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CITATION
Spatial Memory in Captive American Black Bears (Ursus americanus)

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The spatial memory and foraging strategies of four adult captive-born American black bears (Ursus americanus) were explored in four experiments using a simulated foraging task. In the first three experiments, each session consisted of two phases separated by a delay: During the exploration phase, subjects foraged among a set of baited and unbaited sites. During the delay, the same locations were rebaited and subjects were released again and allowed to search the sites (search phase). In Experiments 1a and 1b, different sites were baited each day and the interval between exploration and search was short (4 hr or 15 min). Subjects were not accurate at recovering the food items in either experiment. In Experiment 2, an “informed forager” paradigm was used in which one subject was given privileged knowledge about the location of the food during the exploration phase and was later released with an “uninformed” competitor during the search phase. The bears did not achieve above-chance recovery accuracy even in the presence of a competitor. In Experiment 3, the same two of four sites were continually baited and the bears were released simultaneously over a period of 20 days, with each baiting separated by 2 or 3 days. As a group, the bears’ foraging accuracy with repeated baiting and longer intervals approached greater than chance accuracy. Results suggest some limitations on bears’ use of spatial memory in captive environments, but reveal the potential for use of spatial memory over longer delays.

Keywords: black bears, foraging, spatial memory, captivity

Spatial memory has been investigated in a variety of species, most notably in nonhuman primates, using both win–stay and win–shift paradigms, in which the subjects are expected to either return to or avoid previously baited sites, respectively. These strategies should reflect the behavioral ecology of the species, with animals that experience patchily distributed, rapidly replenishing resources exhibiting win–stay strategies and those who experience slowly replenishing, scattered resources exhibiting win–shift strategies (Olton, Handelmann, & Walker, 1981). Researchers have hypothesized, on the basis of available data, that species foraging over large home ranges, whose food sources are variable and patchily distributed, should have evolved effective spatial learning mechanisms. Bears are good candidates for such mechanisms as they have large home ranges, have large relative brain size, and exploit variable, unpredictable food sources (Gittleman, 1986). However, with the exception of a dissertation by Tarou (2004) and a recent study by Perdue, Snyder, Zhihe, Marr, and Maple (2011), researchers have not explicitly tested spatial memory in bears.

Both Tarou (2004) and Perdue et al. (2011) investigated spatial memory in giant pandas, with Tarou (2004) comparing the foraging strategies of giant pandas to that of spectacled bears, expecting differences in their ecology to affect their foraging behavior. Frugivorous primate species, such as spider monkeys (Ateles geoffroyi), have been found to demonstrate superior spatial memory when compared to foliverous species, such as howler monkeys (Alouatta palliata), which is explained by the fact that fruit is a patchily distributed and rapidly depleting resource (Milton, 1981). In Tarou’s study, spectacled bears, who are frugivorous, made fewer errors (revisits to depleted sites), and relied more heavily on visual cues. The current study aims to explore American black bears’ spatial memory and search strategies in a foraging task. Given that studies of spatial behavior have not yet been conducted in American black bears, the mechanisms of navigation used by this species remain unknown. Even though among the order Carnivora black bears have large relative brain sizes (Gittleman, 1986) and their learning and memory abilities compare favorably with those of dogs, wolves, and nonhuman primates (Bacon & Burghart, 1976a, b), research on their cognitive capacities remains scarce.

The experimental design was based on previous research with nonhuman primates (Gibeault & MacDonald, 2000; MacDonald & Wilkie, 1990) and carnivores (Perdue et al., 2011; Tarou, 2004). Typically, several locations within an enclosure are marked with landmarks and some of them are baited with a preferred food. MacDonald and colleagues tested yellow-nosed monkeys’ (MacDonald & Wilkie, 1990), marmosets’ (MacDonald, Pang & Gibeault, 1994), gorillas’ (Gibeault & MacDonald, 2000; MacDonald, 1994), and orangutans’ (MacDonald & Agnes, 1999).
spatial memory using this paradigm. Subjects were usually re-
leased in two different phases separated by a delay. In the first 
phase, subjects were free to explore the enclosure and thus ob-
tained information about the location of baited sites. They were 
then removed from the enclosure for a retention interval ranging 
from 2 min to 24 hr, during which either the same sites were 
rebaited or the sites that were not baited during the first phase were 
baited. Subjects were subsequently released again and their mem-
ory for the sites and foraging strategies were tested. MacDonald 
and colleagues found that marmosets preferred a win–stay strategy 
(MacDonald, Pang, & Gibeault, 1994), while yellow-nosed mon-
keys were successful using both win–stay and win–shift strategies 
(MacDonald & Wilkie, 1990).

Studies of foraging efficiency have also focused on the tactics 
adopted by individuals that forage in groups and how these tactics 
relate to the social status of each subject in the group. For example, 
six gorillas were tested in pairs (Gibeault & MacDonald, 2000) in 
a win–stay task, with retention intervals ranging from 24 to 48 hr. 
Individuals tended to avoid visiting sites that had been depleted by 
their partner, meaning that they were unlikely to overlap their 
visits. Thus, their foraging decisions depended on the foraging 
behavior of the competitor. It is interesting that orangutans were 
not more accurate when tested with a competitor, although they did 
forage above chance overall (MacDonald & Agnes, 1999). Other 
species have also been tested in competitive foraging tasks. Held, 
Mendl, Devereux, and Byrne (2000) tested domestic pigs in a 
paradigm where the “informed” forager was allowed to forage in 
an arena until it retrieved the food. After the experimenters re-
baited the same site, the informed forager was released again with 
a “naïve” forager that was heavier and thus could be successful at 
monopolizing the food. Results showed that during solitary train-
ing trials, the dominant pig found the baited bucket using a random 
search strategy. However, when foraging with a subordinate in-
fomed pig, the dominant pig followed the subordinate as it investi-
gated the buckets. Switching from a “producing” tactic when 
foraging alone to a “scrounging” strategy when foraging with a 
subordinate increased the dominant pig’s foraging success. In 
addition, the subordinates also modified their foraging decisions 
when paired with scroungers, for example, by increasing the 
distance between them and the exploiter (Held, Mendl, Devereux, 
& Byrne, 2002). These experiments reveal intelligent and flexible 
strategies that are adapted to the species’ social and ecological 
environment.

Such experiments have also revealed whether animals travel 
efficiently between feeding sites. If animals remember where food 
is located they should attempt to minimize the distance traveled or 
travel to particular sites first—such as those where favored food is 
located, or where food that depletes quickly or by competitors is 
located. Several primate species have also been shown to use 
neighbored strategies when choosing among fixed food sites 
(capuchin monkeys, De Lillo, Visalberghi, & Aversano, 1997; 
tamarin monkeys, Garber, 1989; yellow-nosed monkeys, Mac-
Donald & Wilkie, 1990; common marmosets, MacDonald et al., 
1994; orangutans, MacDonald & Agnes, 1999; gorillas, Gibeault 
& MacDonald, 2000; and chimpanzees, Menzel, 1973).

As an alternative, the “look-ahead” rules are an extension of the 
nearest neighbor strategy, and consist of examining a subset of the 
total sites to be visited and choosing the shortest path to visit them 
(Cramer, 1996; Janson, 2000). Foragers might not know the loca-
tion of all the destinations in advance; might revisit some sites 
more than once; might not visit all of the sites in the same trip; 
might not always return to the point of departure; might not always 
know the amount and type of reward available; and might encoun-
ter new sources along the way while traveling. Accounting for 
these differences, Janson (2000) proposed the “shortest path sat-
isfying” strategy. He suggested that to maximize their fitness, 
animals must choose every day, from the available sources, the 
subset that minimizes the total distance traveled and that can 
be visited within a day or fulfills their daily food requirement. In 
order to understand animal movement patterns while foraging, one 
must also take into account the rates of renewal of their primary 
resources. If no spatial memory is assumed and resources do not 
replete quickly, the best strategy is to move in a straight line from 
one source to the next because making turns will probably bring 
the travel or back to the previously depleted source (Cody, 1974). 
Short movements in random directions will be a better strategy for 
sources that replete quickly. Thus, in order to examine the use of 
spatial memory, one might look for nonrandom movements where 
previously baited sites are visited first more often than would be 
predicted by chance.

