Spatial Memory in Dogs (*Canis familiaris*) on a Radial Maze

Krista Macpherson and William A. Roberts
University of Western Ontario

Working spatial memory in dogs (*Canis familiaris*) was tested in Experiments 1 and 2 on an 8-arm radial maze. When dogs chose freely among all 8 arms containing food in Experiment 1, they learned to enter all 8 arms with progressively fewer arm visits over trials. In Experiment 2, 2 groups of dogs were forced to visit 4 randomly chosen arms on the maze and then tested for memory of these arm visits using a win-shift rule for 1 group and a win-stay rule for the other group. Dogs performed better with the win-shift rule than with the win-stay rule. In Experiment 3, reference memory was investigated by using a 4-arm maze on which 0, 1, 3, and 6 pieces of food were consistently placed on different arms. Dogs learned to visit the arms with the larger amounts before the arms with the smaller amounts. Dogs' memory capacity in these studies was found to be surprisingly low.

Keywords: dogs, spatial memory, radial maze

It is generally agreed that spatial cognition is essential for the fitness of animals in their natural environments. Locating and remembering where food, water, mates, and predators are within one's habitat are essential to survival and reproduction. Extensive recent work on spatial cognition indicates that animals use a number of cues and mechanisms accessed in a hierarchical fashion (Healy, 1998; Roberts, 2001; Shettleworth, 1998). These include both intrinsic cues provided by an animal's own movements and extrinsic cues emanating from the environment outside the animal. In the absence of extrinsic cues, many vertebrates have been shown to be able to take a direct path home after making a winding trip to some distant point. Feedback from intrinsic self-generated kinesthetic and vestibular cues provides the basis for a process of path integration. Extrinsic environmental cues allow animals to navigate through spatial environments by using geometric relationships between objects, landmarks as beacons, and by the computation of distance and direction vectors using multiple landmarks.

In addition to the investigation of spatial coding, a number of studies have indicated that many animals have a capacious spatial memory, both in terms of the number of locations that can be stored and in terms of the length of time over which locations in space can be remembered. Clark's nutcrackers bury as many as 33,000 seeds in the fall and recover them throughout the winter. Observations of the locations where they dig in the snow suggest that they are searching at or near buried caches (Tomback, 1980). Black-capped chickadees accurately recover seeds cached in trees in a laboratory at retention intervals as long as 28 days (Hitchcock & Sherry, 1990). Rats tested on radial mazes accurately keep track of locations visited on a 17-arm maze (Olton, Collison, & Werz, 1977) and on a hierarchical maze that involved 32 different locations (Roberts, 1979). Beatty and Shavalia (1980) allowed rats to visit a random subset of four out of eight arms on a radial maze for food reward and then brought the rats back to the maze for testing after a retention interval. Rats entered only the previously unvisited (baited arms) with over 90% accuracy after a 4-hr retention interval and were still above chance accuracy when tested 24 hr later.

Nonhuman primates also have revealed an ability to keep track of a number of different spatial locations visited. In an early study, Tinklepaugh (1932) found that chimpanzees could remember which of two cups placed in different locations contained food when pairs of cups were placed in 16 different rooms and the retention interval was 24 hr. Menzel (1973) reported that chimpanzees shown the location of 18 different food items in an open field accurately retrieved all of the food items and did so by traveling a least distance path between food locations. In a task somewhat analogous to the radial maze, MacDonald and her colleagues had animals search for food in eight different containers placed at different positions in an enclosure. An ability to visit all of the food locations with a very low incidence of revisits was found in yellow-nosed monkeys (MacDonald & Wilkie, 1990), an Old-World species, in marmoset monkeys (MacDonald, Pang, & Gibeault, 1994), a New-World species, and in two species of apes, gorillas (MacDonald, 1994), and orangutans (MacDonald & Agnes, 1999). In further experiments, these primates visited the containers and found that only four of them (randomly chosen) contained food. On a subsequent retention test, they returned to the enclosure and could visit any of the containers, but only the previously baited four containers were rebaited (win-stay task) or only the four previously empty containers were rebaited (win-shift task). In general, all of these species were able to find the baited containers at better than chance accuracy on these tasks.

A number of studies have investigated spatial understanding and spatial navigation processes in dogs. Although earlier studies with dogs concluded that they were capable of tracking the movements of an object placed in a container (displacement device) between several boxes (invisible displacement; Gagnon & Dore, 1992, 1993, 1994), more recent findings suggest that dogs may not understand invisible displacement. Collier-Baker, Davis, and Suddendorf (2004) and Fiset and LeBlanc (2007) found that dogs tended to choose a box adjacent to the position of the displacement box. Thus, when the displacement device was left near the correct target box, dogs performed accurately, but, when it was left near an incorrect box, their performance dropped below chance accuracy.

In studies of spatial navigation in dogs, the role of both egocentric and allocentric cues has been studied in dogs' ability to find hidden rewards. Cattet and Etienne (2004) showed dogs the location of food and then led them over different paths to another location while blindfolded and wearing earphones. When released, dogs went directly to a location near the hidden food, indicating use of path integration. Studies by Fiset and his colleagues suggested that dogs use both egocentric and allocentric cues in a hierarchical fashion. When dogs can take a linear path between their spatial position and a hidden target location, they maintain a vector containing distance and direction information to the target over an interval in which a barrier is placed between them and the target (Fiset, Landry, & Ouellette, 2006). When dogs search for a hidden object that has disappeared or been visibly displaced, their preferred strategy is to use egocentric cues to find it, such as a linear path or dead reckoning. If these cues are unavailable, however, dogs use allocentric cues, such as the position of a target relative to landmarks and global cues (Fiset, Beaulieu, LeBlanc, & Dube, 2007; Fiset, Gagnon, & Beaulieu, 2000). In a further study supporting this position, Fiset (2007) trained dogs to find a buried object placed at a constant distance and direction from two landmarks near the rear wall of a testing room. On tests when the landmarks were shifted parallel, perpendicular, or diagonal to the rear wall, dogs searched at locations that were partially but not completely shifted as far as the landmarks. He concluded that dogs had encoded the target location by using both the landmarks and global cues provided by the testing room.

