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Food-specific spatial memory biases in an omnivorous bird

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The tendency of nectarivorous birds to perform better on tasks requiring them to avoid previously rewarding locations (to win–shift) than to return to them (win–stay) has been explained as an adaptation to the depleting nature of nectar. This interpretation relies on the previously untested assumption that the win–shift tendency is not associated with food types possessing a different distribution. To test this assumption, we examined the specificity of this bias to different food types in an omnivorous honeyeater, the noisy miner (*Manorina melanocephala*). As predicted, we found that the win–shift bias was sensitive to foraging context, manifesting only in association with foraging for nectar, not with foraging for invertebrates.

Keywords: cognitive adaptations; win-shift; spatial memory

1. INTRODUCTION

To understand how evolution shapes cognition, the ecological approach investigates the selective pressures responsible for, and the adaptive value of, observed variations in cognitive abilities. Much of this research has focused on the evolution of spatial memory abilities in response to various ecological pressures (reviewed by Sherry 2006).

One line of investigation has examined functional biases in how spatial information can be used. Various animals have been tested in laboratory settings for their tendency (or ability to learn) to either avoid previously rewarding locations (to win–shift) or return to such locations (to win–stay). Differential performances on these tasks have often been interpreted with respect to the animal's foraging ecology. Nectar is a food resource with a unique spatio-temporal distribution. Under natural conditions, the spatial location of the flower remains constant and, once visited by a forager, will probably be completely depleted of nectar (Kamil 1978). The tendency of nectarivorous species, including various birds (Cole *et al.* 1982; Healy & Hurly 1995; Burke & Fulham 2003) to win-shift has been interpreted as an evolved adaptation to this distribution.

This theory relies to some extent on a largely untested assumption that these same biases are not associated with foods possessing other distributions. One problem is that a variety of non-nectar feeding species have also shown a win–shift bias when tested under laboratory conditions (Olton & Schlosberg 1978; Laughlin & Mendl 2000; Burke *et al.* 2002). While adaptive explanations have been given to explain these results, more compelling evidence would come from demonstrating that the observed win–shift bias is unique to spatially stable, depletable resources and not associated with foods possessing other distributions.

This study examined whether the win–shift bias was food specific, by testing an omnivorous species. The noisy miner (Aves: Meliphagidae, *Manorina melanocephala*) exploits the nectar of a wide variety of plants and consumes a highly varied invertebrate diet (Barker & Vestjens 1984). This variation makes it difficult to hypothesize about the exact distribution of potential prey items, but such prey would be unlikely to share the unique spatio-temporal distribution of nectar. We predicted that the win–shift advantage found in other nectar-feeding birds would manifest in the omnivorous noisy miner, but only in association with foraging for nectar. We predicted no bias associated with invertebrates, and therefore initial chance-level performance for both the shift and the stay invertebrate groups and no difference in performance between these groups.

2. MATERIAL AND METHODS

(a) *Subjects*

Data were collected in August (experiment 1) and November (experiment 2) of 2006 at Macquarie University, Sydney Australia. Subjects were 16 wild-reared noisy miner birds (*M. melanocephala*) of unknown age and sex. Subjects were kept and tested individually in adjacent wire mesh cages measuring approximately 3 m^3. The aviaries were outdoors, so natural temperature fluctuations and light/dark conditions prevailed.

(b) *Apparatus*

Four feeders were arranged at the corners of a 90 cm (experiment 1) or 180 cm (experiment 2) sided vertical square on the front wall of each cage. Each feeder consisted of a balsa wood box (4×4×2 cm) housing a lidded plastic well that would potentially contain the food reward. The balsa wood box remained closed outside of testing and during the retention intervals, and birds were free to explore it but unable to obtain food rewards at these times.

(c) *Procedure*

Prior to testing, samples of the food type to be used in the experiment were placed in the experimental feeders at the time of the daily feed. The birds explored the feeders and learnt how to open the lids of the plastic wells. Testing commenced once birds were readily opening these lids immediately after the food was placed. To avoid influencing the birds' subsequent shift/stay behaviour, food was placed in all four feeders and only once per day during this period.

Birds were given up to three trials per day during experiment 1 and two trials per day during experiment 2, with a minimum intertrial interval of 45 min. Birds took an average of 10 days to complete each experiment (18 trials for experiment 1 and 12 trials for experiment 2) and this did not differ between the groups. Both food type (nectar and invertebrates) and win condition (win–shift and win–stay) were varied between subjects, giving four birds in each experimental group (shift/nectar, stay/nectar, shift/invertebrates, stay/invertebrates). Individuals were maintained in the same group for each experiment.

