



## Chickadees neither win-shift nor win-stay when foraging



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The win-shift versus win-stay distinction supposes that foraging animals use one of two movement rules when searching for food: win-stay to return to locations where they previously found food and win-shift to avoid locations where they previously found food. Win-shift and win-stay rules describe, for example, the behaviour of rats foraging in a radial arm maze, the behaviour of animals in delayed matching and nonmatching to sample tasks, and the behaviour of nectarivorous birds feeding on depleting and replenishing nectar sources. The present study investigated whether black-capped chickadees, *Poecile atricapillus*, searching for food use win-shift and win-stay rules in response to different reward contingencies. Chickadees first searched multiple spatially dispersed sites for food hidden randomly in these sites, then after several minutes returned to find these sites replenished in the win-stay condition, or empty and other sites baited in the win-shift condition. Birds performed no better than chance at returning to baited sites in the win-stay condition or avoiding previously baited sites in the win-shift condition. Instead, chickadees used preferred search patterns regardless of the win-shift or win-stay contingencies they experienced. Search sequences, however, showed greater stereotypy under win-stay than under win-shift conditions even though the locations of baited sites were determined randomly. Chickadees are year-round residents in relatively small home ranges and may forage using well-established movement rules that, in our experiments, led to neither win-stay nor win-shift behaviour. The stereotypy of search does, however, appear to be influenced by win-stay and win-shift foraging outcomes.

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The win-shift versus win-stay distinction is derived from the gambler's dilemma of whether to continue betting on the same outcome or shift to betting on a different outcome depending on the recent history of success (Worthy, Hawthorne, & Otto, 2013). It is a widely used paradigm in research on animal cognition, especially in foraging tasks, and is often invoked as a behavioural mechanism to account for movement rules while foraging. A win-shift bias, for example, has been described as an adaptive specialization of cognition (Sulikowski & Burke, 2012) and win-shift and win-stay strategies may be cognitive adaptations to the depleting or replenishing nature of a food source (Sulikowski & Burke, 2011). Win-shift and win-stay strategies are typically tested in a two-phase procedure. In phase A, animals are presented with a number of locations that contain food and they are allowed to search

until they have retrieved some or all of the food. After a delay, the animals return in phase B to search again. When the rewarded locations are the same in both phases, a win-stay strategy leads to success and when the rewarded locations differ between phases, a win-shift strategy is more successful.

Rats win-shift spontaneously, accurately and rapidly on the radial arm maze (Gaffan & Davies, 1981; Guitar & Roberts, 2015; Olton, Becker, & Handelmann, 1979; Olton, Handelmann, & Walker, 1981; Olton & Schlosberg, 1978; Roberts & Dale, 1981; Tsuda & Imada, 1989), but can also win-stay in response to the appropriate reward contingency (Evenden & Robbins, 1984; Guitar & Roberts, 2015; Means, 1988). Marmosets and mice also win-shift spontaneously while foraging (Locurto, Emidy, & Hannan, 2002; MacDonald, Pang, & Gibeault, 1994). In contrast, pigeons may be predisposed to win-stay and repeat their response to previously rewarded locations (Randall & Zentall, 1997). Avian nectarivores win-shift when foraging in the wild (Gill & Wolf, 1977). Nectar-feeding regent honeyeaters, *Anthochaera phrygia*, win-shift to avoid previously rewarded locations after short intervals and win-stay to return to the same rewarded locations after long intervals

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(Burke & Fulham, 2003). Sulikowski and Burke (2007) have demonstrated a win-shift bias specific to nectar food rewards that does not extend to invertebrate food rewards. Similarly, Healy and Hurly (1995) have shown a win-shift bias in foraging hummingbirds in the wild. Birds that forage on food resources that deplete slowly may use a win-stay strategy (Smith, 1974) while other birds that forage on resources that deplete quickly use a win-shift strategy (Kamil, 1978).

Black-capped chickadees, *Poecile atricapillus*, forage for foods that deplete after a single prey capture, such as insects, and foods that do not, such as clusters of berries, seed heads and fat from animal carcasses (Bent, 1946; Smith, 1991). Chickadees also store food and are able to remember the spatial locations of large numbers of caches (Sherry, 1984). We hypothesized that chickadees would flexibly adopt win-shift and win-stay strategies in response to reward contingencies encountered while foraging. We tested chickadees under both win-shift and win-stay conditions and quantified their use of each strategy in three separate experiments.

Chickadees searched for randomly dispersed food rewards in phase A and after a short interval searched again in phase B, with reward contingencies in phase B following either a win-shift or a win-stay rule. The number of searches birds were allowed to make in phase B was manipulated to vary the cost of a search error. Whether birds encountered nonrewarded sites in phase A was also manipulated to allow birds to self-select the sites that they would return to or avoid under win-stay or win-shift contingencies, respectively.

## GENERAL METHODS

### Birds

Fourteen black-capped chickadees were captured by Potter trap between September 2015 and November 2016 near the Western University campus in London, Ontario, Canada. Birds were housed individually on a 12:12 h light:dark cycle (light onset 0700 hours) and provided with food and water ad libitum except during brief periods of food restriction as described below. Food was powdered sunflower seeds mixed with powdered Mazuri Small Bird Diet (PMI Nutrition International, Brentwood, MO, U.S.A.).

Birds were divided into two groups: the win-shift group ( $N = 7$ ) and the win-stay group ( $N = 7$ ). The same 14 birds were used in all experiments; the win-shift group experienced the win-shift contingency in all three experiments and the win-stay group experienced the win-stay contingency in all three experiments. The win-shift group was tested beginning November 2015 and continued for several months until all experimental conditions were completed. The win-stay group was tested beginning November 2016 and all experimental conditions were likewise completed within several months. Previous studies have found no sex difference in spatial memory, food-caching behaviour, memory for cache sites or relative size of the hippocampus (Petersen & Sherry, 1996) and therefore sex of the birds was not determined.

