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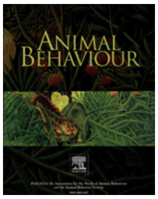

Win shifting in nectarivorous birds: selective inhibition of the learned win-stay response

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A variety of nectarivorous species have demonstrated a bias to ‘win-shift’ (shift away from/avoid locations that have recently yielded food, as opposed to ‘win-stay’ behaviour where the animal returns to such locations). Since recently exploited flowers contain no nectar, the win-shift bias is a candidate for an adaptive specialization of cognition. This bias tends to manifest as faster learning and/or better performance on a win-shift than a win-stay task. In standard win-shift/win-stay tasks (multiple two-phase trials where animals first find rewards in particular locations, and must subsequently avoid, or return to, such locations) noisy miners, *Manorina melanocephala*, and rainbow lorikeets, *Trichoglossus haematodus*, developed patterns of revisits/errors in the exploration phases that corresponded to the spatial contingency they experienced in the test phases: birds reinforced to shift revisited locations in the exploration phase that were unrewarded; birds reinforced to stay revisited rewarded ones. This was true even for birds that failed to shift or stay appropriately in the test phase itself. This suggests that the poorer performance of nectarivorous birds in win-stay than win-shift tasks may not be a consequence of an inability to learn the win-stay contingency. Our results suggest that these birds are equally sensitive to the win-shift and win-stay contingencies. This implies that, if the win-shift bias previously reported in nectarivorous birds is an example of a cognitive adaptation to the depleting nature of nectar, then the specially adapted mechanisms may have more to do with inhibition of the win-stay response than insensitivity to the win-stay contingency.

Many nectarivores engage in ‘win shifting’, the tendency to avoid, rather than return to, recently rewarded locations. It has been observed in wild avian nectarivores (Gill & Wolf 1977; Kamil 1978) and manifests experimentally (Cole et al. 1982; Wunderle & Martinez 1987; Burke & Fulham 2003; Sulikowski & Burke 2007) as an initial shift bias coupled with a learning advantage of shift over stay contingencies. The authors listed above have suggested that the tendency to shift may be an adaptation to the depleting nature of nectar: a flower once visited is an unprofitable place to revisit in the immediate future. The shift bias can reverse to a stay bias after sufficient time has elapsed for a flower to replenish its nectar (Burke & Fulham 2003), and is sensitive to foraging context, manifesting with nectar but not invertebrate rewards (Sulikowski & Burke 2007). A bias to win-shift under appetitive motivation has also been found in a variety of non-nectarivorous species including rats, *Rattus norvegicus* (Olton & Schlosberg 1978), pigs, *Sus scrofa* (Laughlin & Mendl 2000) and echidnas, *Tachyglossus aculeatus* (Burke et al. 2002). Various species-specific adaptive arguments have been put forward to explain these results (although see Gaffan & Davies 1981, 1982 for an alternative perspective).

The typical way to test for a shift bias uses multiple trials, each with an exploration and a test phase. In the exploration phase the animal either freely explores a series of locations, finding food rewards in half of these (Burke & Fulham 2003; Sulikowski & Burke 2007), or undergoes a forced exploration procedure in which it is exposed only to rewarded locations (Cole et al. 1982). After a short retention interval the animal is presented with the locations again (including additional unexplored locations in the case of the forced exploration procedure) to see whether it is more likely, or better able to learn, to search in the previously rewarded (win-stay) or previously unrewarded (win-shift) locations. There are multiple potential mechanisms underpinning successful performance in these tasks (terms such as attention, encoding, retention and integration could be used to describe such hypothesized processes) and any one or combination of these may have been shaped by evolution to produce the shift bias seen in nectarivores. Relatively poor performance from nectarivores in stay compared to shift tasks

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could be attributed, for example, to an attentional bias towards locations in which food has not previously been found, resulting in birds being more likely to ‘notice’ a shift, rather than a stay contingency. Alternatively, birds may only encode those locations in which food has been found (failing to retain any information about unrewarded locations) and rely on a tendency to search in apparently novel locations to produce the win-shift bias. At this stage, however, little is known about the cognitive mechanisms responsible for the observed bias to win-shift and so the above examples are purely hypothetical.