Each trial consisted of an exploration phase and a test phase separated by a 5 min retention interval. For the exploration phase, two of the four feeders were baited with the appropriate food reward (0.3 ml of a 30% w/v sucrose solution for birds in the nectar condition and a dead mealworm for birds in the invertebrate condition). During baiting (in both phases), the experimenter dummy-baited all feeders inside the wooden boxes to obscure the birds' view. The feeders to be baited were selected pseudo-randomly with the restrictions that the six possible combinations of rewarding feeders occurred with equal frequency and none of the feeder contained a reward in the exploration phase more than three trials in a row. This phase was deemed over when the bird had inspected all four feeders at least once and left the array to perch elsewhere in the cage. Following the 5 min retention interval, either the same two feeders (win–stay condition) or the other two feeders (win–shift condition) were baited and presented for the test phase. During this phase, subjects were only allowed to open the lids of

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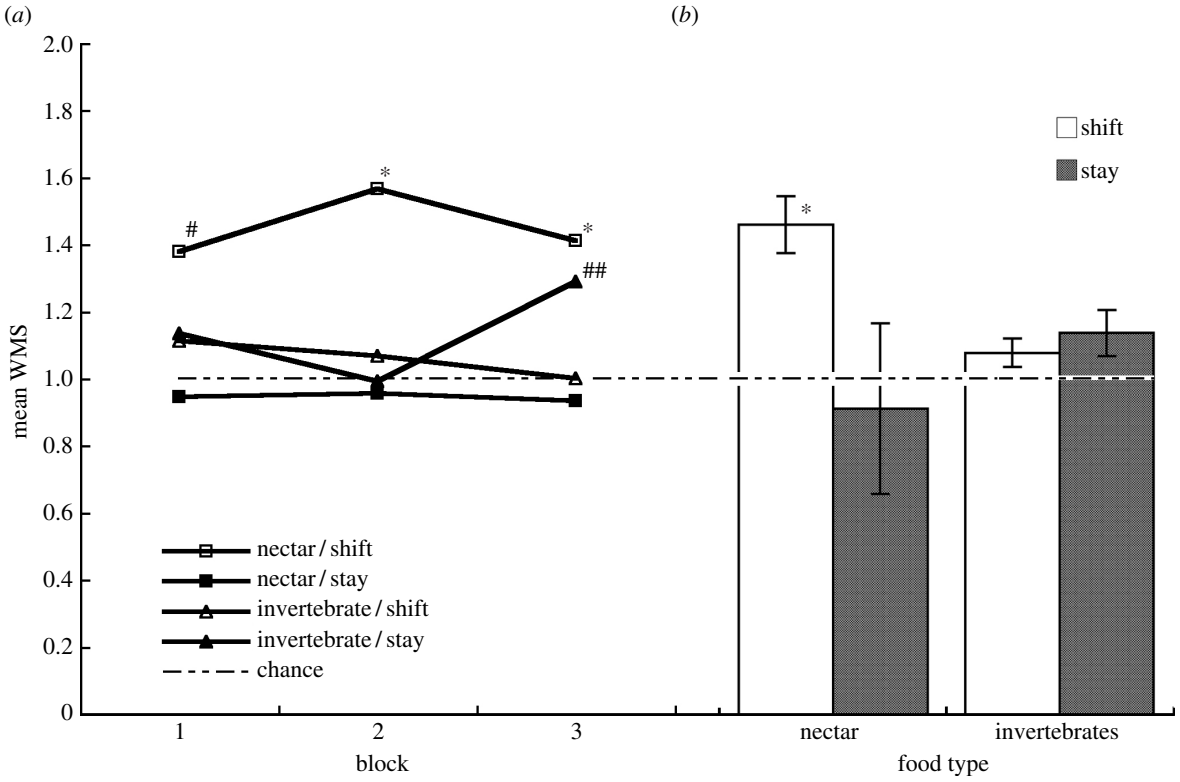

Figure 1. The performance in terms of WMS (± s.e.) of each group of birds ($n=4$ in each of the four conditions) presented (*a*) over three blocks of six trials and (*b*) over all 18 trials of experiment 1. *indicates performance that is significantly above chance as per a one-tailed (for nectar shift) or two-tailed one-sample *t*-test against a score of 1, ($p<0.05$). #$p=0.055$, ##$p=0.071$.

two feeders before being chased off by the experimenter. If either phase exceeded 10 min, the trial was aborted. The number of rewarded feeders visited in the test phase was scored such that each subject received a score of 0, 1 or 2 for each trial.