A number of experiments have shown that dogs attend to human cueing and perform better when cued by a person. Thus, both adult dogs and puppies use human head pointing, head turning, and gaze as cues to the hidden location of food (Agnetta, Hare, & Tomasello, 2000; Hare & Tomasello, 2005; Miklosi, Polgardi, Topal, & Csanyi, 1998; Miklosi, Pongracz, Lakatos, Topal, & Csanyi, 2005; Udell, Giglio, & Wynne, 2008). As an evolutionary account of dogs' sensitivity to human cueing, it has been pointed out that dogs have lived in close association with humans for the last 10,000 to 15,000 years and have been selectively mated by humans for domestication (Csanyi, 2000; Vila et al., 1997). Through human selection, ancestral wolves evolved into dogs that possess traits highly adapted to life among humans, including communicative, social, cooperative, and attachment behaviors (Miklosi & Topal, 2005; Miklosi, Topal, & Csanyi, 2004).

Alternative interpretations of dogs' readiness to be directed by human cueing have been offered recently. One possibility is that dogs have learned to be highly attentive to human cues because human limbs were associated with food delivery during an early critical period of development (Udell, Dorey, & Wynne, 2008;

Udell, Giglio, & Wynne, 2008; Wynne, Udell, & Lord, 2008). A recent study showed that dogs learned to approach a human cooperator who pointed to a container with food and to avoid a human deceiver who pointed to an empty container; however, dogs learned this discrimination just as well when the "cooperator" and "deceiver" were nonhuman objects (black and white boxes; Petter, Musolino, Roberts, & Cole, 2009). Reid (2009) suggested that human domestication of dogs led to a scavenger animal that is biologically prepared to quickly learn about the location of food from the behavior of other organisms.

Although considerable research has been carried out to investigate spatial displacement and navigation in dogs, little or no work has been performed to examine dogs' spatial capacity or ability to remember a number of different spatial locations. If dogs have been selected for human-like abilities, we might expect them to show a capacious spatial memory, as found in humans and in primate studies with monkeys and apes.

An alternate possibility is that dogs have paid an adaptational price for becoming so socially compatible with humans. Frank and Frank (1982) argued that domestication of dogs had actually selected against cognitive processes that may be present in the wolf. In a comparative study of 6-week-old wolves and dogs, they found that wolves outperformed dogs in a problem-solving experiment that required animals to find their way past barriers of varying length. Brauer, Kaminski, Riedel, Call, and Tomasello (2006) hypothesized that dogs should be especially skillful at employing human social cues, whereas apes should be skillful at using causal physical cues provided by objects to be discriminated. It was found that dogs readily used human pointing, which chimpanzees and bonobos did not. By contrast, apes discriminated between containers well when the containers provided differential auditory cues, but dogs did poorly based on these physical properties. In a string-pulling task, dogs failed to be able to infer the path of a baited string when strings were crossed (Osthaus, Lea, & Slater, 2005), but chimps (Kohler, 1925) and ravens (Heinrich & Bugnyar, 2005) readily solved such problems. These studies suggested the possibility that the spatial memory capacity of dogs might be reduced relative to species that did not undergo intense human domestication. Although anecdotes are frequently reported of lost dogs finding their way home over new terrain, Miklosi (2007) argued that there is no good scientific evidence for this ability in dogs and that "most lost dogs never find their homes" (p. 153).

Allometric studies of the effects of domestication on encephalization may be relevant to this issue. The contemporary dog's brain (relative to its body size) is about 30% smaller than that of a wolf (Kruska, 2005). It has often been argued that the hippocampus is a critical brain structure for spatial navigation and memory (O'Keefe & Nadel, 1978; Olton & Papas, 1979). The poodle's hippocampus is 42% smaller than that of a wolf (Kruska, 2005). The hippocampus of smaller and less domesticated lab rats has decreased only 12% in size from that of wild rats (Kruska, 2005).

The purpose of the studies reported here was to examine spatial memory ability in dogs on a radial maze. The radial maze has been used to study spatial memory in rats (Olton & Samuelson, 1976), gerbils (Wilkie & Slobin, 1983), pigeons (Roberts & Van Veldhuizen, 1985), fish (Roitblat, Tham, and Golub (1982), and other animals, but no studies of dogs have been carried out with this apparatus. A large, enclosed 8-arm radial maze was constructed

that accommodated dogs of different sizes. Dogs were given repeated trials on the maze, and a record of their arm entries was kept for analysis. The initial experiment examined dogs' working memory on the maze when all arms were baited and a dog could choose freely among all the arms. The second experiment studied dogs' working memory for arm locations when they had to remember a subset of four random arm locations initially visited. In addition, the second experiment examined whether dogs showed better retention when required to use a win-shift or a win-stay strategy to enter baited arms. The studies of working memory involved memory for recent visits to arms on the maze within a single trial, and arms visited initially changed from trial to trial. In a third study, dogs' ability to form reference memory was examined. Reference memory refers to memory for stable properties of locations that do not change over trials. In Experiment 3, different amounts of food were placed in different arm locations, and dogs' ability to learn and remember these food locations was examined. These experiments allowed us to make some direct comparisons between dogs' spatial memory and that of other species.

Experiment 1

Dogs were trained in an 8-arm radial maze under conditions similar to those used by Olton and Samuelson (1976) in their experiments with rats. All eight of the arms on the maze contained food reward, and dogs were allowed to freely enter arms until they had visited all eight arms and depleted them of food. Rats tested under these conditions show progressive improvement in their ability to enter previously unvisited arms and to avoid revisits to arms previously entered. They reach a level of performance at which they make only about 0.5 errors (revisit a previously entered arm) per trial.

Method

Animals. Five rough collies were tested. Three of the dogs were male and two were female. The dogs were all from a single kennel, ranged in age from 8 months to 12 years at the beginning of the experiment, and all had received some basic obedience training. The performance of the single younger 8-month-old dog did not differ noticeably from that of her older kennelmates.

Apparatus. A large 8-arm enclosed radial maze was constructed for testing dogs (See Figure 1). The overall diameter of the

Figure 1. A picture of the radial maze used in Experiments 1 to 3.

maze was 4.56 m, and the height of the walls was 0.76 m. The center of the maze was octagonal and measured 1.52 m in diameter. Each of the eight arms that branched off the center was 1.52 m long and 0.58 m wide. The maze was made of plywood and painted a flat gray. The center, arms, and sides of the maze were detachable and were held together with metal pins, thus allowing the maze to be transported from one location to another. Guillotine doors were also constructed that could be used to close off the entrance to any arm.

