When a place is not a place: encoding of spatial information is dependent on reward type

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Summary

The adaptationist perspective investigates how an animal's cognition has been shaped by the informational properties of the environment. The information that is useful may vary from one context to another. In the current study we examine how manipulating the foraging context (the type of resource being foraged) could affect the way spatial information is used by the forager. Noisy miner birds (omnivorous honeyeaters) were given spatial working memory tasks in which they searched baited and unbaited feeders for either nectar or invertebrates. We hypothesised that noisy miners would encode the locations of baited and unbaited feeders equally well when foraging for nectar (all flowers, whether containing nectar or not are places to remember and avoid while foraging on a plant). When foraging for invertebrates, however, we predicted that noisy miner birds would not encode the locations of unbaited feeders as effectively as baited feeders (in a natural patch of invertebrates there is no cue to differentiate a point location where a prey item has not been found from the rest of the potentially homogenous patch). As predicted, birds foraging for invertebrates made more revisits to unbaited than baited feeders, with no such difference evident when birds were foraging for nectar.

Keywords: spatial cognition, foraging, resource distribution.

Introduction

Using an animal's ecology to make predictions about its cognitive function is an approach that has yielded important insights into the evolution of

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cognition and its underlying behavioural mechanisms (Shettleworth, 2003; Sherry, 2006). The majority of research in this vein has used foraging ecology to form hypotheses about species differences in spatial cognition (Shettleworth, 2003). Demonstrations that caching birds rely on memory to relocate their caches (Cowie et al., 1981; James & Verbeek, 1985) led several research teams to hypothesise that caching species would outperform closely related non-caching species in laboratory tests of spatial memory, or that degree of dependence on stored food would positively correlate with spatial performance in storing species. While there was substantial evidence for the test hypotheses (Hilton & Krebs, 1990; Kamil et al., 1994; Olson et al., 1995; McGregor & Healy, 1999), they were not unanimously supported (Healy & Krebs, 1992; Healy & Suhonen, 1996). Further studies asked specific questions about which aspects of the laboratory tasks led to a performance advantage for the caching species. These studies revealed some of the underlying behavioural mechanisms involved in the superior spatial cognition of caching birds, such as a tendency to attend to spatial over colour information (Brodbeck, 1994; Brodbeck & Shettleworth, 1995) and an ability to retain spatial information for longer (Hilton & Krebs, 1990; Bednekoff et al., 1997a) with high resistance to interference (Bednekoff et al., 1997b).

A similar, if less expansive, body of research has investigated the spatial memory abilities of nectarivorous birds. Cole et al. (1982) were the first to report a win-shift bias (a spontaneous tendency to avoid recently rewarded locations coupled with faster learning of shift versus stay contingencies) in several species of hummingbirds and suggested that this behaviour represented a cognitive adaptation to the depleting nature of nectar. Since then, a win-shift bias has been reported in other nectarivorous bird families including Australian honeyeaters (Burke & Fulham, 2003; Sulikowski & Burke, 2007) and bananaquits (Wunderle & Martinez, 1987). Studies have also reported that the tendency to win-shift can be sensitive to current foraging context and the passage of time, manifesting only: when the food is nectar not invertebrates (Sulikowski & Burke, 2007); only if the bird depleted the location before leaving (Hurly, 1996); and only if time since the last foraging bout has not been sufficient for a flower to replenish (Burke & Fulham, 2003). This last study was conducted on a population of captive-reared regent honeyeaters (*Xanthomyza phrygia*) that had never experienced the natural depleting and replenishment rates of wild flowers, strongly suggesting that win-shift behaviour, in the honeyeaters at least, is not simply the result of a general spatial learning process being shaped by ontogeny.

Further research on the noisy miner (*Manorina melanocephala*, an omnivorous Australian honeyeater) has shown that as well as win-shifting only in association with nectar, these birds also perform better on spatial working memory tasks when the food is nectar rather than invertebrates (a difference not explicable in terms of motivation), and tend to structure their search differently in response to the different food types (Sulikowski & Burke, 2010). The study we currently report follows from these earlier findings and aimed to further explore the variation in what information is extracted from the environment and how this information is used, as a function of the food type being foraged upon.

The natural distributions of nectar and invertebrates differ substantially. Nectar is a resource with a predictable spatio-temporal distribution. A flower contains small enough quantities that it is typically depleted after a single visit (at least for avian foragers) and so will be an unprofitable place to return to until such time has passed for it to replenish. The flowers on a plant conspicuously signal the potential presence and location of nectar. Each flower represents a precise and discrete point location in space. Upon arriving at a flowering plant to forage, a bird will do best if it visits each flower only once. Irrespective of whether any particular individual flower contained nectar, a bird should remember the locations of *all* flowers it has visited in the patch and avoid these as it continues to search (Pyke, 1978). In the current study we present birds with both baited and unbaited feeders in an array and predict that birds foraging for nectar should be able to avoid revisits to both types of feeder equally well. The Margnial Value Theorem (MVT) dictates that the forager should attend to its rate of success and leave a patch when this rate falls below the average for its territory (Charnov, 1976). We are not, therefore, suggesting that birds foraging for nectar are not likely to distinguish between baited and unbaited locations (in fact, previous research suggests they do, Sulikowski & Burke, 2007), just that both baited and unbaited locations should be avoided with equal efficacy.