Here we examined whether black bears foraged randomly or used 
efficient strategies, when foraging alone, in pairs when only a forager 
was informed as to the location of food, and in competitive groups 
when all were informed. As in Perdue et al. (2011) and Tarou (2004), 
here the bears were first presented with a task in which four of eight 
sites were baited. They were released in two phases separated by a 
retention interval. During the second phase, subjects were tested in 
two conditions: individually (Experiments 1a and 1b) and in pairs 
(Experiment 2). In Experiment 3, we extended the retention interval 
and allowed all of the bears to compete for food simultaneously.

General Method

Subjects

Four adult captive-born American black bears served as sub-
jects. Elsie was an adult female of approximately 160 kg born at 
the Limestone Zoo (Harvest, Alabama) in 1993 and transferred to 
the Mobile Zoo (Wilmer, Alabama) in 1996, where she gave birth 
to three cubs in January 2002: two males, named Brutus (~200 kg) 
and Dusty (~180 kg), and a female named Bella (~125 kg). The 
subjects were group housed and had free access to indoor and 
door enclosures, except when locked inside or outside during 
cage cleaning, feeding, or testing. Subjects were fed by the zoo-
keepers two times a day, at approximately 1000 and 1700 hrs, in 
their indoor enclosure. Each feeding session consisted of 200 g of 
high-protein, dry dog chow (Purina Achiever), and at least two 
pieces of fruit, generally an apple and an orange, distributed to 
each individual.

Brutus participated in a series of two-choice natural concept 
discrimination and matching-to-sample experiments presented on 
a touch-screen computer monitor during a period of 12 months 
between May, 2007 and May, 2008 (Vonk, Jett, & Mosteller, 
2012). Bella briefly (3 months in the spring of 2006) participated in 
an auditory speech discrimination experiment in which she had 
found how left/right to two different vowel sounds (“oo” and “ee”) 
(Sinnott, unpublished data). The other two subjects were experi-
mentally naive. None of the subjects had ever participated in experiments involving spatial memory or foraging.

Testing Area

The study was conducted at the Mobile Zoo (Wilmer, Alabama) in the black bear exhibit, which consisted of two areas: an outdoor enclosure surrounded by a 3.6-m high fence and an indoor enclosure surrounded by a 2.4-m high perimeter fence. The indoor enclosure consisted of two pens (3 m × 2.4 m each) separated by heavy chain link and a 1.2-m wide human access area that spanned the front of the two bear pens. Each pen had a doorway with a vertically sliding gate that allowed access to a pathway leading to the outdoor enclosure. In general, these gates were kept open, allowing the bears free access to both sections of the exhibit. The outdoor enclosure consisted of grass, shrubs, and other natural vegetation. It contained an artificial water pool, a plantation of privet hedge and bamboo canes, and a wooden platform. The experiments were conducted in the outside enclosure, which is depicted in Figure 1.

Materials

Several locations—eight (A–H) for Experiment 1a, five (C–G) for Experiment 1b, and four (C–F) for Experiments 2 and 3—scattered within the enclosure were each marked by a tire affixed horizontally on the ground, that served as a landmark for a food site (see Figure 1). Landmarks were evenly distributed within the enclosure; some sites were located in heavily used areas and others were located in relatively unused areas, but no landmark was located directly in the heavily traveled path around the enclosure. Each tire was fixed to the ground on three sides using three spiral tie-out stakes (40 cm long). This procedure prevented subjects from modifying the landmarks’ original location, and from creating a cue for previously visited sites on a given session. Due to the logistical constraints of introducing and removing each structure after every session, landmarks remained in the same location within the enclosure throughout the study. Keeping the landmarks in place throughout this period was assumed to be a better approximation of the conditions bears may encounter in their natural habitat, where food sites and permanent natural landmarks do not just “appear” and “disappear,” as opposed to food items themselves, which might be eaten by other conspecifics, or be absent due to crop failures.

Because subjects were not familiar with experimentally inserted forage in the outside enclosure, the landmarks were introduced into the enclosure a week before the beginning of the experiments, with the aim of facilitating this activity and familiarizing them with the new landmarks before testing.

Feeding regime. Subjects were fed with 50% of their usual morning ration of dog chow during testing and familiarization sessions. Food was used to bring subjects in and out of their inside pens for testing. No fruits were provided at this time. At the end of each familiarization and testing session, individuals received the balance 50% of their ration of dog chow. Every afternoon, subjects were fed their normal ration of dog chow and fruits. The food rewards for familiarization and Experiment 1a were three grapes in

Figure 1. Schematic view of black bear exhibit. Black ovals depict locations of landmarks. Baited and unbaited sites were randomly determined on a session by session basis until Experiment 3 when sites C and E were always baited for the first 12 sessions then sites D and F were always baited for the last eight sessions.
each site. Originally we planned to use grapes because they gave off little odor. However, for motivation purposes, these were substituted with four vanilla wafer cookies in each site on the search phase of Session 10 (Elsie) and the exploration phase of Session 11 (Brutus, Dusty, and Bella) of Experiment 1a, and were used from that point forward for Experiments 1b, 2, and 3. Food items were placed on the ground in the middle of the open area of each tire during familiarization and Experiment 1a and inside the rim of each tire during Experiments 1b, 2, and 3.

In order to control for subjects relying on odor cues instead of memory for the sites, baking soda was sprinkled in the location where the food items were introduced, as well as on the food items. The odor-masking cues were introduced in every tire whether it was baited or not and were added in every session during the

Figure 2. Number of visits required to retrieve all the food items as a function of trials in the exploration and search phases of Experiment 1a. Brutus (A), Dusty (B) and Bella (C).

4 ZAMISCH AND VONK
baiting procedure. Tires were baited with odor masking (baking soda) in the same order on each session so that experimenters did not provide any visual cues by virtue of their movement patterns and baited sites were not systematically more or less recently baited than unbaited sites. No odor masking was used during the familiarization phase in order to facilitate the process of encouraging them to forage in the landmarked sites. Although more typically, food is placed in all sites but made inaccessible to animals in “unbaited” locations (Bacon & Burghardt, 1976a), we chose not to use this procedure, given the destructive nature of our bears and the high probability that they would eventually be able to access the food in intended “unbaited” sites. We found the method of using baking soda to mask the food to be effective, in that the bears did not locate the food on every trial or travel immediately from one baited site to the next (as can clearly be seen in the results) despite the fact that they were observed to sniff the air during foraging.

Data recording. A Sony DCR-HC28 MiniDV Handycam camcorder was used to record the sessions. Two observers were located at a vantage point in the area between the enclosure fence and the perimeter fence (see Figure 1) and followed the bears with the camera as they foraged throughout the enclosure. Observers tracked the bears’ movements from their entrance into the outdoor enclosure until the foraging session was completed. Two observers were required to ensure that the bear did not become invisible at any point during the session. Once in position at the beginning of sessions, experimenters did not move significantly from the optimum vantage points in order to attempt not to influence the bears’ movement patterns during foraging. Signs were posted on the outside perimeter fence in order to discourage zoo personnel and visitors from moving through the area during testing as well. In addition, most sessions were completed before the zoo opened to the public each day.

