

## Original Article

# Win-shift and win-stay learning in the short-beaked echidna (*Tachyglossus aculeatus*)

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**Abstract.** Numerous previous investigators have explained species differences in spatial memory performance in terms of differences in foraging ecology. In three experiments we attempted to extend these findings by examining the extent to which the spatial memory performance of echidnas (or "spiny anteaters") can be understood in terms of the spatio-temporal distribution of their prey (ants and termites). This is a species and a foraging situation that have not been examined in this way before. Echidnas were better able to learn to avoid a previously rewarding location (to "win-shift") than to learn to return to a previously rewarding location (to "win-stay"), at short retention intervals, but were unable to learn either of these strategies at retention intervals of 90 min. The short retention interval results support the ecological hypothesis, but the long retention interval results do not.

**Keywords.** Echidna - Spatial memory - Foraging ecology

## Introduction

The ecological approach in comparative cognition has been most successfully applied to our understanding of spatial memory. There are now a large number of studies in which some aspect of the ecology of a particular species (generally its foraging ecology) is used successfully to predict performance, or performance differences, in spatial memory tasks. For example, in two different groups of food-storing birds, spatial memory performance typically correlates with dependence on food storing in the wild, although there are also data that are inconsistent with this pattern (Balda et al. 1995; Shettleworth 1995; Gould-Beierle 2000).

In addition to examining differences in *capacity*, previous research has also addressed whether the way in which spatial memory operates has been shaped by ecological demands. When a foraging animal finds food at a particular location, and leaves that location, it is faced with the decision to return to forage there at a later time, or to search in a new location. When this process is studied in controlled settings, returning to a previously rewarding location is referred to as adopting a win-stay strategy, and avoiding a previously rewarding location is referred to as a win-shift strategy.

An animal's tendency to win-shift or win-stay is frequently consistent with its foraging ecology. For example, nectar-feeding birds would be expected to avoid a previously rewarding flower (to win-shift), since it no longer contains nectar. This has been shown to be true of sunbirds (Gill and Wolf 1977), Hawaiian honeycreepers (Kamil 1978), and hummingbirds (Cole et al. 1982; Healy and Hurly 1995), although rufous hummingbirds also have a tendency to return to flowers that they have visited but not emptied (to win-stay; Hurly 1996). In contrast with this tendency in nectar feeders, ovenbirds (Zachs and Falls 1976) and English thrushes (Smith 1974a, b), which feed primarily on worms and other aggregating, ground-dwelling invertebrates, have a tendency to win-stay.

These examples suggest that the critical ecological factor determining the likelihood of an animal having a preference to learn a win-shift task is the utilisation of a food source that can be depleted in a single visit. The current study is an attempt to examine whether the tendency to win-shift or win-stay is affected by ecological factors other than the depletion or non-depletion of a food source. Echidnas feed on ants and termites that are concentrated in spatially isolated, temporally stable patches (nests), scattered throughout their home ranges. Since these food sources contain too much prey to be depleted, we might expect echidnas to show a strong win-stay tendency. However, the prey of echidnas mount chemical and mechanical defences that force them to leave a nest after a relatively short foraging bout (Abensperg-Traun et al. 1991). Abensperg-Traun (1988) recorded a mean feeding bout of 1.63 min in the field. If this ecological factor has resulted in evolved spatial memory biases, echidnas should have a win-shift preference when the retention interval is short (before the chemical defences at a nest have dissipated). Since ant and termite nests are rarely depleted and rarely move, however, they may also have a win-stay preference at longer retention intervals. The current experiments are an attempt to examine these possibilities.

Experiment 1 was designed to examine whether echidnas show the predicted win-shift bias at short retention intervals in a T-maze. Experiment 2 examines whether this bias is present in a more complex task, using a four-arm radial maze. Experiment 3 was designed to test the prediction that the win-shift bias would become a win-stay bias at a longer retention interval.

