bean, 2001). However, gorillas and bonobos show few if any sex differences in foraging. In chimpanzees, the results are somewhat mixed, with sex differences in foraging being reported at some study sites but not others. According to Bean (2001), as habitat quality decreases, sex differences become more apparent in all species of great ape. In great apes such as the bonobo and the gorilla, it might be predicted that there would be no sex differences in spatial memory, because they have similar home range sizes and foraging habits. However, sex differences in spatial memory might be predicted in orangutans given the sexual dimorphism in feeding and range.

It would be most interesting to test for sex differences in chimpanzees on tasks of spatial memory requiring different skills. Chimpanzee males are known to hunt, and it has been hypothesized that chimpanzee predation and human hunting originated from the behavior of a common ancestor (Kawanaka, 1982). Chimpanzee males are believed to hunt to obtain meat to share with other males and strengthen social bonds or coalitions

(Mitani & Watts, 2001). Hunting in females is much more rare than it is in males, occurring only when males are not around (Tuttle, 1986). Therefore, we might expect chimpanzee males to perform better tests of spatial memory involving maze learning than females or than other species of great ape. Because primates differ markedly in their mating systems and home range sizes between the sexes, they might make good subjects for tests of sexual differences in spatial memory.

Sex differences in primates may also be expected on the basis of hormones. If estrogen and testosterone are influential in causing sex differences between male and female humans as well as other species then it is certainly possible that they would be correlated with sex differences between male and female non-human primates. To my knowledge, only one study has been conducted to determine whether sex differences in spatial memory exist in non-human primates. Lacreuse, Herndon, Killiany, Rosene, and Moss (1999) compared 12 young and 14 old rhesus monkeys on tests of object and spatial memory using delayed non-matching-to-sample and delayed-recognition span tests. The results showed that males outperformed females on spatial conditions of a delayed recognition span test. This is in accordance with human studies of cognition in which men are known to outperform women on test of spatial ability. In addition, aged monkeys performed worse than young monkeys on all tasks except trials to reach criterion and object reversal. The observed sex difference in performance on the spatial memory task between males and females decreased with age. Although hormone levels were not measured in this study, these results suggest that sex steroid hormones may be responsible for the observed sex differences in spatial memory. No studies have been conducted to determine whether differing levels of gonadal hormones are associated with different levels of spatial memory performance in non-human primates.

Rarely do studies of spatial memory in animals compare more than one type of spatial learning. Most studies involve either some type of maze or an open field testing environment. Given that human men and women show differences in superiority on tasks designed to test different aspects of spatial memory, it would be interesting to make a priori predictions based on feeding ecology to see if similar differences in spatial ability could be found in other species of animal. For example, a carnivore that hunts for its prey may be more proficient than frugivores on task involving maze learning, but less likely than frugivores to perform well on tasks involving spatial recognition and recall. The results of this study suggested that bears can use spatial memory to locate viable food sources. However, it only tested one type of spatial memory. Specifically, this study examined spatial recall. Species differences on other forms of spatial memory might be predicted. For example, it might be argued that polar bears that live in a relatively impoverished sensory environment would perform more poorly on tests of spatial and visual recall. However, they may outperform other species on tests of maze-learning and way-finding given that they are carnivorous, actively hunting live prey (Stirling, 1990).

7.3 Value of Zoos for Comparative Cognitive Research

For comparative psychology to survive and compete in the intellectual arena with ethology, behavioral ecology and sociobiology, many researchers have argued that it has to become more integrated with these fields by choosing species based on their phylogenetic origins rather than convenience, by increasing fieldwork or research in semi-naturalistic settings, by adopting a more ecological approach, and by incorporating the theory of evolution into the anthropocentric approach in their study of animal behavior (Beer, 1998; Buss, 1995; Domjan, 1987; Domjan & Galef, 1983; Dore & Kirouac, 1987; Galef, 1987; Gottlieb, 1979; Hodos & Campbell, 1969; Janson, 1994; Kamil, 1998; Lockard, 1971; Riley & Langley, 1993; Shettleworth, 1993a; Snowdon, 1983; Tolman, 1987a; Wasserman, 1997; Yoerg & Kamil, 1987). Comparative psychologists are now beginning to promote an ecological or evolutionary approach to formulating hypotheses and conducting research on both animal and human learning and cognition. Recent studies using this approach are finding interesting results that shed light on not only the cause but also the function of certain behaviors and cognitive abilities (Esmorfs-Arranz, Pardo-Vazquez, Vazquez-Garcfa, 2003; Sharps, Villegas, Nunes, & Barber, 2002). It has long been accepted by scientists that environmental pressures could create specializations in sensory, motor or physiological processes in animals through the process of natural selection. It is, therefore, not unreasonable to think that the same environmental pressures could create specializations in memory and brain function. The ecological approach takes into account the natural history of the organism by identifying and designing experiments to test learning abilities that may be important to the organism in nature and determining how and why these capabilities may have evolved. Thus the current field of comparative psychology seems positioned to bridge the gap between psychologists and ethologists by attempting to discover not only similarities but also differences both within and across species based on their phylogeny and evolutionary niche.