At the end of each session, an experimenter entered the enclosure, counted the number of food items left (if any) in each site and recorded this information in the foraging datasheet. Food items were never observed in sites that had been visited. Based on the length of time spent at each baited site, it appeared to us that the bears depleted the sites completely before moving on. A visit was defined as manual searching (subject touches any part of the tire with either paw), or visual examination (subject’s face orienting to landmark at a distance closer than 20 cm). A visit was defined as ending when every part of the subject’s body was a minimum of 1 m away from the site, or the subject was clearly orienting away from the site.

Procedure

Familiarization. The aim of the familiarization sessions was to accustom the bears to the task of foraging in the outside enclosure and to establish the association between the landmark and the presence of preferred foods. Familiarization sessions were conducted in the morning between 0900 and 1200 hr. A total of four familiarization sessions were conducted. During Sessions 1 and 3, all of the tires were baited. During Sessions 2 and 4, only four tires were baited (A, C, E, G and B, D, F, H respectively). Subjects did not have visual access to all landmarks from a single vantage point in the outside enclosure. Before the beginning of a session, subjects were sequestered by two experimenters into the indoor pens. From there, the bears did not have visual access to the outdoor enclosure and thus were not able to observe the experimenters baiting the food sites or the other subjects’ sessions. While the bears were locked in the inside enclosure, the experimenters baited the corresponding sites for that session with three grapes each. After the baiting procedure, the experimenters exited the enclosure and a randomly selected subject was released from the inside enclosure into the pathway that connects with the outside enclosure while the other three animals were kept in the inside pens. Once released, each individual was free to forage until it visited all of the sites or for a maximum of 10 min (whichever occurred first). At the end of the session, individuals were called into the inside enclosure by the experimenters. Typically, subjects went straight to the pathway and into the inside pens when called. The experimenters then entered the enclosure, removed any remaining food items and subsequently rebaited the corresponding food sites for the next subject to be released. The order in which subjects were released was randomized on each familiarization session with a simple random software program created for DOS operating system.

Testing. Subjects were tested individually and in pairs in a win–stay foraging task. In Experiments 1a and 1b, a set of landmarks were baited and subjects were released individually in two phases separated by either a long (Experiment 1a) or a short (Experiment 1b) delay. During the exploration phase, subjects searched within the enclosure until they visited all the sites. Thus, during this phase subjects were informed about the location of the food. During the search phase, the bears were released individually and were given the opportunity to use this information to relocate the food. Experiment 2, the competition task, differed in that subjects were tested in pairs during the search phase. In Experiment 3, all bears were released together and exploration and search were separated by a period of days. In addition, the locations of the baited sites were not varied in Experiment 3. Familiarization and test sessions for the first three experiments were conducted over a 3-month period and every subject was tested once on each testing day.

Reliability. Inter observer reliability was estimated by calculating the percent of agreement between the data recorded in the field on the foraging datasheets and by an independent rater who coded 20% of the sessions in each experiment (which corresponded to three randomly chosen testing days per subject for Experiments 1a and 2, and two testing days per subject for Experiment 1b) from video. For the purposes of analysis, data from the online datasheets were used, as they constituted the entire set of sessions, and the degree of agreement with the sessions coded from video estimated using Cohen's kappa coefficient was high (see Results). For Experiment 3, the entire data set was coded from video by the second author who was familiar with the bears’ appearance and could track their movements as they all foraged simultaneously. Unfortunately, due to a video copying error, Sessions 11 and 12 before the reversal and Sessions 1–5 after the reversal of baiting were permanently lost, thus only data from the first 10 and final three sessions of Experiment 3 can be analyzed and reported here.

Data Analysis

Although Brown and Demas (1994) outlined a sophisticated method for determining the pattern of locomotion between sites in
a foraging task, those methods cannot be readily applied in the current tests, given the small number of sites, and the lack of even distribution of sites. We have chosen to examine the number of successes (visits to baited sites) assuming no replacement (revisits) as described by Tillé, Newman, and Healy (1996), given the relatively few number of revisits observed, and that most revisits occurred after all other sites had been visited first. Thus, following Tillé et al., we calculated z-scores for each individual subject and for the group as a whole, taking into account the total number of sites, baited sites, and nonbaited sites for that experiment, and compared their performance against that z-score, based on sampling without replacement in a memory task with a fixed number of successes. Tillé et al.’s (1996) procedure measures the departures from random exploration in spatial memory tasks specifically. The animals’ actual searches are compared against the number of sites we should expect them to search before they find the number of baited sites or successes that are possible. We also report the number of revisits and compare subjects’ recovery accuracy (number of successful visits) over the first and last halves of the search phase of the experiments as a measure of learning, using dependent-samples t tests.

### Experiment 1

This experiment aimed to explore American black bears’ spatial memory in a foraging task. Based on MacDonald and Wilkie’s (1990) experiments with yellow-nosed monkeys (Cercopithecus ascanius whitesidei), subjects were released and allowed to forage among several food sites in two different phases separated by a retention interval. Of interest was the level of accuracy in retrieving the food during the search phase of the experiment and the strategies used to retrieve it, specifically how subjects organized their search and whether they avoided revisiting previously depleted sites. Subjects were tested under two conditions: in Experiment 1a, the exploration and search phases were separated by a 2-hr delay, while, in Experiment 1b, they were separated by a period ranging from 5 to 15 min.

#### Experiment 1a

Four out of eight sites were baited and the odor masking cues were introduced during the baiting procedure in every session. Baited sites were randomly selected across sessions, and each site was baited equally often for each subject across sessions. There was no particular pattern such that the same four sites were not baited together on particular sessions, that is, A may be baited along with C, D, and F one day, but along with B, G, and H the next, or C, D, and H on another day. In order to avoid leaving residual cues of baited locations the experimenters followed a designated path as they walked through the enclosure during the baiting procedure (A, B, C, D, E, F, G, and H). Thus, they visited all of the sites but only the selected ones were baited for each session. A total of 12 single-trial sessions were conducted per individual over 12 days. The number of sessions was selected for counterbalancing purposes. Overall, each of eight sites was baited six times for a total of 48 baits (four sites baited on each of 12 sessions). Test sessions were usually conducted three times a week. Each session consisted of two phases: exploration and search.

#### Phase 1: Exploration

In this phase, individual subjects were released into the pathway connecting to the outside enclosure and were allowed to explore until they visited all of the sites or for a maximum of 10 min (whichever occurred first). After every site had been visited or 10 min had passed, subjects were called to the inside enclosure through the same procedure used in familiarization. In between subjects, the experimenters entered the outside enclosure, counted and recorded on the corresponding foraging datasheet the number of grapes (if any) that remained uneaten in each baited site, cleaned the sites so that there were no remains of any sort (liquid or solid), baited the randomly selected sites for the next subject’s exploration phase, and added the odor-masking cues.

Phase 1 for every subject took place between 0900 and 1030 hrs, while Phase 2 for every subject took place between 1100 and 1230 hrs so there was a delay of approximately two hours between phases for each subject. This delay allowed time for testing of each subject, baiting of the food sites and maneuvering of the appropriate test subjects by the experimenters. At no time between phases were the bears as a group allowed back out into the outdoor enclosure. The order in which subjects were released was randomized on each testing day, but remained the same across phases. This practice ensured that the delay between both phases for every subject remained equal. Each subject participated equally often in each possible order across the 12 sessions of the experiment.