## **Experiment 1**

This experiment was designed to examine whether echidnas more easily learn to win-stay or to win-shift, using a food reward at short retention intervals. Since we were not sure how many locations echidnas would be able to remember (this has not been previously studied), we decided to test them in the simplest possible situation in which shifting and staying could be examined - a T-maze. Based on the ecological considerations outlined earlier, we expected the echidnas to learn more easily to win-shift than to win-stay at short retention intervals.

## **Methods**

## Subjects

Four short-beaked echidnas (*Tachyglossus aculeatus*) served as subjects in this experiment. All were female and apparently adult, however ages could not accurately be determined. The echidnas were captive animals held at Taronga Zoological Park in Sydney, Australia. Two echidnas were assigned to a win-stay condition and two were assigned to a win-shift condition.

At the time of testing, subjects weighed 3.4, 3.1, 4.4, and 3.7 kg, respectively. The echidnas were housed communally in a 10 × 10-m open enclosure with a substrate of plants, logs, leaf litter, bark, and earth. They were maintained on a high-fat diet of mincemeat (beef), wheatbran, eggs, Glucodin (glucose supplement), olive oil, vitamin E powder (Equine E), Avi Drops (bird vitamins) and calcium carbonate, receiving 100 ml daily, and all had free access to water.

## Apparatus

During the experiment, the echidnas were transported to a 5 × 5-m open enclosure that had a bark and leaf litter surface. The testing apparatus was a T-maze, consisting of marine plywood arms and concrete half-pipe ends, backing onto one of the enclosure walls, also made of marine plywood. The entrance to the maze was 31 cm long and 52 cm wide, and the arms were identical in length (120 cm), width (54 cm), and height (54 cm). Three metal dishes (12 cm diameter, 6 cm height) were placed in the maze with one positioned at the end of the "start" leg to prompt the echidnas to search for food (these were the containers in which they were usually fed). This dish was uncovered. The remaining two were placed one in each arm of the maze, covered by 20 × 20-cm plywood lids to prevent the subjects from detecting the smell of the food contained inside.

## Procedure

In an initial training stage (in the home enclosure) the echidnas learned how to remove the lids (by placing their snout on the undersurface of the lid) after only a few attempts. In a previous study (Quince 1998) we conducted tests to ensure that the echidnas could not locate food on the basis of olfactory cues when the lids were in place. It is clear, in any case, from the results of the experiments reported here that they were not able to do so.

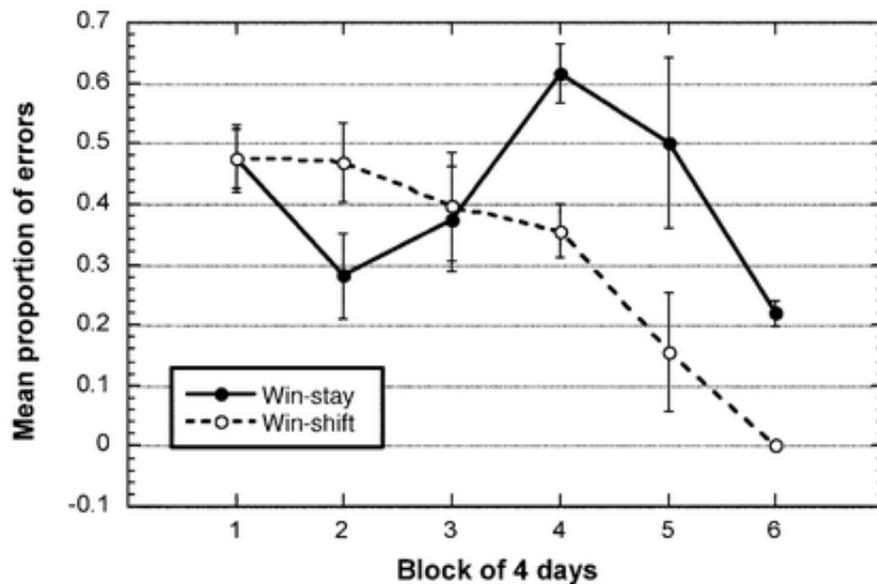
Trials consisted of two parts (the "exposure" and "test" phases), separated by a retention interval of 2 min. In the exposure phase, subjects were placed at the maze entrance and were given the opportunity to explore both arms freely to find a food reward. Only one dish was baited during each phase of a trial, which contained approximately 10 ml of food mixture. After locating and consuming the food, subjects were removed from the apparatus. Following the retention interval, subjects were returned to the maze for the test phase of the trial. Depending on the condition, food was in the previously baited arm (win-stay) or in the previously empty arm (win-shift). The arm that was baited in the exposure phase varied randomly except that we ensured the food was in the left arm as often as it was in the right arm in this phase on any given day (twice in each). The echidnas were removed from the apparatus after finding and consuming the food in the test phase. An interval of 10 min separated each trial. Each echidna completed four trials per day over 24 days (not consecutively - testing occurred on only four days of the week), for a total of 96 trials. Two echidnas were randomly assigned to the win-shift condition and two to the win-stay condition.