‘Invertebrates’ as a source of prey are not as homogenous a group as nectar. There are, however, several characteristics that many types of invertebrate prey (particularly those most relevant to the noisy miner) have in common that distinguish their spatial distribution from that of nectar. We firstly note that ‘patches’ of invertebrates within a territory likely exist in a similar way as the flowers of a plant together form a patch. Microhabitat changes from one part of a bird's territory to another (for example, a damp shady place under the leaf litter at the foot of a tree is a different habitat from the foliage of that tree or a patch of dry unshaded ground) no doubt produce discrete clumps of invertebrate prey within the territory (Dennis et al., 1998; Jonsson et al., 2009). There is no reason to suppose that birds may not be just as aware of these discrete patches and their relative profitability as they are of the flowering plants in their territory. It is within these patches, however, that the important differences between the distributions of nectar and invertebrates exist. While flowers advertise the point location of nectar, no such signal typically marks the spot of invertebrate prey. This is especially true of cryptic prey, which form the majority of the noisy miner insect diet (Dow, 1977; Barker & Vestjens, 1984).

When a bird arrives at a site to forage for invertebrate prey, there are no cues that distinguish a point location where nothing has yet been found from the continuum of other potential point locations, nor is there any useful information attached to any particular point that could be arbitrarily defined until after a prey item is located there. Only after a prey item is located (and typically immediately consumed), is the point location at which it was found differentiated from the rest of the potentially homogenous patch. Since an unbaited feeder is the experimental analogue of an overturned piece of bark that yielded no prey, no different from other unproductive parts of the patch, we predict that birds foraging for invertebrates in the current study will not encode the locations of unbaited feeders as effectively as those of baited feeders and, therefore, that birds ought to make more revisits to the unbaited than to the baited feeders.

The above predictions hinge on the assumption that the birds are using encoding and recall of particular locations to solve the spatial search problem. There is good evidence that noisy miners (and other nectarivorous bird species: Wunderle & Martinez, 1987; Hurly & Healy, 1996) spontaneously attend to and use fine-scale spatial information when foraging for nectar. They display a bias (prior to any reinforcement) to win-shift after a short retention interval, a behaviour that would be impossible without encoding and recalling the point location information (Sulikowski & Burke, 2007). They also perform well-above chance on spatial working memory tasks (Sulikowski & Burke, 2010). The evidence that these birds attend to fine-scale spatial information when foraging for invertebrates is less compelling. This may be because invertebrate prey are often mobile (so a particular point location may only be depleted momentarily) and so high precision spatial information may not be so useful in this context. Noisy miners do not exhibit either a shift or a stay bias when foraging for invertebrates and perform only a little above chance in spatial delayed match-to-sample tasks (Sulikowski & Burke, 2007). When foraging for invertebrates in a spatial working memory task, noisy miners do perform above chance, but not as well as when they are foraging for nectar (Sulikowski & Burke, 2010). This suggests that the birds may not process (encode and/or attend to, etc.) the relevant spatial information as effectively when foraging for invertebrates as when foraging for nectar. One consequence of this for the current study is that if the birds are not compelled to attend to the spatial location information on an appropriate scale when foraging for invertebrates we may fail to find the predicted difference between how effectively they are able to encode the locations of baited versus unbaited feeders. To encourage birds foraging for both food types to attend to and encode the spatial locations of the feeders, rather than adopting a stereotypic search pattern, we used a procedure based on Dubreuil et al. (2003) and interrupted birds on a number of occasions during their search, forcing them to leave the array of feeders. Details of this procedure are described in the methods.

To summarise our predictions; in a series of spatial working memory trials where birds search an array of baited and unbaited feeders, foraging for either an invertebrate or a nectar reward we hypothesised that the natural distributions of these two types of food would influence how effectively the birds encoded the locations of the baited versus the unbaited feeders. We predicted that because all flowers on a plant are to be avoided once visited, irrespective of whether they contained nectar when first visited, that a bird foraging for nectar would encode the locations of baited and unbaited feeders with equal efficacy, seeking to avoid all of these. As a result any revisits that these birds do make should be equally distributed between the baited and unbaited feeders. We predicted that birds foraging for invertebrates on the other hand, would make more revisits to the unbaited than to the baited feeders as, under natural foraging conditions, only locations where invertebrate prey are found are differentiated from the background of the patch.

Material and methods

Subjects, housing and husbandry

Subjects were ten noisy miner birds (Aves: Meliphagidae, *Manorina melanocephala*) trapped from the wild as adults (exact age and sex unknown). The birds had previously participated in social and colour learning studies while in captivity, but not in any spatial experiments or tasks. Birds had been in captivity for 2–4 months prior to the experiment. At the completion of testing the birds were banded and released back into their territories. Observations from several years of research in our lab suggest that levels of survivorship and re-integration into the social group are high following release.

While in captivity birds were held and tested individually in outdoor cages measuring approx. 3 × 3 × 3 m. Birds were maintained on a diet of Wombaroo Lorikeet and Honeyeater Wet Mix (a commercial nectar substitute). During the testing period the daily food was provided a variable time after the end of the testing session, with water for drinking and bathing always available.

