

Painted Turtles Solve a Detour Task Using Proximal Cues

William Kochen^{1,*}, Jeanny Gomerez², and Alice S. Powers²

¹Nova Southeastern University

² Stony Brook University

*Corresponding author (Email: wkochen@nova.edu)

Citation – Kochen, W., Gomerez, J., & Powers, A. S. (2022). Painted turtles solve a detour task using proximal cues. *Animal Behavior and Cognition*, 9(4), 408-415. https://doi.org/10.26451/abc.09.04.04.2022

Abstract – Painted turtles (*Chrysemys picta*) are a common species of pond turtle, which forage for food in shallow water and on land, necessitating navigation around obstacles. A detour problem in the laboratory is one in which an animal is presented with a goal on the opposite side of a barrier, so that the only way the individual can reach the goal is to navigate around the barrier. As such, the detour problem presents a challenge for animals similar to what they find in the wild. They must use their spatial understanding of the environment to navigate around the detour and obtain the food. In this study, we investigated a detour problem in which painted turtles had to find their way around a barrier to obtain food as the reward. We then tested them on their use of intra-apparatus (proximal) and extra-apparatus (distal or room) cues. All turtles solved the problem on the first trial, and almost all of them did so consistently over days. They did not show improvement in speed over trials, and they went to different sides on different days, suggesting that they were not learning the task but were solving it anew each day. When the apparatus was rotated in the room, their behavior did not change, showing that they were using proximal, not distal, cues to navigate the detour. These findings demonstrate that painted turtles can solve a detour without the need for experience with the contingencies of the task and that they rely on intra-apparatus (proximal) cues to do so. They add to the growing body of findings that demonstrate that non-avian reptiles can master a detour task.

Keywords - Chysemys picta, Detour, Spatial cue

Painted turtles (*Chrysemys picta*) are commonly found in North America. They live in ponds and eat fish, insects, and plants (Gibbons, 1967). They hunt for prey on land as well as under water and navigate around rocks or plants while doing so. Furthermore, on land, they migrate short distances between ponds, encountering obstacles, such as bushes and other vegetation, that they must navigate around (Roth & Krochmal, 2015). The cues they use for this navigation are at present unknown. In the laboratory, however, turtles have been shown to utilize room cues to navigate a maze (Lopez et al., 2003; Rodriguez et al., 2002).

A detour task presents a goal to an organism on the opposite side of a barrier, so that the only way the individual can reach the goal is to navigate around the barrier (Kabadayi et al., 2018; Köhler, 1925). As such, this task resembles the problem that animals face when searching for food. Detour behavior may be ecologically meaningful for predator species (Kabadayi et al., 2018). Thus, the behavior of painted turtles in the wild suggests that they would be good at negotiating detours.

One can distinguish between the ability to solve a detour problem on the first trial and the ability to learn the path to the goal over successive trials (Regolin et al., 1995; Smith & Litchfield, 2010; Wynne & Leguet, 2004). The terms *solve* and *solution* will be used here to designate finding the goal on the first trial. Solving the detour problem suggests spatial reasoning about the nature of the task, according to some authors (e.g., Wynne & Leguet, 2004), whereas gradual improvement over trials has been attributed to spatial learning. According to this interpretation, animals show an understanding of the spatial arrangement

of objects in the environment and therefore navigate around the detour to reach the goal. In such a situation, animals could use either proximal cues, within the apparatus, or distal (or room) cues, outside the apparatus (Hebert et al., 2017). Without testing, it is impossible to know which type of cue the animals use. By rotating the apparatus in the room, however, one can determine whether distal cues are being used. If so, rotation would disrupt performance.

Other authors have interpreted solving the task on the first trial as evidence of the ability to inhibit the response to approach the food directly (Kabadayi et al., 2018). In contrast, coming to successfully perform the detour task over multiple trials may be the result of trial-and-error learning by reinforcement principles. Indeed, the use of a detour task to assess inhibition has been questioned, because studies have shown that, over trials, response learning can facilitate the performance (van Horik et al., 2018, 2020).

