An evolved spatial memory bias in a nectar-feeding bird?

DARREN BURKE & BENJAMIN J. FULHAM

Department of Psychology, University of Wollongong

Studies have shown that nectar-feeding birds more easily learn to avoid a previously rewarding location (to win-shift) than to return to such a location (to win-stay). This pattern has been interpreted as evidence of an evolved adaptation to the fact that nectar is a depleting resource; however, such a conclusion requires ruling out the possibility that this tendency is a consequence of the experience of individual birds, and is more compelling if performance in the memory task reveals sensitivity to detailed features of the spatiotemporal distribution of nectar in the environment. We tested the tendency of captive-reared Regent honeyeaters, *Xanthomyza phrygia*, a species of nectar-feeding bird, to win-shift or win-stay at different intervisit intervals. The birds generally avoided rewarding locations after a short retention interval (10 min), but returned to these locations after a long retention interval (3 h). This behaviour tracks the replenishment rate of the flowers exploited by this species in the wild, even though the subjects were born and reared in captivity.

To understand the evolution of cognitive mechanisms, we need to find environmental factors that require particular kinds of cognitive skills and that correlate in a predictable way with performance on controlled cognitive tasks. Most researchers have looked for correlations between some aspect of the ecology of a particular species (frequently its foraging ecology) and performance, or performance differences, in laboratory spatial memory tasks (reviewed by Krebs et al. 1996; Sherry 1998). For example, in two groups of birds, species that cache food and later recover it typically outperform closely related noncaching species on a range of spatial memory tasks (although there is also evidence that is inconsistent with this for both groups; Balda et al. 1995; Hampton & Shettleworth 1996; Gould-Beierle 2000). Food-storers also typically have larger hippocampi than their non-storing relatives (e.g. Healy et al. 1994; Basil et al. 1996), suggesting that this is the neural basis of the adaptation.

Macphail & Bolhuis (2001) and Bolhuis & Macphail (2001) have questioned the utility of attempting to understand learning mechanisms as evolved adaptations, based on both theoretical and empirical concerns. These criticisms are a version of the standard general-process-approach objections to ecologically inspired research (Cosmides 1989; Timberlake 2001). This approach

maintains that a few general, unspecialized, learning and memory mechanisms (such as associative learning) are able to account for all existing data. Differences in performance between species are instead attributed to motivational, perceptual, or other differences, or to interactions between these and the particular task the animals must perform (Macphail 1982).

Without wishing to add to the details of this debate (e.g. Dwyer & Clayton 2002; Hampton et al. 2002; MacDougall-Shackleton & Ball 2002; and see Bolhuis & Macphail 2002), we would make the observation that some of the force of the general process argument depends on a historical accident. Since learning and memory were first systematically investigated from a general process perspective, the onus of proof is usually placed on researchers in the ecological tradition to demonstrate that a general process account is unable to deal with their data. The default position seems to be that learning and memory mechanisms are identical in all species (or at least all vertebrates, excluding humans; Macphail 1982, 1987, 1996). Whatever the merits of each case, it seems clear that this debate will be settled (if it ever is) only by the balance of experimental results, and our study is designed to produce data that bear on the issue.

The recent critiques of Bolhuis and Macphail focused on research that claims to show adaptive differences in spatial memory capacity. Other research has examined the possibility of evolved biases in the use of spatial memory. When a foraging animal finds food at a particular location, and then leaves, it may return to forage there

Correspondence and present address: D. Burke, Department of Psychology, Macquarie University, Sydney, NSW 2109, Australia (email: darrenb@vision.psy.mq.edu.au). B. J. Fulham is at the Department of Psychology, University of Wollongong, Wollongong, NSW 2582, Australia.

at a later time, or search in a new location. In controlled settings, returning to a previously rewarding location is usually referred to as adopting a win-stay strategy, and avoiding a previously rewarding location as a win-shift strategy. The tendency to win-shift or win-stay is frequently consistent with the animal's foraging ecology. Nectar-feeding birds tend to avoid a previously rewarding flower (to win-shift), since, under natural conditions, once visited it no longer contains nectar (Gill & Wolf 1977; Kamil 1978; Cole et al. 1982; Healy & Hurly 1995), although rufous hummingbirds, *Selasphorus rufus*, also return to flowers that they have visited, but not emptied (win-stay; Hurly 1996). In contrast to this tendency in nectar-feeders, ovenbirds, *Seirus aurocapillus* (Zach & Falls 1976) and English thrushes, *Turdus merula* and *T. philomelos* (Smith 1974a, b), which feed primarily on aggregating, ground-dwelling invertebrates, tend to return to previously rewarding locations (to win-stay). There are two potential problems with concluding that these differences in spatial memory bias are a consequence of evolved cognitive adaptations.