Materials

For each trial the birds were presented with a 4 × 4 array of 16 feeders (Figure 1). The feeders consisted of an opaque well (approx. 1 ml capacity) with a lid that birds could lift open with their beaks. These lids fell closed when the bird left the feeder making visited and unvisited feeders visually indistinguishable. A bird was considered to have visited a feeder if it opened the lid and probed inside the well with its beak or tongue. All birds had previous experience opening similar feeders, so no specific training for this experiment was required. Of the 16 feeders presented in each trial, half were baited and half remained empty. For each trial the 8 feeders to be baited were chosen pseudo-randomly with the restriction that every row and column contained at least 1 baited feeder. The baits were half a mealworm (*Tenebrio molitor* larva) or 0.25 ml of a 30% (w/v) sucrose solution (invertebrate- and nectar-rewarded conditions respectively, manipulated between-subjects).

Experimental procedure

The experiment proceeded in three stages; two blocks of 8 time-limited free search trials separated by an intervening block of 16 disrupted search trials. For the 2 blocks of 8 time-limited search trials, birds were presented with the

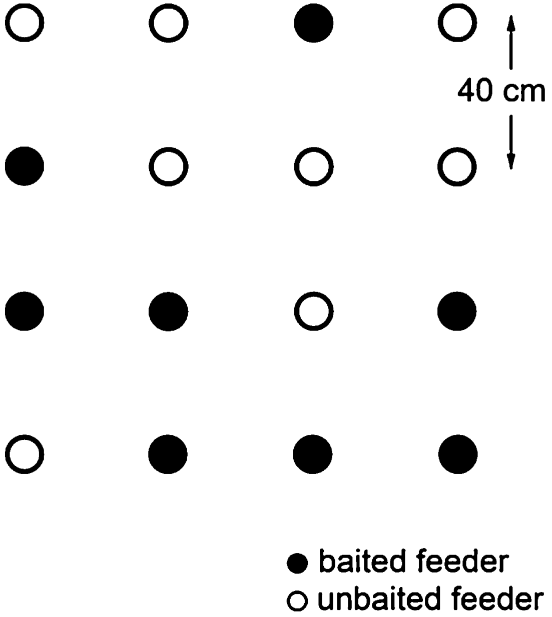

Figure 1. Experimental layout of the array of feeders. For each trial the feeders to be baited were chosen pseudo-randomly with the restriction that every row and every column had to contain at least one baited feeder.

array of feeders and given 15 min to freely search the array. This was more than sufficient time for the birds to thoroughly search the arrays (typically making upwards of 40 visits to the 16 feeders). In order to minimise possible proactive interference from previously rewarded locations, trials were spaced one day apart, and baited feeders were selected randomly, except that identical arrays were used for both foods.

To encourage all of our subjects to attend to the spatial information in an appropriate way we included interrupted search trials, a procedure adapted from the radial-arm-maze (RAM, Olton & Samuelson, 1976) literature. We included a series of 16 trials (between the two 8 trial blocks in which the birds were free to explore the array uninterrupted) that limited the number of visits birds were permitted to make to feeders in the array (so that revisits would carry a cost) and repeatedly interrupted the birds as they searched through the array. We hypothesized that any tendencies to search using movement rules (analogous to the serial search exhibited by rats in the RAM, Dubreuil et al., 2003) would be discouraged by the interrupted trials, in turn encouraging the use of spatial memory to encode specific locations. We hoped this would allow any differences in the effectiveness with which a bird encoded the location of a baited versus an unbaited feeder to be maximized in the second series of free exploration trials.

For the 16 intervening disrupted search trials, each bird was presented with the array and allowed to make a maximum of 16 visits to the feeders. The bird was forced to fly away from the array, after every fourth visit, by the experimenter stepping forward toward the front of the cage until the bird retreated. The experimenter then stepped back again allowing the bird to approach the array once more. All birds quickly adjusted to this disturbance and readily re-approached the array once the experimenter stepped back.

All trials were recorded on mini-DV tape and the data were subsequently scored.

Results

Encoding of baited and unbaited feeder locations

To test our main hypothesis, that there would be an interaction between baited/unbaited status of the feeders and reward type we examined the first 8 visits that birds made to the baited feeders and the first 8 visits birds made to the unbaited feeders in each of the time-limited trials. We recorded how many of these 8 visits constituted revisits (to feeders already visited in that trial). We then calculated for each bird the mean number per trial of these revisits for the baited and unbaited feeders in each of the two blocks of time-limited trials. A GLM ANOVA with within-subjects factors and reward type (2 levels, nectar and invertebrates) as a between-subjects factor revealed a significant feeder status × reward type interaction ($F_{1,8} = 7.879$, $p = 0.023$). There were no significant main effects or interactions involving block (all F values < 3, all p values > 0.1) and Figure 2 shows that while birds foraging for invertebrates appeared to make more revisits than nectar foragers in block 1 only, the pattern of the critical reward type × feeder status interaction is the same in both blocks — that is more revisits to unbaited than baited feeders for invertebrate foragers and more revisits to unbaited feeders for invertebrate foragers compared to nectar foragers. Since we predicted that the reward type × feeder status interaction would be stronger in the second block we also ran the above analysis (without the ‘block’ factor) on the data from each block separately. The effect size of the reward-type × feeder status