A white plastic bowl measuring 24 cm in diameter and 9.5 cm in height was attached to the end of each arm of the maze with double-sided tape. These bowls were perforated colanders that were double stacked and taped together, with extra bait placed between the colanders but unavailable to the dog. In this way, the possibility that a dog would find a baited arm using differential odor cues was controlled. When taped together, the bowls were 10.5 cm high, and dogs could not see their contents from the center of the maze. Chicken frankfurters were used as the bait for the experiment. Each frankfurter was sliced into a dozen small, circular, and consistently sized pieces.

Procedure. Each dog was tested for 24 trials on the maze. Testing was carried out in two sessions, each lasting for 12 trials. These sessions were spaced 1 month apart. Because testing was performed outside in the winter, some snow could accumulate in the maze. The snow was brushed out of the maze between trials.

On each session, the dogs were tested in rotation, so that trials for any given dog were spaced about 20 min apart. Before each trial, the experimenter placed one piece of frankfurter reward in each bowl at the end of each arm. The dog being tested then was lifted by hand by the experimenter and placed in the center of the maze. To not bias a dog in favor of any particular arm or direction, dogs were randomly placed in the maze from different sides and facing in different directions from one trial to the next. A dog was allowed to visit arms on the maze until it had entered all eight arms and collected all of the rewards available. It was then lifted out of the maze by the experimenter and returned to its crate until its next trial. The experiment was conducted outdoors, in a quiet enclosed field at the kennel where the dogs resided. None of the dogs had been on the radial maze prior to this experiment. Although the dogs were kept on a standard diet, they were not fed on the test days prior to being tested on the maze. Each trial was videotaped from a balcony above the maze, and tapes were analyzed for measures of each dog's performance.

Results and Discussion

Dogs learned to deplete the maze of food with increasing efficiency over trials. In Figure 2, the mean number of arm choices that dogs needed to make to enter all eight arms is plotted over blocks of three trials for Sessions 1 and 2. Performance generally improved over blocks in Session 1, with an unexplained rise is arm entries on Block 4. In Session 2, dogs' mean arm entries stayed around 9.0, one arm entry above a perfect score of 8.0. A two-way analysis of variance (ANOVA) was performed on mean choices, with two sessions and four blocks of trials within sessions as the factors. Dogs showed significant improvement in performance from Session 1 to Session 2, $F(1, 4) = 42.18$, $p < .01$, $\eta^2 = .32$, but nonsignificant effects were found for block, $F(3, 12) = 3.32$,
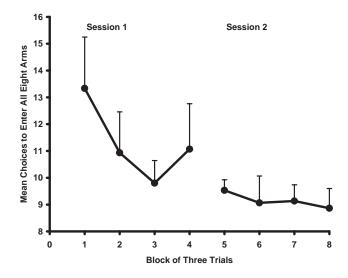
Figure 2. Mean choices required to enter all eight maze arms plotted as a function of blocks of three trials for Sessions 1 and 2 in Experiment 1. Error bars are 95% confidence intervals.

$p > .05$, $\eta^2 = .15$, and the Session $\times$ Block interaction, $F(3, 12) = 2.03$, $p > .05$, $\eta^2 = .09$.

To examine dogs' performance within trials, the proportions of correct choices are plotted as a function of Choices 1 to 8 in Figure 3, with separate curves for Trials 1 to 12 and 13 to 24. These curves are corrected for chance. Because the number of correct (unvisited) arms on the maze decreases over successive choices, the probability of choosing a correct arm by chance declines with each choice. To correct for this decline in chance accuracy, the difference between the chance level of performance (C) calculated for each choice and the observed level of performance (O) was divided by the difference between the chance level and a perfect score of 1.0 for each dog (Corrected Score $= (O - C)/(1 - C)$). Thus, chance performance in Figure 3 is a score of zero at each choice.

The curves for both trial blocks decline over choices, but the curve for Trials 13 to 24 is higher than the curve for Trials 1 to 12. The corrected proportions of correct choices were examined statistically in a 2×8 ANOVA, with eight choices as one factor and two blocks of trials as the other. The analysis revealed significant effects of choice, $F(7, 28) = 18.99$, $p < .01$, $\eta^2 = .58$, but nonsignificant effects of block of trials, $F(1, 4) = 7.40$, $p > .05$, $\eta^2 = .06$, and Choice $\times$ Block of Trials, $F(7, 28) = .92$, $p > .05$, $\eta^2 = .06$.

In general the findings shown in Figures 2 and 3 are similar to those found with rats in the Olton and Samuelson (1976) study with rats. Dogs showed improved ability to find the rewarded arms without revisiting arms as trials progressed. Within trials, accuracy dropped over successive choices, although performance at each choice was corrected for chance. This drop in accuracy can be accounted for by retroactive interference. As successive choices are made on a trial, a dog must remember more and more arms previously visited to avoid revisiting arms already depleted of food. This increase in memory load over choices may interfere with the dog's memory for earlier arms visited, thus causing it to more often revisit early arms entered on the later choices. Support for this interpretation is shown in Figure 4. Total errors made by all dogs on Choice 8 were examined to see which arms among the dogs' previous choices were reentered. Overall, dogs made 58 errors at Choice 8 throughout the 24 trials. Figure 4 shows the proportion of errors that were reentries into the arm chosen first through the arm chosen seventh. It can be seen that most errors were returns to the arm chosen first, followed by revisits to the arms chosen on Choices 2 to 4. Dogs rarely revisited the arms chosen on Choices 5 and 6 and never revisited the arm just previously chosen on Choice 7. The curve suggests that memory for the earliest arm visits declined as further arms were chosen.

Experiment 2

A concern may be raised with the procedure used in Experiment 1 to assess dogs' spatial memory. Dogs could have been using a
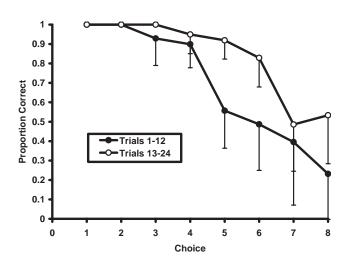

Figure 3. Proportions of correct choices made by dogs on Choices 1 to 8 for Trials 1 to 12 and 13 to 24 in Experiment 1. Error bars are 95% confidence intervals.
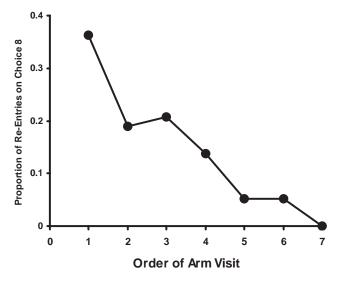

Figure 4. Proportions of errors made on Choice 8 that were revisits to arms entered on Choices 1 to 7 in Experiment 1.

response strategy on the maze that enhanced their performance. The most obvious strategy that might be used is to enter immediately adjacent alleys in a clockwise or counterclockwise direction until all eight arms have been visited. Although this strategy was not seen in the dogs tested in Experiment 1, other possible response patterns might have been used that reduced a dog's dependence on memory.