Prior to testing, birds were given 2–3 h of food restriction and all testing occurred between 1000 hours am and 1300 hours.

### Testing Apparatus

Birds were tested in a  $2.7 \times 2.7$  m indoor room equipped with a one-way mirror to allow live behavioural scoring by an observer. Chickadees could fly freely in the testing room, which contained two 'trees' each comprising a branch supported vertically on a stand. Each tree had several smaller side branches. Small holes were drilled in the branches to create sites that could hold food and each site was labelled with a white marker. Tree 1 was 2 m in

height, had 14 side branches and contained eight holes. Tree 2 was 1.7 m in height, had six side branches and contained four holes. Birds' home cages were attached to the wall of an adjoining holding room. A  $0.2 \times 0.2$  m door in each cage could be opened remotely to admit a bird to the testing room (Fig. 1).

### Training

To ensure birds initially experienced finding food at all 12 locations on the trees, each bird completed seven training trials before the start of experiment 1. In each training trial, food-restricted birds, which had no access to food for 2–3 h prior to testing, were released into the testing room to search for pieces of sunflower seed. All holes were baited with a sunflower seed fragment (sieved through a 3 mm mesh) and plugged with a piece of knotted green yarn. Birds were given 10 min to find all of the seeds and then allowed to fly back to their home cages.

### Ethical Note

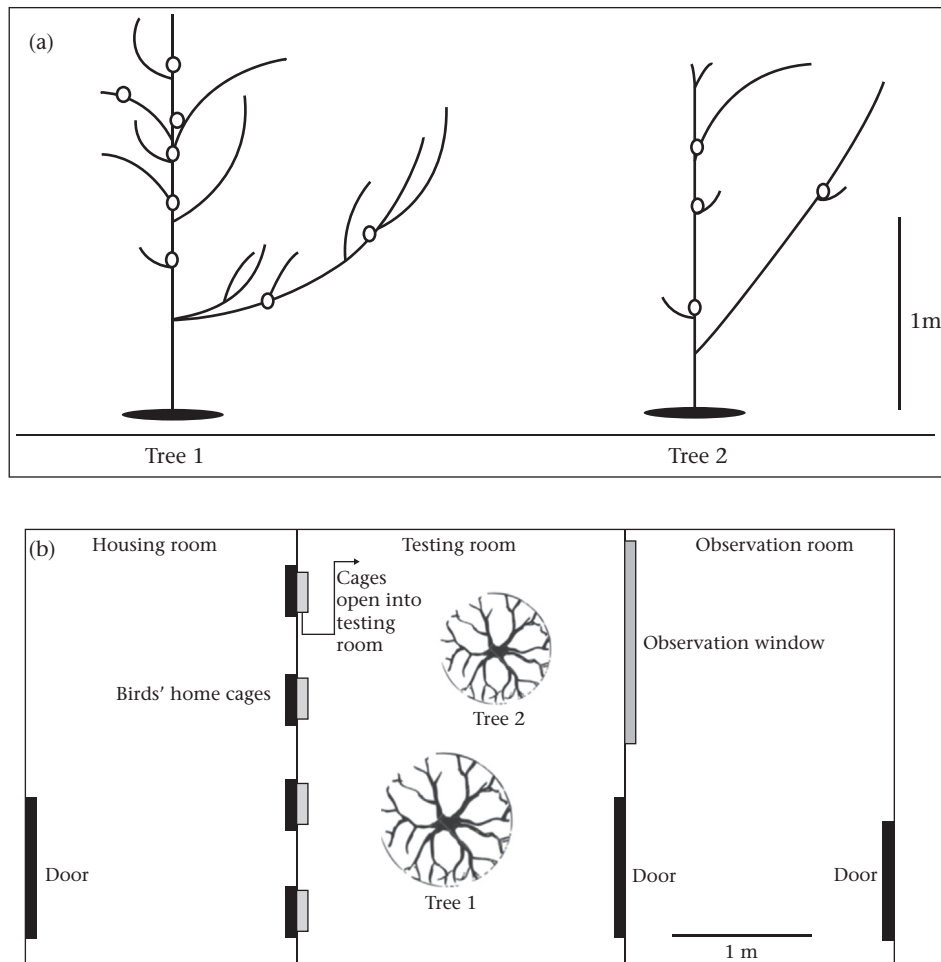
All animals were handled and tested according to the guidelines of the Canadian Council on Animal Care and the ASAB/ABS Guidelines for the Use of Animals in Research. This research was conducted under protocol 2015-019 approved by the Western University Animal Care Committee. Black-capped chickadees were held in captivity under Canadian Wildlife Service Scientific Permit CA 0236. Birds were individually housed in visual and acoustic contact with other chickadees. Daily observation sessions provided enrichment in the form of free flight in a large room containing natural tree branches on which birds searched for food. Food restriction of 2–3 h starting at 1000 hours (3 h following light onset at 0700 hours and morning feeding by the birds) is mild for chickadees. Following completion of the experiments described, all birds participated in a further study involving inhibition of adult hippocampal neurogenesis and were sacrificed for histological examination of brain tissue.

### Experiment 1

The purpose of experiment 1 was to train birds on a task in which perfect performance could be obtained using either a win-stay or win-shift search strategy. The procedure was adapted from radial arm maze win-stay or win-shift experiments and consisted of two phases. In phase A, birds searched the aviary for baited locations and then returned to their home cage. In phase B, birds were given another opportunity to search for baited locations in the aviary. The locations of food rewards in phase B could be predicted based on a win-stay reward contingency for the win-stay group or a win-shift reward contingency for the win-shift group. If, during phase B, birds are able to use the information acquired while foraging in phase A, then we would expect better than chance performance in phase B of the experiment. If chickadees preferentially use a win-stay or win-shift strategy, then we would expect one group to outperform the other in phase B of the experiment.