A few studies have tested the abilities of chelonians to solve or learn detour problems (reviewed in Burghardt, 1977; Szabo et al., 2021). Spigel (1964a, b), for example, showed that painted turtles could solve a detour task in which the reward was to escape from confinement. He allowed unlimited time to escape. Spigel (1964b), again working with painted turtles, studied the effect of confinement before and after a trial on the same detour behavior. Although he found that pre-trial confinement disrupted behavior, he again found that turtles could solve the detour task from the first trial when given unlimited time. Wilkinson et al. (2010) investigated social learning in red-footed tortoises (*Chelonoidis carbonaria*), using a detour task. The tortoises observed a trained tortoise performing a detour task for food and then were able to learn it. Other tortoises that did not observe the model failed to learn the task. In a subsequent study, Wilkinson and Huber (2012) reported further investigations of the same tortoises and showed that those that had observed another tortoise were able to generalize to two different detour configurations and to solve each of them on the first trial. Non-observer animals were again unable to perform the tasks reliably.

In the present study, we examined the ability of painted turtles to solve a detour task for food. Before training, we habituated the turtles to eating in the apparatus on the barrier side to familiarize them with the apparatus. Then, we gave one trial a day on the detour task for five days. Finally, we rotated the apparatus on the next three days, to determine whether the turtles were using proximal or distal cues to navigate around the detour. Our hypothesis was that rotating the apparatus would disrupt their performance, as had been shown in maze learning for turtles (Rodriguez et al., 2002), thus demonstrating that they were using distal cues.

Method

Ethics Statement

All procedures were performed according to the guidelines established by the Society for Neuroscience and the American Psychological Association and were approved by the Institutional Animal Care and Use Committee at Stony Brook University (protocol #267730). All national, international, and institutional guidelines for the care and use of animals were followed.

Subjects and Housing

Eight adult painted turtles (*Chrysemys picta*), weighing from 150 to 400 g, participated in this experiment. They were obtained from www.turtlesale.com (now www.myturtlestore.com), who raised the turtles on their farm in Florida. Although the turtles were of adult size when purchased, their exact ages were unknown. Sex was not recorded.

Once purchased, the turtles were housed in individual tanks made of white plastic (45 X 37 X 19 cm) containing water 5-7 cm deep and a gray slatted plastic platform (15 X 34 cm in area and 7 cm high) to allow them to bask. The tanks were kept in a temperature controlled (26.6 degrees Celsius) room with a 14-10 h day-night cycle and full-spectrum lights. The experiments were performed in an adjacent room with identical temperature control.

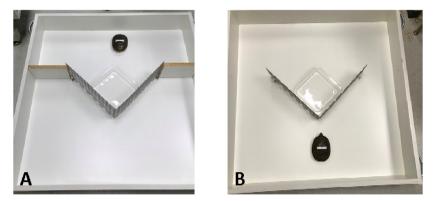
The turtles were fed 12 pieces of Omega One Adult Turtle Sticks and six pieces of Zoo-Med Aquatic Turtle Food in the home tank per day before the experiment began. During the experiment, they received the same amount of food each day, all of it in the experiment. If an animal did not eat in the apparatus during the test session, it was fed the daily ration in its home tank 30 min after running the session. Turtles used in this experiment were kept in the colony for use in future research.

Apparatus

The apparatus used in the experimental stage was similar to the apparatus used by Wilkinson et al. (2010) (Figure 1B). It consisted of a white square box (91 X 91 cm) made of plastic-coated wood with 15 cm high walls. In the center of the box was a V-shaped fence made of a metal grid with sides 40 cm long and holes 4.2 X 1.4 cm, positioned at a 90-degree angle. For the acclimation stage of the experiment (Figure 1A), walls of the same height and color as the perimeter of the apparatus were added to the edges of the detour fence in order to prevent the turtle from seeing the detour problem but allowing it to acclimate to the area.