The science of animal cognition has traditionally involved work with a very limited number of animal species. One reason for this is that the diversity of species available for use in laboratories is limited for financial, practical, and ethical reasons. Much has been learned from both traditional laboratory investigations of spatial memory. However, the comparative research that needs to be conducted to address evolutionary hypotheses cannot adequately be carried out in a traditional research laboratory using standard laboratory animals. The development of an appropriate methodology that can be implemented in a zoological research park is important to the field of comparative psychology and animal cognition for several reasons. The need for accessibility to a wide range of animal species has long been recognized. One of the first comparative psychologists to recognize the importance of animal collections for comparative research was L. T. Hobhouse, who conducted research on several different species of animal at the Belle Vue Gardens in Manchester to determine how animals acquire novel behaviors (Greenberg, 1987). However, zoos were not fully seen as potential laboratories for research until 1969, when Heini Hediger formally endorsed of the use of zoo collections for scientific research. Since this time, more researchers have begun to make use of zoo collections. If comparative psychology is to succeed amidst the growing fields of ethology, behavioral ecology and sociobiology, it must develop a more ecological approach (Galef, 1987; Lockard, 1971). The future of the field of comparative psychology depends on the ability to conduct research with a wide variety of animal species (Wasserman, 1997).

Another advantage of using zoos in cognitive research is their ability to reach the public. According to Wasserman (1997), despite the fact that the public seems to be very interested in animal intelligence "little or no concerted effort to educate the public about the science of comparative cognition has recently been undertaken." He suggests that public education could increase the support of psychological research by a public who is often misinformed of the nature and importance of research by animal rights activists. Zoos provide a unique opportunity to reach a wide range of people, making them a potentially important resource for the future of the field of comparative cognition.

7.4 Value of Comparative Cognitive Research for Zoos and Conservation

Not only would the science of comparative cognition benefit by using zoos as resources, but in many ways the zoos and zoo-housed animals themselves may also benefit from the work conducted by comparative psychologists. Even when comparative psychologists recognized the importance of zoological institutions for scientific research, zoo directors were often unsupportive of their efforts, failing to see the importance of science in their institution (Greenberg, 1987). However, this attitude is changing. Research is now considered to be one of the four main purposes of zoos along with conservation, entertainment, and education. "At a time when zoos are increasingly required to justify their continued existence in terms of conservation, education and research, it is in the interests both of the zoo and the academic community to promote research which is of common interest, but whose goal goes beyond just the better maintenance of animals in captivity" (Hosey, 1997, pp 205-206).

In a recent survey of research in zoos, 88% of zoological institutions were reported to conduct research. However, only 18% reported that the research focused on animal cognition (Stoinski, Lukas, & Maple, 1998). Zoos may, therefore, provide a unique and relatively untapped resource for researchers interested in using both a general and ecological approach to the study of animal learning and cognition (Moran & Sorensen, 1984). Research that is focused on animal learning and cognition could be a valuable in its ability to potentially influence the design and management of captive environments, promote species-appropriate cognitive development, prepare animals for reintroduction, improve animal well-being, and educate the public about the aspects of animal behavior that make each species unique.