### Methods

Phases A and B were separated by 2–5 min. Between phases, the lights in the testing room were turned off and birds returned independently to their home cages. In both phase A and phase B, six of the 12 possible locations contained a seed fragment. Sites were baited pseudorandomly such that an equal proportion of holes were baited on each tree. In phase A, birds searched until they found all six baited locations or until 10 min had elapsed. In phase B, birds searched until they found the six baited locations, which were in the same locations as in phase A for the win-stay group and



**Figure 1.** (a) Trees 1 and 2. Circles indicate food locations. (b) Plan view of housing, testing and observation rooms.

in the six locations not baited in phase A for the win-shift group. Birds completed 18 trials. A search or a revisit was defined as eating the seed fragment found inside the hole, or removing the yarn and inserting the beak fully into the hole, or looking directly into a hole at a distance of less than approximately 2 cm. The measure of performance accuracy in phase B was the number of locations where food was found in the first six searches. Revisits to baited or unbaited sites were counted as incorrect searches.

Performance was analysed using repeated measures ANOVA with trial as a within-subject factor and group (win-shift or win-stay) as a between-subjects factor. When necessary because of violations of sphericity, Greenhouse–Geisser adjustments were made to degrees of freedom. The number of correct searches expected by chance in the first six searches was determined from the binomial distribution assuming 12 locations, six of which were correct, and six search attempts, sampling with replacement. The expected number correct was three for both win-shift and win-stay conditions. The observed mean number of correct searches was compared to the chance value using one-sample *t* tests.

### Results

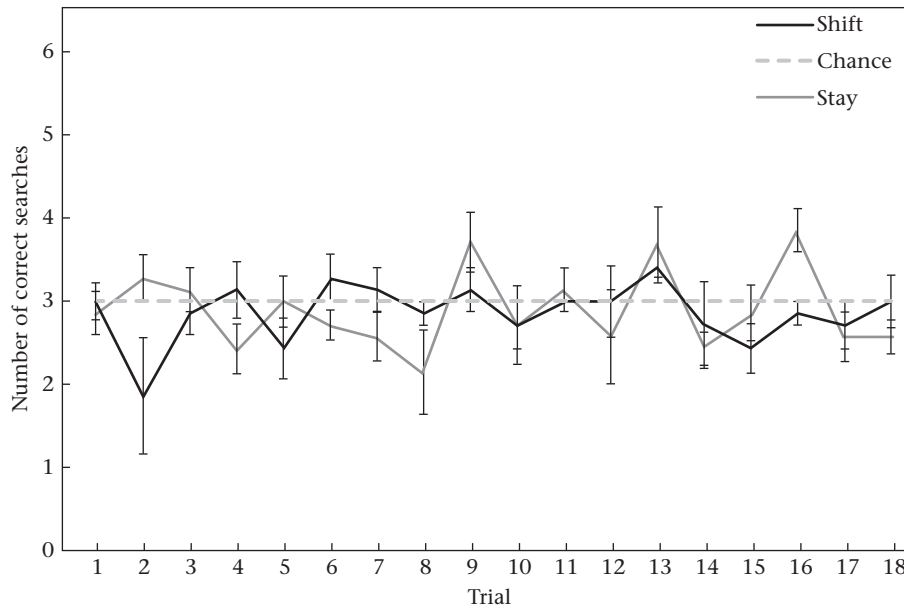
Neither the win-shift nor the win-stay group was more accurate than expected by chance in phase B (win-shift:  $t_{17} = 1.57$ ,  $P = 0.14$ ; win-stay:  $t_{17} = 0.83$ ,  $P = 0.42$ ). There was no significant difference in accuracy in phase B between the win-shift and win-stay groups ( $F_{1,12} = 0.003$ ,  $P = 0.96$ ), no significant effect of trial ( $F_{6,23,74.81} = 1.68$ ,  $P = 0.13$ ) and no significant interaction between trial and win-shift/win-stay condition ( $F_{6,23,74.81} = 1.83$ ,  $P > 0.10$ ; Fig. 2).

In phase A, birds could not know where food was to be found and neither the win-shift nor the win-stay group was more accurate than expected by chance (win-shift:  $t_{17} = 0.00$ ,  $P = 1.00$ ; win-stay:  $t_{17} = 0.81$ ,  $P = 0.43$ ). There was no significant difference in accuracy in phase A between the win-shift and win-stay groups ( $F_{1,12} = 0.54$ ,  $P = 0.48$ ), no significant effect of trial ( $F_{6,87,82.45} = 2.05$ ,  $P = 0.06$ ) and no significant interaction between trial and group ( $F_{6,87,82.45} = 1.86$ ,  $P = 0.09$ ; Fig. 3).

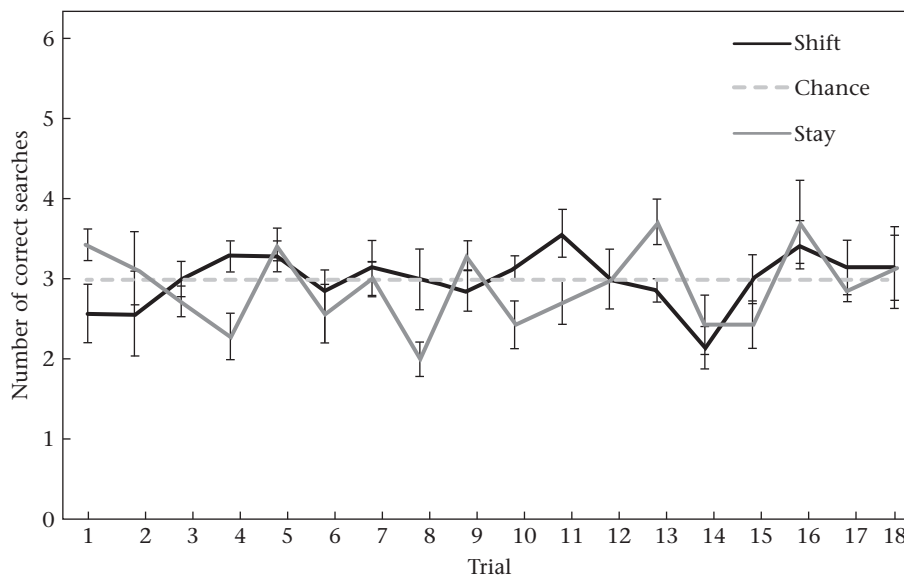
Birds made essentially no revisiting errors during their first six searches in phase A. In the win-stay condition, one bird made one revisiting error in its first six searches out of a total of 90 opportunities per bird to make a revisiting error (18 trials  $\times$  five searches). In the win-shift condition, four birds made one revisiting error each in their first six searches out of 90 opportunities each.

