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Win-Shift and Win-Stay Learning in the Rainbow Lorikeet (*Trichoglossus haematodus*)

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The tendency to win-shift (to better learn to avoid, rather than return to, recently rewarded locations) has been demonstrated in a variety of nectarivorous birds and in honeybees. It is hypothesized to be a cognitive adaptation to the depleting nature of nectar. In the present study we report the first attempt to test for a win-shift bias in a nectarivorous parrot, the rainbow lorikeet (*Trichoglossus hematodus*). This species differs from others tested for a win-shift bias in that it is a facultative, rather than an obligate, nectarivore. We tested a captive-reared population of the birds on a shift/stay task at long and short retention intervals. The data show no evidence of either a win-shift or a win-stay bias. The birds demonstrated efficient spatial search ability and above chance performance for both shift and stay contingencies at long and short delays. These data suggest that an innate tendency to win-shift may not be present in all avian nectarivores, or that the role experience plays in shaping such behaviors is different for different species.

Keywords: spatial cognition, cognitive adaptation, win-shift, win-stay, rainbow lorikeets

To understand how evolution has shaped animals' behavioral and cognitive mechanisms, much research has focused on spatial learning and memory. Species' ecology has been used to predict differences in spatial cognition as a function of sex (Gaulin & Fitzgerald, 1986), season (Galea, Kavaliers, & Ossenkopp, 1996), species (Olson, 1991) and context (Sulikowski & Burke, 2007; reviewed by Sherry, 2006). A line of research examining win-shift biases (the tendency to spontaneously avoid and/or to better learn to avoid than to return to, locations where food has recently been found) of a variety of species has led to the theory that this behavior represents an adaptation to depletable food resources (Burke & Fulham, 2003; Cole, Hainsworth, Kamil, Mercier, & Wolf, 1982; Kamil, 1978; Sulikowski & Burke, 2007; Wunderle & Martinez, 1987).

While many food resources may deplete to some extent, nectar has a uniquely reliable spatiotemporal distribution. It is typically offered in such small amounts that for avian foragers a flower will be depleted after a single visit and will prove an unprofitable place to return to until such time as it replenishes. Field observations (Gill & Wolf, 1977; Kamil, 1978), and field (Healy & Hurly, 1995) and laboratory (Cole et al., 1982; Wunderle & Martinez, 1987) experiments have reported win-shifting behavior in five families of nectarivorous birds. In one of these families, the Meliphagidae (Australian honeyeaters), the win-shift bias was demonstrated in a captive-reared population with no experience of natural nectar distributions (Burke & Fulham, 2003), suggesting that, in this family at least, the behavior is not merely a result of a general learning mechanism being shaped by life experience.

Kamil (1978) examined win-shift behavior in wild Hawaiian honeycreepers within their own territories. He demonstrated that win-shifting resulted in increased foraging efficiency (which correlates with fitness, Pyke, Pulliam, & Charnov, 1977) when compared to the foraging of intruder birds, who lacked information about which flowers had been visited most recently. The win-shift bias in the Meliphagidae is sensitive to time and context in ways consistent with an adaptive explanation. It reverts to a stay bias after an extended delay (Burke & Fulham, 2003), when flowers have refilled with nectar, and manifests only when behavior is reinforced with nectar, not invertebrates (Sulikowski & Burke, 2007), which do not have a reliably, depleting distribution. Furthermore, Hampton and Shettleworth (1996) have reported a stay bias in species that forage on clumped resources that are not easily depleted, such as seeds and insects. This is further evidence that shift/stay behavior maps closely onto foraging ecology.

Shift-stay tasks typically consist of an exploration phase and test phase separated by a delay. In the literature these tasks have differed in the way they conduct the exploration phase. In this study we chose to present the subjects with both the baited and unbaited feeders (as opposed to presenting them with the baited feeders only) to explore in the exploration phase. This was the method used to identify shift/stay biases in honeyeaters (Burke & Fulham, 2003; Sulikowski & Burke, 2007), echidnas (Burke, Cieplucha, Cass, Russel & Fry, 2002) and marmosets (MacDonald, Pang, & Gibeault, 1994). The potential drawback of this method is that, if a bird views an empty flower as an unprofitable place to

