

eScholarship

International Journal of Comparative Psychology

Title

Shortcut taking by ferrets (*Mustela putorius furo*)

Permalink

<https://escholarship.org/uc/item/7fs2s98h>

Journal

International Journal of Comparative Psychology, 17(4)

ISSN

0889-3675

Authors

Perreault, M.
Plowright, C. M. S.

Publication Date

2004-12-31

DOI

10.46867/ijcp.2004.17.04.02

Copyright Information

This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed

SHORT COMMUNICATION

Shortcut taking by ferrets (*Mustela putorius furo*)

M. Perreault and C. M. S. Plowright
University of Ottawa, Canada

A 2 X 2 between-subjects design was used to test for the tendency of domestic ferrets to take novel shortcuts. The cross maze with shortcuts adapted by Poucet (1985) was used to train ferrets to search for a goal (an empty food bowl) while having the possibility of seeing the shortcuts or not during training (i.e., a screen, which was either transparent or opaque, blocked off the shortcut). In the test sessions in which the animals were given access to the shortcuts, the goal was visible for half of the subjects in each training condition and not visible for the other half. Ferrets were more likely to take the shortcut if they had seen it during training, regardless of whether they could see the goal or not during the test: Visual familiarity with the shortcut is sufficient to account for shortcut taking. When the goal was not visible and the shortcut had not been seen prior to the test, performance was no different from chance: There was no evidence for the ability to infer a shortcut. Pronounced individual differences were obtained when the shortcut was visually unfamiliar yet the goal was visible.

The domestic ferret's long scientific name is *Mustela putorius furo*. The word *furo* means thief: Ferrets routinely take household objects and move them to new places. Ferrets are also adept at navigating through tunnels. They have been used to flush rabbits from their holes ("ferreting"), though the practice is now illegal in many parts of the world. They have been used to run wire through narrow tubing in aircraft (Shefferman, 1996). The present study on ferret behaviour was designed with these two characteristics, a motivation to retrieve objects and a predilection for moving through tunnels, in view. While these characteristics make the ferret an ideal subject, questions regarding the adaptive significance or evolutionary origin of these characteristics are not addressed since *Mustela putorius furo* is a domestic animal and is not the same species as the wild North American black-footed ferret (*Mustela nigripes*). Whatever abilities they possess may have been shaped by natural selection and/or artificial selection.

Even though current contents in many journals in animal behaviour display a wealth of interest in spatial navigation in a variety of species (reviewed by Shettleworth, 1998), the literature on ferrets reveals very little in the way of their spatial abilities. The present study begins to fill this void. Ferrets have been studied for the neurophysiology of vision (Crowley & Katz, 1999) and audition (Mrsic-Flogel et al., 2002), sexual behaviour (Kelliher & Baum, 2001) and numerical competence (Davis, 1996). In a maze-learning task, ferrets can be unsuccessful because "despite prolonged periods of food deprivation, animals of this species continue to explore every blind alley on the way to the goal box" (Beach, 1950, p.

This work was supported by a research grant to C.M.S.P. from the Natural Sciences and Engineering Research Council of Canada. We thank Ms Isabel Plowright for discovering the Ferret Rescue Society of Ottawa where Ms Marion Houle kindly allowed us access to the animals and gave invaluable assistance in data collection. Dr. Sylvain Fiset gave constructive suggestions on the experimental design and Ms Dana Church provided helpful comments on the manuscript. The animals in this study were treated in accordance with the standards of the Canadian Council on Animal Care. Correspondence concerning this article may be addressed to CMS Plowright, School of Psychology, University of Ottawa, Ottawa, Ontario, Canada K1N 6N5 (cplowrit@uottawa.ca).

122). They are, however, capable of maze learning (Pollard & Lewis, 1969).