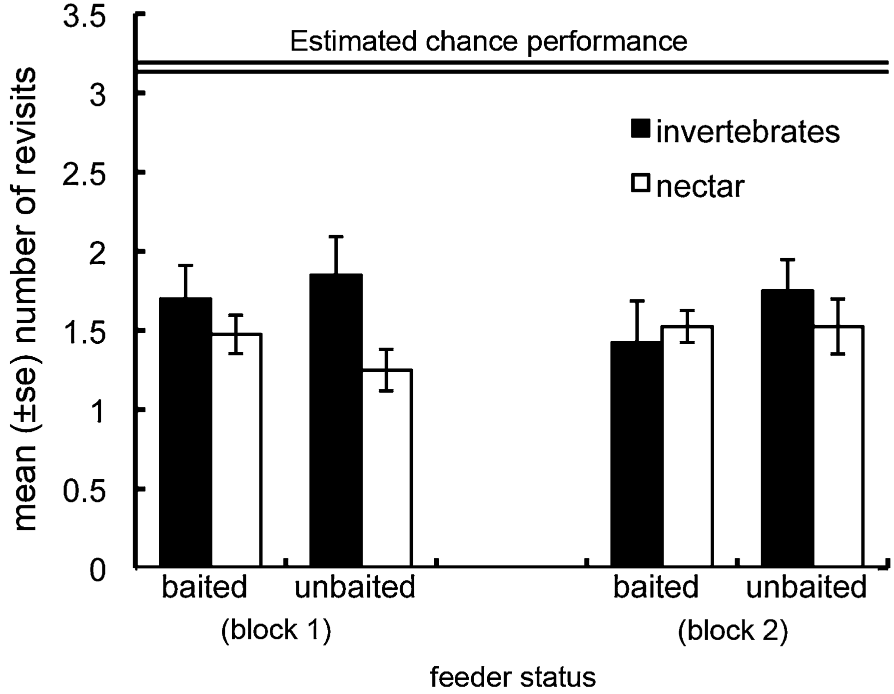

Figure 2. Mean (± SE) number of revisits made in the first eight visits to baited and unbaited feeders, respectively, in block 1 and block 2 of the time-limited trials. The reward type by feeder status interaction was significant, with birds foraging for invertebrates making significantly fewer revisits to baited than unbaited feeders and making significantly more revisits to unbaited feeders than birds foraging for nectar. Estimated chance performance for baited and unbaited feeders is indicated by the two horizontal lines.

interaction was similar in block 1 ($F_{1,8} = 4.545$, $p = 0.066$, $\eta_\rho^2 = 0.362$) and block 2 ($F_{1,8} = 3.841$, $p = 0.086$, partial $\eta_\rho^2 = 0.324$), providing no evidence at all of a difference between the blocks in how baited and unbaited feeders were encoded.

Overall baited and unbaited mean revisit scores were calculated for each bird. One-tailed t-tests were used to test the a priori predictions that birds foraging for invertebrates would make more revisits to unbaited than to baited feeders and that birds foraging for invertebrates would make more revisits to unbaited feeders than birds foraging for nectar. A one-tailed independent-samples t-test revealed that, as predicted, birds made significantly more revisits to the unbaited feeders when foraging for invertebrates (1.80 ± 0.15) than when foraging for nectar (1.39 ± 0.08; $t_8 = 2.366$, $p = 0.023$). There was no difference between the reward types (1.50 ± 0.06 and 1.56 ± 0.19 for the nectar and invertebrate groups, respectively) for the baited feeders, (one-tailed independent-samples t-test, $t_8 = 0.313$, $p = 0.381$). Paired-samples t-tests revealed that birds foraging for invertebrates made significantly more revisits to unbaited than baited feeders ($t_4 = 4.750$, $p = 0.005$) with no difference between baited and unbaited feeders for the birds foraging for nectar ($t_4 = 0.985$, $p = 0.190$).

Random walk simulations (80 in total, 10 through each of the 8 baiting arrays used in the experiment) were conducted to estimate the chance number of revisits to baited and unbaited feeders in the first 8 visits to each. In our model the walker stepped from a feeder in any of the 8 possible directions (up, down, left, right, up-right, etc.), with equal likelihood as long as a move in that direction would encounter another feeder. From this analysis, we calculated a mean chance revisit rate in the first 8 visits to that feeder type of 3.21 ± 0.12 for the baited feeders, and 3.15 ± 0.13 for the unbaited feeders. Birds in all conditions were performing significantly better than this.

Search bout length in the time-limited trials

Previous studies (Sulikowski & Burke, 2007, 2010) have suggested that birds foraging for invertebrates in these types of tasks combine their individual visits into significantly longer search bouts (a bout ending once a bird leaves the array and perches in another part of the cage, and a new bout commencing if a bird returns to the array) than birds foraging for nectar. We found the same effect in this experiment (Figure 3). While there was no significant difference between the nectar and invertebrate groups in the mean number of visits birds made to the array per trial in either the first ($t_8 = 1.339$, $p = 0.109$) or the second ($t_8 = 0.587$, $p = 0.288$) block (Figure 3A,B), invertebrate-rewarded birds organised these visits into significantly longer search bouts. A GLM ANOVA with block (2 levels, first and second) as a within-subjects factor and reward type (2 levels, nectar and invertebrates) as a between-subjects factor revealed a significant main effect of reward type ($F_{1,8} = 9.006$, $p = 0.017$). Though the reward type × block interaction was not significant ($F_{1,8} = 3.221$, $p = 0.110$) post-hoc independent-samples t-tests suggested that the second block ($t_8 = 2.996$, $p = 0.017$) may have been contributing more to the effect than the first block ($t_8 = 0.863$, $p = 0.413$; Figure 3C,D).