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return to (irrespective of whether the bird emptied the flower itself or just found it to be empty) the bird may seek to avoid *all* recently visited sites, irrespective of whether they were rewarded. Previous studies, however, suggest that this is not the case. Both noisy miners (Sulikowski & Burke, 2007) and regent honeyeaters (Burke & Fulham, 2003), prefer to avoid sites that they themselves have recently emptied compared to sites they have recently visited and found to be empty. Hurly (1996) demonstrated that hummingbirds also distinguish between recently visited rewarded and recently visited unrewarded sites. Dynamic nectar replenishment, where the secretion of nectar is mediated by pollinator behavior (Castellanos, Wilson, & Thomson, 2002) may mean that the longer ago a flower was emptied the sooner it is likely to replenish.

Hurly (1996) also demonstrated that hummingbirds preferentially direct their search toward sites that have been previously unexplored, a behavior termed spontaneous alternation (Gaffan & Davies, 1982). Spontaneous alternation has been argued to be a general process seen in many species that facilitates exploration of the environment. It is distinct from win-shifting, which is hypothesized to be a specialized process, adapted to the depleting nature of nectar. The alternative method, to only present subjects with the baited locations in the exploration phase, has also been used (Cole et al., 1982; Wunderle & Martinez, 1987). If a win-shift bias is found with this method, though, it is impossible to rule out spontaneous alternation as an alternative explanation. We chose the former method as it has previously proved effective (and so allowed direct comparisons between the current study and previous data) and is the one that yields the most robust result.

The rainbow lorikeet (Aves: Psittacidae, *Trichoglossus hematodus*) an Australian parrot, is a facultative nectarivore. It feeds on nectar, seeds, fruit, and leaf buds (Cannon, 1982). Despite their varied diet, rainbow lorikeets show morphological adaptations to feeding on nectar including a brush-tipped tongue and shortened intestine (Richardson & Wooller, 1990). Field studies have also reported that movements of wild rainbow lorikeets track the availability of nectar on different plants within their range (Franklin & Noske, 1999). This foraging ecology makes the rainbow lorikeet a suitable candidate to test for a win-shift bias. Such tests have not been previously conducted on any member of the Psittacidae.

While the large bodied honeyeaters (two species of which have been shown experimentally to exhibit win-shift biases) and rainbow lorikeets currently share a common facultative reliance on nectar (Barker & Vestjens, 1984; Cannon, 1979), the honeyeaters evolved from an obligate nectarivore ancestor (Driskell & Christidis, 2004), whereas rainbow lorikeets (a Psittacidae parrot) have presumably never (in their evolutionary history) been obligate nectarivores (de Kloet & de Kloet, 2005). It is most parsimonious at this stage to assume that the win-shift bias seen in the honeyeaters arose in this common ancestor. If this were true it would mean that all avian species in which a win-shift bias has been experimentally demonstrated are, or at least once were, obligate nectarivores. Bananaquits, the only avian nectarivore to not exhibit a win-shift bias (using a hand-reared juvenile population, Wunderle & Martinez, 1987) are also facultative nectarivores (Gross, 1958). Therefore, the current study aims not just to explore spatial memory biases in a previously untested family of nectarivorous birds, but may also provide clues as to the ecological conditions necessary for such biases to evolve. The absence of a win-shift bias at a short delay in the rainbow lorikeet would be consistent with the idea that facultative nectarivory may not provide sufficient selection pressure for win-shift biases to evolve.

In our experiments, we sought to examine the degree to which a captive population of rainbow lorikeets may display a shift/stay bias at short and long delays. If the tendency to win-shift, as observed in other species, is indeed a response to the depleting nature of nectar, we would expect such a behavior to manifest at reasonably short delays only, before a flower would have a chance to replenish. At longer delays, however, when a flower may have replenished, one would predict that the tendency to win-shift would no longer be present and may even be replaced by a win-stay bias. This was the pattern predicted by Cole et al. (1982) and then displayed by a captive reared population of regent honeyeaters (Burke & Fulham, 2003). Provided that a facultative reliance on nectar is sufficient to result in the observed biases, we would predict that our subjects would show a shift bias at the short delay and a stay bias at the long delay.