The questions addressed here are structured by the work of Bennett (1996), described below, in which the evidence on spatial representations in animals is assessed. Prior to Bennett (1996), one predominant framework for the study of spatial knowledge was the “cognitive map”. In a nutshell (for a more detailed history see Shettleworth, 1998), the operational definition for a cognitive map was the behaviour of taking a novel shortcut between two or more locations in the environment (Tolman, 1948). It was thought to reflect an allocentric, as opposed to egocentric, spatial representation of objects and their spatial relationships (Thinus-Blanc, 1988). The notion was further developed by O’Keefe and Nadel (1978) when neurophysiological correlates were discovered. More recent developments include changes in the very definition of cognitive map to be more inclusive (Gallistel, 1990) and difficulties in interpretation of the original criterion for the cognitive map (i.e., novel shortcut taking), which began to emerge in the controversy surrounding whether foraging honeybees could take novel shortcuts (Gould 1986, 2002) or not (Dyer, 1991).

The contributions of Bennett (1996) were, first, to argue that no animals had ever been shown to have a cognitive map as reflected in the ability to take a novel path and, secondly, to recommend abandoning the quest for the cognitive map in favour of more behaviourally-tied discussions of how animals way-find. Bennett reasoned that when an animal takes a novel shortcut, assuming that it is truly a novel shortcut (i.e., not taken before), it can do so for a variety of reasons: (1) It can see the goal from where it is; (2) Even if it can not see the goal, it can remember having seen the shortcut in the past; and (3) It can neither see the goal nor can it remember seeing the shortcut (especially if it has never seen it), but it can infer the shortcut. The animal might infer this shortcut from its memory of relative positions of places it has visited (the elusive “cognitive map”) or from integration of memories of its own trajectories (“path integration”; e.g., Collett & Collett, 2000). The condition for drawing this possible third conclusion (i.e. that the animal infers the shortcut) is to use a testing procedure that ensures that the animal can neither see the goal nor remember seeing the shortcut in the past. Accordingly, we used the controlled environment of the modified cross-maze (described below) and explicitly manipulated the key variables of visual familiarity with the shortcut during training and of visibility of the goal during testing.

This study was designed to address three questions : (1) Do ferrets take shortcuts if they have not been trained to do so? (2) If so, does the shortcut taking depend on visual familiarity with the shortcut and/or visibility of the goal? (3) In the absence of both visual familiarity with the shortcut and visibility of the goal, is there any evidence of shortcut taking?

Method

Subjects

A subject pool of 31 ferrets was available for this study. Seventeen were selected on the basis of their performance during shaping; the rest were comparatively distractable or unmotivated to search for food. One ferret was successfully shaped but did not complete training. The sixteen ferrets that were used, 12 males and 4 females, were aged 2 to 5.5 years. Nine ferrets lived in groups at the Ferret Rescue Society of Ottawa, Ontario, Canada. The others had spent time in the facility before, but lived elsewhere and were borrowed from their owners for this experiment. The animals were

deprived of food for one hour before each training or testing session. They were randomly assigned to four groups ($N = 4$ in each group) of a 2 X 2 between-subjects design. The groups will be referred to first by their training condition (Shortcut Visible (SV) or Not Visible (SNV)) and then by their testing condition (Goal is Visible (GV) or Not Visible (GNV)), described below, and so the 4 group names are SV/GV, SV/GNV, SNV/GV, and SNV/GNV.

Apparatus

The cross maze originated with O'Keefe and Conway (1980) but was adapted with shortcuts by Poucet (1985) and Thinus-Blanc et al. (1987) for use with cats and rats. Four central arms (70 cm long x 18 cm wide x 18 cm high) are arranged in the shape of a cross. The end of each arm is connected to the ends of the two adjacent arms by a diagonal shortcut (18 cm wide x 18 cm high X 99 cm long on the outside and 80 cm on the inside). The four shortcuts are arranged in the shape of a square (Figure 1).

The apparatus was constructed of transparent Plexiglas, but the central arms were made opaque by covering their sides with white plastic sheets fixed with strips of Velcro. A door on top of the intersection of the cross could be opened for daily cleaning of the attached arms with disinfectant soap. During training, plastic squares (20 cm x 20 cm x 0.7 cm) blocked off the entrance from each side of each central arm so that the shortcuts could not be taken. The plastic squares were either solid white, so that the shortcuts were not visible during training or transparent so that they were visible.