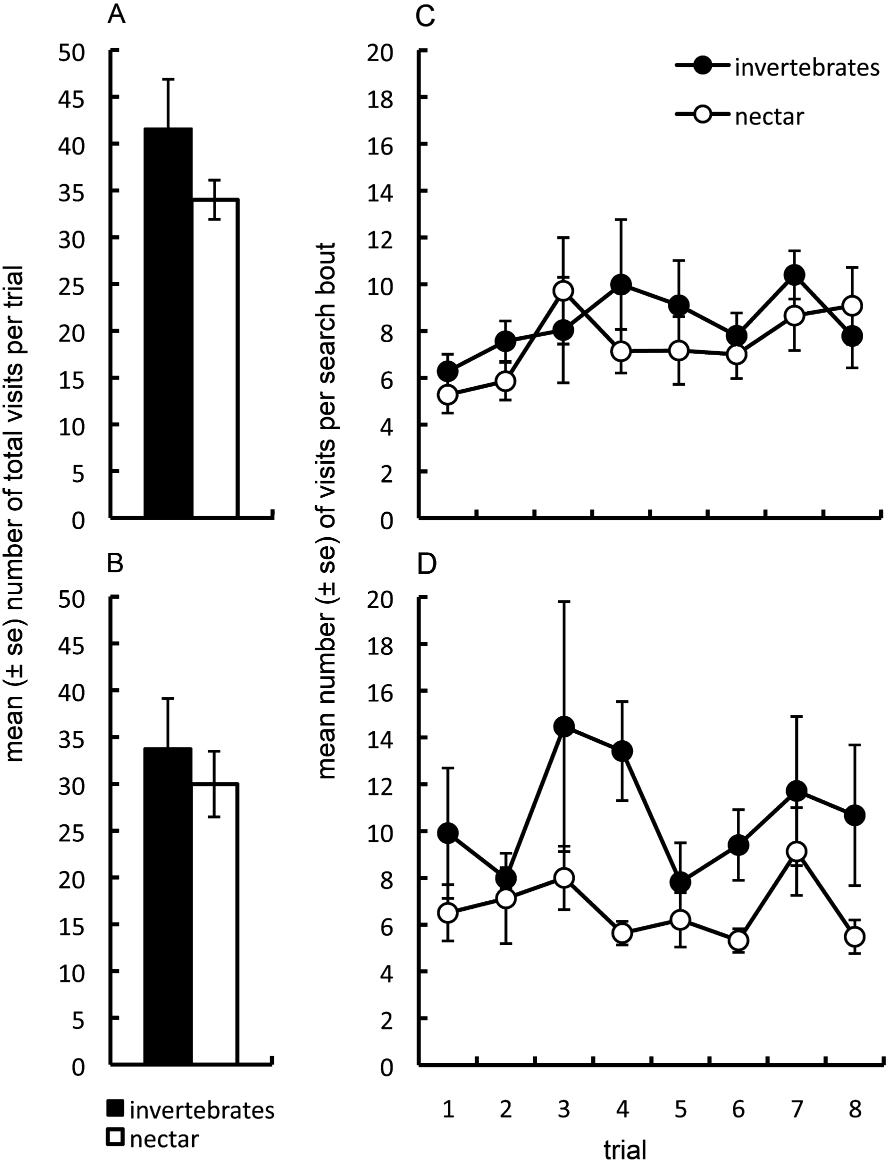

Figure 3. Mean (± SE) number of total visits per trial birds made in block 1 (A) and block 2 (B) of the time-limited trials and visits per search bout made in each trial of block 1 (C) and block 2 (D) of the time-limited trials. While there was no difference in the total number of visits made by birds in the two reward groups, invertebrate-foraging birds grouped these visits into significantly longer search bouts than nectar foragers, especially in block 2.

Performance in the interrupted search trials

In these trials (occurring between the first and second block of the time-limited trials) birds were limited to 16 visits only and forced to leave the array after every fourth visit. As for the time-limited trials we examined the number of revisits made in these trials. For analysis, the 16 trials were divided into four blocks of 4 trials and the mean number of revisits was calculated for each bird for each of the four blocks — the calculation of block means was necessary as file corruption resulted in the loss of footage of several individual trials. The block means were then analysed using a GLM ANOVA with block (4 levels, trials 1–4, 5–8, 9–12 and 13–16) as a within-subjects factor and reward type (2 levels, nectar and invertebrates) as a between-subjects factor. This analysis revealed a significant main effect ($F_{3,24} = 6.065$, $p = 0.003$) and linear contrast effect ($F_{1,8} = 14.156$, $p = 0.006$) of block as both groups of birds made progressively fewer revisits. Despite nectar rewarded birds making fewer revisits in each of the 4 blocks the main effect of reward type was not significant ($F_{1,8} = 1.881$, $p = 0.207$). The reward type × block quadratic contrast interaction, however, approached significance ($F_{1,8} = 5.015$, $p = 0.055$) as nectar-rewarded birds improved their performance more sharply and earlier than invertebrate-rewarded birds (Figure 4).