Method

Subjects

Subjects were 12 rainbow lorikeets (*Trichoglossus hematodus*), of unknown age and sex, on loan from Hunter Valley Zoo, Cessnock, NSW, Australia. They had been reared in captivity in a large social group and had no prior experimental experience. At the zoo, the birds had been maintained on a diet of fruit, cut browse and commercial lorikeet food, and so had no experience with the natural distribution or replenishing rates of nectar.

During the experiment, birds were housed and tested individually in cages measuring approximately 27 m^3 and were maintained on a commercial nectar mix, Wombaroo Lorikeet and Honeyeater Wet Mix. Testing occurred in morning and afternoon sessions and half of the daily food was provided after each session.

Apparatus

The test feeders were made from small opaque plastic wells (approximately 1 cm^3 capacity) with flip-open metal lids, which fell shut after a bird finished feeding. This ensured that visited feeders were visually indistinguishable from those not yet visited. The feeders could be hooked through the metal mesh front of the cages from the outside in such a way that they were accessible to the birds on the inside. During the experiment baited feeders contained 0.4 mL of “nectar” (a 30% wt/vol sucrose solution).

Birds learned how to open the feeders via free exploration before testing began. Initially, several pieces of apple were placed in either two or three feeders such that they held the lids open and were plainly visible. Apple was a preferred food and it quickly drew the birds’ attention to the unfamiliar feeders. These feeders were presented to the birds (not in the locations to be used in the experiment) a few times a day until they were readily consuming the apple. Typically, the birds would approach a feeder and consume a piece or two and then leave, returning sometime later to finish what was left. Each time the feeders were presented they were placed in different locations. The feeders were then presented with the apple inside and the lids closed. The birds were allowed to explore these feeders until they learned how to open the lids with their beaks. The provision of multiple pieces of apple in feeders whose locations changed after each baiting prevented reliable depletion/replenishment of feeder locations during pretraining, thus avoiding any systematic win-shift or win-stay reinforcement. The birds completed pretraining over a period of several days and once a bird was readily opening feeders to retrieve apple it began the experiment.

Procedure

The experiment consisted of a total of 60 trials, 30 in a short delay condition and 30 in a long delay condition. A trial was made up of two phases, the exploration phase and the test phase. In the short delay condition the phases were separated by a 5-min retention interval and in the long delay condition by a 120-min retention interval. All birds completed both delay conditions in counterbalanced order (all 30 trials at one delay were completed before the 30 trials of the other delay condition commenced). By using a series of trials to examine shift/stay behavior we were able to inspect the way this behavior emerged over the course of the experiment. It allowed us to compare the rate of learning of the shift and stay contingencies as well as assess whether the birds would exhibit any spontaneous tendencies to either shift or stay.

For the exploration phase a bird was presented with an array of six feeders (arranged as shown in Figure 1), three of which were baited. The locations of the baited feeders varied randomly from trial to trial with all feeders containing baits an equal number of times by the end of the experiment. The bird was allowed to freely explore the feeders and eat all the food rewards. Once feeders were removed at the end of this phase, it was confirmed that all rewards had been completely consumed. The exploration phase ended when the bird, having consumed all rewards, either left the array or made a maximum of 12 visits. Allowing birds to explore both the baited and unbaited feeders in the exploration phase, rather than presenting them with feeders at the baited locations only, prevents mechanisms of spontaneous alternation (Gaffan & Davies, 1982) resulting in an apparent win-shift bias.

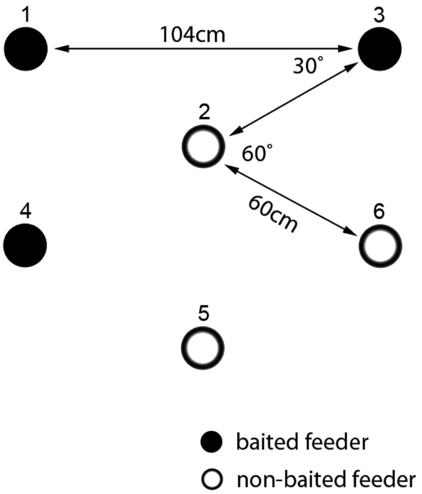

Figure 1. Shows the formation of the array of feeders that was placed on the front wall of the birds' cages during the exploration and test phases of each trial; the location of the baits in the exploration phase was randomized from trial to trial.