Figure 1

The Detour Apparatus



Note. A: The detour apparatus used in the acclimation stage (Stage 1), B: The apparatus used in the experimental stage (Stage 2).

The food used was the same as the food given in the home tank and in the same amount. Because painted turtles swallow their food underwater, the food was placed in a transparent plastic container 23.6 cm square, which contained water 1.25 cm deep. The rest of the apparatus was dry. Turtles are typically fearful of humans; therefore, all trials were video recorded with the experimenter out of sight, monitoring from behind an opaque barrier located left of the apparatus when viewed from the front, as seen in Figure 1.

Throughout both stages of the experiment, the water in the food dish was replaced after each trial, and the apparatus was wiped down with alcohol wipes.

Procedure

The experiment had two stages, an acclimation stage, during which the turtles were taught to eat in the apparatus, and an experimental stage, in which the turtles were given the opportunity to solve and learn the detour problem. During the acclimation stage of the experiment, each turtle was placed at the location in the apparatus shown in Figure 1A, and given 15 min a day to eat the food. They were removed when they finished eating the food or when 15 min had elapsed. Training continued for six days, one trial per day. Turtles that did not eat in the apparatus were not fed in the home cage during this stage, to encourage eating. Only turtles that ate in the apparatus for four consecutive days within the acclimation stage were admitted into the experimental stage.

During the experimental stage, each turtle was placed on the outside of the fence, opposite the food (Figure 1B), and given five minutes from the time it was placed in the apparatus to solve the problem. It was removed after it ate the food or after five min had elapsed, whichever came first. On the subsequent four days, the animals were again tested on the problem, to give them an opportunity to learn it or to improve their performance if they had solved it on previous days. On days six, seven, and eight, the apparatus was rotated 90 degrees clockwise per day, prior to experimentation, and the turtles were again given one trial per day.

The experiment was conducted five days per week. The turtles received their daily ration in the experiment but were fed additional food on Fridays, 30 min after they had been run in the detour task. This is a standard procedure in our laboratory. No animal lost weight during the experiment.

Coding and Analysis

Success was defined as reaching the goal within the five min trial limit. The time to complete the task was recorded. In addition, two types of "errors" were measured: number of reverses of direction (*reverses*) and number of times the turtle touched the barrier (*touches*). These definitions of errors in detour behavior have each been used in prior studies. MacLean et al. (2014), comparing detour performance in 26 species of birds and mammals, defined an error as touching the outside of a transparent cylinder (the barrier) instead of going directly to the opening and the goal. On the other hand, stopping or reversing the direction of travel was counted as an error by others (Frank & Frank, 1982; Krichbaum & Lazarowski, 2022; Smith & Litchfield, 2010).

All videos were independently reviewed by at least two observers, and Cohen's Kappa was used to assess interobserver reliability.

Because of the small number of subjects, nonparametric statistics were calculated using IBM SPSS Statistics 25. A binomial test was used to determine the probability of success of the turtles on the first trial. Friedman's ANOVA for signed ranks was used to analyze daily behavior: time to complete the task, reverses, and touches. Wilcoxon signed rank tests were used to compare behavior on the first five days of the study to behavior on the last three days, when the detour apparatus was rotated in the room. Chi-square was used to analyze side preferences. Alpha was set at .05 for all comparisons.

Results

Interobserver reliability statistics were calculated from the videos for two observers on all of the trials, for successes, touches, and reverses. The observers were always in agreement (Cohen's Kappa, k = 1.00 for all measures).

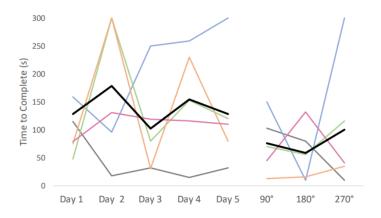
Five of the eight turtles tested in the acclimation stage passed the requirements to be admitted into the experimental stage.