7.4.1 Improvement and Management of the Captive Environment

Only about half of the animals that have been reintroduced have come from zoos (Beck 1995). Though zoos are generally not the main initiators and providers for reintroduction programs, it is one area of conservation to which zoos can contribute. Zoos interested in participating in reintroduction programs could potentially benefit from studies of learning and cognition in several ways. First, knowledge of the appropriate environment in which to raise a particular species could be useful in designing and managing environments in a way that promotes or encourages the development of appropriate cognitive skills. Animals that are born or kept in captivity for many years are often behaviorally deficient (Beck, 1995; Kleiman, et al., 1986) and have trouble foraging and traveling efficiently when released back into the wild (Beck, personal communication). To survive in the wild, captive animals must have the appropriate skills for finding food, engaging in appropriate social interactions, coping with extremes in temperature, defending territories, avoiding predators, etc. Preparing captive animals for these types of situations requires that they be exposed to them before they are released. As pointed out by Beck (1995), creating a truly naturalistic environment, as opposed to an aesthetic naturalistic environment, may involve a drastic reduction in animal welfare.

This might be true for teaching anti-predatory behaviors or preparing animals for extremes, however, other forms of preparation such as the testing and improvement of skills such as those involved in finding food could be very positive and rewarding. Finding food has been found to be a problem for reintroduced captive born animals, even for those that have successfully killed or processed food in captivity. For example, two young fishers (*Martes pennanti*) that showed proficiency at killing porcupines in captivity starved to death after being reintroduced to the wild because they were unable to search for and find food (as cited in Miller et. al., 1998).

A second reason why the study of animal learning and cognition is important for zoos is its potential contribution to the cognitive development of their zoo-housed animals. It is known that experience with enriched environments can influence both behavior and overall brain development (Rosenzweig, 1979). Studies have shown that the development of exploratory behavior and spatial memory, both of which are believed to be important in information gathering and finding food, can be influenced by relatively simple and positive changes in the captive environment. For example, rats raised in a perceptually-enriched environment (large cage with objects that were changed regularly) were observed to explore a novel, open-field environment more than those raised in a perceptually impoverished environment (Gardner, Boitano, Mancino, D'Amico, & Gardner, 1975). Moreover, rats raised in a restricted environment exhibit a limited behavioral repertoire characterized by stereotyped, engage in repetitious patterns of movement, are less attentive to stimuli, and have more trouble learning a given task than rats raised in and enriched environment (Joseph & Gallagher, 1980).

Rearing environment not only influences overall exploration of novel environments, but it can also affect the quality of the interaction with the environment. Renner (1987) found that rats that had spent 30 days in an enriched environment (larger home cage with stimulus objects that changed daily) showed a greater diversity of behavior toward the objects in their environment. In addition, they engaged in longer and more complex interactions with those objects. Similar results were found by Widman and Rosellini (1990) when rats were exposed to just two hours of enrichment each day. Therefore, an animal's rearing environment can result in both quantitative and qualitative behavioral differences later in life. According to Renner (1987), exploration allows an animal to gather information. Having a more diverse exploratory repertoire would allow an animal to broaden the range of information that is available during an interaction.

In support of the information-gathering hypothesis of exploration, several studies have found that animals housed in enriched environments are not only more exploratory but also perform better on tasks involving spatial ability. In a study conducted by Joseph (1979), rats were housed in either an enriched or impoverished environment at 20 days of age following weaning from their mothers. For animals housed in the enriched environment, the location of the home cage was shifted every other day and objects were changed daily for the first 45 days. After 45 days, changes were made on a weekly basis. At 100 days of age the rats were housed in standard laboratory cages, and were tested using a T-maze at 120 days. The results showed that enriched animals of both sexes performed better those raised in the impoverished environments. In addition, the restricted rats engaged in less exploratory behavior than the enriched rats. Janus, Koperwas, Janus and Roder (1995) found that mice raised in an enriched environment (objects and running wheel in standard cage) made fewer errors and found the goal more quickly in an 8-arm maze than rats raised in a standard environment. Interestingly, the impoverished and enriched rats did not differ on a less complex 4-arm maze.

One of the most interesting studies examining the effect of rearing environment on spatial learning was conducted by Kiyono, Seo, Shibagaki, and Inouye (1985). Pregnant rats were housed in either an enriched, impoverished, or standard cage. Those housed in the enriched cage were housed socially in a dynamic environment. The impoverished rats were housed alone in a cage with solid walls and a mesh floor. They were removed from these environments just prior to parturition. The cubs were tested using a Hebb-Williams maze when they were 21-25 days of age. The results showed that the cubs of mothers housed in the enriched environments performed better on the maze than the cubs born to impoverished animals. There were no differences between cubs of enriched and standard housed mothers or between cubs of impoverished and standard housed mothers. In a second experiment, pregnant female rats were again housed in either an enriched, impoverished or standard condition. However, the enriched females were also allowed to explore the Hebb-Williams maze for one hour a day, three days a week. It was found that the cubs of these enriched mothers performed significantly better on the Hebb-Williams maze than the cubs of females raised in either the standard or the impoverished environments. There was no difference in performance between cubs born to mothers raised in impoverished and standard environments. These results indicate that the prenatal environment may be just as important as the post-natal environment.