At the end of the exploration phase the feeders were removed and the retention interval began. After the retention interval (either 5 min or 120 min) the feeders were replaced in the same formation for the test phase. The location of the baits in this phase was dependent upon whether a subject was in the win-shift or win-stay reinforcement condition (varied between subjects, 6 birds in each condition, with a bird remaining in the same reinforcement condition for all of its 60 trials). If a bird was in the stay condition, the same three feeder locations were baited as in the exploration phase. For a bird in the shift condition, only the other three feeders were baited. In the test phase, birds were only allowed to visit three feeders and the number of baits they recovered was scored as the measure of performance.

The feeder arrangement was staggered (as shown in Figure 1) so that birds could, for example, visit feeder 1 and then feeder 3 without having to go straight past feeder 2 in between (and be tempted to open it just because it was nearby). The staggering was not entirely successful, as birds often did not bypass feeders that were above or below their line of travel. In case the shape of the array affected birds' second and subsequent choices, as well as analyzing all three choices birds made in the test phase, we also looked at just the first choice data separately. Both exploration and test phases were video-recorded using a Sony DCR-HC28E mounted on a tripod placed in front of the bird's cage. Test-phase visits were scored by the first author during testing and the order of visits during the exploration phase was scored by the first author subsequently, using the video footage. It was unambiguous (in both real time and from the video footage) whether a bird had probed a feeder and so the scoring did not involve any subjective judgments. As such, there was no need to engage a second scorer to gauge reliability.

Results

Shift and Stay Performance

The number of correct feeders visited in the test phase of each trial was analyzed using a GLM repeated measures ANOVA with reinforcement (shift, stay) and first delay condition completed (5 min, 120 min) as between subjects factors and delay (5 min, 120 min) and block (1–5, 6 trials per block) as within-subjects factors. An alpha value of 0.05 was adopted for this and all subsequent analyses.

The birds were able to learn both the shift and stay contingencies and improved over the course of the experiment (from the first to the last block) as reflected by the significant main effect, $F(4, 32) = 4.039$, $p = .009$, $\eta_p^2 = 0.335$, and significant linear contrast effect, $F(1, 8) = 11.480$, $p = .010$, $\eta_p^2 = 0.589$, of block. This improvement was largely restricted to the delay condition birds completed first, though, with a significant three-way linear contrast interaction of delay × block × first delay, $F(1, 8) = 9.440$, $p = .015$, $\eta_p^2 = 0.541$, with performance stable across whichever delay condition the bird completed second (Figures 2a & 3a).

The primary result of interest, the interaction between reinforcement and delay was not significant, $F(1, 8) = 0.504$, $p = .498$, $\eta_p^2 = 0.059$, with no evidence that birds performed better at the shift task at the short delay (Figure 2b) or the stay task at the long delay (Figure 3b). There was a borderline significant main effect of

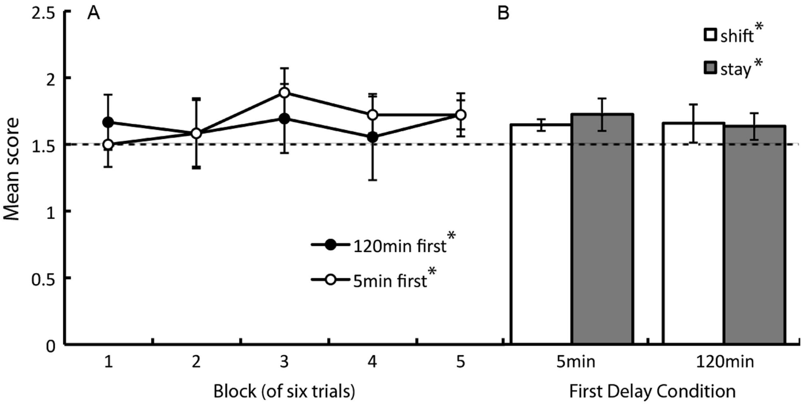

Figure 2. Shows the mean score (number of baits found in the test phase; error bars represent 95% CI) of birds during the 5-min delay trials; the dashed line represents chance performance; * indicate performance that is significantly above chance. A. Birds performed significantly above chance overall regardless of whether they had completed the 120-min delay condition prior to these trials or not. B. Both shift- and stay-reinforced birds performed above chance overall, with no difference in performance between these groups overall, or as a function of which delay condition they completed first.

delay, $F(1, 8) = 5.323$, $p = .050$, $\eta_p^2 = 0.400$, with birds performing better in the 5-min than the 120-min delay condition.