On the first trial of the experimental stage, all five turtles solved the detour problem. A one-tailed binomial test yielded a probability of this event being due to chance of .031. Only one solved the problem without touching the barrier or reversing direction, however.

Over the 25 trials run by five turtles in five days, the turtles reached the goal on 22 trials. No turtle failed to reach the goal on more than one trial: two animals failed on Day 2 and one on Day 5. The times to complete the detour did not vary significantly from day to day (Figure 2; Friedman's ANOVA by ranks: F_r (N = 5, k = 5) = 1.64, p = .65).

Figure 2

Time (in seconds) for each Turtle to Complete the Detour Problem Each Day

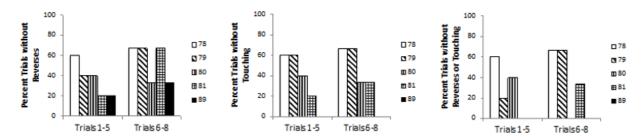


Note. The dark line shows the mean performance for the five turtles that were tested. On test days 6, 7, and 8, the apparatus was rotated through 90 degrees prior to the start of the test session.

When errors were examined, there were marked differences in the turtles' behavior from day to day. All turtles had trials in which they reached the goal without reversing direction, and four out of five had trials in which they did not touch the barrier. No animal demonstrated such trials consistently, however. Figure 3 shows the individual data for percentage of trials without a reverse, percentage of trials without touching the barrier, and percentage of trials in which neither error was made. As the figure shows, the maximum percentage for all three measures was 60%, and one turtle (#89) had no trials in which it did not touch the barrier. Number of reverses did not differ across days, F_r (N = 5, k = 5) = 0.92, p = .91, nor did number of trials on which the turtle touched the barrier, F_r (N = 5, k = 5) = 9.08, p = .16.

Figure 3

Individual Error Data



Note. Each bar represents the percentage of trials from a single turtle. The top graph shows the individual percent of trials without a reverse, the middle graph shows the individual percent of trials without touching the barrier, and the bottom graph shows the individual percentage of trials in which neither error was made.

The turtles did not show a side preference either in their initial choice of side, or in their final entrance into the goal enclosure. For the five turtles, the mean percent initial choice of the left side in the first five days was 23%, which is not significantly different from chance, f(1) = 6.6, p = .20. The final choice of the left side was 31%, which is also not significantly different from chance, f(1) = 2.9, p = .45. Two animals consistently chose left as the initial choice, but the other three went to the right on some initial choices, and no animal consistently went into the goal area on one side.

The turtles did not show any significant change in behavior when the maze was rotated on Days 6-8 (Figure 2). Wilcoxon signed ranks tests were used to compare performance on Days 1-5 with performance on Days 6-8. There was no significant difference on any measure: time (T + (N = 5) = 15, p = .08, reverses) (T + (N = 5) = 13.5, p = .10), touches: T + (N=4) = 8.0, p = .26, both reverses and touches: T + (N = 4) = 7.0, p = .46. Also, initial and final side preference did not differ significantly between the two stages of the experiment: both T + (N = 5) = 11, p = .14.

Discussion

These results demonstrate that painted turtles can solve a detour task for food on the first trial. Spigel (1964a, b) had already shown that painted turtles could detour to escape from confinement on the first trial, but our results extend his findings to detouring for a food reward, a behavior that is no doubt common in the life of this species of turtle in the wild. Our findings also failed to confirm our hypothesis that the turtles would use distal (room) cues to find the food. Of course, we do not know if they use distal cues in the wild.

Another group of non-avian reptiles, lizards, has also been shown to be capable of successful detour performance. Three studies have looked at detour behavior in lizards. Szabo et al. (2019) studied eastern water skinks (*Eulamprus quoyii*) in a cylinder detour task, in which the lizard faced the side wall of the cylinder and had to navigate to enter it from the end. They first trained the skinks to retrieve a piece of food from an opaque cylinder, then tested them on a transparent cylinder made of aluminum insect screen. Five of 20 skinks solved the transparent cylinder task on the first trial, but the mean number of trials that they retrieved the food over 10 trials was only 3.1.