#### Phase 2: Search

During the retention interval, the experimenters rebaited the same food sites from Phase 1 for each bear. Subjects were again released individually, and in the same order as in the exploration phase and were allowed to forage for 10 min. Phase 2 was never terminated before the completion of the 10-min period, even if subjects had visited all food sites and had depleted the baited ones. This maximum interval allowed the experimenters to record the number of revisits to both baited and unbaited sites within a set time period for all subjects.

### Results

Interrater agreement for the order of visits to sites was high (Cohen’s K = 0.93). Subjects foraged within the enclosure recovering all of the food items during almost all of the sessions, except for Elsie. Elsie visited on average 6.75 sites during the exploration phase and in half of the sessions she failed to visit all of the baited sites. Subjects were expected to investigate fewer sites to recover all of the food items during the search phase than during the exploration phase. In our experiment, the mean number of visits required for each subject to recover all of the food items approximated eight, which is the total number of sites to be visited, and did not greatly differ between phases: Brutus: mean \( M_{\text{Search}} = 8.17 \) (standard deviation \( SD = 1.64 \)); Dusty: \( M_{\text{Search}} = 7.50 (SD = 2.32) \), \( M_{\text{Exploration}} = 8.67 (SD = 1.44) \); Bella: \( M_{\text{Search}} = 6.78 (SD = 1.09) \), \( M_{\text{Exploration}} = 7.78 (SD = 2.17) \) (see Figure 2). Because Bella did not visit all of the baited sites in the search phase of Sessions 5, 7, and 10, the data corresponding to these sessions were excluded from this calculation. Because Elsie did not visit all four baited sites in the exploration phase of nine sessions and the search phase of 10 sessions out of a total of 12 sessions, we did not include this subject in the analysis. In comparing the mean number of visits against chance using adjusted z-scores assuming no replacement...
Brutus and Dusty searched for longer than would be expected by chance during exploration ($z = 1.84, p < .05$, and $z = 1.59, p = .05$, respectively, one-tailed $z$ tests). The same was true for the three bears that foraged reliably, as a group ($z = 4.01, p < .001$). This is expected given that the bears would not know which sites were baited during exploration. The bears could search for longer than would be expected by chance during exploration if they had preferred routes that made their searches nonrandom or revisited depleted or unbaited sites before baited sites, as was sometimes the case. During search, the bears’ performance did not differ from chance, either individually, or as a group.

If learning was taking place, subjects’ performance was expected to improve across sessions. However, no significant differences were found between recovery accuracy (number of successful visits) in the initial and final blocks of six sessions of the search phase, dependent samples $t$ tests, $t(3) = 0.66, p = .56$. If subjects were using spatial memory, no revisits to either depleted sites during a session, or unbaited sites in any of the phases of the experiments would be expected. In general, Brutus and Dusty made one or two revisits per session before they retrieved all of the food items; Bella revisited only one site in the search phase of one session before recovering all the baits: Brutus: $M_{\text{search}} = 1.33$ ($SD = 1.44$), $M_{\text{exploration}} = 1.83$ ($SD = 2.89$); Dusty: $M_{\text{search}} = 0.83$ ($SD = 1.53$), $M_{\text{exploration}} = 1.25$ ($SD = 1.14$); Bella: $M_{\text{search}} = 0.08$ ($SD = 0.29$), $M_{\text{exploration}} = 0.89$ ($SD = 1.17$). Taken together, the above results show that, in general, Brutus, Dusty and Bella visited all eight sites with only a few revisits in between before they retrieved all of the food items in both phases of the experiment. After visiting all of the sites, subjects usually continued to search around the enclosure, making several revisits during the 10-min period of the search phase. On some sessions the bears visited five or six sites, then returned to the path into the indoor enclosure for a couple of minutes and came back out to investigate sites that had not been visited, as well as some of the previously visited sites. No significant differences were found between the mean number of revisits to previously baited and unbaited sites, $t(3) = 1.69, p = .19$.

Subjects did not show any fixed movement patterns while foraging throughout the enclosure, but there was a tendency to move to adjacent sites. For example, after visiting site A, Bella always moved either to site C (91%) or B (9%), both sites being the closest to A. In addition, subjects showed a preference for the sites most proximate to the entrance to the outside enclosure; in all 12 sessions, either site A, B, or F was chosen first by every bear. Nevertheless, this preference was not influenced by whether the site was baited or not. Brutus’s first choice was to site A on the search phase of all 12 sessions, but this site was baited on only half of the sessions. A similar situation was observed with Bella and Dusty in both phases. For every subject the first choice accuracy during the exploration phase did not differ from that of the search phase. In addition, after making their first choice, Brutus and Bella visited an adjacent correct site on only 50% of the sessions which is what would be expected by chance. Dusty and Elsie’s performances were less consistent (Dusty visited an adjacent correct site on 42% of the sessions and Elsie on only 25% of the sessions). Thus, the bears tended to travel between adjacent sites regardless of whether these were baited or not.

The enclosure in which the bears were tested was small, and thus the costs of foraging were negligible as compared with the costs that black bears face in their natural habitat. By introducing eight sites in this small enclosure, subjects were exposed to a large site density; they required little deviation from their path to inspect nearby sites on their way to a specific further site. This led to several revisits that did not represent any consequential extra cost for the bears. Thus, it is possible, that even if they knew and remembered which sites were baited, they might have investigated unbaited sites on their way to baited sites simply because the cost for doing so was negligible. In addition, there was no competition for the food during their sessions, and no real time pressure since the food did not degrade or expire during the session.

It is also possible that subjects did not demonstrate the use of spatial memory because the retention interval was too long for them to retain the location of the food sites. Several studies that reported spatial memory in nonhuman primates applied shorter retention intervals that ranged from 2 to 15 min (MacDonald & Wilkie, 1990; MacDonald et al., 1994; Menzel, 1973), but this was not the case for captive lowland gorillas, which were able to remember the location of food after a retention interval of up to 24 hr (MacDonald, 1994).

The results show that subjects performed similarly in both phases of the experiment, visiting every available site in a relatively efficient manner (using an adjacency pattern, with few revisits in between) and depleting the sites that contained food along the path. This pattern was consistent across all sessions. It was anticipated that the bears would use the food location information acquired during the exploration phase to efficiently forage throughout the enclosure during the search phase. Even though the subjects encountered both baited and unbaited sites in each session, the bears quickly learned to associate the tires with the presence of food, but they never learned the task, that is to use the information acquired during exploration to effectively seek out sites that were baited during this phase immediately during search, throughout the experiment.

The failure to demonstrate spatial memory in this experimental setting may be due to the fact that the subjects did not have the necessity of memorizing baited locations in the first phase. Because they were food adjusted (i.e., not provided with their regular morning feed on the days of testing), it was expected that the bears would run to the outside enclosure to search for food once released from the inside pens. However, only Brutus and Dusty completed their testing sessions relatively quickly. Bella and mainly Elsie moved very slowly during testing. It was also expected that they would continue searching until they had searched in all of the sites during the exploration phase, but this was not always the case.

When grapes were substituted with cookies, Elsie immediately started to forage at all of the sites and to recover all of the food items. Her foraging behavior improved as soon as the food reward was switched, suggesting that she was lacking motivation in the previous sessions.
during the search phase. Rather, the bears went from searching below chance during exploration to searching at chance during search.

In summary, subjects in this task did not have time or energy constraints, and thus did not need to use a strategy, such as remembering the location of food sites, to minimize the costs. Their strategy was to search in all of the sites which required little extra effort, and eventually they retrieved the food. Based on the results of Experiment 1a it was unclear whether subjects lacked the ability or the motivation to demonstrate the use of a spatial memory strategy in a foraging task. In Experiment 1b, we set out to reduce the demands of the task in an attempt to optimize the likelihood the ability would be expressed if it were present.