A better test of spatial working memory that has been employed with rats is to force an animal to choose a randomly determined set of four arms on the maze, after which it is returned to the maze for a test of its memory for the arms previously entered (Beatty & Shavalia, 1980; Zoladek & Roberts, 1978). Response patterns cannot play a role here because the arms initially visited vary from trial to trial and are chosen by the experimenter and not the animal.

In Experiment 2, new dogs were tested on the 8-arm radial maze using a procedure in which a dog could visit only four randomly chosen arms on Phase 1 of a trial. About 5 min later, the dog was returned to the maze for Phase 2 of the trial in which all eight of the arms were open. Two groups of dogs were tested, and each group could obtain food in Phase 2 by following one of two strategies. For one group, a win-shift strategy of going to the arms not entered in Phase 1 led the dog to the arms containing food. For the other group, dogs needed to pursue a win-stay strategy of going to the same arms visited in Phase 1 to obtain food.

Groups of rats trained with a win-shift strategy perform much better than those trained with a win-stay strategy (Haig, Rawlins, Olton, Mead, & Taylor, 1983; Olton & Schlosberg, 1978), and similar findings have been reported with pigs (Laughlin & Mendl, 2000) and echidnas (Burke, Cieplucha, Cass, Russell, & Fry, 2002). The superiority of the win-shift strategy may arise from an evolved foraging predisposition to avoid return to patches that have been recently depleted and to explore new patches. However, recent studies of nectar-feeding birds indicated that the tendency to shift is context specific. Regent honey eaters shifted after a short 10-min retention interval but stayed after a long 3-hr retention interval (Burke & Fulham, 2003). Noisy miners shifted after visiting locations with nectar but not after visiting locations with invertebrate prey (Sulikowski & Burke, 2007). If dogs have become highly dependent on humans for food, and are usually fed at the same place, it is possible that they might not show superior performance when required to perform a win-shift task. Perhaps they might actually show better spatial memory when required to perform a win-stay task.

Method

Animals. Sixteen dogs of several different breeds were used in this experiment. These included one standard poodle, one smooth fox terrier, three Labrador retrievers, one Labrador retriever cross, three rough collies, one bichon frise, one Australian shepherd, one cairn terrier, one border collie cross, one poodle/miniature schnauzer cross, and two large mixed-breed dogs. The dogs varied in age from 3 years to approximately 10 years. Seven of the dogs were male, and nine of the dogs were female. The dogs' owners had responded to an article in a local newspaper and had volunteered their dogs for the study. All the dogs were house pets and had received some obedience training.

Apparatus. The same 8-arm radial maze used in Experiment 1 was used in Experiment 2. Guillotine doors were used to block access to four of the arms in Phase 1 of each trial.

Procedure. Sixteen dogs were assigned to two groups of eight dogs each, a win-shift group and a win-stay group. The assignment was semirandom, with dogs of the same breed and size balanced across groups as far as possible. Each dog received 24 trials of training, which were divided into four daily sessions, each containing six trials. There was approximately a one week interval between successive daily sessions. Dog owners were asked not to feed their dogs before testing on the day of a session, and dogs readily ate all of the rewards placed on the maze. Data collection took place in an indoor dog training facility that measured 6.1 × 10.6 m. Ample extramaze cues were provided by windows, doors, and furniture in the facility.

Each trial consisted of two phases. In Phase 1, four randomly selected arms on the maze were blocked at their entrances by guillotine doors. The other four arms of the maze were open and baited with one piece of chicken frankfurter. A different set of four randomly chosen arms was open on each trial. Phase 1 began when a dog was placed in the center of the maze and was completed when the dog had entered all four open arms and consumed the rewards. The dog was removed from the maze while the experimenter baited the appropriate arms for Phase 2 and removed the guillotine doors so that all eight arms were open. If a dog was in the win-shift group, food was placed in the bowls at the ends of the arms not visited in Phase 1. If a dog was in the win-stay group, food was placed in the bowls at the ends of the arms that had been visited in Phase 1. Phase 2 began after an interval of approximately 5 min. The dog was placed in the center of the maze and allowed to enter arms freely until it had entered the four arms that contained reward. The dog's choices were videotaped from an elevated tripod and later used to evaluate its performance.

Results and Discussion

As a measure of maze completion performance, the number of arm entries required to enter the four-correct (baited) arms in Phase 2 was counted on each trial for each dog. The mean arm entries to complete Phase 2 are plotted over blocks of three trials for the win-shift and win-stay groups in Figure 5. It is clear from these data that dogs in the win-shift group entered the four-baited arms sooner that dogs in the win-stay group. As was the case in rat experiments on the radial maze (Olton & Schlosberg, 1978), dogs showed a preference for shifting over staying that was present on the initial block of trials and persisted over all eight blocks. A block of Trials × Group (win-shift vs. win-stay) ANOVA showed a significant effect of group, $F(1, 14) = 24.04$, $p < .01$, $\eta^2 = .26$, but not of block of trials, $F(7, 98) = .64$, $p > .05$, $\eta^2 = .02$, or of the Block of Trials × Group interaction, $F(7, 98) = .70$, $p > .05$, $\eta^2 = .03$. Overall, dogs in the win-shift group took 6.85 ($SD = .77$) mean arms entered to find all four-food arms, and dogs in the win-stay group took 10.23 ($SD = 1.03$) mean arms entered.