First, the bias may simply reflect an individual bird's experience of the environment. Wild-caught adult bananaquits, *Coreba flaveola*, more easily learn a win-shift than a win-stay task but wild-caught juveniles learn both tasks equally easily (Wunderle & Martinez 1987). This suggests that the bias present in wild adult birds (the kind of subjects used in all other studies) may be a consequence of a long history of being rewarded for win-shifting (by exposure to the replenishment rates of natural flowers). This, in turn, raises the possibility that the win-shift and win-stay biases found with other species are not, in fact, the result of an evolved adaptation.

Although Wunderle & Martinez (1987) did not discuss them in this way, their findings are also consistent with the possibility that nectar-feeders have an evolved predisposition to learn to win-shift more easily than they are able to learn to win-stay, and that this interacts with exposure to the natural replenishment rates of flowers to produce the observed bias in adults. A mechanism of this kind appears to be responsible for hippocampal differences between storing and nonstoring birds. For example, Clayton (1995a b, 1996, 2001; Patel et al. 1997) has found that food-storing parids have an enlarged hippocampus only if they have experienced food caching, suggesting the cognitive adaptation for food storing is a change in the responsiveness of the hippocampus to particular kinds of experiences.

In our experiment, we used adult birds that were born and reared in captivity, and so had never been exposed to natural flower replenishment rates. Our aim was to examine whether they nevertheless showed win-shift and win-stay tendencies that reflected these rates, so ruling out a simple experience-based explanation.

A second potential shortcoming with previous evidence for evolved spatial memory biases is that the observed biases are merely consistent with the species' foraging ecology. Researchers seeking evidence of ecological influences on spatial memory capacity have usually compared the performance of related species on identical spatial tasks. If animals that depend on food storing consistently outperform those that do not, then this is much more compelling evidence for an adaptive specialization than simply showing that a food-storing bird can, for example, remember many locations for a long time. Since related species with different foraging ecologies (a nectar-feeder and a nonnectar-feeding relative, for example) have not been tested on comparable win-shift and win-stay tasks, the evidence that the win-shift bias in nectar-feeders is a consequence of an adaptive specialization is much less compelling. In fact, Gaffan & Davies (1981, 1982) have argued that this win-shift bias is a simple consequence of animals avoiding recently visited places. Clearly, without a comparison of some kind, it is impossible to rule out the operation of less specialized mechanisms in producing the win-shift bias in nectar-feeders.

Of course, as Macphail (1982, 1987, 1996) and others have pointed out, there are also difficulties associated with validly comparing the performance of different species, prompting a range of possible solutions (Kamil 1988; Shettleworth 1993; Lefebvre 1995; Carlier & Lefebvre 1996; Lefebvre et al. 1996). Because they have tended to focus exclusively on human cognitive and social mechanisms, evolutionary psychologists have sought evidence for adaptive specializations without making interspecies comparisons (e.g. Cosmides 1989; Barkow et al. 1992). Essentially, this approach involves testing predictions about the way in which an hypothesized cognitive module should function if it was 'designed' to solve a particular evolutionary problem. If the prediction is detailed enough then it is unlikely that alternative (general process) explanations are able to account for the results. This approach is particularly well suited to situations where a cognitive bias of some sort is predicted and it is the technique we have used in the current experiment.

A unique feature of our study is that we examined the tendency of Regent honeyeaters, *Xanthomyza phrygia*, to win-shift or win-stay at different intervisit intervals. Previous studies have shown only that nectar-feeders have a tendency to win-shift at short intervisit intervals. While a nectar-feeding bird that avoided only recently visited flowers (and otherwise searched randomly) would probably forage reasonably efficiently, it would be failing to exploit the fact that a flower that contains nectar now will eventually do so again. A win-shift-only strategy may, in fact, have evolved in birds that live in environments with plentiful, dispersed nectar sources (such as hummingbirds). If, however, nectar sources are clumped, then the most efficient foraging strategy is to combine a short-term win-shift tendency with a long-term win-stay tendency. Since Regent honeyeaters derive over 90% of their nectar from patchily distributed flowers of various eucalyptus species (Franklin et al. 1989; McGoldrick & MacNally 1998), we predicted that they would show a win-shift tendency at short intervisit intervals but a win-stay tendency after a period long enough for a flower to have refilled with nectar (about 3 h, House 1997).