Experiment 1b

This experiment was designed to simplify the task, making it easier for subjects to retain the location of the sites and to demonstrate the use of spatial memory. Because subjects went to sites A and B first in almost every session during Experiment 1a, and site density had to be decreased in order to reduce the likelihood of nearby revisits, those two sites, as well as site H, were removed. The reduction in number of sites, and number of baited sites together reduced the memory demands of the task. Furthermore, in order to increase the cost of foraging, while the size of the enclosure could not be increased, the food rewards were introduced inside the rim of the tires. This way the food would not be so readily available and subjects would have to manipulate the site to have access to the food. In addition, three out of five sites were baited in each session, increasing subjects' probabilities of visiting a baited site. A time constraint was added in the search phase of Experiment 1b; the session was terminated after the subject had visited all of the baited sites or after 5 min had passed (whichever occurred first), regardless of whether it had visited all unbaited sites. Finally, the delay between phases was reduced from 2 hr to a range of 5 to 15 min. This shorter period was designed to be short enough for subjects to retain the spatial information previously acquired. This period was necessary to clean and rebait the same sites, and get the subject back into the enclosure. Variability between intertrial intervals simply reflected the differential amount of time required to lure different subjects on different test days back into the enclosure. Sometimes this was a function of which other subject they were enclosed with on that particular day, among other factors. Note that, in this condition the search phase for each subject immediately followed the exploration phase for that subject. That is, no other bears foraged in the enclosure in between the exploration and search phases of their sessions. Sessions were conducted between 0900 and 1030 hrs on 10 days. A total of 10 single-trial sessions were conducted for counterbalancing purposes. Overall, each of the five sites was baited six times for a total of 30 baatings (three sites baited on each of 10 sessions). The order in which subjects were released was randomized on each testing day, but remained the same across phases.

Results

Interrater agreement for the order of visits to sites was high (Cohen’s $K = 0.95$). Subjects visited all five sites in the exploration phase and recovered all of the food items in the search phase of all 10 sessions, except for Elsie who did not visit one of the baited sites in the search phase of Session 2. The mean recovery accuracy (number of baited searches visited out of the first three visits) of the exploration phase approached 2 for every subject: Brutus: $M_{\text{Search}} = 2.00$ (SD = 0.67), $M_{\text{Exploration}} = 1.90$ (SD = 0.74); Dusty: $M_{\text{Search}} = 2.00$ (SD = 0.67), $M_{\text{Exploration}} = 1.90$ (SD = 0.74); Bella: $M_{\text{Search}} = 2.00$ (SD = 0.82), $M_{\text{Exploration}} = 1.67$ (SD = 0.71); Elsie: $M_{\text{Search}} = 2.10$ (SD = 0.74), $M_{\text{Exploration}} = 2.00$ (SD = 0.47). This number did not significantly differ from that of the search phase ($t(3) = 1.67, p = .19$). As in Experiment 1a, subjects' performance did not improve across sessions; no significant differences were found between recovery accuracy in the initial and final blocks of five sessions of the search phase, $t(3) = 0.66, p = .55$.

The mean number of visits required for each subject to recover all of the food items ranged around five, which is the total number of sites to be visited, and did not greatly differ between phases: Brutus: $M_{\text{Exploration}} = 5.50$ (SD = 2.17), $M_{\text{Search}} = 5.10$ (SD = 1.45); Dusty: $M_{\text{Search}} = 4.80$ (SD = 1.23), $M_{\text{Exploration}} = 4.60$ (SD = 1.26); Bella: $M_{\text{Search}} = 4.20$ (SD = 1.03), $M_{\text{Exploration}} = 5.10$ (SD = 1.20); Elsie: $M_{\text{Search}} = 4.30$ (SD = 2.06), $M_{\text{Exploration}} = 6.00$ (SD = 1.63) [see Figure 3]. In this experiment, only Elsie searched more than would be expected by chance, $(z = 2.24, p < .01)$, while all of the other bears searched at chance levels during exploration.

The number of revisits that subjects made before retrieving all the food items was variable, with Bella and Dusty making fewer revisits overall: Brutus: $M_{\text{Search}} = 1.20$ (SD = 1.62), $M_{\text{Exploration}} = 0.80$ (SD = 0.92); Dusty: $M_{\text{Search}} = 0.80$ (SD = 0.63), $M_{\text{Exploration}} = 0.50$ (SD = 0.85); Bella: $M_{\text{Search}} = 0.10$ (SD = 0.32), $M_{\text{Exploration}} = 0.60$ (SD = 0.70); Elsie: $M_{\text{Search}} = 0.70$ (SD = 1.16), $M_{\text{Exploration}} = 1.30$ (SD = 1.42). The total number of revisits did not decrease across sessions for any of the subjects.

Subjects’ movement patterns were not consistent across sessions but as in Experiment 1a, there was a tendency to move to adjacent sites. Dusty often traveled from site E to G even though G was farther from E than some of the other sites were. However, this pattern was observed regardless of whether G was baited or not (only 37% of the times that Dusty traveled from E to G, the latter was baited). The bears also showed a preference to visit particular sites first, going mostly to C, F (Brutus, Dusty, and Elsie), or G (mainly Bella) which were the closest sites to the starting point.

Discussion

Subjects’ foraging behavior improved in this experiment relative to Experiment 1a. They visited all of the sites in the exploration phase and retrieved all of the food items in the search phase (except for Elsie in one session). This can be explained by the
Figure 3.

BLACK BEAR SPATIAL MEMORY

Figure 3.

Figure 3.
switch from grapes to cookies as food reward, which might have increased their motivation to forage, especially Elsie’s. The bears’ performance was expected to improve in this experiment, given that the number of sites to be remembered was reduced to three, the probabilities of visiting a baited site were greater and the retention interval was shorter than in Experiment 1a. It was assumed that these factors would simplify the task by decreasing the memory demands. However no sign of learning or use of spatial memory by any of the subjects was observed.

By introducing the food in the rim of the tires, an extra cost was added. In general subjects obtained the food by pulling it out with their paws. This forced them to spend extra time at the baited sites. However, the total costs of foraging within the enclosure were still negligible because of the short distances between sites. As in Experiment 1a, the bears’ strategy was that of visiting all of the sites with few revisits in between, and collecting the food as they encountered it. In general subjects moved from one site to the next adjacent site regardless of whether it was baited or not. The fact that subjects did not demonstrate spatial memory when recovering the food even after the memory load was reduced is most likely due to the small energy demands that the bears have in captivity, combined with the low costs of foraging in this relatively small enclosure.

**Experiment 2**

Even though the demands of the task were reduced in Experiment 1b, relative to 1a, it remains possible that bears have the capacity for spatial memory even though they did not demonstrate it in these experiments, because of a lack of cost or impetus that would motivate them to forage efficiently and make use of the information acquired during exploration. Experiment 2 was designed to increase the costs of foraging through the introduction of a competitor during testing. In this context subjects were expected to be motivated to forage more efficiently, gaining access to the food before their competitor. In addition, to further reduce the memory load, only two sites out of four were baited. Site G was selected to be removed from the enclosure in order to maintain two groups of sites equidistant from the starting point (C–D and E–F). Of interest was whether subjects, who had been given the opportunity to be knowledgeable as to the location of food during exploration, would increase their accuracy in retrieving food items in the presence of a competitor, and whether this would relate to the social status of each pair member.