As a measure of accuracy during the early arm visits, we counted the number of correct arms entered during the first four arm visits in Phase 2. The mean number of correct choices is plotted over trial blocks in Figure 6. The win-shift group made more mean correct choices than the win-stay group at every block. A Block of Trials × Group ANOVA yielded a significant effect of
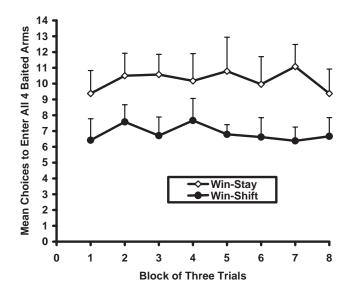
Figure 5. The mean number of choices required by dogs in win-shift and win-stay groups to enter all four-baited arms in Phase 2 of Experiment 2. Error bars are 95% confidence intervals.

group, $F(1, 14) = 18.80$, $p < .01$, $\eta^2 = .17$, but nonsignificant effects of block of trials, $F(7, 98) = 1.17$, $\eta^2 = .05$, and Block of Trials $\times$ Group, $F(7, 98) = 1.05$, $p > .05$, $\eta^2 = .04$. Figure 6 shows that a perfect retention score was 4.0. Both groups were far below a perfect score. The overall mean correct choices made were 2.18 ($SD = .14$) in the win-shift group and 1.74 ($SD = .22$) in the win-stay group. The chance line shows the expected number of correct responses based on random selection of arms. A chance value of 1.65 was used based on the assumption that each arm was chosen randomly with replacement of chosen arms. This value is calculated by summing the probabilities of a correct choice on each of four successive trials. On the first choice, the probability of entering a correct arm is $4/8 = 0.5$. On the second choice, the probability of entering a correct choice is $(4 - 0.5)/8 = 0.44$, and so on. The high numbers of choices required to enter the four-correct arms shown in Figure 5 suggest that the sampling with replacement assumption is justified. When the mean number of correct responses was tested against chance, the win-shift group was significantly above chance, $t(7) = 8.89$, $p < .01$, but the win-stay group was not, $t(7) = 1.41$, $p > .05$.

Several things are striking about these findings. First, dogs, like rats and other animals tested on the radial maze, show better retention of arms entered when required to use a win-shift strategy than when required to use a win-stay strategy. It appears that dogs have a preference for visiting new locations. Given this preference, however, it is surprising that dogs performed only somewhat better than chance when using the win-shift strategy and were far short of entering all of the baited arms on the first four visits in Phase 2. Finally, it is also striking that dogs showed no significant improvement in performance over 24 trials of training. Rats and other animals generally show increasing proficiency on this task. The dogs' tendency to enter only a little over two baited arms in the first four choices remained constant from the early trials to the late trials.

Experiment 3

Experiments 1 and 2 explored dogs' ability to perform working memory tasks on the radial maze. These tasks involved memory for arms that changed from trial to trial, either from variation in a dog's choices in Experiment 1 or from forced entrances into randomly chosen arms in Experiment 2. In Experiment 3, we examined dogs' ability to form reference memory on the radial maze. The reference memory task requires the dog to learn permanent properties about the maze and to use them to its advantage. Four arms on the 8-arm radial maze were closed to form a cross maze that was used throughout the experiment. Four different quantities of food were placed in each arm, with the same quantities always placed in the same arms over repeated trials. The arms were baited with zero, one, three, and six pieces of food. When rats have been trained on a reference memory task of this sort, they learn to visit the arms in descending order of food quantity, thus going to the arms with the most food before those with less food (Hulse & O'Leary, 1982; Olthof, Sutton, Slumskie, D'Adetta, & Roberts, 1999; Roberts, 1992). Such behavior suggests that rats are following an optimal foraging strategy for the acquisition of food (Roberts, 1992). Experiment 3 was performed to see if dogs would learn to perform in a similar manner.

Method

Animals. Fourteen dogs of various breeds were tested. These included two German shepherds, two Chihuahuas, two Australian cattle dogs, one rough collie, one bull terrier, one beagle, one Shetland sheepdog, and four dogs of mixed breed. Ten of the dogs were male, and four were female. The dogs ranged from 6 months to 10 years of age. The performance of the younger 6-month-old dog did not differ noticeably from that of the other 13 dogs. They were recruited from an obedience school and had experienced different levels of obedience training.

Apparatus. The same radial maze used in Experiments 1 and 2 was used in Experiment 3. The entrances to alternate arms on the
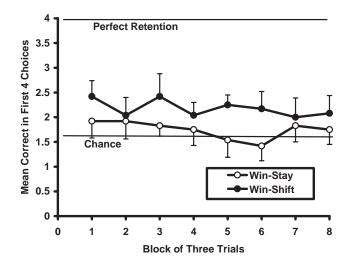

Figure 6. The mean correct (baited) arm entrances in the first four choices made by dogs in the win-shift and win-stay groups in Phase 2 of Experiment 2. Error bars are 95% confidence intervals.

maze were closed with guillotine doors to form a 4-arm cross maze that was used throughout the experiment. Pieces of chicken frankfurter were used as the reward placed in the arms of the maze. The experiment took place at a dog training facility, in a room that measured 7.3 × 12.2 m.

Procedure. Dogs were trained for 10 trials, with five trials on each of 2 days that were spaced 2 days apart. For each dog, zero, one, three, and six pieces of frankfurter were placed in different arms of the maze, and the amounts placed in different arms stayed constant over the 10 trials. The dogs were divided into three subgroups of five, five, and four subjects. The assignments of amounts of food to different arms of the maze varied between these groups to control for any possible preferences for or aversions to particular arms or locations in the test room.

A dog was placed into the center of the maze to start a trial, with the orientation of the dog varying from trial to trial. The dog was allowed to visit all four arms on the maze and to consume all of the rewards available. It was then removed from the maze and returned to its owner for an intertrial interval that lasted about 20 min within a daily session. The dogs' movements through the maze were videotaped, and the tapes were later analyzed for the orders in which arms were visited.

Results and Discussion

The orders in which a dog entered the arms containing different quantities of food were recorded in order from Choice 1 to the final choice required to enter all arms and consume their contents. The rank of entry into each arm containing a different amount was determined, and the mean rank was calculated for each amount for each dog over Trials 1 to 5 and 6 to 10. The mean rank of entry into arms containing zero, one, three, and six pieces of food is plotted for all 14 dogs in Figure 7. These findings show that mean rank of entry declined as the amount of food increased and that this
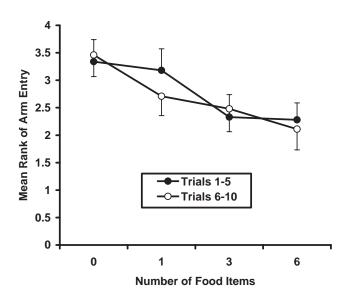

Figure 7. Mean rank of arm entry plotted as a function of number of food items on each arm in Experiment 3. Error bars are 95% confidence intervals.

relationship was somewhat more marked on Trials 6 to 10 than on Trials 1 to 5.