## Results

For each subject the total number of errors made on a day was recorded. An error involved travelling down the arm that did not contain food and lifting the lid off the food container in the test phase. Failure to find food invariably resulted in the echidna heading directly to the food container in the other arm, and therefore finding food. Since the echidnas were removed from the apparatus after they had found and consumed the food, they could only make one error per trial, and only then when it was their first choice that was wrong.

To reduce variability in the data, these daily error scores (out of four) were converted to proportion of errors (by dividing by 4), and these daily proportion of errors were averaged to create 4-day blocks. So, for each echidna, the data analysed were the mean proportion of errors across six 4-day blocks.

As can be seen from Fig. 1, both groups of echidnas began performing at about chance levels, but after 20-24 days of testing (blocks 5 and 6) the echidnas in the win-shift group were making far fewer errors than those in the win-stay group. A condition (stay or shift)  $\times$  block (six levels) factorial analysis of variance (ANOVA) on these data produced a significant main effect of block ( $F_{5,10}=6.39$ ,  $P=0.006$ ) and a significant block  $\times$  condition interaction ( $F_{5,10}=3.52$ ,  $P=0.043$ ) at the 0.05 alpha level, but a non-significant main effect of condition ( $F_{1,2}=3.34$ ,  $P=0.21$ ).



**Fig. 1.** Experiment 1: the mean proportion of errors as a function of blocks of days for echidnas in the win-shift and the win-stay conditions in a T-maze. *Error bars* represent  $\pm 1$  standard error

## Discussion

The results obtained in this experiment are consistent with the possibility that the foraging ecology of the echidna has shaped its spatial learning mechanisms. At a short retention interval (2 min), echidnas were better able to learn to avoid a location that had contained food (to win-shift) than to learn to return to a previously rewarding location (to win-stay). It is important to be clear that this short-term avoidance of rewarding locations is not a bias built in to the echidna's foraging behaviour; it is a bias in the ease with which they can *learn* to avoid or return to previously rewarding locations.

If as a result of evolution echidnas had a tendency to avoid previously rewarding locations (at least in the short-term), then the differences between the groups would have been present at the beginning of training. Instead, the results clearly show that the advantage enjoyed by the echidnas in the win-shift condition emerges over blocks of trails, suggesting that the bias is in the ease with which the two tasks can be learnt. In other words, evolution appears to have produced a predisposition to more easily *learn* certain spatio-temporal distributions of food, rather than an unlearned bias to forage in a particular way. The fact that the differences were not apparent early in training, and that both groups originally performed at chance levels, is further evidence that the echidnas could not use olfactory cues to locate the baited dish.

## Experiment 2

Although Experiment 1 provides evidence that echidnas are better able to learn to avoid a previously rewarding location (to win-shift) than to return to such a location (to win-stay) at short retention intervals, and this was predicted on the basis of ecological considerations, we wished to examine the generality of this effect with a slightly more realistic number of locations, and using new echidnas - with so few subjects available, we may have randomly allocated better learners to the win-shift condition in Experiment 1.