Overall performance at the 5-min delay (see Figure 2) was significantly above chance (as determined by a one-sample *t* test against chance at 1.5) for both the shift, $t(5) = 4.392$, $p = .007$, Cohen's $d = 4.339$, and stay, $t(5) = 4.339$, $p = .007$, Cohen's $d = 4.392$, conditions. Overall performance at the 120-min delay (see Figure 3) condition was only above chance for the subgroup of birds that had previously completed the 5-min delay condition, $t(5) = 3.639$, $p = .015$, Cohen's $d = 3.639$.

When just the first trial each bird completed was considered (irrespective of whether the bird was to be reinforced to shift or to stay), the birds displayed no spontaneous tendencies to shift at the short delay (a mean of 1.33 ± 0.44 95% CI of each bird's three choices were shifts) or to stay at the long delay (a mean of 1.67 ± 0.56 95% CI of each bird's three choices were stays). In considering just the first choice made by each bird in its first trial there were four shifts and two stays at the short delay and two shifts and four stays at the long delay, giving no significant association between delay length and shift/stay choice (Fisher's exact test, $p = .567$).

In case the shape of the test array had affected second and third choices in the test phase (see Discussion) the same analysis described above was also carried out on data from just the first choice made in the test phase from each trial (Figure 4a and b). For these data there was also no reinforcement × delay interaction, $F(1, 8) = 0.116$, $p = .742$, $\eta_p^2 = 0.014$. Performance as measured by these data was also only marginally above chance, significantly so for birds in the 5-min delay condition (as determined by a one-

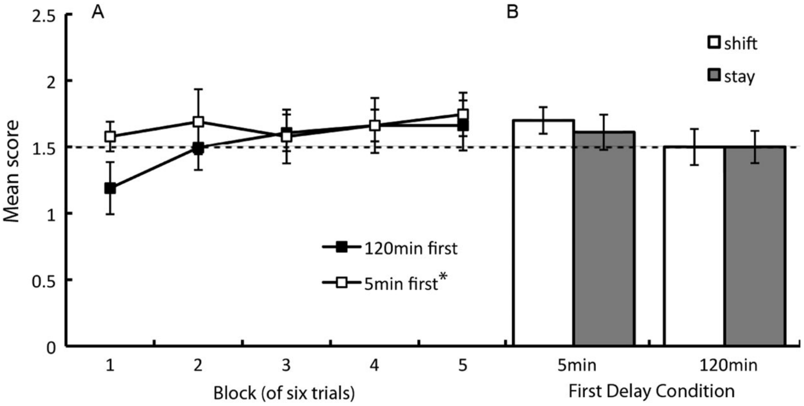

Figure 3. Shows the mean score (number of baits found in the test phase, error bars represent 95% CI) of birds during the 120-min delay trials; the dashed line represents chance performance; * indicates performance that is significantly above chance. A. Only birds that had previously completed the 5-min delay condition performed significantly above chance overall, although birds that completed the 120-min delay trials first did show improvement. B. There was no difference overall between performance of shift- and stay-reinforced birds, both groups were above chance if they had previously completed the 5-min delay condition and at chance overall if they had not.