### Discussion

Even though the baited locations in phase B could be perfectly predicted from their locations in phase A, birds' performance in phase B did not differ from chance for either group. This suggests that black-capped chickadees are not influenced by memory for foraging outcomes in a recent previous bout of foraging while searching for food rewards in this experiment. This stands in contrast to their ability to avoid revisiting errors in the short term when searching in phase A. The win-stay and win-shift groups did not differ in performance in phase B, indicating that black-capped chickadees do not spontaneously adopt either a win-stay or a win-shift strategy.



**Figure 2.** Mean number of correct searches in the first six search attempts for the win-stay and win-shift groups in phase B of experiment 1. Error bars equal  $\pm 1$  SE of the mean.



**Figure 3.** Mean number of correct searches in the first six search attempts for the win-stay and win-shift groups in phase A of experiment 1. Error bars equal  $\pm 1$  SE of the mean.

In this experiment birds were able to do an exhaustive search of possible reward locations in phase B and the cost in time and energy of a search error was small. It is possible that chickadees could remember which sites were baited in phase A and could have used this information to direct their search in phase B, but instead used a systematic search strategy because of the relatively low cost of searching exhaustively.

### Experiment 2

In this experiment we modified the experimental design to increase the cost of errors and encourage birds to adopt either a win-stay or win-shift strategy. Like experiment 1, experiment 2 consisted of two phases. In phase A, birds searched until they found the baited sites, and in phase B, they searched for baited sites again

under either win-shift or win-stay reward contingencies. In phase B, however, we limited the number of searches birds could make to six, making exhaustive search of all locations in phase B impossible.

### Methods

The method was identical to experiment 1 except that, in phase B, birds were limited to only six searches. After the birds completed six searches, the lights were turned off in the testing room to halt searching and the birds returned to their home cages. Birds completed 10 trials.

### Results

Neither the win-shift nor the win-stay group was more accurate than expected by chance in phase B (win-shift:  $t_9 = 0.08$ ,  $P = 0.94$ ; win-stay:  $t_9 = 0.14$ ,  $P = 0.90$ ). There was no significant difference in

accuracy in phase B between the win-shift and win-stay groups ( $F_{1,12} = 0.03, P = 0.86$ ), no significant effect of trial ( $F_{4,94,59,28} = 1.72, P = 0.14$ ) and no significant interaction between trial and group ( $F_{4,94,59,28} = 2.16, P = 0.07$ ; Fig. 4).

In phase A, birds could not know where food was to be found and neither the win-shift nor win-stay group was more accurate than expected by chance (win-shift:  $t_9 = 0.113, P = 0.91$ ; win-stay:  $t_9 = 0.327, P = 0.80$ ). There was no significant difference in accuracy in phase A between the win-shift and win-stay groups ( $F_{1,12} = 0.008, P = 0.93$ ), no significant effect of trial ( $F_{5,48,65,86} = 1.49, P = 0.20$ ) and no significant interaction between trial and group ( $F_{5,48,65,86} = 1.19, P = 0.32$ ; Fig. 5). As in experiment 1, birds made very few revisiting errors in the first six searches in phase A. Two birds in the win-stay group made one revisiting error each and two birds in the win-shift group made one revisiting error each in 50 opportunities (10 trials  $\times$  five searches).

### Discussion

As in experiment 1, black-capped chickadees failed to adopt either a win-stay or a win-shift strategy despite repeated experience with reward contingencies that favoured these search strategies. Removing the opportunity to engage in an exhaustive search in phase B did not appear to influence the performance of the birds, suggesting that either the cost of errors was not a factor in their failure to adopt the appropriate search strategy or the cost of an error was not great even when the number of searches was limited to six in phase B.

Although the experimental design used in experiments 1 and 2 was adapted from the standard radial arm maze procedure, there is one notable difference, which is that in some radial arm maze experiments rats make their own choices of which maze arms to visit in phase A, rather than searching until they find rewarded locations as our birds did. It is possible that being presented with assigned instead of self-selected locations in phase A disrupts birds' ability to engage in the appropriate search strategy in phase B. Birds may be better able to encode spatial locations they have chosen themselves, because of their apparent salience to the bird, leading to better performance under both win-shift and win-stay conditions. Allowing birds to choose phase A sites themselves might lead to more successful search under win-stay conditions if birds learned to visit again in phase B the sites they preferred in phase A. Allowing birds to self-select phase A sites might also lead to better win-shift performance if birds are better able to continue a search

sequence across phases when they have initiated the sequence with sites they have chosen themselves.

### Experiment 3

In experiment 3 we modified our spatial search procedure so that birds chose their baited locations in phase A. This modification increased the similarities between our procedure and win-stay/win-shift procedures used in radial arm maze studies in which win-shift and win-stay behaviour is often observed.

### Methods

Experiment 3 used the same method as experiment 2 except that in phase A, all 12 locations were baited. Birds were allowed to find food at exactly six locations and consume the seed fragments they found before the lights were turned off and birds returned to their home cage. Birds completed seven trials.

### Results

In phase B, birds in the win-stay group performed significantly better than expected by chance whereas performance by birds in the win-shift group was significantly below chance (win-stay:  $t_6 = 10.68, P = 0.00$ ; win shift:  $t_6 = 4.70, P = 0.00$ ). There was a significant difference between the win-shift and win-stay groups in phase B ( $F_{1,12} = 22.49, P = 0.00$ ), no significant effect of trial ( $F_{4,42,53,05} = 0.468, P = 0.78$ ) and no interaction between group and trial ( $F_{4,42,53,05} = 1.09, P = 0.37$ ; Fig. 6).