Two other studies assessed side preferences in common wall lizards (*Podarcis muralis*, Csermely et al., 2010) and common chameleons (*Chamaeleo chameleon*, Lustig et al., 2013), using a detour task. In both studies, the apparatus was an elevated runway from which the lizards viewed a prey (frozen mealworm in Csermely et al., moving cockroach in Lustig et al.) through a window in a partition that blocked access to the prey. There were two arms going left and right around the partition, and the lizards had to choose one or the other to get to the reward and consume it. Csermely et al. defined successful completion as including an effort to consume the mealworm, which was under a glass petri dish, and they found that all lizards completed more than half of the 10 trials they ran. They do not report choice on the first trial. Lustig et al. reported that the chameleons captured the cockroaches on all trials. Although not designed to examine whether lizards could perform a detour task, these studies clearly show that they can.

We had hypothesized that the turtles would be using distal (room) cues to navigate to the food and that rotation of the apparatus would disrupt the turtles' detour behavior. Our hypothesis was not confirmed, however. The detour behavior did not change significantly on the three test days in which the apparatus was rotated. The turtles were not slower, and, except for one animal on one trial, they did not fail to find the food. This finding suggests that the turtles were using proximal cues, inside the apparatus, to navigate (Hebert et al., 2017). Those cues would not change with rotation of the test apparatus. Turtles have been shown to use room cues in maze learning (Lopez et al., 2003; Rodriguez et al., 2002), but maze learning differs from the detour problem because the food reward is not visible in a maze. The food was visible throughout our detour task and the turtles could locate it by attending to the local cues in the apparatus, including the visual and olfactory cues from the food.

Although we tried to prevent olfactory cues by wiping down the apparatus between animals with alcohol wipes, it is possible that olfactory cues played a role in the turtles' ability to perform the detour task. The use of alcohol wipes between animals would have eliminated olfactory cues from other animals, but not olfactory cues from the food, which were necessarily present. Turtles have been shown to have good senses of smell (Boycott & Guillery, 1962; Munoz, 2004; Schwenk, 2008). In addition, the food used as reinforcement was the same food the turtles ate in their home tank and in the acclimation phase of the experiment so that they were familiar with its odor. Olfactory cues would not have been present in Spigel's (1964a, b) experiments.

Previous studies of detour learning in chelonians (Spigel, 1965a, b; Wilkinson et al., 2010; Wilkinson & Huber, 2012) did not count reverses or barrier touches as errors. In studies in which these behaviors are reported, the emphasis is usually on errors as an index of inhibition. We report those behaviors but do not count them in determining whether the turtles solved the detour task. Only one turtle reached the goal without reversing direction or touching the barrier, however. If those behaviors were to be counted as constituting failure to achieve solution, then only one turtle solved the problem. All turtles except one had several error-free trials. All turtles had trials with no reverses, and four out of five had at least one trial without touching the barrier.

We did not see evidence of learning over the five days of the experiment. Learning would have been demonstrated by faster completion of the task or fewer reverses or touches of the barrier, facilitating their getting to the food more quickly. The fastest time shown by any turtle was 15 s (on Day 4); thus, there was the potential for animals to show increased speed. Instead, the average time to complete the task stayed constant over the five trials, and the reverses and touches did not decline. The turtles solved it on the first trial and re-solved it on each subsequent trial throughout the experiment, going different ways and at the same speed as on the first trial. If they were remembering the original day's solution, they would be expected to increase their speed from day to day and always go to the same side. The finding that they used both sides of the fence on different trials also demonstrates that they were not forming a motor habit but rather finding their way around the fence to the food, suggesting that they had understood the spatial layout of the apparatus.