Not only can behavior be affected by the environment, but it can also be accompanied by actual physiological changes known to influence spatial memory. In a study conducted by Paylor, Morrison, Rudy, Waltrip, and Wehner (1992), rats just weaned from their mothers were housed in an enriched environment for either 6 or 12 days. They were then tested using a Morris water maze task. An analysis of the result showed that a 12-day exposure to an enriched environment improved performance on the Morris water maze task. Moreover, an analysis of their brains showed increased hippocampal protein kinase C activity. Those rats housed in the enriched environment for only 6 days were not different from control animals. However, it is impressive that only 12 days of an enriched environment were enough to produce significant changes in both spatial ability and physiology. The rats were tested when they were very young, not long after being housed in an enriched environment.

The finding that rats housed in enriched environments engage in more exploratory behavior than those housed in impoverished environments may not be universal in all animals. For example, pigs housed in a barren environment were found to be more exploratory of a novel object than those housed in an enriched environment (Wood-Gush, Vestergaard, & Petersen, 1990). However, this study differed from those conducted with rats in that the novel object was placed in the animal's home environment. Most researchers test the behavior of their subjects in a completely novel environment. It is possible that an animal raised in a barren environment might be more anxious or fearful in an entirely new environment than one that was raised in a more enriched environment. It would be interesting to conduct a study that compared exploratory behavior of enriched and impoverished animals in their home environment and novel environments.

Despite the fact that zoos are getting better at providing for the psychological well-being of their animals through enrichment (Mellen, Shepherdson, & Hutchins, 1998), many animals are still fed and provided water in a relatively constant location within their environment each day. This type of environment may or may not be ideal for encouraging efficient foraging behavior depending on the foraging strategy of the species in the wild. It is known that being reared in a static environment can affect behavior and learning in tasks involving spatial memory. For example, gerbils raised in an environment in which the location of their food and water is changed from day to day were found to be more proficient at avoiding previously depleted food sites in a 17-arm radial arm maze than animals raised in an environment in which their food and water sources were constant (Takai & Wilkie, 1986). According to the authors, being housed in a dynamic environment caused the gerbils to develop a "shift" strategy in which they shifted their search location each time they were fed. This tendency to shift generalized to the radial arm maze. This study does not tell us if these same animals would be impaired on a task requiring them to stay at a location. Presumably, improvement in the ability to shift would only be desirable for those species of animal whose resources are either completely depleted and/or are not replenished quickly after a visit. This study may not necessarily suggest that improvement on this type of task is good for the animal, but it does show that the way animals are fed can also affect learning on cognitive tasks. It is currently unknown how different types of feeding practices in captivity (scatter feeding, hiding food, unpredictable schedules of reinforcement) might positively or negatively affect cognitive development. It is possible that random scatter-feeding, a feeding practice designed to increase time spent foraging in captivity, could be beneficial in encouraging movement and combating boredom but detrimental to an animal that needs to learn to make associations between stimuli and food.

There is still a lot to learn about the nature of enrichment programs and their effect on behavior and cognitive development. However, it is possible that "enrichment of captive rearing environments can help ensure the success of reintroduction programs by providing animals with the opportunity to learn from, and adapt to, new environments" (Shepherdson, 1994). Understanding the nature of environmental enrichment in terms of cognitive development could be a rich area of research. For example, one question that is still unanswered refers to the level of enrichment necessary to consider an environment enriched. How much enrichment is enough? The finding that just two hours of daily exposure to an enriched environment can influence behavior (Widman & Rosellini, 1990) suggests that enrichment does not necessarily have to be provided for long amounts of time to exert a positive effect on stimulating cognitive behavior. Zookeepers are often very busy and have trouble providing continual enrichment to the animals under their care. Enrichment that is less time-consuming and relatively inexpensive will be more likely to be maintained in zoos. Another questions is, when should enrichment be provided to obtain the greatest effect? Because most studies are conducted to determine the effect of early rearing environment on behavior, it would also be important to know whether there is a developmental window of opportunity after which an enriched environment no longer exerts an effect on learning. Early research suggests that, whereas all animals exposed to a complex environment performed better on a Hebb-Williams maze, those exposed to the environment immediately after weaning performed the best (Forgays & Read, 1962). Managers of captive animals may be able to use this information to narrow their focus on those animals or age-groups that would benefit the most from enrichment.