A Number of Food Items (4) × Block of Trials (2) × Subgroups (3) ANOVA was performed on mean rank of entry data. It revealed a significant effect of number of food items, $F(3, 91) = 10.62$, $p < .01$, $\eta^2 = .30$, but nonsignificant effects of subgroup, $F(2, 11) = .26$, $p > .05$, $\eta^2 = .006$, and block of trials, $F(1, 91) = 1.62$, $p > .05$, $\eta^2 = .003$. None of the interactions was significant. Pairwise comparisons were performed using t tests to examine significant differences between quantities, with the Bonferroni correction applied to reduce alpha from .05 to .008. The arm with zero food items was entered significantly later than the arms with three and six items, and the arm with one food item was entered significantly later than the arm with six items.

These findings clearly indicate that dogs learned or formed reference memory for the locations of different quantities of food. Like rats tested on this type of task, they tended to visit locations with large quantities before those with small quantities or no food.

General Discussion

Three experiments were performed to study spatial memory capacity in dogs on the radial maze. The first two experiments examined working memory, in which dogs had to remember locations previously visited on the maze and the locations changed from trial to trial. Thus, on each trial, a dog had to keep track of the places most recently visited. When allowed to choose freely among all eight arms in Experiment 1, dogs showed clear improvement over trials in their ability to visit all eight arms without revisiting arms. By the final trials of testing, they were entering all eight arms in an average of about nine arms visited. Declines in retention were found primarily on Choices 6 to 8 and appeared to arise from retroactive interference caused by increasing memory load. Because performance in Experiment 1 could have been enhanced by dogs executing preferred response patterns or routes through the maze, this factor was controlled in Experiment 2 by forcing dogs to visit four randomly chosen arms for food in Phase 1 of a trial and then bringing them back to the maze after a short retention interval to test their memory in Phase 2 with all eight arms open. The rule for finding food in Phase 2 differed between two groups. Dogs in the win-shift group had to go to the arms they had not visited in Phase 1, and dogs in the win-stay group had to return to the arms they had visited in Phase 1. Dogs in the win-shift group performed far better than dogs in the win-stay group and showed retention scores that were significantly above chance. Experiment 3 tested reference memory in dogs by placing different amounts of food on the same arms of a 4-arm cross maze over 10 trials. Dogs readily learned to visit the arms with larger amounts before the arms with smaller amounts. This experiment is important because it showed that dogs formed a representation of the maze and its contents and took advantage of this representation to forage in an optimal manner by taking the larger caches of food before the smaller ones.

The spatial memory effects shown in these experiments with dogs match up nicely with many of the effects found with rats. Rats improve over trials of free choice among all eight arms, as the dogs did in Experiment 1, and rats also show retroactive interference that leads to lower performance on later choices than on earlier choices (Olton & Samuelson, 1976). Like the win-shift and

win-stay groups of dogs tested in Experiment 2, rats show far better memory for previous arms visited when required to shift than when required to stay on a retention test (Haig et al., 1983; Olton & Schlosberg, 1978). Finally, dogs learned the locations of arms on the maze in which different quantities of food were placed in Experiment 3 and visited locations of larger quantities before locations of smaller quantities, just as rats do (Hulse & O'Leary, 1982; Olthof et al., 1999; Roberts, 1992).

Given these similarities in the patterns of effects obtained, the most surprising aspect of these results is that dogs' spatial memory capacity was low compared to other species that have been tested. Over the first 10 trials of testing in Experiment 1, an examination of the first eight choices showed that the five dogs made 83% mean correct choices. In a rat experiment on an 8-arm radial maze (Olton & Samuelson, 1976, Experiment 4), 12 rats made 90.21% mean correct choices in the first 10 trials. Because Olton and Samuelson (1976) reported data for individual rats (Appendix Table A2), it is possible to test the difference between the dog and rat mean percentages correct. Rat performance was significantly higher than dog performance, $t(15) = 2.74$, $p < .05$, $d = 1.66$. Although nonhuman primates have not been tested on a radial maze, tests with eight distributed containers baited with food indicated low levels of revisits (errors) to locations in which food had already been found. No errors were reported over five trials of testing in two yellow-nosed monkeys (MacDonald & Wilkie, 1990) and a gorilla (MacDonald, 1994). Four marmoset monkeys made 85% mean correct choices in the first eight visits over 10 to 14 trials (MacDonald et al., 1994), and three orangutans made 93.9% correct choices in the first eight visits over five to 10 trials (MacDonald & Agnes, 1999).

The differences are even more marked when dogs' performance in Experiment 2 is compared with that of rats. In Experiment 2, dogs were forced to visit four randomly chosen arms in Phase 1 of a trial and then chose freely among all eight arms in Phase 2, with food in the previously baited arms for the win-stay group and food in the previously nonbaited arms for the win-shift group. Dogs in the win-stay group chose a correct (baited) arm on only 43.5% of their first four choices, and dogs in the win-shift group chose a correct arm on only 54.5% of their first four choices. Furthermore, the dogs showed no improvement in accuracy over 24 trials of testing. By contrast, rats tested on a win-shift task achieved about 95% accuracy (Beatty & Shavalia, 1980). Data from MacDonald et al.'s (1994) study of marmoset monkeys showed that one monkey tested on a win-stay task made 73% correct choices in the first four visits on 12 trials. In a win-shift task, the performance of two monkeys was close to that of dogs, with 53.8% visits to correct locations in the first four visits on 14 trials.

One interpretation of these results is that through intense selective domestication that led to downsizing of the brain and particularly the hippocampus (Kruska, 2005), dogs may have lost spatial memory abilities that might be found in wolves (Frank & Frank, 1982). A test of this hypothesis would require testing wolves on comparable spatial memory tasks. Further testing of dogs' spatial memory ability will be necessary before any firm conclusions can be reached. It may be that dogs were tested under conditions that were not favorable to a demonstration of their true spatial memory ability (Bitterman, 1960). For example, dogs were not deprived of food before testing, as rats are in most radial maze experiments. On the other hand, dogs did consume the rewards avidly on the maze, and the nonhuman primate tests discussed did not use food deprivation. Another possibility is that dogs would perform better on a modified radial maze. It has been shown that rats' radial maze performance is higher when long arms are used than when short arms are used (Brown, 1990; Brown & Huggins, 1993). Longer arms spread the spatial locations of food farther apart and force animals to do more work (travel farther) to obtain food. Dogs might show higher spatial memory performance in a maze with arms extended in length.