**Dominance Testing**

In order to analyze subjects’ performance in the competition task with regard to their social status, a dominance test was conducted during the initial sessions of the competition task. Two subjects were sequestered at the front of one of the inside pens. An experimenter located at the front of the enclosure presented the subjects with a vanilla wafer cookie and subsequently placed it on the pen’s floor, or held it in her hand, equidistant from both subjects. The bear that ate the cookie was considered dominant with regards to its competitor (subordinate) in that trial. A total of eight trials were conducted for each pair. A bear was considered dominant over its partner if it obtained the cookie on six of those eight pairings. No clear dominance was determined if one of the bears obtained the cookie on less than six of the eight trials within a pairing.

**Procedure**

In this experiment, two out of four sites (half) were baited in each session. A total of 48 single-trial sessions were conducted across 12 days. The number of sessions was determined so that within each pairing, the same sites would be baited equally often for each subject. The sites to be baited were determined randomly across sessions, as before. Each subject served once as the test subject and once as a competitor per test day. Each subject was released a total of eight times with every other subject (four times serving as the test subject and four times serving as a competitor). The order in which pairs were tested was randomized, but every pair was tested in each order (first, second, third, fourth) an equal number of times across testing days. Each bear participated in 12 sessions as subject, four times with each of the other subjects as competitor, in random order. However, each subject was released with each other subject as competitor before any pairings repeated.

**Phase 1: Exploration.** The basic procedure for the exploration phase was the same as in Experiment 1b, with the exceptions noted above.

**Phase 2: Search.** After a retention interval ranging from 5 to 15 min, the same food sites as in Phase 1 were baited and both the test subject and the competitor were released simultaneously, from the same inside pen, and allowed to forage in the outside enclosure. The search phase was terminated once the test subject had visited the two baited sites or after 5 min had passed (whichever occurred first). The time of the session began as soon as the test subject emerged from the path. If the test subject never emerged from the path and the competitor had foraged for 5 min, the session was aborted.

**Results**

No clear dominance pattern was observed between Dusty, Bella, and Elsie. Brutus was clearly dominant over all the other subjects, eating all of the food in all of the dominance trials (see Table 1). Brutus and Dusty foraged in the enclosure during both phases of the experiment visiting all the sites during the exploration phase and making few revisits in between. Bella did not visit one of the sites during one of her exploration phases but she always foraged during the search phase, as opposed to Elsie who failed to go out of the inside pens during the search phase of five sessions.

**Table 1**

<table>
<thead>
<tr>
<th>Pairs</th>
<th>Dusty</th>
<th>Bella</th>
<th>Dusty</th>
<th>Elsie</th>
<th>Bella</th>
<th>Elsie</th>
</tr>
</thead>
<tbody>
<tr>
<td># Sessions</td>
<td>8</td>
<td>0</td>
<td>8</td>
<td>0</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td># Sessions</td>
<td>5</td>
<td>3</td>
<td>5</td>
<td>3</td>
<td>4</td>
<td>4</td>
</tr>
</tbody>
</table>
Interrater agreement for the order of visits to sites was high (Cohen’s $K = 0.94$). The mean number of correct choices during the exploration and search phases approached 1 for Brutus, Dusty, and Bella, which is what would be expected by chance: Brutus: $M_{\text{Search}} = 1.00$ ($SD = 0.60$), $M_{\text{Exploration}} = 1.17$ ($SD = 0.39$); Dusty: $M_{\text{Search}} = 1.17$ ($SD = 0.58$), $M_{\text{Exploration}} = 0.92$ ($SD = 0.51$); Bella: $M_{\text{Search}} = 1.08$ ($SD = 0.67$), $M_{\text{Exploration}} = 0.92$ ($SD = 0.67$); Elsie: $M_{\text{Search}} = 1.00$ ($SD = 0.82$), $M_{\text{Exploration}} = 1.00$ ($SD = 0.60$). Because Elsie did not forage during the search phase of five sessions, her recovery accuracy during this phase was computed from only seven sessions. Although the subject’s foraging was undoubtedly affected by the presence of the competitor, their success should still have been above chance because only they were knowledgeable as to the presence of the food during search. However, performance for all of the subjects in both search and exploration was at chance ($z$ tests, all $p > 1.0$). No significant differences were found between recovery accuracy during exploration and search phases, $t(3) = 0.29, p = .79$.

An analysis of the bears’ performance across sessions with regards to the competitor they were paired with, showed that Brutus was able to recover more food items when tested with Bella and Elsie than when tested with Dusty. Overall, Elsie was able to retrieve very few items, regardless of the competitor she was paired with. The subject that was able to recover more food items when competing with another bear was Brutus. However, the test subject recovered all of the food items in only a few sessions. Thus in most sessions, the competitor was able to recover food from at least one site. Recovery success for each bear as a function of their foraging partner appears in Table 2.

Competitive behaviors between the different pairs were variable and no clear relationship was observed with regards to the individual’s social status, sex, or kin relationship. Aggressive events were observed on only three sessions. On one occasion Brutus chased Dusty away as they were both approaching site C. On another occasion Elsie bit Dusty as he approached her while she was foraging in site D and, on a third occasion, Elsie guarded an unbaited site (F) during the entire session and vocalized toward Brutus each time this subject approached her. Displacement from a site was observed only when Bella was foraging in pairs. She was displaced while eating at a baited site on five sessions, three of them while competing with Dusty and two while competing with Brutus. However she was the knowledgeable subject on only two of these sessions, so it is unlikely that either Dusty or Brutus were exploiting their competitor’s knowledge to access the food.

On 42% of the sessions, subjects would visit first a site opposite to the site that the competitor was visiting (i.e., if Dusty went to C first, Bella would go to F first and vice versa). This was mostly the case for Bella regardless of the competitor she was paired with. Elsie and Dusty also showed this behavior mostly when paired with Brutus. Avoidance was also observed when Brutus was paired with Elsie; on two occasions, Brutus moved toward a site where Elsie was foraging, stopped at distance of about 2 m and turned around. Thus, the bears did not use the strategy observed in Held et al. (2000) by the pigs, which exploited competitors’ knowledge.

### Discussion

In this experiment, a subject was given privileged knowledge about the location of food and was subsequently tested with an uninformed competitor. Because subjects did not demonstrate the ability to use spatial memory during Experiments 1a and b, it was expected that, if they were indeed capable of doing so, the presence of a competitor would serve as an incentive to use spatial memory to increase foraging efficiency. The informed subject was expected to visit first the two baited sites, obtaining all of the food in the search phase, while the uninformed subject should use one of two strategies: forage at random or exploit the informed subject’s knowledge to obtain as much food as possible as in Held and colleagues’ study with pigs as foragers (2000).

However, our results show that each subject used the same strategy when serving as competitor and test subject. There was no greater evidence here that subjects were able to utilize spatial memory to increase returns. Even though Brutus appeared to be the dominant subject in the group, he avoided Elsie on a few occasions when he was paired with her. This is not surprising given that in general when not being tested, Elsie displayed aggressive behavior toward Brutus. That Bella was displaced from a baited site on several sessions by Dusty and Brutus and that Elsie foraged during all of her exploration phases (in which she was released individually) but only on seven of her search phases (in which she was released with a competitor), suggest that these subjects maintain a low status in the group’s hierarchy. Furthermore, in general males were better able to recover more food items when competing with the females than when competing with each other. It is unlikely that Brutus and Dusty exploited Bella’s knowledge during those sessions in which they displaced her, because she was not the knowledgeable subject in most of them. They probably observed her as she ate at a particular site and, through local enhancement, followed her to that site. However, the general pattern appeared to be one of avoiding sites where others were foraging, even when dominant animals could have displaced subordinates. This is similar to what MacDonald and Agnes (1999) found with orangutans, and may be a pattern demonstrated by nonsocial foragers.