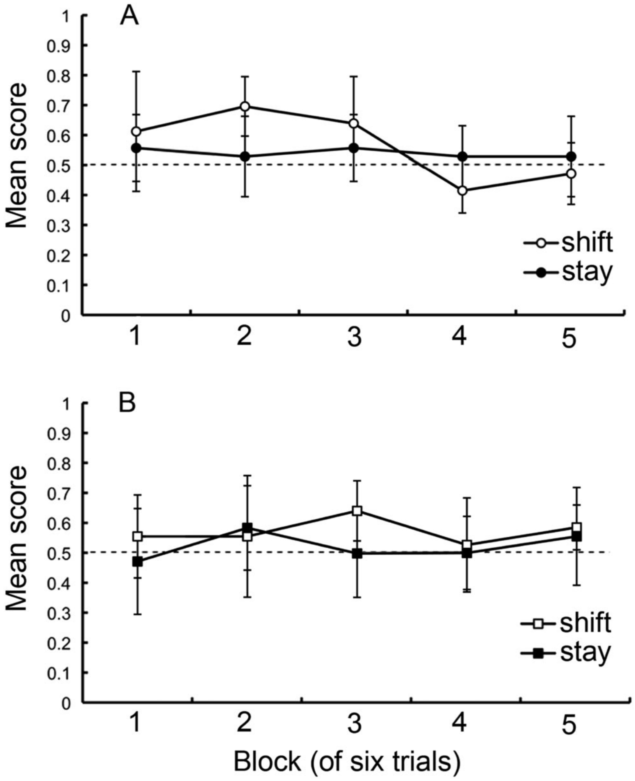

Figure 4. Shows the mean score (error bars represent 95% CI) of just the first choice made in the test phase; the dashed line represents chance performance. A. There was no difference in performance between the shift-reinforced and stay-reinforced birds at the 5-min delay, with overall performance marginally but significantly above chance. B. There was also no difference in performance between groups at the 120-min delay, with overall performance not significantly above chance.

sample *t*-test 0.5, $t(11) = 2.299$, $p = .042$, Cohen's $d = 2.528$), but not so for birds in the 120-min delay condition, $t(11) = 1.751$, $p = .108$, Cohen's $d = 1.751$.

Search Performance During the Exploration Phase

The number of revisit errors the birds made to previously visited feeders before visiting all six feeders in the exploration phase of the trials was first analyzed in a GLM ANOVA with the same factors as described above for shift and stay performance. This revealed a significant delay × first delay interaction, $F(1, 8) = 5.449$, $p = .048$, $\eta_p^2 = 0.405$, with birds performing better in whichever delay condition they completed second (Figure 5a). Considering that the delay period follows the exploration phase in each trial (and that the above analysis revealed no other effects of delay), the data were reanalyzed as a series of 60 trials, ignoring delay.

A GLM ANOVA with reinforcement (shift, stay) as a between subjects factor and block (1–10, 6 trials in each) as within-subjects factors, also revealed evidence of learning with a significant effect of block, $F(9, 90) = 2.826$, $p = .006$, $\eta_p^2 = 0.220$, and a significant linear contrast of block, $F(1, 10) = 13.330$, $p = .004$, $\eta_p^2 = 0.571$. It is interesting to note that there was also a significant block × reinforcement linear contrast, $F(1, 10) = 6.700$, $p = .027$, $\eta_p^2 = 0.401$, with birds in the shift reinforcement condition improving more steadily and making fewer errors in the majority of blocks than birds in the stay reinforcement condition (Figure 5b).

Discussion

Performance in the Shift/Stay Task

Contrary to findings with other nectar feeding species, the rainbow lorikeets in this study did not show any evidence of either an initial bias toward win-shifting behavior, or an ability to better learn the shift versus the stay contingency over a short delay period. Unlike the behavior of the captive regent honeyeaters (Burke & Fulham, 2003), there was also no evidence of a stay bias at the long delay period. As far as we are aware, there is only one other account in the literature of a nectarivorous bird failing to show a win-shift bias when tested under experimental conditions. Wunderle and Martinez (1987) tested hand-reared juvenile bananaquits and found no shift/stay bias and concluded that the shift-bias seen in wild adult bananaquits was experience dependent (although the study confounded experience with maturation).

Even though birds were able to perform at above chance for both contingencies at both delays (and somewhat better at the shorter delay), mean levels of performance never exceeded 2 (out of a possible 3) correct. One possibility is that birds were not sufficiently motivated. We think this is unlikely as birds routinely approached the array once the experimenter had retreated from the front of the cage, and birds typically made the maximum number of allowed visits in the exploration phase, only leaving the array when the experimenter approached to remove the feeders. A more likely explanation may be a lack of spatial problem solving experience, due to a life in captivity. Although laboratory rodents can produce more competent performance on similar tasks (Floresco, Seamans & Phillips, 1996; Olton & Samuelson, 1976; Olton & Schlosberg, 1978) these rodents are typically bred from laboratory strains and so are somewhat adapted to a captive lifestyle (Boice, 1981) and are often experienced in experimental problem solving.