For these reasons, the current experiment expanded the learning task to a four-arm radial maze, two arms of which contained food, and two arms of which were empty, and used a retention interval of 5 min. Again, two echidnas were required to learn to win-shift and two to learn to win-stay.

## **Methods**

### **Subjects**

Four new female echidnas served as subjects in this experiment. They were aged 3 years, 6 months; 4 years, 1 month; 6 years, 3 months; and 4 years, 2 months and weighed 3.2, 3.6, 4.2, and 3.3 kg, respectively, at the time of testing. As in experiment 1, the echidnas were housed together and were transported individually to the testing enclosure.

### **Apparatus**

A four-arm radial maze constructed from marine plywood served as the apparatus for this experiment. Each arm measured 215 cm in length and 70 cm in width and was 40 cm high. Single layers of plastic sheet were placed down the lengths of the arms to prevent the echidnas from probing the soil for additional food. Positioned at the end of each arm was a metal dish covered by a wooden lid (as used in experiment 1).

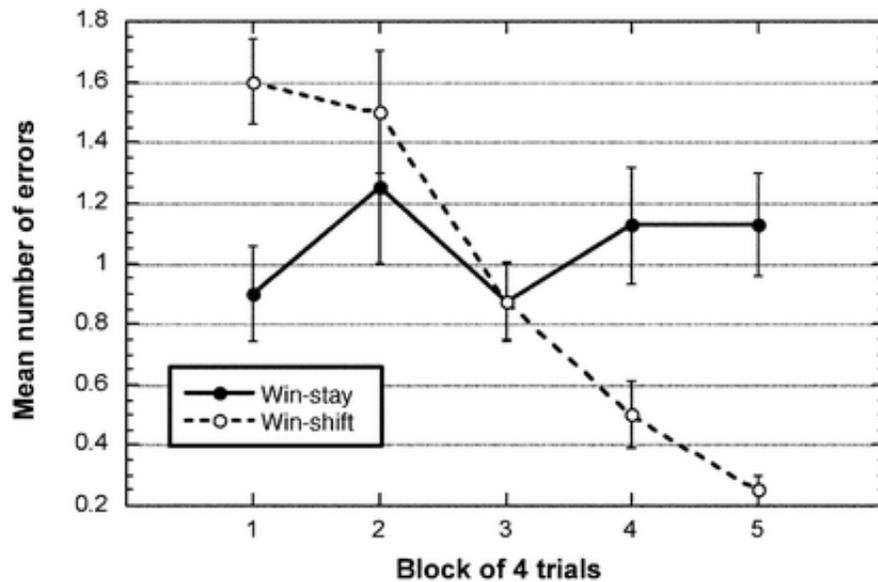
### **Procedure**

As in experiment 1 a trial consisted of two visits to the maze, with visits being separated by a 5-min retention interval. In the exposure phase of the trial, echidnas were placed in the centre of the maze facing randomly chosen arm ends and were given free access to all arms. Two of the arms were randomly baited with food. After each arm had been visited and both food dishes had been emptied, subjects were removed from the maze for a period of 5 min. During this time, the same (win-stay) or the opposite (win shift) arms were re-baited. Following the retention interval, subjects were returned to the maze and the order of arm visits was recorded. Subjects were removed from the maze after they found and consumed the food within both baited dishes. After each trial, subjects were returned to their home enclosure.

Each echidna was given 20 trials, with 2 trials being administered per day for most days (but again, non-consecutively). On days with 2 trials, there was an inter-trial interval of approximately 90 min.

## **Results**

The number of times an echidna travelled to the end of an unbaited arm (and touched the lid) in the test phase was recorded as the number of errors for that trial. As in experiment 1 the error scores from individual trials were pooled as average errors for a block of four trials for each echidna, and the block error scores were used in the analysis of variance. These are plotted in Fig. 2.