The lack of evidence for improvement over trials contrasts with the results of Spigel (1964a, b), who found dramatic improvement in his turtles' speed in solving the problem over days. This difference might be due to the use of an acclimation stage in the present experiment, in which turtles had the opportunity to habituate to the cues of the box. In addition, the presence of olfactory cues could also have increased the turtles' ability to find the food on each trial.

In summary, we demonstrated that painted turtles could solve a detour problem for food on the first trial. They showed no evidence of improvement over trials, and they did not follow the same path each day. When the apparatus was rotated, their performance did not change significantly, showing that they were not using distal (room) cues to locate the food. These findings suggest that their performance was based on an understanding of the spatial arrangement of the problem and the use of proximal visual (and possibly olfactory) cues and did not require learning. Taken together with other studies of non-avian reptiles, this study contributes to the understanding of detour behavior in this group and suggests that detour solution is a behavior that might have been present in the ancestors of mammals.

Data Availability Statement: The data that support the findings of this study are available on request from the corresponding author.

Funding: JG was supported by a summer fellowship from the McNair Program of St. John's University, Jamaica, NY.

Conflict of Interest: The authors declare that they have no conflicts of interest.

References

- Boycott, B. B., & Guillery, R. W. (1962). Olfactory and visual learning in the red-eared terrapin, *Pseudemys scripta* elegans (Wied.). Journal of Experimental Biology, 39(4), 567-577.
- Burghardt, G. M. (1977). Learning processes in reptiles. In C. Gans & D.W. Tinkle (Eds.), *Biology of the Reptilia*. *Ecology and Behaviour A* (Volume 7) (pp. 555–681). Academic Press.
- Csermely, D., Bonati, B., & Romani, R. (2010). Lateralisation in a detour test in the common wall lizard (*Podarcis muralis*). Laterality: Asymmetries of Body, Brain and Cognition, 15(5), 535-547. https://doi.org/10.1080/13576500903051619
- Frank, H., & Frank, M. G. (1982). Comparison of problem-solving performance in six-week-old wolves and dogs. *Animal Behaviour*, 30, 95–98. <u>https://doi.org/10.1016/s0003-3472(82)80241-8</u>