Though environmental enrichment does produce changes in behavior and physiology that seem to be related to finding food, it remains to be seen whether these changes would result in improvements in survivorship of reintroduced captive animals. Environmental enrichment that focused on foraging and locomotion did not seem to confer any long-term advantage to reintroduced golden lion tamarins (*Leontopithecus rosalia*) of the Golden Lion Tamarin Conservation Program (Castro, Beck, Kleiman, Ruiz-Miranda, & Rosenberger, 1998). However, success was measured in terms of overall survival. The main causes of death in reintroduced tamarins as discussed by Beck (1995) did not include the inability to locate food. Whereas decreased foraging efficiency and the inability to adequately locate preferred, higher-quality food may not affect actual survival rates, it could possibly affect the general health and nutrition of the individual as well as the amount of time an individual could devote to other activities. Castro and colleagues (1998) did note that it appeared to subjective observers that the animals provided with pre-release training focusing on foraging and locomotion showed behavior more characteristic of that of wild-born animals than the untrained animals. Research will be necessary to determine how factors such as the quality, complexity, manipulability, variety, and length of exposure to the enrichment items influence the ability of an environment to improve foraging efficiency. In addition, enrichment items related to feeding are often associated with preferred foods and are provisioned in addition to the regular diet that is fed in constant location (Molzen & French, 1989). It would be interesting to see if there are differences in the development of learning and performance on cognitive tasks between animals reared in an environment in which enrichment is in addition to a standard feeding regime and animals reared in an environment in which all of their daily provisions are presented in foraging devices.

7.4.2 Measuring and improving behavioral deficiencies

Knowledge of the foraging skills and learning capabilities of a species could also be helpful for choosing individual animals for reintroduction. Individual differences are often observed within a species in studies of animal learning, and radial maze performance is no exception. Teskey, Ossenkopp, Kavaliers, Innis, and Boon (1998) found that individual differences in the performance of meadow voles on a radial arm maze corresponded with individual differences in locomotor behavior. They hypothesized that those animals that showed greater behavioral flexibility and higher rates of locomotion may be more likely to be dispersers or animals that show less fidelity to their natal site. This research suggests that it might be possible to conduct pre-tests of individuals to determine their likelihood of expressing a certain behavioral trait in the wild (disperser/non-disperser, leader/follower). Understanding the relationship between performance on laboratory tests of cognition and behavior in the wild could be extremely important for managers choosing individuals for reintroduction. This in turn could lead to the development of cognitive/behavioral tests that could be administered to animals prior to release. There were large individual differences across the giant pandas and spectacled bears. It would be interesting if those individual differences could be used as predictors for success were any of the individuals chosen for release back into the wild.

Wild-born individuals that are re-released in the wild after spending some time in captivity tend to have better survival rates than captive-born individuals (Castro et. al., 1998). A comparison of the performance of wild-born individuals with captive-born individuals on a battery of traditional cognitive tests could lead to the determination of basic skills necessary for post-release survival. Pre-testing could be conducted to establish a mean level of performance by a species on a particular cognitive task about which individuals within a population (captive or wild) fall, allowing researchers to identify either performance superiority or deficiency in individuals. Those individuals with average performance or above might be chosen for release, whereas those with less than average performance might be put into a training program. Or, individuals that performed less adequately on the pre-release tests might be paired with an individual that scored above-average and released together with the hopes that observational learning could occur between the two individuals. "Tutors" are known to improve the success of reintroduction programs (Beck, 1995). It is unknown whether pre-release tests of learning and cognition could be designed that would predict future success in the wild. However, the development of a simple battery of tests capable of predicting individual differences in post-release success could prove to be valuable.