**Fig. 2.** Experiment 2: mean number of errors as a function of trial block for echidnas in the win-shift and the win-stay conditions in a four-arm radial maze. *Error bars* represent  $\pm 1$  standard error

As can be seen from Fig. 2, the echidnas in the win-shift condition again learned the task more rapidly than those in the win-stay condition. The results of a  $2 \times 5$  (condition  $\times$  block) factorial ANOVA confirm this, again showing a significant main effect of block ( $F_{4,8}=4.004$ ,  $P=0.045$ ) and a significant block  $\times$  condition interaction ( $F_{4,8}=4.693$ ,  $P=0.030$ ), but a non-significant main effect of condition ( $F_{1,2}=5.378$ ,  $P=0.146$ ).

Indeed it is not clear from Fig. 2 that the echidnas in the win-shift condition are learning the task at all. As is explained below, their performance is not very different from that we might expect from an echidna searching randomly in the test phase, if we assume that revisiting arms does not occur. In fact, the echidnas were very unlikely to revisit arms they had already tested in either phase of a trial. In the exposure phase, echidnas almost always visited all four arms systematically, starting with the one they were randomly oriented towards at the start of the trial, and then entering each adjacent arm in turn. We removed them after they had visited all four arms.

In the test phase echidnas were removed after they had consumed the food in both of the baited dishes. Given that they almost never returned to a dish they had visited, this means that they almost never made more than two errors per trial. If we assume that they do not revisit arms, then there are 24 possible patterns of arm visits (1234, 1243, etc.). If we assume that arms 1 and 2 are baited, then there are only 4 ways of searching randomly that will result in zero errors (1234, 1243, 2134, and 2143). By similar reasoning, there are 8 ways of making one error (1423, for example, since they are removed after they consume the food in arms 1 and 2), and 12 ways of making two errors. So if the echidnas search randomly except that they do not revisit arms, then they will (on average) make a total of 32 errors  $[(4 \times 0)+(8 \times 1)+(12 \times 2)]$  in 24 trials, or 1.33 errors per trial. The echidnas in the win-stay condition did not perform much better than this.

## Discussion

This experiment, in common with experiment 1, found that echidnas were better able to learn to avoid previously food-containing locations (to win-shift) than to learn to return to them (to win-stay) at short retention intervals. If this bias is a cognitive adaptation shaped by the foraging ecology of the echidna we might expect it to be specific to the use of a food reward and to short retention intervals. A test of this hypothesis, therefore, would be to examine whether the win-shift bias persists when using a long retention interval.

## Experiment 3

Experiments 1 and 2 have provided evidence that echidnas more easily learn a win-shift task than a win-stay task at short retention intervals using a food reward. We predicted this bias on the basis of the fact that the prey of echidnas (ants and termites) mount defences that keep foraging bouts at a given nest short. Since these defences do not immediately dissipate, and echidnas do abandon nests after a short foraging bout, we reasoned that they may have a bias to learn to avoid a rewarding location in the short term. Once the defences of a nest have dissipated, however, it would then be advantageous for an echidna to be able to return to this food-rich location. So, if the spatial learning mechanism of echidnas also reflects this aspect of the spatio-temporal distribution of their prey, we might expect them to be better able to learn to win-stay than to learn to win-shift at longer retention intervals.