Birds chose which holes to visit in phase A of experiment 3, and all choices were rewarded, so performance is not shown for phase A. As in experiments 1 and 2, birds made very few revisiting errors in phase A: no revisiting errors for the win-stay group and one revisiting error each by two birds in the win-shift group out of 35 opportunities (seven trials  $\times$  five searches).

### Discussion

For the win-stay group, choosing their preferred locations in phase A resulted in more correct searches in phase B than observed in experiments 1 and 2. For birds in the win-shift group, the locations they preferred in phase A were never the correct holes in phase B, resulting in lower numbers of correct searches than observed in experiments 1 and 2. Chickadees visited preferred locations, regardless of reward contingency. The significant difference in accuracy between win-stay and win-shift group occurred

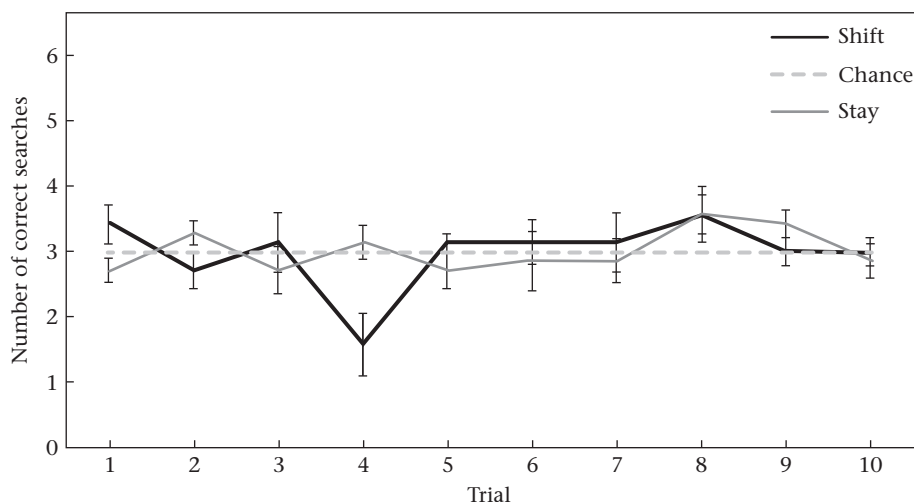
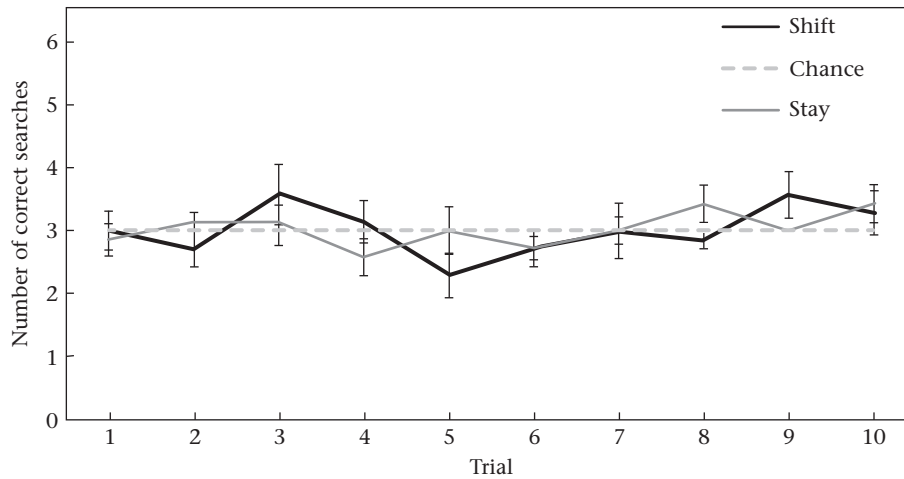
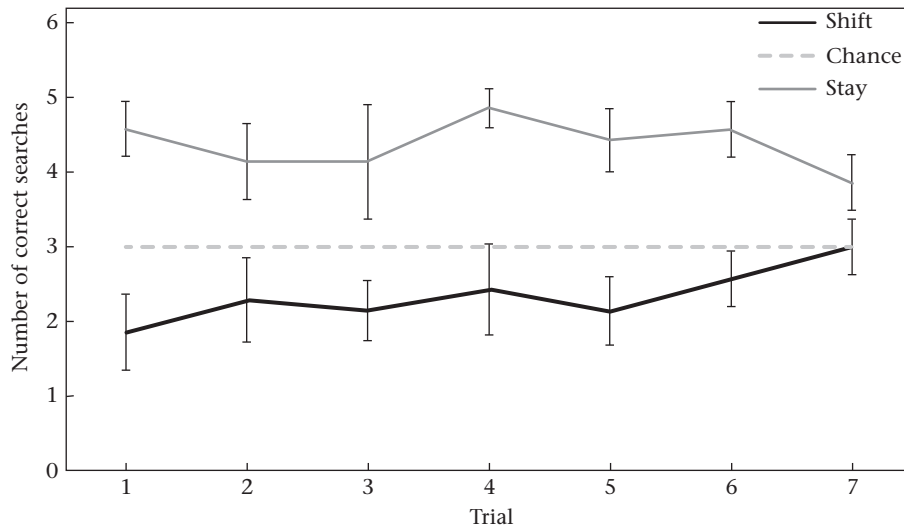


Figure 4. Mean number of correct searches in the first six search attempts for the win-stay and win-shift groups in phase B of experiment 2. Error bars equal  $\pm 1$  SE of the mean.



**Figure 5.** Mean number of correct searches in the first six search attempts for the win-stay and win-shift groups in phase A of experiment 2. Error bars equal  $\pm 1$  SE of the mean.