We tested two nectarivores, the noisy miner, *Manorina melanocephala*, and rainbow lorikeet, *Trichoglossus haematodus*, in a win-shift/win-stay paradigm. For this study, we were concerned with the effect of reinforcement contingency (whether rewards were present in the win-shift or win-stay locations in the test phases) on the behaviour of birds in the exploration phases of trials only. The performances of the birds in the test phases of these trials are reported elsewhere (Sulikowski & Burke 2007; Sulikowski & Burke 2011a).

Initially, we aimed to determine whether systematic differences in behaviour in the exploration phases might account for differences in performance in the test phases of win-shift/win-stay tasks. Sulikowski & Burke (2007) reported a shift bias for noisy miners rewarded with nectar, but no bias for birds rewarded with invertebrates. This was originally interpreted as a nectar-specific bias to win-shift (avoid recently rewarded locations), a potential adaptation to the depleting nature of nectar. If nectar-rewarded birds behaved differently from invertebrate-rewarded birds in the exploration phases, this may have exposed the two groups of birds to different information (and thus different learning opportunities), influencing their performance in the test phases. For example, if only nectar-rewarded birds tended to make many more revisits to the rewarded than the unrewarded locations, during the exploration phase, a tendency to avoid the more familiar locations would manifest as the observed win-shift bias. If invertebrate-rewarded birds had the same tendency to avoid more familiar locations but revisited rewarded and unrewarded feeders equally often, this would account for the lack of a shift bias seen in this group of birds. Discounting differences in exploration phase behaviour related to reward type would therefore strengthen the case for interpreting nectar-specific win-shift biases as potential adaptations to the depleting nature of nectar. In the current paper, therefore, we present analyses of search behaviour exhibited during the exploration phases of shift-stay tasks, completed by noisy miners searching for either a nectar or an invertebrate reward. We also present the same analyses applied to search behaviour of rainbow lorikeets in a similar experiment, for comparative purposes.

METHODS

Subjects

Subjects were 16 noisy miners and 12 rainbow lorikeets (age and sex not known). The miners were trapped and held in captivity for several months before testing. The lorikeets were reared in captivity. Birds were held and tested individually in outdoor cages measuring 3 × 3 × 3 m.

Ethical Note

Data were collected with the approval of the Macquarie University Animal Ethics Committee under approval numbers 2005/001 and 2007/035 and data collection complied with the Animal Research Act 1985, Animal Research Regulation 2005 and The Code of Practice in New South Wales. Permission to trap, hold and release wild noisy miners was granted by National Parks and Wildlife Service NSW under licence number S12057.

Water was provided ad libitum, and the daily food, which consisted of Wombaroo Lorikeet and Honeyeater mix (and mealworms for noisy miners, and apple for rainbow lorikeets) was provided at the completion of test sessions. Food deprivation was not used. The cages were fitted with leafy branches for perching.

Noisy miners were trapped using a walk-in cage baited with flowers, cake crumbs or mealworms. The trap was visually monitored at all times and trapped birds were immediately transported within the covered trapping cage to the holding/test aviaries. Birds were always trapped within a few minutes’ walk of the aviaries. Noisy miners are active breeders at most times of the year, so all trapped birds were visually inspected for a brood patch (indicating they were a nesting female). Any birds with a brood patch were released immediately. As noisy miners breed co-operatively, with several nonbreeding females and males feeding at each nest, the removal of a small number of nonbreeding females or males from a territory is not detrimental to breeding activities. At the completion of the study the noisy miners were banded (using standard metal and coloured plastic bands, approved by the Australian Bird and Bat Banding Scheme) and released at the sight of capture. Anecdotal observations in subsequent months and years confirmed that released birds successfully reintegrated into their social groups.