Discussion

Consistent with predictions we found evidence that noisy miner birds encode the locations of baited and unbaited feeders equally well when foraging for nectar, a resource distributed over discrete locations. In contrast, the locations of unbaited feeders are not as effectively encoded for avoiding revisits as the locations of baited feeders when birds are foraging for invertebrates, a potentially continuously distributed resource. These patterns of information-use coincide with the types of information we predicted would be useful and salient when birds foraged for nectar and invertebrates under natural conditions. We do not adhere to the notion that all learning and memory differences between species or, as is the case here, between contexts, can be accounted for by a few unadapted general processes being shaped by a variety of life experiences (Bolhuis & Macphail, 2001). We feel that the weight of evidence against this view is overwhelming (Hampton et al., 2002;

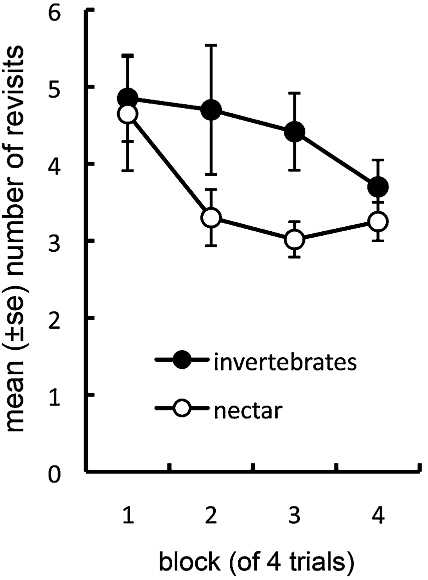

Figure 4. Mean (± SE) number of revisits made during the 16 trials, where feeding was interrupted after every 4th trial. Data are presented for the two reward groups, and divided into sequential blocks of 4 trials.

Timberlake, 2002; Sherry, 2006). Nor are we of the view that every piece of adaptive behaviour is indicative of an evolved adaptation in the cognitive mechanism underlying that behaviour. We instead view the behavioural phenotype of the animal in the same way as the morphological phenotype; the traits expressed are a result of complex interactions between the genes and the environment. Comparative and developmental studies are, therefore, required to start unravelling the ways in which these interactions produce the observed behaviours (for example, what are the predispositions and potential of different species and what learning experiences are necessary to realise this potential?). From that perspective, the extent to which this particular finding is indicative of an evolved adaptation, which has equipped the species with various specialised cognitive systems that it can engage in appropriate foraging contexts, is still an open question.

Irrespective of the ultimate causes of these differences, from a proximate perspective, the birds were obviously not responding to differences in the distributions of the rewards as these were held constant between the food types in the experiment. Rather birds must have been responding to some perceptible difference in the taste/texture, or perhaps nutrient content via gut physiology, of the reward types. Further research, independently manipulating these features, is required before we can justify speculation on this point.

The nature of the reported differences in response to the food types and what they may indicate collectively, however, does warrant some consideration. The difference in encoding of unbaited locations reported here joins a string of cognitive and behavioural differences observed in response to nectar or invertebrate rewards. Birds foraging for nectar attend to spatial location information spontaneously and exhibit a win-shift bias, while birds foraging for invertebrates, appear to attend less effectively to spatial information but tend to search in longer bouts, being less likely to disrupt their own movement while searching. We suggest that it may be appropriate to describe these differences collectively as qualitatively different cognitive strategies, which selectively process different information to produce different behavioural responses. Such an interpretation is reminiscent of the behavioural systems approach to learning (Timberlake & Lucas, 1989; Timberlake, 1993), which hypothesised that behaviour was the outcome of a series of systems (a foraging system, a mating system, etc.) each adapted to extract and process the relevant information and produce appropriate behaviours. If it is the case that qualitatively different strategies are engaged then this raises the possibility of the existence of highly specific encapsulated behaviour systems. Again, though, we stress that the existence of such strategies in and of itself does not necessarily imply anything about their phylogenetic and ontogenetic roots.

While we deduced our hypotheses based on the types of information the birds would use to forage efficiently within a patch, our findings are also consistent with the types of information the birds would need to make between-patch foraging decisions. The MVT (Charnov, 1976) states that animals calculate their instantaneous rate of energy gain while foraging, as well as keeping an estimate of the average rate of energy gain available within their territory. For animals to optimise their energy intake, the MVT predicts that animals should leave the patch they are currently foraging in and move to another when their instantaneous rate of energy gain falls below the average of that for their territory. When foraging in a patch of flowers on a plant, birds would need information about all the available flowers — all the flowers they have visited and the amount of nectar in these flowers μ to judge the profitability of the plant versus other plants in their territory (Pyke, 1978). When foraging for a potentially continuously distributed prey such as invertebrates, however, only information about the number of items found and where they were found is needed to make judgements about the relative profitability of different areas within the territory, with patch boundaries defined by the relative densities of available prey in various areas, rather than the more discrete patch determination afforded by a flowering plant (see Arditi & Dacarogna, 1988, for a lengthy discussion of the application of MVT to continuously distributed resources). Therefore, the way birds encoded the available information in our experiment is consistent with the information they would typically use to make within- and between-patch foraging decisions when exploiting nectar and invertebrates, respectively, under natural conditions.