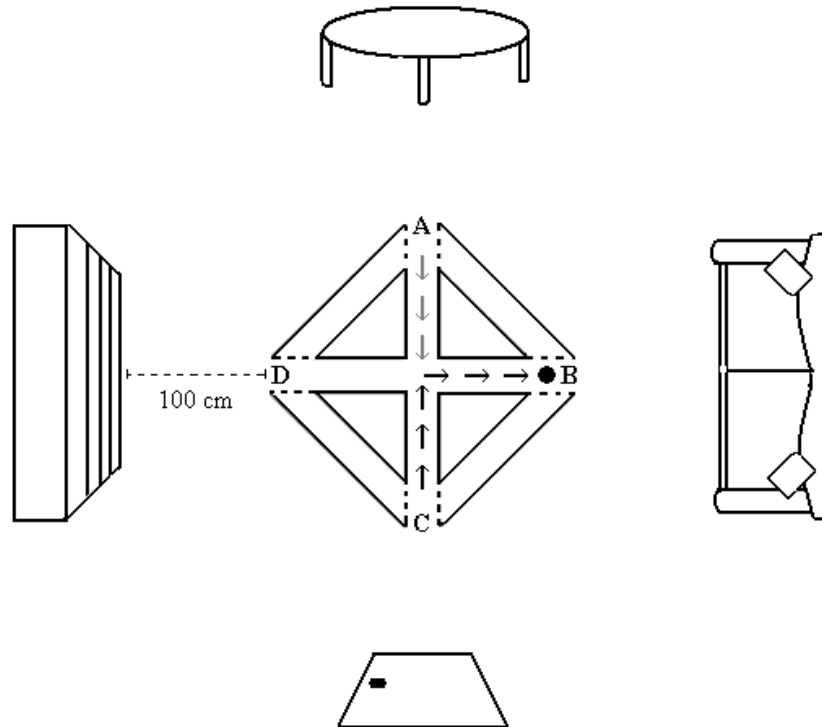


Figure 1. Top view of the cross-maze with shortcuts. During training the shortcuts are either blocked by a transparent square so that the shortcuts are not visible (dotted lines) or by an opaque square so that the shortcuts are not visible. In the test, for half of the ferrets the goal (B) is visible from the starting point (A or C) and for the other half the goal is not visible from the starting point because it is recessed into the central arm. The positioning of A, B, C and D vis-à-vis the extra-maze cues was counter-balanced across subjects. The arrows indicate the paths taken by the ferrets during training.

Procedure

The maze was placed in a room (5.6 m x 6.3 m) adjacent to the one where the ferrets of the Ferret Rescue Society of Ottawa were housed. The center of the maze was positioned under two 60 W ceiling-lights. Extra-maze spatial cues were placed 100 cm from each entrance point to define the location of the goal (B). The cues (a table, a couch, a door and a bookshelf, none of which were moved during the experiment) for each point remained constant for each subject, but were counter-balanced across subjects. The subjects were used during shaping, training and testing in the same order each day.

Shaping. Each ferret was first given about 10 min to become familiar with the four central arms of the maze (but not with the shortcuts). Then, a white plastic bowl (15 cm diameter, 10 cm high) that contained treats (8 in 1 Ferret Bites; Fruits & Crunch Ferret Treat) was placed on the floor 100 cm in front of the subject. The experimenter showed the food to the animal and then covered the bowl with a lid. When the ferret then approached and touched the bowl with its nose or paw, the experimenter took the lid off the bowl and handed the ferret a treat. In this way, the subjects became motivated to search for the bowl, which was subsequently replaced by an identical empty bowl in training and testing. Each trial began when a subject was released with verbal commands such as “go” or “find the toy” and ended when the subject touched the bowl. Shaping ended when the ferrets walked spontaneously towards the bowl for 5 consecutive trials. Usually, this criterion for success was attained in the first 10 trials. Training then began on the same day.