The rainbow lorikeets were loaned from Hunter Valley for the duration of the study. They were transported to and from the zoo in timber bird transport boxes, in an air-conditioned car. The birds were on loan for approximately 5 months and during this time each bird spent about 2 months housed individually while it was undergoing testing (moving birds from group housing to individual housing for testing each day would have been unacceptably disruptive) and the remainder of the time housed in a cage with several other birds. Although housed individually during testing, rainbow lorikeets were not socially isolated during this period. They were kept adjacent to other rainbow lorikeets, separated only by metal mesh and so maintained vocal, visual and (even limited physical) contact with other birds through the mesh. Noisy miners were also housed individually throughout their time in captivity (the potential for aggression prevents housing them in groups) but were able to maintain the same contact with conspecifics as described above.

Apparatus

The miners’ feeders consisted of opaque plastic wells (approximately 1 ml capacity) fitted inside small balsa wood boxes (4 × 4 cm and 2 cm high) that were permanently affixed to the front wall of each bird’s cage. The outside wall of each box was missing so the wells could be baited from the outside of the cage (empty wells were dummy baited). Once the wells were baited the experimenter removed the boxes’ lids, allowing the test bird access to the feeders. Each well had a flip-top lid, which birds were able to open, so that a bird could not see whether a feeder contained food before visiting it (previous studies presenting a combination of baited and unbaited feeders have provided no evidence that birds can detect baits via smell, Sulikowski & Burke 2010a, 2011b). The rainbow lorikeets’ feeders consisted of a larger plastic well (1.5–2 ml) attached to a hook. The lids of these feeders always fell closed, making visited feeders visually indistinguishable from unvisited feeders. The feeders were hooked on the front wall of each cage at the beginning of each phase of a trial and removed thereafter.

The baits used in testing were a mealworm (*Tenebrio molitor* larva, invertebrate-rewarded condition) and 0.3 ml of a 30% w/v

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sucrose solution (nectar-rewarded condition) for the miners and 0.4 ml of the same sucrose solution for the lorikeets. These baits were sufficiently meagre that birds tended to empty all feeders on the initial visit. Birds learnt how to flip the lids via free exploration of baited feeders with lids propped partially open.

Procedure

Both species received similar trials. Each trial consisted of an exploration phase and a test phase separated by a retention interval. In each exploration phase birds were presented with an array of feeders (four for the miners, six for the lorikeets), half of which were baited (Fig. 1). For both species the locations of baits was chosen such that any individual feeder would contain a bait during the exploration of exactly half the trials (and be unbaited for the other half of trials), and the particular feeders baited in the exploration of particular trials was the same for shift-reinforced as for stay-reinforced birds. Birds freely explored the array and consumed the baits. Once a bird had eaten all the baits and left the array voluntarily (or after a maximum of 12 visits for the lorikeets) the retention interval commenced. For noisy miners, the lids of the boxes were replaced so that birds had no access to the plastic well inside during the retention interval, and for rainbow lorikeets the feeders were removed during the retention interval. After the retention interval the feeders were rebaited and replaced for the test phase. For birds being reinforced to ‘win-stay’ the baits were placed in the same feeder locations as in the exploration phase; for ‘win-shift’ birds the baits were placed in the previously empty feeder locations. The shift/stay contingency was manipulated between subjects for both species. During the test phases birds were only allowed as many visits as there were baits present (two for the miners, three for the lorikeets). For each species, the locations of the feeders were held constant throughout the experiment, but which of these feeders were baited varied from trial to trial.