The data reported here add to a series of previous studies that have shown more proficient spatial cognitive performance by noisy miner birds when foraging for nectar compared to when foraging for invertebrates (Sulikowski & Burke, 2007, 2010 and data in submission). Previous studies also suggest that noisy miners are less likely to interrupt the movement of their search and to rely on movement-based search strategies when foraging for invertebrates than when foraging for nectar. The same was true in this study, with invertebrate foragers searching in significantly longer bouts than nectar foragers in the time-limited trials.

The findings discussed above are consistent with the conclusions drawn from previous studies and with the logic used to derive the hypotheses in the current study. The evidence, in terms of differential performance, we found here for use of memory versus movement strategies when birds are foraging for nectar and invertebrates respectively, however, is not as strong as those reported previously. One potential causal factor is the size and shape of the array used in this study versus that used in previous studies. This study used 16 feeders in a symmetric 4 × 4 array, while previous studies (Sulikowski & Burke, 2010 and data in submission) used 8 feeders arranged in asymmetric arrays within a 4 × 4 grid. The increased size and symmetric nature of the array used in the current study may not have facilitated a memory-based strategy while being more conducive to a movement-based strategy.

With respect to the movement-based strategy, the 16-feeder array used in this study meant that from any given feeder birds could potentially move in any of up to 8 directions and/or move repeatedly in the same direction. This is in contrast to the 8 feeder arrays (with 8 of the potential locations not containing feeders) where birds had less freedom of choice with respect to direction to the nearest feeder, and the irregular shape of these arrays would often make repeated movements in the same direction unlikely. With respect to the memory-based strategy, the irregular nature of the 8-feeder arrays provided for unique configural relationships for each of the feeders with respect to their nearest neighbours. For example, only one of the 8 feeders may have had one feeder directly above and another immediately to the left. In the current 16-feeder array, however, none of the configural relationships were unique, with all feeders surrounded by immediately adjacent feeders (with the obvious exception of those at the edge). If the configuration of surrounding feeders is one of the cues used by a spatial memory strategy, and evidence from hummingbirds suggests it might be (Healy & Hurly, 1998), then the square layout of the 16-feeder array would reduce the discriminability of these cues. Working together, these two effects may have encouraged the nectar-foragers to increase their reliance on a movement-based strategy resulting in a decrease in the behavioural differences between the reward-type groups, relative to that seen in previous studies.

A surprising aspect of the current study is that even though the behaviour of the birds changed over the course of the 16 interrupted trials, this did not lead to the anticipated enhancement of the difference between revisits to baited and unbaited feeders in the birds foraging for invertebrates in block 2. It is possible that the level of interruption we used was simply insufficient to strongly encourage greater use of a spatial memory strategy, or that birds were already using such a strategy (which is likely in the case of those foraging for nectar). We were reluctant to interrupt the birds after every visit in case this led to them abandoning the task altogether. While the lack of an effect of this manipulation is curious, the critical result is that the predicted food-type difference between revisits to baited and unbaited feeders occurred.

In summary, this paper reveals a new important difference in the way information is processed when birds are foraging for a discrete versus a potentially continuously distributed resource. All discrete locations appear to be encoded equally well when birds are foraging for nectar, while locations containing a reward are encoded more effectively than unbaited locations when birds are foraging for invertebrates. This difference is consistent with the information animals need to make optimal within-patch and between-patch foraging decisions under natural conditions with respect to the different resources. It also adds to the growing list of differences in cognitive function that can be detected in the lab as proximate responses to nectar and invertebrate forage, respectively. Collectively these differences (in tendency to spontaneously attend to location information, organisation of search bout structure, presence/absence of a win-shift bias and now encoding of baited and unbaited locations) may be interpreted as indicative of qualitatively different and functionally adaptive spatial strategies being engaged, the ultimate causes and ontogenetic origins of which are yet to be determined. Whatever the mechanisms ultimately turn out to be, and it already seems likely that there will be more than one, there is mounting evidence that evolution has shaped these mechanisms to function adaptively in ecologically appropriate contexts. The fact that using a different food reward can trigger the use of one spatial strategy over another, despite identically structured spatial tasks, raises serious questions about the generality of the cognitive mechanisms (in this case spatial) uncovered in any particular experimental paradigm. Data reported here and previously (Sulikowski & Burke, 2007, 2010 and data in submission) instead suggest that evolution may have engineered independent cognitive mechanisms to meet particular ecological demands, suggesting, in turn, that to fully understand spatial cognition, for example, we first need to carefully consider the multitudinous ways in which spatial information is used in an animal's everyday life.

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References

Arditi, R. & Dacorogna, B. (1988). Optimal foraging on arbitrary food distributions and the definitions of habitat patches. — Am. Nat. 131: 837-846.

Barker, R.D. & Vestjens, W.J.M. (1984). The food of Australian birds II: Passerines. — Melbourne University Press, Melbourne, VIC.

Bednekoff, P.A., Balda, R.P., Kamil, A.C. & Hile, A.G. (1997a). Long-term spatial memory in four seed-caching corvid species. — Anim. Behav. 53: 335-341.

Bednekoff, P.A., Kamil, A.C. & Balda, R.P. (1997b). Clark's nutcracker (Aves: Corvidae) spatial memory: interference effects on cache recovery performance? — Ethology 7: 554-565.

Bolhuis, J.J. & Macphail, M.M. (2001). A critique of the neuroecology of learning and memory. — Trends Cogn. Sci. 5: 426-433.