In summary, we examined whether the win-shift bias found previously for nectar-feeding birds is a consequence of an adaptive specialization. We chose a species

with a foraging ecology that enabled us to predict that the tendency to win-shift or win-stay will reverse as a function of intervisit interval. We also used captive-reared birds that had never been exposed to the replenishment rates of the flowers that are hypothesized to have driven the evolution of the cognitive adaptation. If the birds' win-shift and win-stay tendencies were nevertheless sensitive to the details of natural flower replenishment rates, this would constitute strong evidence that these tendencies are due to a cognitive adaptation.

METHODS

Subjects

Twelve captive-born, and experimentally naïve, adult Regent honeyeaters (four female) were housed and tested individually. All birds were part of a captive breeding colony at Taronga Zoo. The birds were from six clutches (with separate mothers and probably fathers, but paternity was not determined) from breeding seasons in the 2 previous years. The birds were therefore between 1.5 and 2.5 years old and weighed between 20 and 25 g at the beginning of the experiment. No birds lost weight during the experiment.

Apparatus

Birds were individually housed and tested in cages measuring 1×1 m and 1.6 m high all of which were within a large holding facility that received a natural dark/light cycle (ca. 13:11 h), and natural temperature fluctuations (8–20°C). Eight feeders were used to provide the nectar rewards during the experiment. The feeders were made from yellow and green plastic tape wrapped around a transparent syringe (15 cm long and 3.5 cm in diameter) the tip of which (20 mm long and 6 mm in diameter) functioned as the corolla of the 'flower'. The tape was used to make the feeders more salient. During testing, four feeders were presented at each end of the cage, arranged in a square (Fig. 1). A perch was positioned ca. 60 cm from each end of the cage providing equal access to each of the feeders, although birds tended to perch on the wire of the cage when feeding. In all trials each baited feeder contained 50 µl of a commercial artificial nectar solution. All birds were fed on their usual diet of nectar, fruit and insects at the completion of a day's testing.

Procedure

The experiment started with a familiarization period of 3 days, in which the birds were housed in the new cages and single feeders were presented at random intervals and locations, three times during the day. We used a random number generator (http://www.randomizer.org/) to select three times from 0600 to 1800 hours and three walls (from one to four) to determine the time and wall that contained the feeder for each bird for that day. Birds quickly adapted to the new cages and to drinking from
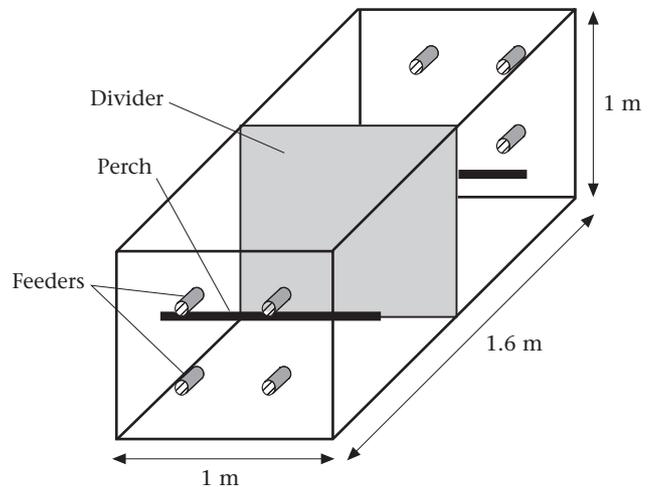
Figure 1. Schematic illustration of the test cage. The four feeders and perch at each end of the cage are shown. A removable divider was used to keep the bird in one half of the cage while the other side was baited.

the feeders. On the second day all birds approached the feeders within 30 s of their introduction. After this, three birds were randomly assigned to each of four experimental groups: win-stay/short-delay, win-stay/long-delay, win-shift/short-delay and win-shift/long-delay.