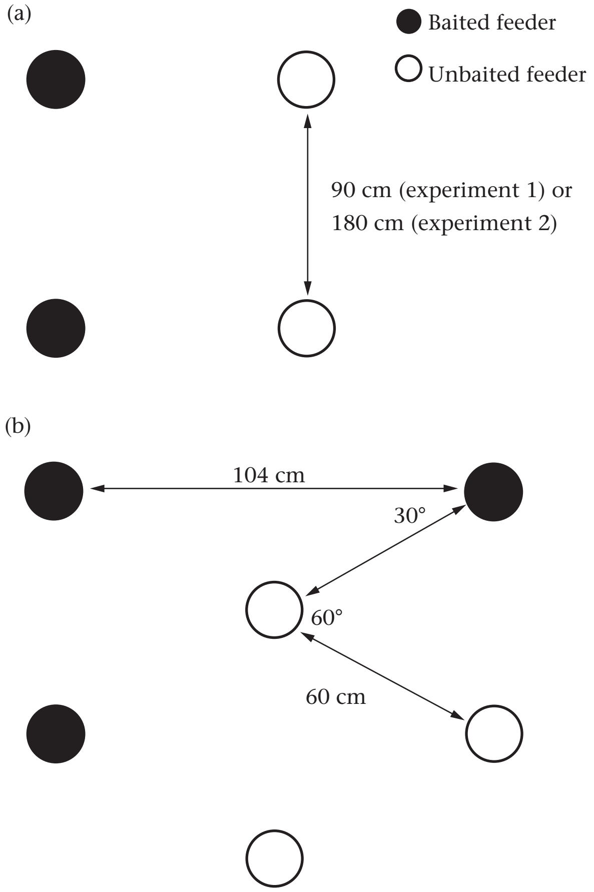

Figure 1. Schematic of the test arrays, as viewed from front on, used for (a) the noisy miners and (b) the rainbow lorikeets.

For the noisy miners two experiments were conducted (18 trials and 12 trials, respectively), with the feeders being closer together in experiment 1 than in experiment 2. The distance between the feeders was increased to increase the salience of the spatial cue, but as all birds completed experiment 1 first, it was not possible to differentiate the effect of feeder distance from the effect of experience with respect to the current data; consult Sulikowski & Burke (2007) for a complete rationale for the design of these experiments. There were two food rewards, invertebrates and nectar, manipulated between subjects and birds were kept in the same reinforcement contingency (shift or stay) and reward type (nectar or invertebrate) conditions over all 30 trials. The retention interval was 5 min for all trials.

For the rainbow lorikeets one experiment was conducted containing 60 trials. Retention interval was varied within subjects with each bird completing 30 trials at a 5 min retention interval and 30 trials at a 120 min retention interval, blocked and counterbalanced for order. The length of the retention intervals was related to the replenishment time of flowers, but was not necessarily expected to affect exploration phase behaviour; Sulikowski & Burke (2011a) provide the complete rationale for the design of this experiment.

Analysis

For this study we were concerned with behaviour in the exploration phases only. We investigated the pattern of errors (a revisit to a feeder previously visited, while there are still unvisited feeders remaining) and revisits (all revisits made, including those made after all feeders had been previously visited) of birds as they were exploring the array. We calculated a search bias score for each bird for each trial: $(F-E)/(F+E)$, where F (full) and E (empty) are the total number of errors (for noisy miners) or revisits (for rainbow lorikeets, which made few errors) made to feeders that were initially full or initially empty, respectively, at the start of that exploration phase. This produced a search bias score between -1 and 1, with positive scores indicating a tendency to be more likely to make repeated visits to feeders that were initially baited (similar to win-stay behaviour but without a retention interval between the ‘win’ and the ‘stay’), and a negative score indicating that the bird was more likely to make repeated visits to nonbaited feeders (similar to win-shift behaviour). We then calculated the mean bias score for each bird over blocks of trials (only trials in which the bird made errors/revisits contributed a score to this mean). If a bird made no errors/revisits in a block, then a bias score of 0 was entered for that block. The means for these blocks were then analysed to test for differences in search bias as a function of shift/stay contingency in the test phase. All analyses were conducted using PASW Statistics 17.0.2 for Mac.

RESULTS

Analyses revealed that shift/stay contingency influenced search behaviour with both species directing errors/revisits to feeders that had initially been full if they were in the stay condition or initially empty if they were in the shift condition.