The few occurrences of agonistic interactions and competitive behaviors observed during this experiment were unexpected. Our results can be explained by a general lack of motivation to compete for food with other members of the group, especially by Elsie who “allowed” her competitors to eat the food items during most of her sessions. This latter finding may not be so surprising, given that the other subjects were Elsie’s offspring. In the wild, mothers typically have no direct contact with their offspring after family breakup, and avoidance of offspring by the mothers has been reported (Rogers, 1987).

<table>
<thead>
<tr>
<th>Competitor</th>
<th>Brutes</th>
<th>Dusty</th>
<th>Bella</th>
<th>Elsie</th>
</tr>
</thead>
<tbody>
<tr>
<td>Test subject</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brutus</td>
<td>1.00</td>
<td>1.75</td>
<td>1.75</td>
<td></td>
</tr>
<tr>
<td>Dusty</td>
<td>0.75</td>
<td>1.50</td>
<td>1.75</td>
<td></td>
</tr>
<tr>
<td>Bella</td>
<td>0.75</td>
<td>1.50</td>
<td>1.70</td>
<td></td>
</tr>
<tr>
<td>Elsie</td>
<td>0.25</td>
<td>0.0</td>
<td>0.25</td>
<td></td>
</tr>
</tbody>
</table>
Experiment 3

Because of the concern that the methodological procedure of changing the sites that were baited on each experimental testing session may have made it difficult for the bears to understand the relationship between exploration and search phases, a decision was made to present them with a situation in which the same sites were always baited, as in Tarou (2004) and Perdue et al. (2011). In addition, due to the possibility that bears may not anticipate sites to replenish over short intervals, sites were rebaited on subsequent test days (2 or 3 days apart), rather than after 4-hr or 15-min intervals, as in the previous experiments. Furthermore, in order to maintain the competitive costs that would reduce the likelihood that bears would simply investigate all four sites, all bears were released to forage simultaneously. If black bears exhibit win–shift rather than win–stay strategies, they should avoid the continually baited sites.

Procedure

The same four sites were used as in Experiment 2; two along the fence facing their indoor enclosure (sites F and C) and two along the opposite, back fence (D and E). Only sites C and E were always baited for 12 sessions. F and C were approximately equidistant to the tunnel from which the bears emerged from the inside enclosure, as were D and E, which were further away. When the bears were locked in the indoor enclosure for their morning feeding, an experimenter entered the outdoor enclosure and walked from tire C, D, E, and F, baiting tires C and E with a handful of vanilla wafer cookie pieces and placing baking soda in each of the four tires to mask the scents. The doors to the indoor pens were then raised releasing two of the bears with a slight head start over the other two bears (two bears feed in each of the indoor pens). However, the bears typically do not run out of the pens into the outside enclosure immediately upon release, particularly after feeding, so releasing the second door at a slight delay did not impact upon the order with which bears entered the outdoor exhibit.

A second experimenter was positioned inside the perimeter fence with a clear view of all four tires to videorecord the bears’ foraging as they entered the outside enclosure. Filming continued until the baited sites had been depleted and at least one of the bears had visited all four sites. Sessions were later coded from video for the order in which each bear visited the sites. One session was conducted each test day 3 days a week for a period of 6 weeks on Sundays, Tuesdays, and Fridays.

After 12 testing days, a decision was made to reverse the baiting of the sites, such that tires D and F were baited and tires C and E were not baited, in order to determine whether bears could flexibly alter an established bias to search first at site C. The baiting at sites D and F continued for eight test days. Other aspects of the procedure were identical.

Results

Due to an unfortunate computer malfunction, video for Sessions 11 and 12 and Sessions 1–5 after the reversal were permanently lost and could not be coded. Therefore only data from the first 10 and last three sessions will be analyzed and reported. In this experiment there was no real distinction between exploration and search. After the first session, all test days could be considered search sessions. None of the individual subjects foraged at above chance levels according to adjusted $z$ tests (all $ps > .10$, Tillé et al., 1996). Elsie’s data was not analyzed because she seldom foraged at all before the other bears had depleted the sites. Not all bears foraged on all sessions and one bear typically depleted the sites before any other bears foraged on each test session. However, the video was still coded for the order in which each bear traveled to each site. The number of visits required to achieve success (recovering food at both baited sites for an individual bear) is depicted in Figure 4.

In addition to conducting adjusted $z$ tests, because of the nature of the data set for this experiment—that being several missing cells for each subject—instead of analyzing only the number of successes, we also calculated the exact probability of visiting each baited site by chance as a function of whether the previously visited site had been baited or not baited, and the implications for each remaining site, for each bear on each session. That is, there was a 50% chance of going first to a baited site given that half of the sites were baited so the probability of success for the first visit was .5. This probability was subtracted from 1.0 and multiplied by 0 or 1 depending on the subject’s success. The probability of success on the second visit declined to .33 (1/3 of the remaining sites were baited) if the subject had already visited a baited site on the first visit, or went up to .67 if the subject had not visited a baited site on the first visit (2/3 remaining sites were baited), and so on. We multiplied the score of 1 or 0 representing success by $1 – p$, where $p$ represented the probability of success to obtain the rate of success for each visit. In this manner, higher scores reflected more accurate performance. Then we added all $p$ values for each novel visit (first visit to a site) per session together to obtain a score for each individual for each session. Possible scores ranged from 0 to 1.17. The scores were then standardized by dividing each score by the maximum possible score (1.17), which produced a distribution with a mean of .65. Each subject’s average score was then compared to the mean standardized score of .65 using one-sample Kolmogorov–Smirnov tests. Only Bella’s performance ($M = .86$) was above chance, $p = .04$. Brutus’ performance tended to be below chance ($M = .57$, $p = .06$). Unfortunately, Dusty ($M = .89$) did not forage reliably until after the reversal. While he foraged primarily in the baited sites on the last three sessions, without the data to show that this was indeed a reversal of prior behavior, it is impossible to determine whether this is indicative of use of spatial memory or a coincidence in that he preferred to search from the opposite sites that were first approached and depleted by the other dominant bears, especially Brutus, who always searched first at C, even after the reversal, thus accounting for his (Brutus’) overall poor performance.

Discussion

As in the previous experiment, there was little indication that the bears attempted to exploit resources before competitors could deplete previously baited resources. They often visited adjacent sites even when the adjacent site had never been baited, rather than passing it over to reach a baited site before a competitor could deplete it. However, there were some test sessions in which some subjects traveled to the two baited sites first, bypassing unbaited
sites. In fact, subjects’ performance on this experiment was superior to that of previous experiments in which subjects rarely went exclusively to the baited sites first. At least one bear, Bella, provided some evidence that bears may use spatial memory when the same sites are repeatedly baited over longer test intervals. It is also possible that Dusty would have revealed similar use of spatial memory but the loss of critical data immediately before and after the reversal of baited sites makes that impossible to determine. It appears that he was learning the location of the sites, based on increased performance from the beginning to the final sessions. In addition, Bella had stopped foraging after the reversal so it was impossible to determine how the reversal affected her performance. However, it is obvious that Brutus did not utilize spatial memory, and simply traveled the same preferred route despite the reversal of baiting and competition from his siblings. Brutus’ below chance performance was likely due to his inability to reverse his particular foraging route once the baiting of sites was reversed, explaining why performance was below chance rather than random or above chance.