7.4.3 Improvement of Animal Well-being

Not only can cognitive testing benefit zoos in management and environmental design, but it may also enhance the welfare of the animals themselves. There is evidence suggesting that animals prefer to work for their food, even when free food is readily available (for reviews see Inglis, Forkman, & Lazarus, 1997; Osborne, 1977). This phenomenon has been referred to as contrafreeloading and appears to be widespread among animals. In fact, of the 16 species tested thus far, only the domestic cat has failed to exhibit contrafreeloading. Contrafreeloading has been most recently explained in terms of the information primacy model which proposes that animals have an inherent need to gather information from their environment concerning the availability, predictability, and optimality of various food sources (Inglis, et al., 1997). The continuous updating of information concerning available food sources would be adaptive, particularly for animals that live in a changing environment. Given the potential relationship between contrafreeloading and the need to explore (referred to colloquially as curiosity), it is perhaps ironic that the one species that failed to engage in contrafreeloading was the domestic cat.

Tasks designed to assess spatial memory may be particularly well-suited for enhancing animal welfare and satisfying an animal's need for information. In most tasks of spatial memory and foraging, either the food is completely hidden or the viability of a patch of food is initially unknown. Hiding food appears to be one factor that elicits or maintains the behavior of contrafreeloading (Forkman, 1996; Inglis, Forkman, & Lazarus, 1997), even when the patch that requires work is unprofitable. For example, gerbils were presented with several experimental conditions in which a profitable food source was paired with a non-profitable food source in which the food was either hidden or not hidden. The animals came to prefer the non-profitable food source only when work was required to find or search for the food. The authors suggested that when food is hidden there is always a level of uncertainty about the amount of food that could be present. Therefore, they have a need to know if the profitability might have changed.

Devices originally designed to provide enrichment can actually be used and manipulated by comparative psychologists to study cognition. For example, puzzle feeders available commercially from the company Primate Products, Inc., have been used to stimulate foraging activity and object manipulation in non-human primates. These puzzle feeders consist of a 5 x 5 matrix of columns and rows of oval holes. The animal inserts its finger into the holes to push food horizontally to an opening at one end of the row. Once pushed through the hole, the food item drops either all the way through to the bottom of the apparatus, where the animal can retrieve it, or it drops to the next row level. Partitions can be moved to increase the complexity from one to five rows, creating a maze-like configuration. The puzzle feeders have been shown provide an opportunity for the rhesus monkeys to manipulate their environment, as well as decrease some forms of stereotypic behavior (Bloom & Cook, 1989; Novak, Kinsey, Jorgensen & Hazen, 1998).

Not only do these devices seem to be an effective form of environmental enrichment, but Watson, Shively and Voytko (1999) have recently found that the puzzle feeder can also be used for cognitive screening. They developed nine mazes of increasing difficulty and compared performance between young and old cynomolgus monkeys (*Macaca fascicularis*). Their results showed that young monkeys were able to solve the first level more quickly than older monkeys and solved the mazes at the highest levels of difficulty. Therefore, this enrichment device seems to not only stimulate foraging, but it also can be used to learn something about the cognitive functioning of individuals. Tasks designed to assess the cognitive abilities of animals in basic research, particularly in studies examining food search and foraging efficiency, can potentially be very enriching for animals that are generally not challenged by their captive environment.

7.4.4 Potential Influence of Research on People's Perception and Appreciation of Animals

"The ultimate reason we study animals in the laboratory is to increase our appreciation of their beauty and sophistication outside of the laboratory, in the field.

Awareness of the cognitive abilities of [corvids] forever changes our perception of them and their place in nature, and ours" (Balda & Kamil, 1998).

One of the questions that the public often asks about animals in the zoo is, "How smart are they?" Though this is a very difficult question for a scientist to answer because we prefer to discuss species characteristics in terms of adaptation to the environment, the public certainly seems to have a need to rank animals in terms of intelligence. According to Wasserman (1997), research has shown that people are strongly influenced by their perception of a species' intelligence. A national survey conducted in the United States found that intelligence was the third most important factor influencing public preference for a species, after size and aesthetic appeal (Kellert, 1989). In an interesting study conducted by Driscoll (1995), respondents were asked to rate 33 species of animal on the basis of factors such as usefulness, importance, intelligence, responsiveness, lovability, and safety. The species were grouped on the basis of similarity of scores using a cluster analysis. Based on high ratings on each of the factors, one cluster was distinguishable as the most popular. This cluster included chimpanzees, monkeys, dogs, horses, humans and dolphins. These were all animals that scored very highly on the intelligence scale. The giant panda (along with cats and sea otters) might have been expected to be included in the most popular group. However, they received lower scores, particularly on those factors associated with usefulness and intelligence.