Training. Each ferret was taught to attain the goal at the end of one arm by taking two different L-shaped paths. They were individually released both from points A and C (Figure 1). The position of the goal (B) vis-à-vis an external cue (table, sofa etc.) was never the same for two subjects tested consecutively, so that if the goal was found, it was not because of any possible scent traces left by the previous subject. Position D was not used as a release point. The positions of release (A and C) varied randomly from trial to trial.

For each trial, Experimenter 1 (E1) held the subject in front of the releasing arm (A or C) and Experimenter 2 (E2) moved the empty bowl in front of the ferret. When the subject’s “interest” in the bowl was manifested behaviourally (by fixating the object, stretching its neck and struggling), E2 moved the bowl to position B while E1 maintained the subject for 3 s at the entry of the arm, made sure not to orient the animal’s body to one side or another, and then released the ferret with a verbal command. A choice was recorded by E2 as correct if the subject took the arm leading to the goal, and incorrect otherwise. The ferrets virtually always moved directly and completely (all four legs) into one of the arms. Dithering was almost never observed, though if the animal merely poked its nose into one of the arms, this was not counted as a choice. When the subject touched the bowl, both E1 and E2 gave some verbal praise to the animal and E2 immediately gave it a treat. After the animal had eaten the food, which took less than 30 s, a new trial began. If the subject made an incorrect choice, E1 would move to the end of this arm, catch the ferret when it arrived, and start a new trial. On occasion, after having made an incorrect choice, subjects attempted to backtrack, in which case E1 would capture the ferret, count the choice as incorrect and take the animal to begin a new trial. No food was given after an incorrect choice.

One ferret was excluded from the experiment after a failure in training; instead of attaining the goal, it returned to the point of release on four consecutive trials on two separate training sessions. For the remaining subjects, training was divided in two sessions of 11 trials each, both taking place within 24 h (after about 8 trials the ferrets apparently lost their motivation as the error rate increased slightly). Subjects had to reach the criterion of 18 correct trials out of 22 consecutive trials to proceed to testing.

Half the subjects (Shortcut Not Visible in Training, SNV) were trained to take two L-shaped paths to attain the bowl without the possibility of seeing the shortcuts. Opaque Plexiglas squares were slid in front of the entrance of every shortcut to prevent the subjects from either entering or even just seeing the shortcuts. The other half of the subjects (Shortcut Visible in Training, SV), were trained with the possibility of seeing the shortcut leading directly to the goal. Transparent squares were slid in front of the entrance of the shortcuts to block access while allowing the ferrets to see the goal.

Testing. Subjects were tested on the day following the last training day at approximately the same time of day. Ferrets were released from their two usual L-shaped paths but all barriers were

removed, giving all subjects access to the shortcuts. Prior to release, the experimenter held the ferrets for about 3 s during which time they always moved their heads around. For half of the subjects in each training group, the bowl was visible and positioned at the same spot as in training (Goal Visible at Test, GV). For the other half (Goal Not Visible at Test, GNV), the bowl was placed in a central arm not at the extremity as in Figure 1, but slightly inwards so that it was just out of view from the starting point. The test session consisted of 12 trials and subjects were released from their two usual starting points. In accordance with Poucet (1985), to maintain their motivation, subjects were given a piece of treat each time they touched the bowl with their paw and nose, as in training, whatever path they took (training path or new path). Five subjects did not complete all 12 trials and so their choice proportions are based on fewer trials (see Table 1).

Predictions. We first tested for the main effects of object visibility and visual familiarity of the shortcuts. Even if performance were enhanced by these variables, it might still be possible for an animal to infer the existence of a shortcut, which would be evidenced by above chance performance in the cell SNV/GNV (i.e., shortcut not visible in training, goal not visible in testing). Accordingly, we also tested for the deviation of choice frequencies from chance. Although three arms were available at the moment of choice, the ferrets never took the arm leading to D, and so the response could be treated as binary. Accordingly, rather than use a chance value of 33%, we used a more stringent value of 50% to test whether the frequency of shortcut taking was greater than the frequency of taking the only other way taken, which was the L-shaped long-path through the center of the maze to B.