On each day that trials were run, the ad libitum nectar feeders (which were attached to a side wall of the cage, rather than one of the ends) were removed from cages at 0600 hours and experimental trials began 30 min later. All birds had access to a dish containing fruit and mealworms at all times during the experiment. This was to ensure that they always had adequate access to food. It did not appear to interfere with their desire for nectar, as the results indicate. For both win-shift and win-stay conditions, the sampling phase of a trial consisted of the introduction of eight feeders into the cage, half of which (randomly) contained nectar, and the other half of which were capped, and so could be generally explored, but not probed. We used a forced-choice procedure, rather than allowing the birds to visit any four of the baited feeders before the retention interval, to prevent them from simply learning a consistent foraging pattern. We capped the unrewarding feeders to ensure that they were completely unrewarding. With such narrow wells it was difficult to be sure that an emptied feeder had no trace of nectar (even after careful cleaning). We did not fill the unbaited feeders with water since this may have reduced the salience of the difference between baited and unbaited sites. Since the caps were present only in sample phases, they may have also provided the birds with a reliable cue to remember the locations containing nectar. The sampling phase ended when birds had emptied all of the baited feeders.

In the test phase of a trial the feeders were reintroduced to the cages, after 10 min for the short-delay groups or after 3 h for the long-delay groups. Each bird was run in three trials per day, with 30-min intertrial intervals. The feeders were removed after the birds had emptied all of them or after 30 min.

If a bird was in a win-stay condition, the feeders that contained nectar in the sample phase were rebaited in the test phase. All nonbaited feeders contained water in the test phase to make them visually indistinguishable from the baited feeders, but nonrewarding. If a bird was in a win-shift condition, all the feeders that had contained nectar in the sample phase now had only water, and the previously empty feeders now contained nectar. Because we were interested in the extent to which a tendency to shift after a short delay and stay after a long delay was learnt during the experiment, each bird completed 20 trials in the condition to which they were initially allocated (Session 1), and then a further 20 trials in the alternative delay condition (Session 2). We selected 20 trials because that has proved long enough to reveal any differences in the ease with which win-stay and win-shift tasks can be learnt (based on previous research with a wide range of species).

We judged a bird to have sampled a feeder when it probed the feeder tip with its tongue. During the test phase, sampling a feeder that did not contain nectar was counted as an error. The number of errors made before a bird found all four nectar-containing feeders was used to compare performance across the groups. Revisits to a water-containing feeder were not counted (and were rare) so the maximum number of errors on a trial was four.

All birds were returned to the large group enclosure after the experiment.

RESULTS

Figure 2 shows mean errors for all conditions in Sessions 1 and 2. The data were pooled into five trial blocks only for data presentation; all ANOVAs were conducted with trial (not block) as the independent variable. There was a tendency for performance to improve across each of the 20-trial sessions for all birds, but the most obvious result is that at short delays the birds performed much better in the win-shift task, and at long delays they performed much better in the win-stay task.

The data from Session 1 (trials 1–20) and Session 2 (trials 21–40) were analysed in two separate 2 (win-stay or win-shift) × 2 (long or short delay) × 20 (trial) mixed-factorial ANOVAs (in which trial was a within-subjects factor and the other two factors were between-subjects factors). In Session 1 there was a significant main effect of Trial ($F_{19,152}=2.74$, $P<0.001$). Inspection of Fig. 2 suggests that this is because performance improved over trials, but since this variable did not interact significantly with any other variables, this improvement was independent of Condition (stay or shift) and Delay. There was also a significant main effect of Delay ($F_{1,8}=10.05$, $P=0.013$), since birds made fewer errors with shorter delays, and, most importantly, a strong interaction between Condition and Delay ($F_{1,8}=206.23$, $P<0.001$), reflecting the win-shift bias at the short delay but a win-stay bias at the long delay.