The absence of a win-shift bias in our data could be a consequence of the lack of natural foraging experience our subjects had. Captive-reared and fed commercial bird food, our subjects had no exposure to the natural depleting and replenishing rates of nectar. Although Burke and Fulham (2003) showed that exposure of this kind is not necessary to develop a win-shift bias in captive regent honeyeaters, Wunderle and Martinez (1987) found that natural foraging experience was necessary for a shift-bias to emerge. If such a bias were present in the rainbow lorikeet as a consequence of convergent evolution, one would not necessarily predict that this behavior would follow the same ontogeny, or have the same experiential requirements to properly develop, as in other groups. Another consideration is the extent to which rainbow lorikeets rely on nectar in the wild. The only two nectarivorous avian species to fail to show a reliable win-shift bias (rainbow lorikeets and bananaquits) have both been facultative (rather than obligate) nectarivores. These considerations suggest that future research needs to examine the dual roles of nectar reliance and experi-

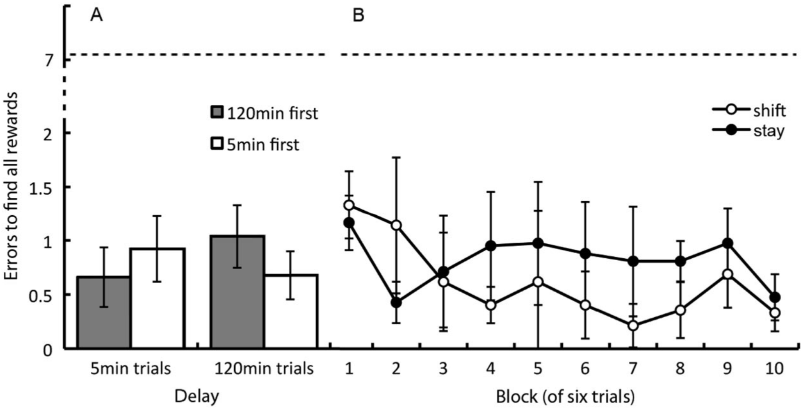

Figure 5. Shows the mean number of errors (error bars represent 95% CI) birds made before finding all rewards in the exploration phases of the trials. The dashed line represents chance performance as predicted by random walk simulations. A. Birds made fewer errors in whichever delay condition they completed second. B. Analyzed as a series of 10 blocks of 6 trials, ignoring delay, shift-reinforced birds improved more steadily and made fewer errors in the majority of blocks than stay-reinforced birds.

ence to determine how win-shift behavior emerges in different groups and to understand its absence in some captive-reared populations.

Search Performance During the Exploration Phase

Birds searched efficiently in the exploration phase of the experiment, performing much better than would be predicted by a random walk, from the first block of trials onward. The contingency of the reinforcement (shift or stay) impacted on search efficiency with birds in the shift condition making fewer revisit errors in the exploration phase than birds in the stay condition. In an experiment of this nature, with repeated exploration and test phases, in order to search efficiently in the exploration phase, an animal must avoid the most recently visited locations in favor of locations not so recently visited. The shift contingency also requires birds to avoid locations based on whether food was recently found there. The stay contingency, however, requires animals to return to, rather than avoid, salient locations. It is possible, therefore, that there is interference occurring between reinforcement in the exploration and test phases in the stay condition and not in the shift condition, resulting in the observed differences. There is no evidence, though, of this hypothesized interference producing differential shift/stay performance in the test phase (that is, the interference occurring in the opposite direction).

Conclusion

In this study a captive-reared population of nectarivorous parrots was tested for win-shift/win-stay biases at both long and short delays. There was no evidence of a bias at either delay, contrary to what has been demonstrated in a variety of other nectarivorous species. The lack of a bias could be attributed to the captive-reared status of the population or their facultative reliance on nectar. Further research examining the effects of experience and development on shift/stay learning in rainbow lorikeets (and other nectarivorous species) is needed to investigate these possibilities before firm conclusions can be drawn.

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