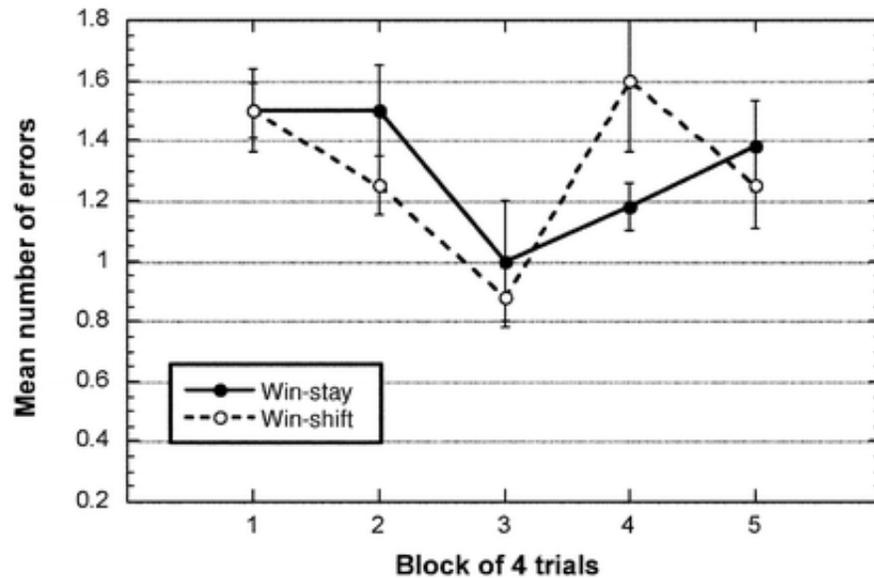
## Methods

Because of limits on the availability of subjects, two echidnas from experiment 2 and two new echidnas participated in this study. The two echidnas from the previous experiment were kept in the same win-stay or win-shift condition as in experiment 2, and the two new echidnas were randomly allocated, one to each condition. The two new female echidnas weighed 2.9 and 3.8 kg, respectively, at the beginning of the experiment.

The apparatus and procedure were identical to experiment 2 except that the retention interval was increased from 5 min to 90 min, and this resulted in our only being able to run one trial per day for each echidna. A retention interval of 90 min was selected because this was certainly long enough for the defences of all potential prey species to have dissipated.

## Results

The results were analysed in the same way as in experiment 2. As can be seen from Fig. 3, neither group appears to improve across the 20 trials of the experiment, with performance starting and ending at about the chance level of 1.33 errors per trial. This is confirmed by the ANOVA, which revealed no significant effects (block,  $F_{4,8}=2.44$ ,  $P=0.132$ ; condition,  $F_{1,2}=0$ ,  $P=1$ ; block  $\times$  condition,  $F_{4,8}=1.15$ ,  $P=0.401$ ).



**Fig. 3.** Experiment 3: mean number of errors as a function of trial block for echidnas in the win-shift and the win-stay conditions in a four-arm radial maze. *Error bars* represent  $\pm 1$  standard error. Performance remains at about chance level (1.33 errors/trial)

## Discussion

In this experiment we predicted that if the spatial memory mechanism of echidnas has been precisely shaped by the spatio-temporal distribution of its prey, then a long retention interval would result in a win-stay preference rather than the win-shift preference observed in the first two experiments. In contrast with this, the echidnas showed no evidence of successfully learning to win-shift or to win-stay, despite the fact that two of the echidnas had previously learnt the same strategy at a shorter retention interval. This suggests that the echidnas were simply unable to remember which locations they had visited (or had not yet visited) after 90 min.

## General discussion

The experiments reported in this article were motivated by a search for evidence of a new foraging ecology effect on spatial memory performance. The current study differs from those conducted previously because it examined the effect of exploiting a prey type that becomes aversive after a short foraging bout (rather than whether the prey can be depleted in a single visit), because it used a phylogenetically unusual species (echidnas), and because it examined whether the win-shift bias would reverse at long retention intervals. The results from experiments 1 and 2 parallel those found previously with nectar-feeding birds and extend the generality of the short-term win-shift bias. Experiment 3 represents a previously unexplored extension of the ecological approach to long retention intervals. We found no evidence of a win-stay bias at the long retention interval. There are a number of mismatches between our test situation and the natural environment of the echidna (the spatial scale over which they foraged, for example), which may account for failing to find such evidence. It is also possible, however, that echidnas (and hummingbirds and rats) have only evolved a short-term spatial memory strategy, or that win-shift behaviour at short retention intervals is not a foraging adaptation at all (Gaffan and Davies 1981). Deciding between these possibilities requires research that compares performance across a range of species (facing a variety of foraging constraints), in a range of tasks, at a range of delays (and possibly also varying the spatial scale and

nature of the reinforcer). The current experiments are a step in that direction.

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