The data from Session 2 show essentially the same pattern, except that Delay was not significant as a main effect, but did interact significantly with Trial ($F_{19,152}=2.23$, $P=0.004$). This seems to be because birds
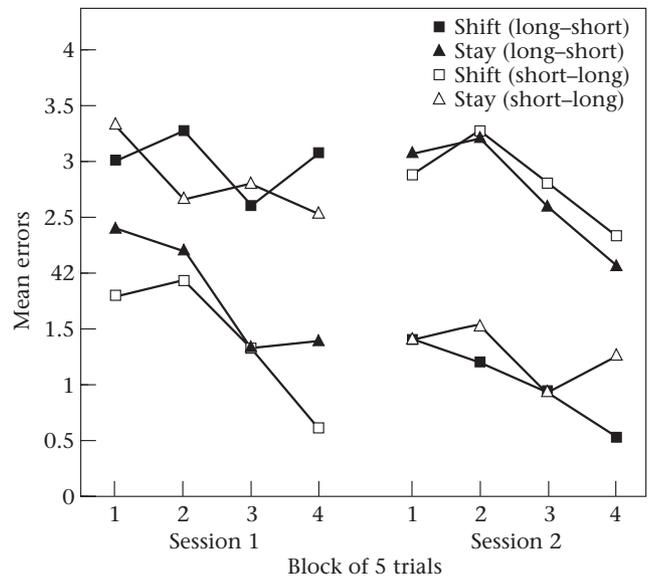
Figure 2. The performance of each group in terms of the mean number of errors (maximum 4) made before finding the four baited feeders. Data are pooled into blocks of five trials for clarity. For each group, the first 20 trials (the first four blocks of trials, or Session 1) were at either the long (3 h) or the short (10 min) delay and the second 20 trials (Session 2) were at the other delay. 'Shift (long-short)' indicates birds that were in the win-shift condition throughout the experiment, but in the long-delay condition in Session 1 and the short-delay condition in Session 2, etc.

that were moved to the short delay in Session 2 showed more evidence of improving over trials than birds moved to the long delay. As in Session 1, there was a significant main effect of Trial ($F_{19,152}=3.38$, $P<0.001$) and a highly significant interaction between Condition and Delay ($F_{1,8}=404.52$, $P<0.001$).

Taken together, these results show that the birds made fewer errors as trials progressed but that this improvement did not depend on whether they were in a win-shift or a win-stay condition. In other words, there was little evidence that the birds learned to win-shift more easily than they learned to win-stay. Instead, they either had a strong unlearned tendency, or rapidly learned, to revisit flowers that contained nectar at long delays, but to avoid those flowers at short delays. The clearest indication that these tendencies did not depend strongly on learning during the experiment is the rapid change in performance when the birds were switched from a short to a long delay or from a long to a short delay in Session 2 (after trial 20). While a performance decrement might be expected when the delay suddenly changes, it would be difficult to account for a sudden improvement in terms of learning, particularly when the change is from a short delay to a long one (as occurred in the stay group switched from a short to a long delay). To investigate the effect of this switch from Session 1 to Session 2 we conducted a 2 (Session) × 2 (Condition) × 2 (First-delay: the delay for that bird in Session 1) × Trial (20) mixed-factorial ANOVA. This revealed significant main effects of Session ($F_{1,8}=42.98$, $P<0.001$) and Trial ($F_{19,152}=4.15$, $P<0.001$), suggesting that performance improved both

within a session (across trials) and across sessions. This analysis also revealed significant interactions between Session and First-delay ($F_{1,8}$=24.39, P=0.001) and Condition and First-delay ($F_{1,8}$=5.72, P=0.044), but these are probably a consequence of the strong Session × Condition × First-delay interaction ($F_{1,152}$=982.27, P<0.001). This interaction reflects the fact that the pattern of results found in Session 1 (birds in the win-shift long-delay and win-stay short-delay conditions performed much worse than birds in the win-shift short-delay and win-stay long-delay conditions) reversed in Session 2, when the birds were moved to the other delay.

While it is clear that performance improved in all conditions, suggesting a role for learning, it is also informative to determine in which conditions searching was significantly better than chance. We used the Z test (Tille et al. 1996, equations 8 and 9) for this comparison. According to equation 8, random searching, without revisits, is expected to uncover all four rewards in 7.2 visits (or after 3.2 errors). The critical Z value for a one-tailed test at an α level of 0.05 is 1.65, so, with three birds in each cell tested, mean errors of less than 2.267 represent significantly better than chance performance. In Block 1 of Session 1, only birds in the win-shift short-delay condition performed significantly better than chance, suggesting an unlearned bias to shift at short delays. Performance in the other conditions was not significantly different from chance, and was close to chance in the shift-long and stay-short conditions. By Block 4 of Session 1, birds in the win-shift short-delay and win-stay long-delay (all three birds made an average of 1.4 errors for this block) conditions were performing significantly better than chance. Birds in the win-stay, short-delay and win-shift, long-delay conditions were still not performing better than chance. In Block 1 of Session 2, when the delay conditions were reversed, birds in the win-stay short-delay (stay (long-short) in Fig. 2) and win-shift long-delay (shift (short-long)) conditions did not perform better than chance, but birds switched to the win-stay long-delay (stay (short-long)) and win-shift short-delay (shift (long-short)) immediately performed better than chance. By Block 4 of Session 2 birds in the shift (long-short) and in the stay (short-long) conditions were still performing significantly better than chance. The performance of birds in the stay (long-short) condition in Block 4 is the only instance of birds in an unfavourable condition performing better than chance.