According to Burghart and Herzog (1989), people value smart animals. Mental similarity and behavioral plasticity are two of the factors that weigh strongly in the determination of the ethical treatment of animals (Burghardt & Herzog, 1980). Therefore, knowledge of the intelligence of a species may change the way people treat and/or demand a species to be treated (Bekoff, 1994; Burghart & Herzog, 1989). But what if the cognitive researcher discovers through his or her research that one species or another has difficulty learning a particular task. This may not be as important as the effect the testing itself has on perception. Will people be less inclined to help save the "less intelligent" species? I would argue that seeing the testing itself is enough to change perceptions. People are often amazed when given the opportunity to see an animal attempting to solve a task. For example, the simple act of a giant panda opening a lid on a feeder to obtain food or pushing open a sliding window on a door to get the attention of a keeper seems to evoke awe and amazement in people (personal observation). Therefore, it is possible that people's opinion of a species can increase through observation of simple environmental actions even if the animal ultimately proves to be incapable of learning a particular task. In addition, poor performance on a particular task could be used to educate the public about the inherent differences and limitations each species has in their ability to learn new tasks and adjust to changes in their environments. It might be argued that the effects of human incursion would be worse for those animals that cannot adapt as easily to environmental disruption.

Regardless of the performance of animals on tests of learning and cognition, conducting cognitive research in zoos and other public institutions provides a unique opportunity to reach out to a wide range of people and educate them about the evolution of particular behavioral traits in endangered species. This in turn may alter their perceptions of animals and encourage them to contribute to and support efforts to save and protect critically endangered animals.

7.5 Conclusion

Researchers in the field of comparative psychology have begun to stress the need for a more ecological or evolutionary approach to species comparisons than has been taken in the past. It has been known for many years that there are biological constraints on learning (Bitterman, 1975; Breland & Breland, 1961). Predictions of both within-species and between-species differences in a variety of behaviors and cognitive abilities can be made on the basis of foraging ecology, habitat, environmental exploitation, and social behavior. Spatial memory is one of the few areas of cognition in which within-species and between-species differences have been hypothesized and tested using an ecological approach. Optimal foraging theory makes a number of predictions concerning prey choice, handling time, encounter rate, and staying time within a patch. Models have been developed to predict the behavior of a foraging animal. However, most models predict the behavior of animals that have already encountered a food resource. Studies of perception, learning and spatial memory, areas of research in which comparative psychologists are well experienced, can provide insight into the ways in which animals can increase the efficiency with which they search for food.

There is a large amount of research that suggests that animals that either hoard food or feed on widely dispersed resources whose locations are predictable in both space and time can maximize foraging efficiency by using spatial memory. Species differences have been observed both within and between species on tests examining spatial memory, and in most cases these differences have been predictable on the basis of the foraging ecology of the animal. However, with the exception of the rigorous program of research that has been conducted with food-storing birds, very few direct comparisons of species have been conducted using a multidisciplinary approach. For instance, despite the availability of a theory of primate intelligence outlining the environmental factors that might be predictive of species differences in brain size and foraging skills, very few studies have been conducted in which two primate species were directly compared to test those predictions. Moreover, it is difficult if not impossible to compare species across different studies conducted in different laboratories because researchers rarely use the same methodology or even the same criterion for learning.

The purpose of this study was to examine hypotheses concerning species differences in associative learning and spatial memory in two species of bear based on habitat, dietary niche and evolutionary history. Both giant pandas and spectacled bears foraged more efficiently in the exploratory task than would be expected had they been foraging randomly. They adopted an adjacency strategy of responding that minimized travel time between food sites. Minimizing costs of traveling between food sites would be particularly important for species such as giant pandas that are required to consume a large amount of food to maintain baseline levels of nutritional requirements. Both the spectacled bears and giant pandas were able to use spatial memory to locate viable food sources. This would allow them to travel directly to known food sites and avoid areas of the habitat that are unlikely to provide viable resources. Neither the spectacled bears nor the giant pandas learned to use an olfactory cue to travel directly to resources. There are many reasons why learning may not have occurred including an inability to detect the odor, an inability to differentiate the odor, a dissipation of the odor following application, overshadowing of the cue by another cue, or the cue was extrinsic or unassociated with a type of food that would normally be in the diet of the bears. The visual cue did, however, learn to associate the visual cue when it was the only cue that could be used to locate baited feeders. The giant pandas only learned to use a visual cue in the final foraging task in which the visual cue was repeatedly paired with a particular spatial location before being dissociated from that spatial location. It is possible that this pairing enhanced learning of the visual cue. The giant pandas may have learned the association between the visual cue and the presence of food in the visual task had they been exposed to more trials. However, the results would still indicate that spectacled bears learned the task more quickly than the giant pandas. The relative ease with which the spectacled bears learned the association may reflect a species difference based on the adaptive value of being able to make visual associations between naturally occurring stimuli and the presence of food in the wild. Finally, the spectacled bears made fewer visits to previously depleted feeders in each of the six foraging experiments. Their behavior supports the hypothesis that frugivores would make fewer errors than folivores on tasks designed to measure choice accuracy. The results of the present experiments suggest that bears may forage through a combination of both associative learning, which would be particularly useful for locating new sources of food between seasons, and spatial learning for remembering the location of these food sources within seasons.