**General Discussion**

One of the most important functions of spatial memory in animals is to provide individuals with fitness advantages through optimal foraging. As proposed by Milton (1981), one of the functional aspects of spatial memory in nonhuman primates is also that of maximizing their food consumption by reducing the costs of foraging in the tropical rain forest, where food is patchily distributed both in space and time. American black bears are subject to high energy demands because they must obtain most of their annual food during a period 6 to 8 months (Beeman & Pelton, 1980). During this time, they must consume enough food to ensure normal body maintenance and accumulation of fats to survive the winter. Mature females face an additional constraint because they produce and nurse their cubs during hibernation. Those individuals that fail to maximize their food intake during late summer and fall, have compromised survival and reproductive success. The substantial temporal and spatial variation of high quality foods within most of black bears’ range is likely to place high demands on this species’ abilities to learn and remember the location of these sources. In addition, black bears’ movement patterns have been associated with food availability, with seasonal shifts of home ranges occurring especially during summer and fall (Garshelis & Pelton, 1981). Based on these ecological challenges, and on reports of individual black bears traveling hundreds of kilometers and returning to the same small areas to den on a monthly and yearly basis (Rogers, 1986), we expected this species to demonstrate
some capacity for spatial memory task as presented in these experiments.

Given this expectation, the results of our study were surprising. After a total of 54 sessions in a win–stay foraging task, the subjects in our experiments did not achieve above chance accuracy in recovering the food items, with the exception of Bella in the final experiment. However, it would be premature to conclude that American black bears have poor spatial memory abilities based on these experiments. The enclosure in which the bears were tested measured approximately 625 m². For a species that is used to traveling several kilometers daily in the wild, the costs of traveling in such a reduced space are most likely negligible. In a study with adult chimpanzees, Harrison and Nissen (1941) showed that the memory for the location of food was directly related to the spatial separation of potential food sites. Thus, it is possible that, due to the reduced area of the enclosure, the spatial separation between sites was not large enough to compel the bears to bypass unbaited food locations en route to baited locations. In this sense, all of the food sites together might have been represented as a large food patch instead of several different patches with and without food.

Because the overall density of food was high (50% of the tires baited in Experiments 1a, 2, and 3, and 60% in Experiment 1b), the payoff for an exhaustive search may have been enough, and hence the bears were not motivated to learn and remember food locations. In a series of experiments Roberts, Mitchel, and Phelps (1993) showed that squirrel monkeys (Saimiri sciureus) failed to demonstrate spatial memory when 30 out of 48 sites were baited, but remembered the location of food when four out of 48 sites were baited. In their experiments, however, the location of baited sites remained the same across 24 days of testing and there was only one phase in the experiment, making it easier for the subjects to learn the location of the sites. In our study, we did not intend to train the bears to learn the location of particular sites; we aimed for them to learn that the exploration phase signaled where the food would be hidden during the search phase. We did not want to teach them to use spatial memory. We wanted to determine if this was a strategy they would spontaneously adopt. Furthermore, a strategy of baiting the same sites each day might lead to local or stimulus enhancement or automatic level preferences for particular sites—mechanisms that would allow for accurate performance but would not indicate the use of spatial memory. For this reason, in the first three experiments, the location of baited sites changed from session to session, but remained the same within the two phases of each session, a design that might have been confusing for our subjects. They may have failed to ever make the connection between the two phases, learning that the same sites that were baited in exploration were also baited during search. They may have simply viewed each time they were released into the exhibit as a separate session in which the sites that were baited were randomly determined, given the frequency with which the location of the baited sites was changed. Some evidence for such a supposition is supported by the finding that at least one bear, Bella, demonstrated above chance foraging success, using conditional probabilities, when the same sites were continually baited in Experiment 3. However, our experimental setting was initially designed based on studies of spatial memory with other species (specifically nonhuman primates) in which baited sites were randomized across sessions, in an attempt to allow for cross species comparisons.

We set up our experimental task using a win–stay paradigm to reflect the conditions we thought would match those faced in the natural environment of bears. Our data did not suggest that the bears were using a win–shift strategy because they did not perform significantly below chance in the search phases. However, it might be useful to compare black bears’ performance on a win–shift paradigm to determine whether they are better able to learn that task.

It is possible that the bears performed an exhaustive search of all of the sites, failing to discriminate between baited and unbaited sites, because of the low cost associated with a visit to an empty site beyond finding it empty, particularly because the unbaited sites were often located en route to a baited site. In their experiments with spider monkeys, Roberts and colleagues (1993) attempted to make the unbaited sites aversive by introducing rubber snake replicas. One of the two subjects showed learning, but not perfect retention, of the location of the baited sites in this condition. The authors suggested that the use of an aversive stimulus might enhance spatial memory in a squirrel monkey.

Future research on spatial memory in American black bears should be conducted in substantially larger enclosures, under semi-naturalistic conditions, or even better, in the wild. This should allow for an appropriate arrangement of food sites far enough from each other to allow discrimination. In addition, the overall density of food should be low enough that an exhaustive search of all of the sites would not be an efficient strategy. Subjects almost immediately began to use a strategy of exhaustively searching all of the sites starting at the closest site to the starting point. They then followed an adjacency or “nearest neighbor” strategy to visit the rest of the sites. An adjacent-site bias tends to minimize the total distance traveled (Spetch & Edwards, 1986). Using an adjacency pattern would have been an efficient strategy for the exploration phase, in which subjects did not have information about the location of the food and thus had to visit all the sites. However, they used the same strategy during the search phase of each session in all three experiments, further suggesting a failure to use memory for which sites were baited.

One particular feature of the subjects tested in this experiment is that they were all captive born. Captive organisms live in less complex environments, which restrict physical movement and memory-based experiences and demands. Black bears in captivity are not able to express many ecologically relevant behaviors, such as returning to dens to hibernate, delimiting territories, and searching for mates. In addition, they do not need to travel long distances in search of food because they are supplied regularly with ready-processed food. The inability to express the species natural behaviors in a confined environment has consequences on many levels, one of which is brain development. A large body of research has focused on the role of experience, physical activity, and environmental enrichment on brain and behavioral development (e.g., Kempermann, Khun, & Gage, 1998; Nilsson, Perfílieva, Johansson, Orwar, & Erikson, 1999; van Praag, Christie, Sejnowski, & Gage, 1999). For example, food storing passerine birds, which rely heavily on spatial memory to recover their caches, have larger hippocampal areas relative to the rest of the telencephalon than nonstoring bird species (Krebs, Sherry, Healy, Perry, & Vaccarino, 1989). Of interest, this difference in hippocampal volume is not present in the nestlings of storing and nonstoring species, but arises later in development, after they reach nutritional independence.
Clayton and Krebs (1994) showed that food-storing experience, and not age, is responsible for the increase in the volume of the hippocampus of food-storing marsh tits (Parus palustris). They found that the hippocampal region of control birds, which were prevented from storing food, was smaller in volume, had fewer neurons and a higher proportion of apoptotic cells than that of the experienced group. Thus, the hippocampal growth in food-storing birds is triggered by experience. Maguire et al. (2000) studied the effects of spatial experience on brain structure in a group of London taxi drivers that had a wide range of navigating experience. The results of their experiments indicated that taxi drivers had a significantly greater volume in the posterior hippocampus than the control group. In addition, right hippocampal volume correlated with the amount of time spent as a taxi driver, providing further evidence of the interaction between experience and brain plasticity. Similarly to the control birds in Clayton and Krebs’s (1994) experiment, our subjects may have been prevented from learning hippocampally dependent tasks (by being held in captivity from birth). Comparisons of the hippocampal area of captive-born and wild bears should provide further understanding of whether this process is restricted to food storing or it can be extrapolated to mammalian species.1

In general, the results of this study have implications that suggest the need for future comparative studies between captive and wild populations of bears and other species in species-typical and potentially impoverished environments. These findings might inform bear management and conservation efforts focused on critically endangered American black bear populations.

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1 Even though birds and mammals have evolved independently for more than 310 million years, the avian and mammalian hippocampi are considered evolutionary homologues (Sherry, 1998).

References


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