DISCUSSION

In this experiment, Regent honeyeaters that had no experience of the spatiotemporal distribution of nectar in their natural environment nevertheless showed strong tendencies to visit flowers in a manner that closely reflected aspects of this pattern. Although there was evidence of learning during the experiment (errors decreased over trials in all conditions) there was no evidence that the shift or stay tendencies were learned during the experiment, since trial did not interact with any of the other factors. It seems that the learning that occurred was superimposed on existing tendencies to

shift at short delays and stay at long delays. Since the birds had also had no opportunity to learn these tendencies before the experiment, they seem likely to be manifestations of an unlearned foraging strategy shaped by evolution to exploit the distribution of nectar in the birds' natural environment. In their home enclosures the birds were exposed to a few, essentially inexhaustible, nectar feeders that were available throughout the day. They were used by all of the communally housed birds, and so were empty at unpredictable times. If anything, this was likely to encourage a win-stay tendency at any intervisit interval. It is difficult to imagine how it could have resulted in the tendencies displayed in the current experiment.

Since the birds in this study could not have learned about natural flower replenishment rates, this is much stronger evidence for an evolved bias in the way in which spatial memory is used than that collected previously. Of course, we do not believe that this means that evolution has not shaped the spatial memory mechanisms of the species studied previously, as we explain below. First, however, it is necessary to rule out a possible alternative account of our data.

As mentioned earlier, Gaffan & Davies (1981, 1982) attempted to explain alternation behaviour in radial maze tasks (of which this is an analogue) using mechanisms different from those we propose and from those proposed in other ecologically inspired investigations. Using rats, *Rattus norvegicus*, as subjects, they showed that the tendency to shift in a radial maze was actually weaker if the rat found food at the end of an arm than if they did not (although it persisted), so referring to this behaviour as win-shift may be misleading. They proposed instead that rats (and possibly hummingbirds) have a bias towards simply shifting their short-term search behaviour, because they avoid arms with which they are familiar. This proposal is relevant to our experiment because they also suggested that this shift tendency would fade with time, as the memory of the visited arms faded. At long intervisit intervals they predicted that rats would be more likely to show a win-stay tendency, because the straightforward operation of the law of effect (returning to rewarding places) would be able to reveal itself in the absence of the short-term shift tendency. In fact, they were consistently unable to find any evidence of a win-stay bias at long intervisit intervals (18–20 min) in six experiments, and rats actually learn win-stay tasks better than win-shift at short intervisit intervals when escape from water is the reward (Means 1988), both of which are problematic for their account, but since the explanation is at least plausible we decided to examine our data from this perspective.

Two aspects of our results are inconsistent with the explanation put forward by Gaffan & Davies. First, the birds visited both capped and uncapped feeders in the sampling phase of each trial (although they were able to empty only those that were uncapped). Gaffan & Davies attributed shift behaviour to differential familiarity with locations: in the short term, animals preferentially visit less familiar locations. Since the birds were free to visit all locations in the sampling phase, and since the feeders at

each end of the cage were close together, they were probably all equally familiar in the test phase of a trial. Second, Gaffan & Davies proposed that win-stay behaviour at long intervisit intervals is due to basic place learning, and so this tendency should gradually emerge over trials. In contrast with this account, there is no evidence in our experiment that the learning that occurred in the win-stay conditions or in the long-delay conditions was different from that occurring in the win-shift or short-delay conditions. Gaffan & Davies would also predict that once an animal had learnt that returning to a location was rewarded (in the win-stay, long-delay condition, for example) this behaviour would persist. They would not predict that an animal switched to a short delay would show a sudden and persistent drop in performance as we found (when the win-stay, long-delay birds were switched to a short delay).