Results

Effects of Experimental Variables

The individual frequencies with which the ferrets took the shortcut to the goal during the test are given in Table 1. Because the data are binary choice proportions (i.e., a ferret either took a shortcut or did not), a logistic model was fit to the data using GLIM version 4.0 (Francis, Green, & Payne, 1993). The ferrets were more likely to take the shortcut when they had seen it before during training (Table 1): The effect of visual familiarity with the shortcut was significant, $\chi^2(1) = 32.53$, $p < 0.00001$. It did not matter whether the goal was visible or not: the effect of goal visibility was not significant, $\chi^2(1) = 0.20$. No interaction between the two variables was detected, $\chi^2(1) = 1.88$.

Comparison with Theoretical Value of Chance

Given that there was no difference between the groups for which the goal was visible vs. not visible during testing, those groups were combined for each training condition (so each training group considered included 8 ferrets). A replicated goodness-of-fit test using the G-statistic (Sokal & Rohlf, 1981) was used to test whether the two group proportions in Table 1 (86 % vs. 50% for the Shortcut Visible vs. Not Visible, respectively) differed from chance. Each test generates both a G_p value (P for Pooled), which tests for whether the group proportion differs from a theoretical proportion (50:50 in our case), and a G_H value (H for Heterogeneity), which tests for individual differences. The G statistic is tested against a χ^2 value.

For the SV in training groups, the group proportion of 86% exceeded the chance value of 50%, $G_p(1) = 55.68$, $p < 0.00001$. No individual differences were detected, $G_H(7) = 13.19$. A different picture is evident for the SNV in training groups, where the overall proportion of 50%, did not differ from chance, $G_p(1) = 0.04$. Individual differences, however, were significant, $G_H(7) = 24.01$, $p < 0.005$, and so the total G value ($G_p + G_H$) was partitioned into individual components to

Table 1

Individual Frequencies in which Individual Ferrets Took the Shortcut During the Test for Each of Four Experimental Conditions.

In Test, goal is:										
	Visible (GV)					Not Visible (GNV)				
During Training	Ferret	Shortcuts	Trials	Proportion	First Choice	Ferret	Shortcuts	Trials	Proportions	First Choice
Shortcut is:										
Visible (SV)	1	10	12	0.83	1	5	8	10	0.80	1
	2	12	12	1.00	1	6	12	12	1.00	1
	3	12	12	1.00	1	7	9	11	0.82	1
	4	9	12	0.75	0	8	5	7	0.71	1
Mean: 0.90					Mean: 0.83					
Mean for Visible Shortcuts: 0.86										
Not Visible (SNV)	9	2	12	0.17	0	13	7	12	0.58	1
	10	10	12	0.83	1	14	6	12	0.50	1
	11	4	6	0.67	1	15	6	12	0.50	1
	12	1	12	0.08	0	16	7	10	0.70	0
Mean: 0.44					Mean: 0.57					
Mean for Not Visible Shortcuts: 0.50										

Note. The frequencies are also expressed as proportions. The first choice in the test (1 for a shortcut and 0 for the long-path) is also given.

identify individual proportions that deviated significantly from chance. None of the four ferrets in the GNV at test had choice proportions that differed significantly from chance: The null hypothesis of chance performance in the cell SNV/GNV could not be rejected for any of the animals. Only in the other group (SNV/GV) were individual differences significant for three of the four ferrets. Moreover, they compensated for each other: Ferrets 9 and 12 (Table 1) took the shortcut significantly less often than chance, $G(1) = 5.82$, $p = 0.016$ and $G(1) = 9.75$, $p = 0.0018$, respectively, and ferret 10 took it significantly more often $G(1) = 5.82$, $p = 0.016$.