- Gibbons, J. W. (1967). Variation in growth rates in three populations of the painted turtle, *Chrysemys picta*. *Herpetologica*, 23, 296-303.
- Hébert, M., Bulla, J., Vivien, D., & Agin, V. (2017). Are distal and proximal visual cues equally important during spatial learning in mice? A pilot study of overshadowing in the spatial domain. *Frontiers in Behavioral Neuroscience*, 11, 109. <u>https://doi.org/10.3389/fnbeh.2017.00109</u>
- Kabadayi, C., Bobrowicz, K., & Osvath, M. (2018). The detour paradigm in animal cognition. *Animal Cognition 21*, 21–35. <u>https://doi.org/10.1007/s10071-017-1152-0</u>
- Köhler, W. (1925). The mentality of apes. Harcourt, Brace & World.
- Krichbaum, S., & Lazarowski, L. (2022). Reward type affects dogs' performance in the cylinder task. *Animal Behavior* and Cognition, 9(3), 287-297. <u>https://doi.org/10.26451/abc.09.03.03.2022</u>
- Lopez, J. C., Vargas, J. P., Gomez, Y., & Salasc, C. (2003). Spatial and non-spatial learning in turtles: the role of medial cortex. *Behavioural Brain Research*, 143(2), 109-20. <u>https://doi.org/10.1016/s0166-4328(03)00030-5</u>
- Lustig, A., Ketter-Katz, H., & Katzir, G. (2013). Lateralization of visually guided detour behaviour in the common chameleon, *Chamaeleo chameleon*, a reptile with highly independent eye movements. *Behavioural Processes*, 100, 110-115. <u>https://doi.org/10.1016/j.beproc.2013.08.002</u>
- MacLean, E. L., et al. (2014). The evolution of self-control. *Proceedings of the National Academy of Scienes USA*, *111*, E2140–E2148. <u>https://doi.org/10.1073/pnas.1323533111</u>
- Munoz, A. (2004). Chemo-orientation using conspecific chemical cues in the stripe-neck terrapin (*Mauremys leprosa*). Journal of Chemical Ecology, 30, 519-530. <u>https://doi.org/10.1023/b:joec.0000018626.55609.31</u>
- Regolin, L., Vallortigara, G., & Zanforlin, M. (1995). Object and spatial representations in detour problems by chicks. Animal Behaviour, 45, 195-199. https://doi.org/10.1016/0003-3472(95)80167-7
- Rodriguez, F., Lopez, J. C., Vargas, J. P., Gomez, Y., Broglio, C., & Salas, C. (2002). Conservation of spatial memory function in the pallial forebrain of reptiles and ray-finned fishes. *Journal of Neuroscience*, 22(7), 2894–2903. https://doi.org/10.1523/JNEUROSCI.22-07-02894.2002
- Roth, T. C., & Krochmal, A. R. (2015). The role of age-specific learning and experience for turtles navigating a changing landscape. *Current Biology*, 25, 333–337. <u>http://dx.doi.org/10.1016/j.cub.2014.11.048</u>
- Schwenk, K. (2008). Comparative anatomy and physiology of chemical senses in nonavian aquatic reptiles. In J.G.M. Thewissen & S. Nummela. (Eds.), Sensory evolution on the Threshhold: Adaptations in Secondarily Aquatic Vertebrates (pp. 65-81). University of California Press.
- Smith, B. P., & Litchfield, C. A. (2010). How well do dingoes, *Canis dingo*, perform on the detour task? *Animal Behaviour*, 80, 155–162. <u>https://doi.org/10.1016/j.anbehav.2010.04.017</u>
- Spigel, I. M. (1964a). Learning, retention, and disruption of detour behavior in the turtle. *Journal of Comparative and Physiological Psychology*, *57*, 108-112.
- Spigel, I. M. (1964b). Antecedent confinement and detour learning in turtles. Psychological Reports, 14, 915-918.
- Szabo, B., Noble, D. W. A., & Whiting, M. J. (2019). Context-specific response inhibition and differential impact of a learning bias in a lizard. *Animal Behaviour*, 22, 317-329. <u>https://doi.org/10.1007/s10071-019-01245-6</u>
- Szabo, B., Noble, D. W. A., & Whiting, M. J. (2021). Learning in non-avian reptiles 40 years on: advances and promising new directions. *Biological Reviews*, 96(2), 331-356. <u>https://doi.org/10.1111/brv.12658</u>
- van Horik, J. O., Langley, E. J. G., Whiteside, M. A., Laker, P. R., Beardsworth, C. E., & Madden, J. R. (2018). Do detour tasks provide accurate assays of inhibitory control? *Proceedings of the Royal Society B, 285*, 20180150. <u>http://dx.doi.org/10.1098/rspb.2018.0150</u>
- van Horik, J. O., Beardsworth C. E., Laker, P. R., Whiteside, M. A., & Madden, J. R. (2020). Response learning confounds assays of inhibitory control on detour tasks. *Animal Cognition*, 23, 215–225. https://doi.org/10.1007/s10071-019-01330-w
- Wilkinson, A., Huber, L. (2012). Cold-blooded cognition: reptilian cognitive abilities. In J. Vonk and T. K. Shackelford (Eds.), *The Oxford Handbook of Comparative Evolutionary Psychology* (pp. 129–141). Oxford University Press.
- Wilkinson, A., Kuenstner, K., Mueller, J., & Huber, L. (2010). Social learning in a non-social reptile (*Geochelone carbonaria*). *Biology Letters*, 6, 614-616. <u>https://doi.org/10.1098/rsbl.2010.0092</u>
- Wynne, C., & Leguet, B. (2004). Detour behavior in the Quokka (*Setonix brachyurus*). *Behavioural Processes*, 67, 281–286. <u>https://doi.org/10.1016/j.beproc.2004.04.007</u>