The present study is important in that it is the first study to examine associative and spatial learning in giant pandas and spectacled bears. Only one study has been conducted to examine learning in any species of bear prior to this study (Bacon & Burghardt, 1974). Furthermore, it is the first comparative study of two bear species (or even two species of carnivores) in which a prior hypotheses of species differences were predicted in learning and cognitive ability on the basis of the evolutionary history of the animals. Though the open-field conditions were limiting in terms of environmental control and methodological design, this type of research would not have been possible in a traditional research laboratory. To truly remain a science of comparative psychology and conduct research using an ecological approach, researchers are going to have to move beyond the traditional laboratory. Zoological institutions may provide valuable resources for researchers interested in testing hypotheses based on foraging and social ecology. Not only might comparative psychology benefit from the use of zoo institutions for their research, but I also think that zoos and zoo-housed animals could benefit from the research conducted by comparative psychologists for several reasons.

First, basic research is necessary for fully understanding the species zoological institutions are trying to save, sometimes leading to important findings that may be useful in ways we can not yet imagine. Second, the tasks designed to assess the cognitive abilities of animals in basic research can be very enriching for animals that are generally not challenged by their captive environment, improving their welfare and making them better exhibit animals. Third, knowledge of the foraging skills and learning capabilities could be useful in preparing animals for introduction or in choosing animals that would be good candidates for reintroduction. Reintroduction is often cited as the ultimate goal of the two main breeding and research centers of giant pandas in Wolong and Chengdu, China. Animals that are kept in captivity for many years have trouble foraging efficiently when released back into the wild. Consequently they often have to be provisioned with food. Studies that can improve foraging efficiency in captive animals and stimulate naturalistic foraging behavior may be helpful for increasing the speed with which reintroduced animals can support themselves in the wild. Finally, not only would cognitive research on zoo-educate the public about the scientific field of animal or comparative cognition, but it may also alter their perception of animals. As stated by Laughlin (1975), "It seems wasteful to maintain a variety of rare animals primarily, if not solely, for exhibit purposes; more especially when the discovery and organization of knowledge about those animals may assist us in ensuring their ultimate survival." Research on associative learning and spatial memory may have broad implications for both scientific theory development and applied management and education.

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APPENDIX 1

Bear Foraging Study Ethogram

Self-directed	Focal scratches body with arm/leg or sucks or bites on fur.
Inactive	Focal is stationary, not performing any of the behaviors listed on the ethogram.
Feed	Focal is chewing or ingesting food; also includes drinking water.
Locomote	Focal walks on ground or climbs on structure.
Object Exam	Focal sniffs the wall, climbing structure, ground, or window, either while standing or walking. The focal manipulates an object with nose, mouth or paw. Does not include behaviors directed toward any of the doors.
	Must indicate what object is being examined. Includes the feeders or "other" for any other part of the exhibit.
Scent Mark	Focal lifts tail and rubs anogenital region back and forth or in circular motion against any part of the exhibit; may be against vertical or horizontal space.
	Must indicate the object on which the focal is scent-marking. Includes the feeders or "other" for any other part of the exhibit.
Door Directed	Focal is scratching on door, trying to look through door, has paws on door, hitting door, biting door, or is digging on ground beneath any of the doors that open to the outside area of the test room.
Vocalization	Focal animal emits a bleat during the test session.
Other	Any behavior not included on the ethogram.
	Includes walking bipedally along the wall. If focal is bipedal and facing the door it will be called "door directed".
Not Visible	Record if the behavior of the focal cannot be seen.