Noisy Miners

Data from all 30 trials were analysed together. Mean search bias scores were calculated for each bird for five blocks (of six trials) by

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considering the errors made in the exploration phase. A general linear model (GLM) repeated measures ANOVA on these scores with block (five levels, 1–5) as a within-subjects factor and reinforcement contingency (two levels, shift and stay) and reward type (two levels, nectar and invertebrates) as between-subjects factors revealed a significant main effect of reinforcement contingency ($F_{1,12} = 7.529$, $P = 0.018$), with birds in the stay reinforcement condition more likely to revisit previously baited feeders (indicated by a more positive search bias score) than birds in the shift reinforcement condition. There was also a significant block*reinforcement interaction ($F_{4,48} = 9.042$, $P < 0.001$) and a significant block*reinforcement linear contrast interaction ($F_{1,12} = 31.598$, $P < 0.001$; Fig. 2a), revealing that search bias scores tended to become more positive for stay-reinforced birds and more negative for shift-reinforced birds. Independent-samples *t* tests were applied to each block. Only in the last block were the search bias scores significantly different between the reinforcement conditions ($t_{14} = 8.546$, $P < 0.001$, Bonferroni-corrected alpha of 0.01 applied; all other $t_{14} < 1.7$, all $P > 0.1$). One-sample *t* tests confirmed the mean search bias in the fifth block was significantly above zero for the stay birds ($t_7 = 5.656$, $P = 0.001$), and significantly below zero for the shift birds ($t_7 = 6.766$, $P < 0.001$). Examining the reward type groups separately (Fig. 2b) using independent-samples *t* tests showed that this difference between the reinforcement conditions was significant for both nectar-rewarded ($t_6 = 10.451$, $P < 0.001$) and invertebrate-rewarded ($t_6 = 4.619$, $P = 0.004$) birds in the fifth block.

Rainbow Lorikeets

Mean search bias scores for the rainbow lorikeets were calculated for six blocks (of 10 trials) using all revisits made during the exploration phases (errors during search were rare for rainbow lorikeets, but considering all revisits, including those made after all rewards were found, allowed data from 95% of trials to be included). Data were averaged over the two retention intervals as preliminary analyses revealed no effect of retention interval on search bias scores. A GLM repeated measures ANOVA with block (six levels, 1–6) as a within-subjects factor and reinforcement contingency (two levels, shift and stay) as a between-subjects factor revealed a significant effect of block ($F_{5,50} = 2.526$, $P = 0.041$) and a significant block*reinforcement linear contrast interaction ($F_{1,10} = 6.125$, $P = 0.033$) as the search bias scores of the two reinforcement groups diverged (with search bias scores of shift-reinforced birds becoming more negative and those of stay-reinforced birds becoming more positive) over the course of the experiment (Fig. 2c).

DISCUSSION

In this study we found no evidence of reward-type mediated effects, suggesting that differential exposure to information does not explain previously reported performance differences on shift/stay tasks between noisy miners foraging for nectar and those foraging for invertebrates (Sulikowski & Burke 2007). We did, however, find evidence of a dissociation of the search mechanisms engaged in the exploration phases and those engaged during the test phases. These results suggest that insensitivity to the win-stay contingency does not explain the nectar-specific win-shift bias exhibited by noisy miners, with sensitivity to both the shift and stay contingencies being evident from behaviour in the exploration phases. Following from this, we investigated the search biases of a second nectarivorous bird, the rainbow lorikeet, to examine the extent to which the effect of shift/stay contingency on exploration phase behaviour is a general finding. These birds also exhibited search biases that were influenced by shift/stay contingency.

These results demonstrate that both species exhibited sensitivity to the shift/stay contingencies between exploration and test phases, via the patterns of search errors/revisits exhibited during the exploration phase. With respect to behaviour during the exploration phase, shift-reinforced birds tended to make errors/revisits to feeders that had initially been empty, while stay-reinforced birds tended to make errors/revisits to feeders that had initially been full. The emergence of this behaviour from two species suggests it is not a spurious observation, but a genuine phenomenon that deserves consideration.