The fact that the win-shift and win-stay biases that we observed emerged without experience of the replenishment rates of natural flowers is central to our claim that they are a consequence of evolved predispositions. This is convenient because it allows us to rule out unequivocally competing explanations based on previous learning, but it should not be seen as a suggestion that evolution has not engineered predispositions to learn particular things or in particular ways. For example, as discussed earlier, Wunderle & Martinez (1987) showed that only adult bananaquits showed a win-shift bias at short intervisit intervals (juveniles learned win-stay as easily as win-shift). This could result from any of three possibilities, only one of which does not involve an evolved predisposition. First, the birds may develop a bias exclusively on the basis of learning about the fact that flowers emptied of nectar are bad places to revisit (in the short term). Second, adult birds may have a bias because of maturation alone, a bias that would emerge when they reach adulthood, regardless of the kinds of experiences they have had with natural flowers. Third, the bias may be present in adults as a consequence of learning, but adults may be predisposed (in some way) to learn to avoid flowers they have recently visited. Which of these possibilities is true could be addressed by experiments that manipulated the learning experiences of captive-born birds. Such experiments are crucial if we are to understand how evolution has shaped cognitive mechanisms.

Acknowledgments

References

Balda, R. P., Olson, D. J., Kamil, A. C. & Nims, P. J. 1995. Performance of four seed-caching corvid species in operant tests of nonspatial and spatial memory. *Journal of Comparative Psychology*, **109**, 173–181.

Barkow, J. H., Cosmides, L. & Tooby, J. (Eds) 1992. *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. Oxford: Oxford University Press.

Basil, J. A., Kamil, A. C., Balda, R. P. & Fite, K. V. 1996. Differences in hippocampal volume among food storing corvids. *Brain, Behavior and Evolution*, **47**, 156–164.

Bolhuis, J. J. & Macphail, E. M. 2001. A critique of the neuroecology of learning and memory. *Trends in Cognitive Sciences*, **5**, 426–433.

Bolhuis, J. J. & Macphail, E. M. 2002. Everything in neuroecology makes sense in the light of evolution. *Trends in Cognitive Sciences*, **6**, 7–8.

Carlier, P. & Lefebvre, L. 1996. Differences in individual learning between group-foraging and territorial Zenaida doves. *Behaviour*, **133**, 1197–1207.

Clayton, N. S. 1995a. The neuroethological development of food-storing memory: a case of use it, or lose it. *Behavioural Brain Research*, **70**, 95–102.

Clayton, N. S. 1995b. Comparative studies of food-storing, memory, and the hippocampal formation in parids. *Hippocampus*, **5**, 499–510.

Clayton, N. S. 1996. Development of food-storing and the hippocampus in juvenile marsh tits (*Parus palustris*). *Behavioural Brain Research*, **74**, 153–159.

Clayton, N. 2001. Hippocampal growth and maintenance depend on food-caching experience in juvenile mountain chickadees (*Poecile gambeli*). *Behavioral Neuroscience*, **115**, 614–625.

Cole, S., Hainsworth, F. R., Kamil, A. C., Mercier, T. & Wolf, L. L. 1982. Spatial learning as an adaptation in hummingbirds. *Science*, **217**, 655–657.

Cosmides, L. 1989. The logic of social exchange: has natural selection shaped how humans reason? Studies with the Wason selection task. *Cognition*, **31**, 187–276.

Dwyer, D. M. & Clayton, N. S. 2002. A reply to the defenders of the faith. *Trends in Cognitive Sciences*, **6**, 109–111.

Franklin, D. C., Menkhorst, P. W. & Robinson, J. L. 1989. Ecology of the Regent honeyeater. *Emu*, **89**, 141–153.

Gaffan, E. A. & Davies, J. 1981. The role of exploration in win-shift and win-stay performance on a radial maze. *Learning and Motivation*, **12**, 282–299.

Gaffan, E. A. & Davies, J. 1982. Reward, novelty and spontaneous alternation. *Quarterly Journal of Experimental Psychology*, **34B**, 31–47.

Gill, F. B. & Wolf, L. L. 1977. Non-random foraging by sunbirds in a patchy environment. *Ecology*, **58**, 1284–1296.

Gould-Beierle, K. 2000. A comparison of four corvid species in a working and reference memory task using a radial maze. *Journal of Comparative Psychology*, **114**, 347–356.

Hampton, R. R. & Shettleworth, S. J. 1996. Hippocampus and memory in a food-storing and in a nonstoring bird species. *Behavioral Neuroscience*, **110**, 946–964.

Hampton, R. R., Healy, S. D., Shettleworth, S. J. & Kamil, A. C. 2002. Neuroecologists are not made of straw. *Trends in Cognitive Sciences*, **6**, 6–7.

Healy, S. D. & Hurly, T. A. 1995. Spatial memory in rufous hummingbirds, *Selasphorus rufus*: a field test. *Animal Learning and Behavior*, **23**, 63–68.