The difference between the two training groups was unchanged when the data set was restricted to the first 6 trials, which were completed by all subjects (so the individual choice proportions are based on the same sample sizes). The mean proportions were 48% vs. 85% for the SNV and SV conditions, respectively. Further restricting the data to only the first choice (Table 1), since it is the only truly spontaneous choice, gives the following: 5 out of 8 of the ferrets took the shortcut in the SNV in training condition and 7 out of 8 did so in the SV condition. Given that the first choice was to take a shortcut, the overall proportion of shortcuts was 0.88 for the SV in training group, and 0.62 for the SNV group.

Discussion

This experiment used four groups of ferrets that differed in their training conditions (shortcut visible or not) and their testing conditions (goal visible or not). In answer to our three questions: (1) Do ferrets spontaneously take novel shortcuts? Yes, performance in the cross-maze with shortcuts revealed that ferrets will take a shortcut, but only under certain conditions. Ferrets do not always take the long-path for its own sake.

(2) Does the shortcut taking depend on familiarity with the shortcut and/or visibility of the goal? Shortcut taking certainly depends on having seen the shortcut before: the ferrets in the SV in training group were much more likely to take the shortcut than those in the SNV in training group, where performance did not deviate from chance. In other words, visual familiarity with the shortcut is sufficient to account for shortcut taking by the ferrets in this study. Whether the goal is visible or not, however, did not seem to matter, in accordance with the suggestion that ferrets may not use visual cues to attain goals (Pollard & Lewis, 1969). Given the failure to find a main effect of the visibility of the goal at the time of testing, it is possible that the ferrets did not attend to, or perhaps even see, the goal at the time of testing. This possibility seems unlikely given that the experimenter did not release the animal until it was looking around and that the bowl, at 10 cm high and 15 cm large, was hardly inconspicuous. Nonetheless, whether the ferrets in the GV during test groups attended to the goal at the time of testing or not, we can conclude that the observed shortcut taking was not attributable to the fact that the goal could be seen at the time of the test.

(3) In the absence of visual familiarity with the shortcut and in the absence of visibility of the goal, is there any evidence of shortcut taking? No, performance was no different from chance for any of the animals in this group. Bennett (1996) has previously argued that there is no reason to invoke a “cognitive map” for any species, and our study is no exception. Methodological variations, however, might perhaps lead to above chance performance.

The fact that the ferrets spontaneously took shortcuts only under certain conditions argues against some possible experimental artifacts. If there were a “Clever Hans” phenomenon at work, then the ferrets would have taken the shortcuts in all conditions, which they did not. We can identify nothing in the testing procedure that suggests the possible post-hoc explanation that the experimenters somehow “gave away” what turned out to be the important variable (i.e., the animal’s training condition). Also, if there were a bias in the direction in which the ferrets were released at the starting point, then it too would be constant across conditions. Finally, the fact that the ferrets were rewarded during testing, so as to maintain their motivation, may well have had an amplifying effect on behaviour, even though the reinforcement was nondifferential. Nonetheless, the explanation that our ferrets simply continued to take shortcuts if it had been their first choice can not account for the data: given that the first choice was a shortcut, the overall mean (Table 1) was smaller in the SNV during training groups (0.62) than in the SV groups (0.88): The ferrets still had a tendency to take fewer shortcuts after the first shortcut if the shortcut had not been seen during training.

Pursuing the cognitive map controversy may well involve challenging the failure to reject the null hypothesis that ferrets would show no tendency to take shortcuts in the SNV/GNV group. Alternatively, other indices of cognitive maps might be adopted, such as the use of detours (Tolman, 1948). Although we used the cognitive map framework as the impetus for this study, it is only one of several possible avenues for further research on the spatial behaviour of ferrets, of which we enumerate three: (1) Species differences remain to be investigated. Comparisons with cats can not be made here because although Poucet (1985) used the same apparatus and found that cats learned to use shortcuts, the procedure differed from ours in one important way: the cats always had access to the shortcut, and a gradual increase in the frequency of shortcut taking was observed over four days. In our experiment, the testing conditions differed from the training conditions. (2) Although extra-maze spatial cues were provided in our experiment, their role in way-finding by ferrets is unknown. Ferrets may possibly rely on purely geometric cues (Cheng, 1986). (3) One further question is raised not by theory but by our own data: The pronounced individual differences in the SNV/GV group were unexpected. Two ferrets almost never took the shortcut and one almost always took it. Possibly competition between an environmental stimulus (the goal) and a representation in memory (of the route well-travelled) competed for control over behaviour. For some animals, the past may have prevailed over the present, and for others, the reverse, in which case behaviour in space might ultimately be understood in terms of time.