Brodbeck, D.R. (1994). Memory for spatial and local cues — a comparison of a storing and a nonstoring species. — Anim. Learn. Behav. 22: 119-133.

Brodbeck, D.R. & Shettleworth, S.J. (1995). Matching location and color of a compound stimulus: comparison of a food-storing and a nonstoring bird species. — J. Exp. Psychol. Anim. B. 1: 64-77.

Burke, D. & Fulham, B.J. (2003). An evolved spatial memory bias in a nectar-feeding bird? — Anim. Behav. 66: 695-701.

Charnov, E.L. (1976). Optimal foraging, the marginal value theorem. — Theor. Popul. Biol. 9: 129-136.

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.

Cowie, R.J., Krebs, J.R. & Sherry, D.F. (1981). Food storing by marsh tits. — Anim. Behav. 29: 1252-1259.

Dennis, P., Young, M.R. & Gordon, I.J. (1998). Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. — Ecol. Entomol. 23: 253-264.

Dow, D.D. (1977). Indiscriminate interspecific aggression leading to almost sole occupancy of space by a single species of bird. — Emu 77: 115-121.

Dubreuil, D., Tixier, C., Dutrieux, G. & Edeline, J.M. (2003). Does the radial arm maze necessarily test spatial memory? — Neurobiol. Learn. Mem. 79: 109-117.

Hampton, R.R., Healy, S.D., Shettleworth, S.J. & Kamil, A.C. (2002). 'Neuroecologists' are not made of straw. — Trends Cogn. Sci. 6: 6-7.

Hilton, S.C. & Krebs, J.K. (1990). Spatial memory of four species of *Parus*: performance in an open-field analogue of a radial maze. — Q. J. Exp. Psychol. 42: 345-368.

Healy, S.D. & Hurly, T.A. (1998). Rufous hummingbird' (*Selasphorous rufus*) memory for flowers: patterns or actual spatial locations? — J. Exp. Psychol. Anim. B. 24: 396-404.

Healy, S.D. & Krebs, J.R. (1992). Comparing spatial memory in 2 species of tit: recalling a single positive location. — Anim. Learn. Behav. 20: 121-126.

Healy, S.D. & Suhonen, J. (1996). Memory for locations of stored food in willow tits and marsh tits. — Behaviour 133: 71-80.

Hurly, T.A. (1996). Spatial memory in rufous hummingbirds: memory for rewarded and non-rewarded sites. — Anim. Behav. 51: 177-183.

Hurly, T.A. & Healy, S.D. (1996). Memory for flowers in rufous hummingbirds: location or local visual cues? — Anim. Behav. 51: 1149-1157.

James, P.C. & Verbeek, N.A.M. (1985). Clam storage in a Northwestern crow (*Corvus caurinus*): dispersion and sequencing. — Can. J. Zool. 63: 857-860.

Jonsson, M., Yeates, G.W. & Wardle, D.A. (2009). Patterns of invertebrate density and taxonomic richness across gradients of area, isolation, and vegetation diversity in a lake-island system. — Ecography 32: 963-972.

Kamil, A.C., Balda, R.P. & Olson, D.J. (1994). Performance of 4 seed-caching corvid species in the radial-arm maze analog. — J. Comp. Psychol. 108: 385-393.

McGregor, A. & Healy, S.D. (1999). Spatial accuracy in food-storing and non-storing birds. — Anim. Behav. 58: 727-734.

Olson, D.J., Kamil, A.C., Balda, R.P. & Nims, P.J. (1995). Performance of 4 seed-caching corvid species in operant tests of nonspatial and spatial memory. — J. Comp. Psychol. 109: 173-181.

Olton, D.S. & Samuelson, R.J. (1976). Remembrance of places passed: spatial memory in rats. — J. Exp. Psychol. Anim. B. 2: 97-116.

Pyke, G.H. (1978). Optimal foraging in hummingbirds: testing the marginal value theorem. — Am. Zool. 18: 739-752.

Sherry, D. (2006). Neuroecology. — Annu. Rev. Psychol. 57: 167-197.

Shettleworth, S. (2003). Memory and hippocampal specialization in food-storing birds: challenges for research on comparative cognition. — Brain Behav. Evol. 62: 108-116.

Sulikowski, D. & Burke, D. (2007). Food-specific spatial memory biases in an omnivorous bird. — Biol. Lett. 3: 245-248.

Sulikowski, D. & Burke, D. (2010). Reward type influences performance and search structure of an omnivorous bird in an open-field maze. — Behav. Process. 83: 31-35.

Timberlake, W. (1993). Animal behavior: a continuing synthesis. — Annu. Rev. Psychol. 44: 675-708.

Timberlake, W. (2002). Niche-related learning in laboratory paradigms: the case of maze behavior in Norway rats. — Behav. Brain Res. 134: 355-374.

Timberlake, W. & Lucas, G.A. (1989). Behavior systems and learning: from misbehavior to general laws. — In: Contemporary learning theories: instrumental conditioning theory and the impact of biological constraints on learning (Klein, S.B. & Mowrer, R.R., eds). Lawrence Erlbaum Associates, Hillsdale, NJ, p. 237-275.

Wunderle, J.M. & Martinez, J.S. (1987). Spatial-learning in the nectarivorous bananaquit: juveniles versus adults. — Anim. Behav. 35: 652-658.