Still another factor to be considered is the height of the dog relative to the maze walls. It may be that many dogs could not see over the walls, and that this factor restricted access to extramaze cues. The rough collies tested in Experiment 1 stood approximately 61 to 66 cm at the withers and the walls of the maze were 76 cm high. A particularly tall collie may have been able to see over the walls, but no differences in performance according to height were noticed. In Experiments 2 and 3, a variety of breeds were used, with some that were clearly shorter than the walls of the maze and others that were clearly taller than the walls. It was not found that the shorter dogs performed worse than the taller dogs. In the future, however, dogs might be tested on mazes with short walls that all dogs could see over.

Dogs are often described as scavengers. Whereas wolves are hunters, it is hypothesized that dogs survived over the centuries by scouring human dumpsites for discarded food (Coppinger & Coppinger, 2001). It is possible that the enclosed nature of a radial maze is not well suited to dogs, and they might do better if tested in a nonmaze task. A task in which food is hidden in different locations in an open field or arena, as used in MacDonald's primate studies (MacDonald, 1994; MacDonald & Agnes, 1999), might yield higher levels of dog performance.

In conclusion, this article presents an initial set of studies of dog spatial memory based on their behavior in a radial maze. The findings are interesting for two reasons. First, they indicate that similar spatial memory processes are at work in dogs and other species. In working memory studies (Experiments 1 and 2), dogs, like rats, showed progressive loss of memory from retroactive interference as successive choices were made, and performed better when required to use a win-shift strategy than when required to use a win-stay strategy. In a reference memory study (Experiment 3), dogs again behaved like rats by visiting arms with the largest quantities of food before those with less food or no food. Second, they raise questions about the spatial memory capacity of dogs compared to other species that need to be addressed by further experiments that vary the dogs' motivation and the type of spatial memory test. Further research may confirm the finding of limited spatial memory capacity in dogs or may reveal that it is comparable to that of other species when tested under more favorable conditions.

References

Agnetta, B., Hare, B., & Tomasello, M. (2000). Cues to food location that domestic dogs (*Canis familiaris*) of different ages do and do not use. *Animal Cognition, 3,* 107–112.

Beatty, W. W., & Shavalia, D. A. (1980). Spatial memory in rats: Time course of working memory and effect of anesthetics. *Behavioral and Neural Biology, 28,* 454–462.

Bitterman, M. E. (1960). Toward a comparative psychology of learning. *American Psychologist, 15,* 704–712.

Brauer, J., Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2006). Making inferences about the location of hidden food: Social dog, causal ape. *Journal of Comparative Psychology, 120,* 38–47.

Brown, M. F. (1990). The effects of maze-arm length on performance in the radial-arm maze. *Animal Learning & Behavior, 18,* 13–22.

Brown, M. F., & Huggins, C. K. (1993). Maze-arm length affects a choice criterion in the radial-arm maze. *Animal Learning & Behavior, 21,* 68–72.

Burke, D., Cieplucha, C., Cass, J., Russell, F., & Fry, G. (2002). Win-shift and win-stay learning in the short-beaked echidna (*Tachyglossus aculeatus*). *Animal Cognition, 5,* 79–84.

Burke, D., & Fulham, B. J. (2003). An evolved spatial memory bias in a nectar-feeding bird? *Animal Behaviour, 66,* 695–701.

Cattet, J., & Etienne, A. S. (2004). Blindfolded dogs relocate a target through path integration. *Animal Behaviour, 68,* 203–212.

Collier-Baker, E., Davis, J. M., & Suddendorf, T. (2004). Do dogs (*Canis familiaris*) understand invisible displacement? *Journal of Comparative Psychology, 118,* 421–433.

Coppinger, R., & Coppinger, L. (2001). *Dogs: A startling new understanding of canine Origin, behavior, and evolution.* New York, NY: Scribner.

Csanyi, V. (2000). *If dogs could talk: Explaining the canine mind.* New York, NY: North Point Press.

Fiset, S. (2007). Landmark-based search memory in the domestic dog (*Canis familiaris*). *Journal of Comparative Psychology, 121,* 345–353.

Fiset, S., Beaulieu, C., LeBlanc, V., & Dube, L. (2007). Spatial memory of domestic dogs (*Canis familiaris*) for hidden objects in a detour task. *Journal of Experimental Psychology: Animal Behavior Processes, 33,* 497–508.

Fiset, S., Gagnon, S., & Beaulieu, C. (2000). Spatial encoding of hidden objects in dogs (*Canis familiaris*). *Journal of Comparative Psychology, 114,* 315–324.

Fiset, S., Landry, F., & Ouellette, M. (2006). Egocentric search for disappearing objects in domestic dogs: Evidence for a geometric hypothesis of direction. *Animal Cognition, 9,* 1–12.

Fiset, S., & LeBlanc, V. (2007). Invisible displacement understanding in domestic dogs (*Canis familiaris*): The role of visual cues in search behavior. *Animal Cognition, 10,* 211–224.

Frank, H., & Frank, M. G. (1982). Comparison of problem-solving performance in six-week old wolves and dogs. *Animal Behaviour, 30,* 95–98.

Gagnon, S., & Dore, F. Y. (1992). Search behavior in various breeds of adult dogs (*Canis familiaris*): Object permanence and olfactory cues. *Journal of Comparative Psychology, 106,* 58–68.

Gagnon, S., & Dore, F. Y. (1993). Search behavior of dogs (*Canis familiaris*) in invisible displacement problems. *Animal Learning & Behavior, 21,* 246–254.

Gagnon, S., & Dore, F. Y. (1994). Cross-sectional study of object permanence in domestic puppies (*Canis familiaris*). *Journal of Comparative Psychology, 108,* 220–232.

Haig, K. A., Rawlins, J. N. P., Olton, D. S., Mead, A., & Taylor, B. (1983). Food searching strategies of rats: Variables affecting the relative strength of stay and shift strategies. *Journal of Experimental Psychology: Animal Behavior Processes, 9,* 337–348.

Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Science, 9,* 439–444.

Healy, S. (1998). *Spatial representation in animals.* Oxford, England: Oxford University Press.

Heinrich, B., & Bugnyar, T. (2005). Testing problem solving in ravens: String-pulling to reach food. *Ethology, 111,* 962–976.

Hitchcock, C. L., & Sherry, D. F. (1990). Long-term memory for cache sites in the black-capped chickadee. *Animal Behaviour, 40,* 701–712.

Hulse, S. H., & O'Leary, D. K. (1982). Serial pattern learning: Teaching an alphabet to rats. *Journal of Experimental Psychology: Animal Behavior Processes, 8,* 260–273.

Kohler, W. (1925). *The mentality of apes.* London, England: Routledge and Kegan Paul.