**Figure 6.** Mean number of correct searches in the first six search attempts for the win-stay and win-shift groups in phase B of experiment 3. In phase A, all 12 locations were baited and birds searched until they had taken food from any six. Error bars equal  $\pm 1$  SE of the mean.

because win-stay birds were rewarded for continuing to visit their preferred set of holes trial after trial, whereas win-shift birds were not.

#### Further Analysis of Search Sequences

Better than chance performance by win-stay birds and worse than chance performance by win-shift birds in experiment 3 might indicate that black-capped chickadees are able to search using a strategy based on recent foraging experience and show a preference for use of a win-stay strategy. Alternatively, these results can be explained by birds consistently choosing to search the same preferred locations, regardless of feedback from the win-stay and win-shift reward contingencies. This latter explanation would be consistent with the findings of experiments 1 and 2 in which birds failed to use previous foraging outcomes effectively to direct their search in phase B. We conducted further analyses to examine the relation between search in phases A and B of all three experiments.

Birds appeared to search locations in the trees in a preferred sequence that differed between birds. It is therefore likely that the accuracy of search in phase B of each experiment showed little

effect of experience in phase A, because search in phases A and B followed an individual preferred sequence, uninfluenced by the win-shift and win-stay contingencies. We used Kendall rank correlations to examine the relation between choices in phases A and B of each experiment.

#### Methods and results

For each bird in each trial we determined the Kendall rank correlation between the sequence of choices in phase A and the sequence of choices in phase B. We counted the number of significant positive and negative Kendall rank correlations for each bird and calculated the mean number of significant positive and negative correlations for win-shift and win-stay groups in experiments 1, 2 and 3. We determined the number of significant positive and negative Kendall rank correlations expected by chance by simulation, drawing holes at random from a set of 12 for experiments 1 and 2 and from a set of six for experiment 3. The mean number of significant correlations expected by chance for each experiment, assuming seven birds per group and 18 trials for experiment 1, 10 trials for experiment 2 and seven trials for experiment 3, was

calculated and the simulation was repeated  $10^6$  times to obtain the chance values shown in Fig. 7.

There were significantly more positive correlations between phases A and B than expected by chance for win-shift and win-stay groups in all experiments, with the exception of the win-shift group in experiment 2 (Fig. 7, Table 1). There were no more negative correlations than expected by chance. There were significantly more positive correlations between phases A and B for the win-stay group than for the win-shift group ( $F_{1,12} = 8.72, P = 0.01$ ). There was no difference in the number of significant positive correlations among experiments ( $F_{1,22,14.65} = 3.91, P = 0.06$ ), and no interaction between group and experiment ( $F_{1,22,14.65} = 0.18, P = 0.72$ ). There was no difference in the number of significant negative correlations between the win-shift and win-stay groups ( $F_{1,12} = 0.54, P = 0.48$ ), no difference in the number of significant negative correlations between experiments ( $F_{1,44,17.31} = 3.32, P = 0.07$ ) and no interaction between group and experiment ( $F_{1,44,17.31} = 0.77, P = 0.44$ ).

We also determined whether phase A search sequences were affected by win-shift and win-stay conditions by calculating Kendall's coefficient of concordance,  $W$ , across all phase A trials for each bird in each experiment. We compared the mean value of Kendall's  $W$  to the mean value expected by chance, determining the chance value by drawing random sequences of six phase A searches for the appropriate number of trials in each experiment, calculating the value of  $W$  for each bird and repeating this simulation  $10^6$  times. The mean value of Kendall's  $W$  was significantly greater than chance for all conditions of all experiments except for the win-shift condition in experiment 1 (one-sample  $t$  tests:  $t_6 > 2.59, P < 0.04$ ; Fig. 8). Birds in win-stay conditions had a significantly higher mean value of Kendall's  $W$  than birds in win-shift conditions ( $F_{1,12} = 10.83, P = 0.006$ ), indicating greater similarity in the sequence of phase A searches across trials for birds in win-stay conditions (Fig. 8). The difference between experiments that can be seen in Fig. 8 was also significant ( $F_{2,24} = 7.04, P = 0.004$ ), possibly because experiments 1, 2 and 3 differed in the number of

**Table 1**

One-sample  $t$  tests comparing the number of observed positive and negative Kendall rank correlations between phases A and B to the number expected by chance for the win-shift and win-stay groups in all experiments

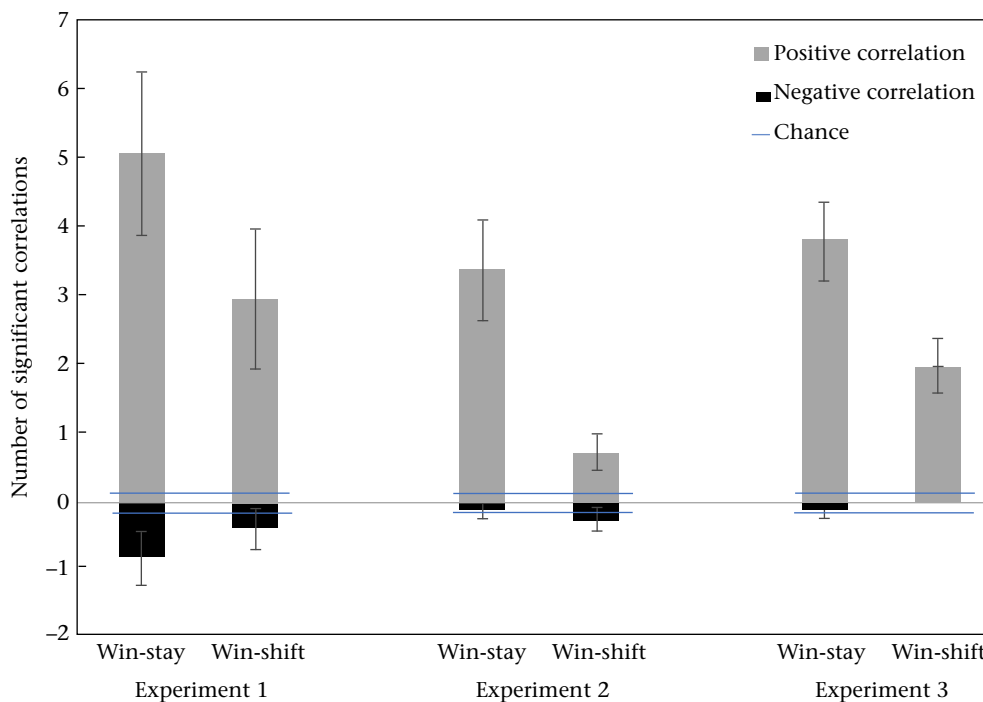
Correlation	Experiment	df	$t$	$P$
Win-shift Positive	1	6	2.72	0.03
	2	6	2.21	0.07
	3	6	4.45	0.004
Negative	1	6	0.94	0.38
	2	6	1.10	0.31
	3 <sup>a</sup>	–	–	–
Win-stay Positive	1	6	4.08	0.006
	2	6	4.45	0.004
	3	6	6.40	0.001
Negative	1	6	1.80	0.13
	2	6	0.42	0.69
	3	6	0.59	0.58