References

- Beach, F. A. (1950). The snark was a boojum. *American Psychologist*, **5**, 115-124.
- Bennett, A. T. D. (1996). Do animals have cognitive maps? *Journal of Experimental Biology*, **199**, 219-224.
- Cheng, K. (1986). A purely geometric module in the rat’s spatial representation. *Cognition*, **23**, 249-178.
- Collett, T. S., & Collett, M. (2000). Path integration in insects. *Current Opinion in Neurobiology*, **10**, 757-762.
- Crowley, J. C., & Katz, L. C. (1999). Development of ocular dominance columns in the absence of retinal input. *Nature Neuroscience*, **2**, 1125-1130.

- Davis, H. (1996). Numerical competence in ferrets (*Mustela putorius furo*). *International Journal of Comparative Psychology*, **9**, 51-64.
- Dyer, F. C. (1991). Bees acquire route-based memories but not cognitive maps in a familiar landscape. *Animal Behaviour*, **41**, 239-246.
- Francis, B., Green, M., & Payne, C. (1993). *GLIM: The statistical system for generalized linear interactive modelling. Version 4.0*. New York: Oxford University Press.
- Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT Press.
- Gould, J. L. (1986). The locale map of honeybees: Do insects have cognitive maps? *Science*, **232**, 861-863.
- Gould, J. L. (2002). Can honey bees create cognitive maps? In M. Bekoff, C. Allen, & G.M. Burghardt (Eds) *The cognitive animal: Empirical and theoretical perspectives on animal cognition*. (pp. 41-45). Cambridge, MA: MIT Press.
- Kelliher K. R., & Baum, M. J. (2001). Nares occlusion eliminates heterosexual partner selection without disrupting coitus in ferrets of both sexes. *Journal of Neuroscience*, **21**, 5832-5840.
- Mrsic-Flogel, T. D., King, A. J., Jenison, R. L., & Schnupp, J. W. H. (2002). Listening through different ears alters spatial response fields in ferret primary auditory cortex. *Journal of Neurophysiology*, **86**, 1043-1046.
- O'Keefe J., & Conway, D.H. (1980). On the trail of the hippocampal engram. *Physiological Psychology*, **9**, 229-238.
- O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford, UK: Oxford University Press.
- Pollard, J. S., & Lewis, R. F. V. (1969). Ferrets do learn mazes. *Journal of Biological Psychology*, **10**, 40-43.
- Poucet, B. (1985). Spatial behaviour of cats in cue-controlled environments. *Quarterly Journal of Experimental Psychology*, **37B**, 155-179.
- Shefferman, M. R. (1996). *The ferret: An owner's guide to a happy healthy pet*. New York: Howell Book House.
- Shettleworth, S. J. (1998). *Cognition, evolution, and behavior*. New York: Oxford University Press.
- Sokal, R. R., & Rohlf, F. J. (1981). *Biometry. Second edition*. San Francisco: WH Freeman.
- Thinus-Blanc, C. (1988). Animal spatial cognition. In L. Weiskrantz (Ed) *Thought without language* (pp. 371-395). Oxford: Oxford University Press .
- Thinus-Blanc, C., Bouzouba, L., Chaix, C., Chapuis, N., Durup, M., & Poucet, B. (1987). A study of spatial parameters encoded during exploration in hamsters. *Journal of Experimental Psychology: Animal Behavior Processes*, **13**, 418-427.
- Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, **55**, 189-208.

Received February 15, 2004.

First revision received April 19, 2004.

Second revision received May 12, 2004.

Accepted May 28, 2004.