Kruska, D. C. T. (2005). On the evolutionary significance of encephalization in some eutherian mammals: Effects of adaptive radiation, domestication, and feralization. *Brain, Behavior and Evolution, 65,* 73–108.

Laughlin, K., & Mendl, M. (2000). Pigs shift too: Foraging strategies and spatial memory in the domestic pig. *Animal Behaviour, 60,* 403–410.

MacDonald, S. E. (1994). Gorillas' (*Gorilla gorilla gorilla*) spatial memory in a foraging task. *Journal of Comparative Psychology, 108,* 107–113.

MacDonald, S. E., & Agnes, M. M. (1999). Orangutan (*Pongo pygmaeus abelii*) spatial memory and behavior in a foraging task. *Journal of Comparative Psychology, 113,* 213–217.

MacDonald, S. E., Pang, J. C., & Gibeault, S. (1994). Marmoset (*Callithrix jacchus jacchus*) spatial memory in a foraging task: Win-stay versus win-shift strategies. *Journal of Comparative Psychology, 108,* 328–334.

MacDonald, S. E., & Wilkie, D. M. (1990). Yellow-nosed monkeys' (*Cercopithecus ascanius whitesidei*) spatial memory in a simulated foraging environment. *Journal of Comparative Psychology, 104,* 382–387.

Menzel, E. W. (1973). Chimpanzee spatial memory organization. *Science, 182,* 943–945.

Miklosi, A. (2007). *Dog behaviour, evolution, and cognition.* Oxford, England: Oxford University Press.

Miklosi, A., Polgardi, R., Topal, J., & Csanyi, V. (1998). Use of experimenter-given cues in dogs. *Animal Cognition, 1,* 113–122.

Miklosi, A., Pongracz, P., Lakatos, G., Topal, J., & Csanyi, V. (2005). A comparative study of the use of visual communicative signals in interactions between dogs (*Canis familiaris*) and humans and cats (*Felis catus*) and humans. *Journal of Comparative Psychology, 119,* 179–186.

Miklosi, A., & Topal, J. (2005). Is there a simple recipe for how to make friends? *Trends in Cognitive Science, 9,* 463–464.

Miklosi, A., Topal, J., & Csanyi, V. (2004). Comparative social cognition: What can dogs teach us? *Animal Behaviour, 67,* 995–1004.

O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map.* Oxford, England: Oxford University Press.

Olthof, A., Sutton, J. E., Slumskie, S. V., D'Adetta, J., & Roberts, W. A. (1999). In search of the cognitive map: Can rats learn an abstract pattern of rewarded arms on the radial maze? *Journal of Experimental Psychology: Animal Behavior Processes, 25,* 352–362.

Olton, D. S., Collison, C., & Werz, M. A. (1977). Spatial memory and radial arm maze performance of rats. *Learning and Motivation, 8,* 289–314.

Olton, D. S., & Papas, B. C. (1979). Spatial memory and hippocampal function. *Neuropsychologia, 17,* 669–682.

Olton, D. S., & Samuelson, R. J. (1976). Remembrance of places passed: Spatial memory in rats. *Journal of Experimental Psychology: Animal Behavior Processes, 2,* 97–116.

Olton, D. S., & Schlosberg, P. (1978). Food-searching strategies in young rats: Win-shift predominates over win-stay. *Journal of Comparative and Physiological Psychology, 92,* 609–618.

Osthaus, B., Lea, S. E. G., & Slater, A. M. (2005). Dogs (*Canis lupus familiaris*) fail to show understanding of means-end connections in a string-pulling task. *Animal Cognition, 8,* 37–47.

Petter, M., Musolino, E., Roberts, W. A., & Cole, M. (2009). Can dogs (*Canis familiaris*) detect human deception? *Behavioural Processes, 82,* 109–118.

Reid, P. J. (2009). Adapting to the human world: Dogs' responsiveness to our social cues. *Behavioural Processes, 80,* 325–333.

Roberts, W. A. (1979). Spatial memory in the rat on a hierarchical maze. *Learning and Motivation, 10,* 117–140.

Roberts, W. A. (1992). Foraging by rats on a radial maze: Learning, memory, and decision rules. In I. Gormezano & E. A. Wasserman (Eds.),

Learning and memory: The behavioral and biological substrates (pp. 7–23). Hillsdale, NJ: Erlbaum.

Roberts, W. A. (2001). Spatial representation and the use of spatial codes in animals. In M. Gattis (Ed.), *Spatial schemas and abstract thought* (pp. 15–44). Cambridge, MA: MIT Press.

Roberts, W. A., & Van Veldhuizen, N. (1985). Spatial memory in pigeons on the radial maze. *Journal of Experimental Psychology: Animal Behavior Processes, 11,* 241–260.

Roitblat, H. L., Tham, W., & Golub, L. (1982). Performance of *Betta splendens* in a radial maze. *Animal Learning & Behavior, 10,* 108–114.

Shettleworth, S. J. (1998). *Cognition, evolution, and behavior.* New York, NY: Oxford University Press.

Sulikowski, D., & Burke, D. (2007). Food-specific spatial memory biases in an omnivorous bird. *Biology Letters, 3,* 245–248.

Tinklepaugh, O. L. (1932). Multiple delayed reaction with chimpanzees and monkeys. *Journal of Comparative Psychology, 13,* 207–243.

Tomback, D. F. (1980). How nutcrackers find their seed stores. *Condor, 82,* 10–19.

Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2008). Wolves outperform dogs in following human social cues. *Animal Behaviour, 76,* 1767–1773.

Udell, M. A. R., Giglio, R. F., & Wynne, C. D. L. (2008). Domestic dogs (*Canis familiaris*) use human gestures but not nonhuman tokens to find hidden food. *Journal of Comparative Psychology, 122,* 84–93.

Vila, C., Savolainen, P., Maldonado, J. D., Amorin, I. R., Rice, J. E., Honeycutt, R. L., . . . Wayne, R. K. (1997). Multiple and ancient origins of the domestic dog. *Science, 276,* 1687–1689.

Wilkie, D. M., & Slobin, P. (1983). Gerbils in space: Performance on the 17-arm radial maze. *Journal of the Experimental Analysis of Behavior, 40,* 301–312.

Wynne, C. D. L., Udell, M. A. R., & Lord, K. A. (2008). Ontogeny's impacts on human-dog communication. *Animal Behaviour, 76,* e1–e4.

Zoladek, L., & Roberts, W. A. (1978). The sensory basis of spatial memory in the rat. *Animal Learning & Behavior, 6,* 77–81.