<sup>a</sup> Win-shift birds in experiment 3 showed no significant negative Kendall rank order correlations between phases A and B.

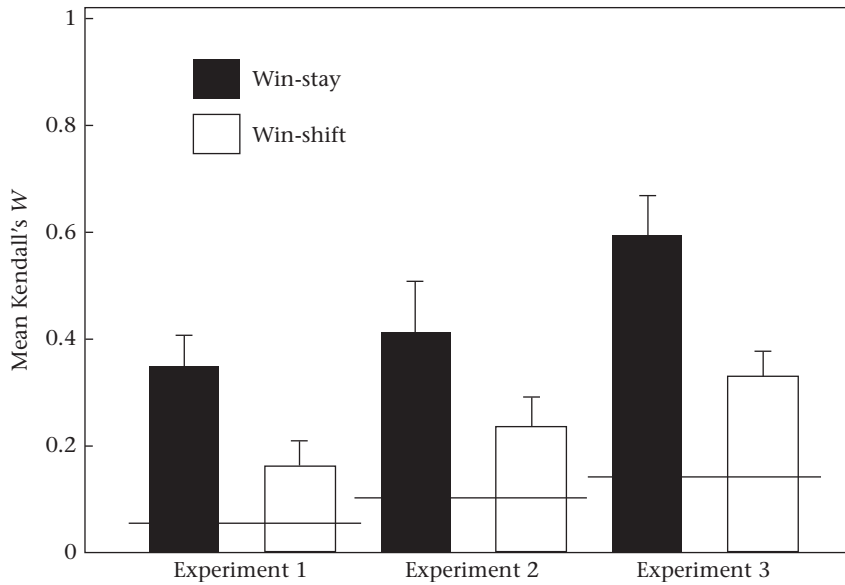
trials (18, 10 and 7, respectively) or due to birds' increasing experience with the testing conditions. There was no significant interaction between win-shift/win-stay conditions and experiment ( $F_{2,24} = 0.37, P = 0.693$ ). The number of significant Kendall's coefficients of concordance was also consistently greater than chance for both win-stay and win-shift conditions (Fig. 9), using the chance value for the number of significant  $W$ s obtained from the simulation described above. Because the number of significant Kendall's  $W$ s is a single value for each win-stay/win-shift condition in each experiment, it is not possible to compare this number statistically to the number expected by chance.

**Discussion**

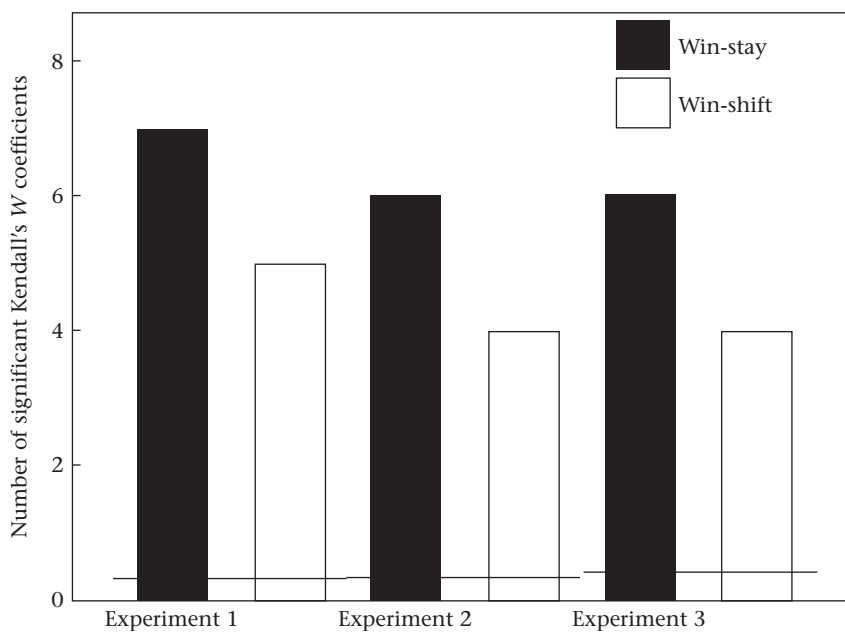
These results show that overall, birds tended to search the trees in similar sequences in both win-shift and win-stay conditions. There were, nevertheless, more significant correlations in win-stay



**Figure 7.** Mean number of significant Kendall rank order correlations ( $P < 0.05$ ) between the sequences of search in phases A and B for all three experiments. The total number of possible correlations equals the number of trials: 18 for experiment 1, 10 for experiment 2 and 7 for experiment 3. Errors bars equal  $\pm 1$  SE of the mean. Horizontal lines show the number of significant correlations expected by chance: experiment 1:  $\pm 0.1490$ ; experiment 2:  $\pm 0.0827$ ; experiment 3:  $\pm 0.1177$ .