(**d**) ***Statistical analysis***

Since the probability of finding one, two or zero baited feeders in the test phase was unequal, a weighted mean score (WMS) for each subject was calculated according to the formula

$$\mathrm{WMS}=\frac{\left(\frac{1}{P_1\cdot N_1\cdot 1}\right)+\left(\frac{1}{P_2\cdot N_2\cdot 2}\right)+\left(\frac{1}{P_0\cdot N_0\cdot 0}\right)}{\left(\frac{1}{P_1\cdot N_1}\right)+\left(\frac{1}{P_2\cdot N_2}\right)+\left(\frac{1}{P_0\cdot N_0}\right)},$$

where $P_{1,2,0}$ denotes the probability of a bird finding one, two or zero baited feeders in the test phase, respectively and $N_{1,2,0}$ denotes the number of trials in which a bird did actually find one, two or zero baited feeders in the test phase, respectively. As the probability of finding one baited feeder alone was four out of six and the probability of finding either two or zero baited feeders was one out of six, the above formula is equivalent to:

$$\frac{(N_1+8N_2)}{(N_1+4N_2+4N_0)}.$$

3. RESULTS

(a) *Experiment 1*

Weighted mean scores were initially calculated for each subject in blocks of three, six and nine trials, respectively. GLM repeated measures ANOVAs were conducted on the resultant datasets (with food type and win condition as between-subjects factors and block as a within-subjects factor with either 6, 3 or 2 levels accordingly). In all cases, there were no significant effects or interactions involving block (all Fs <1).

A GLM univariate ANOVA conducted on the WMS for all 18 trials for each bird (food type and win condition as fixed factors) found an interaction approaching significance ($F_{(1,12)}=4.717$, $p=0.051$) between these factors (figure 1*b*). *Post hoc* independent samples *t*-tests were used to examine the effects of food type within each win condition and vice versa. A one-tailed test was used to test the *a priori* prediction that performance in the shift/nectar group would exceed that in the stay/nectar group. For all other comparisons, two-tailed tests were applied. Superior performance was found in the shift/nectar group when compared with the stay/nectar group ($t_6=2.049$, $p=0.043$) and the shift/invertebrate group ($t_6=4.015$, $p=0.007$). There were no other significant differences between groups (all $t<1$).

(b) *Experiment 2*

In experiment 1, neither invertebrate group performed significantly above chance overall, so one possible explanation for the absence of a bias is a floor effect. To facilitate performance, the distance between the feeders was doubled in experiment 2 to increase the salience of the spatial cue.

WMS were initially calculated in blocks of three and six trials and repeated measures ANOVAS (with the same variables listed for experiment 1) were conducted. There were no main effects of block (all Fs <1), although as a two-level factor block interacted with food-type ($F_{(1,12)}=5.255$, $p=0.041$) as performance decreased in the invertebrate groups from block 1 to block 2, but increased in the nectar groups (figure 2*a*).

A univariate ANOVA (food type and win condition as fixed factors) conducted on the WMS for all 12 trials found a highly significant interaction ($F_{(1,12)}=10.303$, $p=0.007$) between these factors and a main effect of condition ($F_{(1,12)}=7.154$, $p=0.02$) most likely brought about by the interaction (figure 2*b*).