The effect of test phase reinforcement on exploration phase behaviour could be viewed as a type of behavioural generalization across contexts. From this perspective it is not a particularly

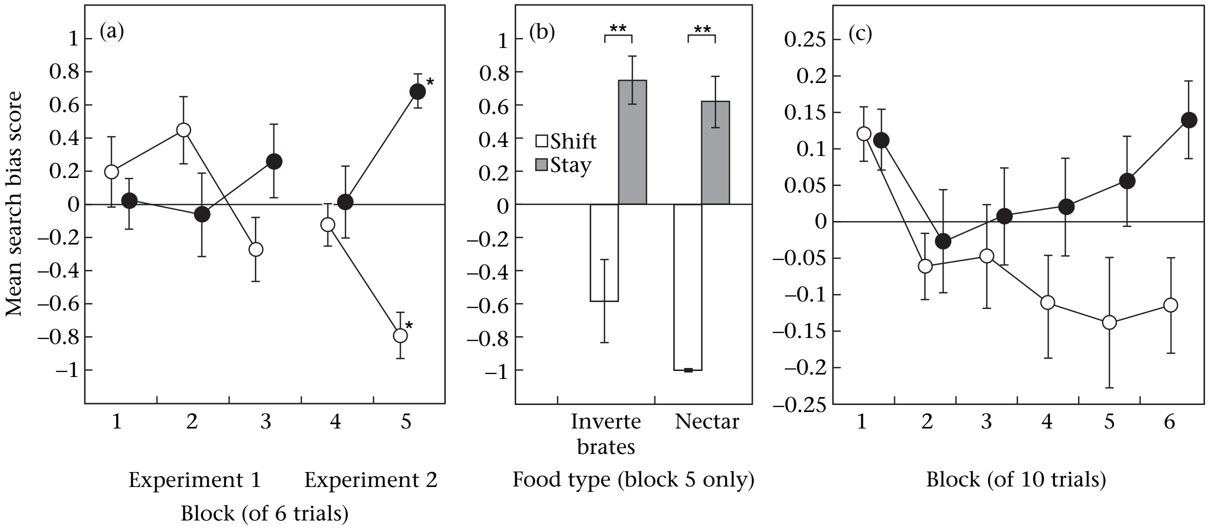

Figure 2. (a) Mean ± 1 SE search bias scores for the noisy miners in experiment 1 and experiment 2. Black dots indicate stay-reinforced birds ($N = 8$) and white dots indicate shift-reinforced birds ($N = 8$). (b) Mean ± 1 SE search bias scores for the noisy miners in block 5 only, with the food types shown separately ($N = 4$, for each reinforcement contingency/food type group). (c) Mean ± 1 SE search bias scores for the rainbow lorikeets, averaged over both delays. Black dots indicate stay-reinforced birds ($N = 6$) and white dots indicate shift-reinforced birds ($N = 6$). Positive scores indicate a tendency to revisit baited feeders and a negative score a tendency to revisit nonbaited feeders. *Significantly different from zero, $P < 0.001$; **significant difference between shift and stay, $P < 0.005$.

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surprising result, although we are not aware of previous reports of this behaviour in the literature. What is remarkable is that the birds showed this pattern of generalization, even when their behaviour in the test phase suggested they were unable to learn the shift/stay contingencies. In the case of the noisy miners rewarded with nectar, birds being reinforced to win-stay in the test phase performed below chance (Sulikowski & Burke 2007). These birds continued to engage in win-shift behaviour during the test phase of trials in spite of the reinforcement to win-stay. For these birds an account of generalization across contexts can only explain their pattern of revisits in the exploration phase if one assumes that they did in fact learn the win-stay contingency between exploration and test phases, but did not manifest their win-stay response in favour of win-shifting behaviour. It is also worth noting that in the case of noisy miners reinforced to win-shift, there was no difference between the nectar and invertebrate-rewarded groups in the tendency to revisit initially unrewarded locations while searching in the exploration phase, even though the tendency to shift in the test phase was much stronger for birds reinforced with nectar.

It is also possible that the birds' behaviour during the exploration phase was affected by the reinforcement they received while searching. One could argue that within the exploration phase birds were reinforced each time they located a reward and so may have been more likely to return to these locations during that particular exploration phase. This could potentially have created the pattern of revisits shown by birds reinforced to win-stay, without those birds needing to be sensitive to the win-stay contingency. This explanation, however, is unlikely to account for the data for two reasons. First, all birds, regardless of the reinforcement contingency they received between the exploration and test phases, would have experienced the same reinforcement while searching in the exploration phase. One would predict, therefore, one of two outcomes. Either all birds would show a tendency to revisit the baited feeders in the exploration phase (if generalization across contexts were not occurring) or one would predict that the win-stay birds would show a stronger bias of revisits in the exploration phase than win-shift birds (if both generalization and exploration phase reinforcement were occurring). Neither of these outcomes is the case.