**Figure 8.** Mean values of Kendall's coefficient of concordance,  $W$ , among phase A search sequences for all experiments. Horizontal lines show mean values expected by chance: experiment 1: 0.056; experiment 2: 0.100; experiment 3: 0.142. Error bars equal  $\pm 1$  SE of the mean.



**Figure 9.** Number of significant Kendall's coefficient of concordance,  $W$ , among phase A search sequences for all experiments. The maximum number of significant correlations equals 7, the number of subjects in the win-stay and win-shift groups. Horizontal lines show mean values expected by chance: experiment 1: 0.347; experiment 2: 0.348; experiment 3: 0.420. Error bars equal  $\pm 1$  SE of the mean.

conditions than in win-shift conditions, indicating that birds more closely repeated the phase A search sequence during phase B under the win-stay contingency.

## GENERAL DISCUSSION

Chickadee search strategies were for the most part insensitive to win-stay and win-shift reward contingencies in these experiments, even though chickadees forage on foods likely to promote both strategies. In experiments 1 and 2 they performed no better than chance at returning to previously rewarded sites in the win-stay condition or avoiding these sites in the win-shift condition. In

experiment 3, in which repeating their preferred search sequence would cause them to visit the same sites in phases A and B, they performed significantly above chance in the win-stay condition and significantly below chance in the win-shift condition. It is unlikely that chickadees do not possess the spatial working and reference memory abilities required to successfully win-shift or win-stay. It seems more likely that the cost of using a preferred search sequence was low enough that the birds did not use a possibly more effortful foraging strategy involving memory for the outcome of search at previously visited sites. Black-capped chickadees made very few revisiting errors during their phase A searches for baited sites, which requires memory for recent experience. Nevertheless,



they did not take recent experience into account when foraging bouts were separated by 2–5 min in their home cage. Instead, chickadees used individual search sequences to move among the sites on trees. In all experiments, birds in the win-stay condition showed a greater number of significant Kendall rank correlations between phases A and B than win-shift birds, indicating that they were affected by the reward contingency. Similarly, birds in the win-stay condition showed more significant Kendall coefficients of concordance among their phase A searches over multiple trials than birds in the win-shift condition, indicating that they repeated their phase A search sequences more precisely under win-stay conditions. Chickadees in our experiments appeared to forage according to preferred movement rules between sites where food was likely to be found. The win-stay contingency caused these movement rules to be repeated more consistently from one bout of searching to the next, both between phases A and B and across successive phase searches. This was the case even though the movement rules themselves were not rewarded under win-stay conditions because baited sites were determined at random for phase A of both experiments 1 and 2. Chickadees are not the only animals that do not show the expected response to win-shift and win-stay contingencies. Dogs (Macpherson & Roberts, 2010) and sheep (Hosoi, Swift, Rittenhouse, & Richards, 1995) fail to learn either win-shift or win-stay contingencies. Goats are strongly influenced by negative experience when foraging (Hosoi et al., 1995) and avoid unrewarded locations during subsequent foraging bouts (i.e. use a lose-shift strategy). Cows also adopt a lose-shift strategy to avoid previously unrewarded locations (Pfeiffer & Nowak, 2006). Motivation and testing conditions can play important roles in win-shift and win-stay responses. Rats consistently win-shift above chance in a radial arm maze (Tsuda & Imada, 1989), but acquire a win-stay response more readily than win-shift in the Morris water maze (Means, 1988). In contrast, mice learn a win-shift strategy more readily than a win-stay strategy when motivated to escape water (Locurto et al., 2002). Rainbow lorikeets, *Trichoglossus moluccanu*, are facultative nectarivores and show no preference for a win-shift or win-stay strategy (Sulikowski & Burke, 2011) and neither do noisy miners, *Manorina melanocephala*, when rewarded with invertebrates (Sulikowski & Burke, 2007).

Because prey can influence an animal's foraging strategy (Sulikowski & Burke, 2015), chickadees may have failed to respond to reward contingencies because of the food reward used in these experiments. Choice of foraging strategy in the wild might be determined not by current reward contingencies, but by longer-term experience with whether current food resources are replenishing or nonreplenishing. Although chickadees eat both animal and plant material, invertebrates make up about 70% of their diet in the wild and seeds and fruit about 30% of their diet (Bent, 1946; Smith, 1991). A different food reward, specifically invertebrate food, might produce a different result in the win-stay and win-shift conditions we used in these experiments. It is possible that birds simply did not learn that the location of food in phase B depended on where food was found in phase A under either the win-shift or the win-stay condition. If birds treated phases A and B simply as repetitions of a single condition in which food was distributed randomly on the trees, they would not be expected to show either win-shift or win-stay behaviour. Birds may have treated their return to their home cage as a period of replenishment of sites where food was sometimes found. We think this is unlikely, but this idea could be tested by manipulation of context to distinguish phase A from phase B. Manipulation of context can successfully serve as a cue to the location of food for rats (Roberts, Guitar, Marsh, & MacDonald, 2016). Finally, the influence of the win-stay and win-shift contingencies on the consistency of search sequences is perhaps the most interesting finding of these experiments. In

general, individual search sequences were very consistent under both win-stay and win-shift conditions. The win-stay contingency promoted more consistent search sequences, however, even though there was no relation between a bird's individual preferred search sequence and the locations where food was to be found in phase A of successive trials. Birds preferred to check for possible baited sites using a stereotyped search sequence and were more likely to do this under win-stay conditions, even though they did not use the win-stay contingency to go directly to baited sites in phase B. Birds may have encoded the win-stay and win-shift contingencies as food being found in roughly the same places or roughly not the same places without encoding the exact locations where food was found in phase A and instead increasing the consistency with which they repeated their preferred search sequence between phases A and B and across successive phase As. Subtle effects such as these on search strategy, occurring without any obvious immediate impact on foraging success, are relatively little explored and would repay further investigation of their cause and possible function.

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