Healy, S. D., Clayton, N. S. & Krebs, J. R. 1994. Development of hippocampal specialisation in two species of tit (*Parus* spp.). *Behavioural Brain Research*, **61**, 23–28.

House, S. M. 1997. Reproductive biology of Eucalypts. In: *Eucalypt Ecology, Individuals to Ecosystems* (Ed. by J. Williams & J. Woinarski), pp. 30–55. Cambridge: Cambridge University Press

Hurly, T. A. 1996. Spatial memory in rufous hummingbirds: memory for rewarded and nonrewarded sites. *Animal Behaviour*, **51**, 177–183.

Kamil, A. C. 1978. Systematic foraging by a nectar-feeding bird, the Amakihi (*Loxops virens*). *Journal of Comparative and Physiological Psychology*, **92**, 388–396.

Kamil, A. C. 1988. A synthetic approach to the study of animal intelligence. In: *Nebraska Symposium on Motivation. Vol. 35* (Ed. by D. W. Leger), pp. 257–308. Lincoln: University of Nebraska Press.

Krebs, J. R., Clayton, N. S., Healy, S. D., Cristol, D. A., Patel, S. N. & Jolliffe, A. R. 1996. The ecology of the avian brain: food-storing memory and the hippocampus. *Ibis*, **138**, 34–46.

Lefebvre, L. 1995. Ecological correlates of social learning: problems and solutions for the comparative method. *Behavioural Processes*, **35**, 163–171.

Lefebvre, L., Palameta, B. & Hatch, K. K. 1996. Is group-living associated with social learning? A comparative test of a gregarious and a territorial columbid. *Behaviour*, **133**, 241–261.

MacDougall-Shackleton, S. A. & Ball, G. F. 2002. Revising hypotheses does not indicate a flawed approach. *Trends in Cognitive Sciences*, **6**, 68–69.

McGoldrick, J. M. & MacNally, R. 1998. Impact of flowering on bird community dynamics in some central Victorian eucalypt forests. *Ecological Review*, **13**, 125–139.

Macphail, E. M. 1982. *Brain and Intelligence in Vertebrates*. Oxford: Clarendon Press.

Macphail, E. M. 1987. The comparative psychology of intelligence. *Behavioral and Brain Sciences*, **10**, 645–656.

Macphail, E. M. 1996. Cognitive function in mammals: the evolutionary perspective. *Cognitive Brain Research*, **3**, 279–290.

Macphail, E. M. & Bolhuis, J. J. 2001. The evolution of intelligence: adaptive specializations versus general processes. *Biological Review*, **76**, 341–364.

Means, L. W. 1988. Rats acquire win-stay more readily than win-shift in a water escape situation. *Animal Learning and Behavior*, **16**, 303.

Patel, S. N., Clayton, N. S. & Krebs, J. R. 1997. Spatial learning induces neurogenesis in the avian brain. *Behavioural Brain Research*, **89**, 115–128.

Sherry, D. F. 1998. The ecology and neurobiology of spatial memory. In: *Cognitive Ecology: The Evolutionary Ecology of Information Processing and Decision Making* (Ed. by R. Dukas), pp. 261–296. Chicago: University of Chicago Press.

Shettleworth, S. J. 1993. Where is the comparison in comparative cognition? Alternative research programs. *Psychological Science*, **4**, 179–184.

Smith, J. N. M. 1974a. The food searching behaviour of two European thrushes: 1. Description and analysis of search paths. *Behaviour*, **48**, 276–302.

Smith, J. N. M. 1974b. The food searching behaviour of two European thrushes: 2. The adaptiveness of the search patterns. *Behaviour*, **49**, 1–61.

Tille, Y., Newman, J. A. & Healy, S. D. 1996. New tests for departures from random behavior in spatial memory experiments. *Animal Learning and Behavior*, **24**, 327–340.

Timberlake, W. 2001. Integrating niche-related and general process approaches in the study of learning. *Behavioural Processes*, **54**, 79–94.

Wunderle, J. M. & Martinez, J. S. 1987. Spatial learning in the nectivarous bananaquit: Juveniles versus adults. *Animal Behaviour*, **35**, 652–658.

Zach, R. & Falls, J. B. 1976. Ovenbirds hunting behaviour in a patchy environment: an experimental study. *Canadian Journal of Zoology*, **54**, 1863–1879.