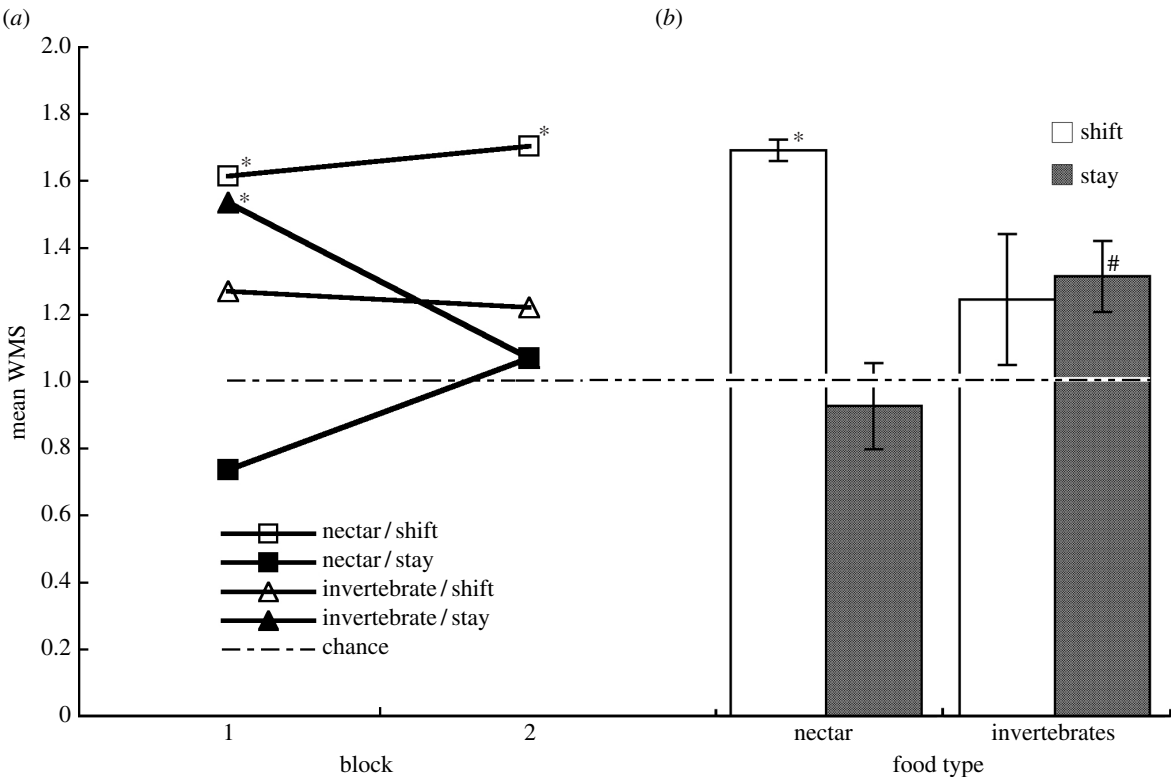

Figure 2. The performance, in terms of WMS (± s.e.) of each group of birds ($n=4$ in each of the four conditions) presented over (*a*) two blocks of six trials and (*b*) all 12 trials of experiment 2. *indicates performance that is significantly above chance as per a one-tailed (for nectar/shift) or two-tailed one-sample *t*-test against a score of 1, ($p<0.05$), #$p=0.060$.

Post hoc independent samples *t*-tests were applied as in experiment 1 and revealed significantly better performance in the shift/nectar group when compared with the stay/nectar group ($t_{(6)}=5.761$, $p<0.001$) and no difference in performance between the invertebrate groups ($t_{(6)}<1$). There was also somewhat better performance, though not significantly so, in the shift/nectar group compared with the shift/invertebrate group ($t_{(6)}=2.239$, $p=0.066$) and in the stay/invertebrate group when compared with the stay/nectar group ($t_{(6)}=2.326$, $p=0.059$).

4. DISCUSSION

In this study, we tested the tendency of an omnivorous bird, to win–shift or win–stay in response to two distinct food types; nectar and invertebrates. In both experiments, as predicted, an initial win–shift tendency manifested in the nectar-rewarded conditions, with no apparent bias in invertebrate groups, supporting the interpretation of these biases as evolved adaptations to the distribution of nectar.

The nectar/shift groups performed above chance during all blocks of both the experiments suggesting that the observed shift tendency was either learnt very quickly (within the first few trials of experiment 1 and then maintained during the three months between the experiments) or may represent a pre-experimental bias. The latter interpretation is supported by previous demonstrations of spontaneous shift biases in other nectarivorous birds (Wunderle & Martinez 1987; Healy & Hurly 1995; Burke & Fulham 2003). Although the nectar/shift bias appears spontaneous, nectar/stay birds do not perform significantly below chance and this is most likely due to some sensitivity to the stay contingency in this group. If there was no initial bias at all, performance in both groups would be similar at the start of experiment 1 and this is clearly not the case. It seems most likely then that the learning which has occurred has been superimposed onto an initial shift bias. In the invertebrate groups there was, as predicted, no initial or overall bias and, if anything, there was a learning advantage for the stay task over the shift task in these groups.

Whether these, and other reported spatial memory biases, represent an evolved cognitive adaptation or the results of experience (or indeed an interaction between the two) have been an area of past debate (Wunderle & Martinez 1987). Captive-reared adult regent honeyeaters, however, a close relative of the miner, exhibited adaptive spatial memory biases in spite of having had no prior experience of the natural distribution of nectar (Burke & Fulham 2003), providing evidence against a purely experiential account of the data, at least in this family of birds.

This is the first study to demonstrate that the win–shift bias is food specific. The results also imply that the nectar/shift biases reported here and elsewhere are a response to some intrinsic quality of the food, for example, taste or nutritional content. Further investigations are now required to determine the mechanisms by which such factors might be influencing cognition and behaviour.

All research was conducted with the approval of the Macquarie University Animal Ethics committee (protocol 2005/01) and complied with the NSW Animal Research Act 1985.

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