Second, one would predict that, if the choice of feeders to visit in the exploration phase was affected by the reinforcement of finding rewards during that phase, then birds given arrays of baited and unbaited feeders to search, without subsequent test phases, should tend to make more revisits while searching these arrays to the baited than to the unbaited feeders. Previous data from noisy miners suggest that when birds are rewarded with invertebrates the opposite is the case. In the absence of a test phase (and so no exploration–test phase contingency is present) these birds tend to make more revisits to the unbaited feeders, while birds rewarded with nectar make an equal number of revisits to the baited and unbaited feeders (Sulikowski & Burke 2010a).

The current study confirms that although birds in a nectar-foraging context were unable to perform above chance on a task requiring them to win-stay (Sulikowski & Burke 2007), these birds nevertheless learnt the stay contingency (and so attended to, encoded, retained and integrated the relevant information between the exploration and test phases). This learning then manifested in the exploration phase, but not the test phase. This suggests that the mechanisms underpinning win-shift behaviour in nectarivores probably involve inhibition of learned potential responses at the specific times these responses would be ecologically maladaptive. They do not, it seems, reflect an inability to learn the ecologically incongruent contingencies, as previously concluded by other authors, including ourselves (Cole et al. 1982; Wunderle & Martinez 1987; Burke & Fulham 2003; Sulikowski & Burke 2007).

With respect to the potential ecological cues that trigger the hypothesized inhibition of learned win-stay responses, the evidence we have currently amassed from a variety of studies with noisy miners (Sulikowski & Burke 2007, 2010a, b, 2011b) suggest that a string of behavioural differences (of which the win-shift bias is one) occur in the laboratory foraging situation as a function of whether the birds are rewarded with nectar or invertebrates. These occur as immediate proximal responses to the reward and seem to be independent of how well they help the bird solve the laboratory task at hand. Therefore, the most parsimonious interpretation we can offer at this stage is that ingestion of a sucrose solution at a particular location acts as a trigger to inhibit returning to that location (once the current search bout has ended), irrespective of recent reinforcement experience. Whether the potential of sucrose to do this is affected by lifetime experience is not yet known.

Although not discussed by those authors the current interpretation is consistent with the findings of Burke & Fulham (2003): regent honeyeaters, *Xanthomyza phrygia*, that had initially performed well on a task requiring them to win-stay after a delay of 3 h failed to perform above chance when the delay was reduced to 10 min. In this study the win-stay contingency had already been learnt, meaning that a general insensitivity to this contingency could not explain poor performance on the win-stay task at the 10 min delay interval. As well as an important step in understanding the specific case of win-shifting behaviour, this insight is valuable in illustrating how aspects of learning, memory and cognition have been shaped by evolution to allow organisms to behave in functionally adaptive ways.

Although this phenomenon has helped illuminate the way win-shifting mechanisms might work, there is no reason to presume that the effect of test phase reinforcement on exploration phase behaviour is itself a specialized mechanism unique to nectar-feeding birds. It may reflect unspecialized mechanisms of generalization across contexts that may be present in a wide variety of species. Indeed, the rainbow lorikeets exhibited this effect, but did not exhibit a win-shift bias at a short delay (or a win-stay bias at a long delay) in the test phase of their trials (Sulikowski & Burke 2011a), suggesting that the search bias reported in the current study and the win-shift bias exhibited by noisy miners in response to nectar are cognitively dissociated.

These results not only help us to understand the cognitive mechanisms that produce win-shift behaviour in nectarivorous birds. They also encourage us to consider the possibility that the mechanisms that underpin adaptive behaviours are multifaceted, and that evolution may have worked on any or all of the sub-mechanisms to produce the adaptive outcome. These findings suggest that it is only through a careful and detailed examination of each of the cognitive processes involved in producing ecologically relevant behaviour that we will fully understand how evolution has produced cognitive adaptations.

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