

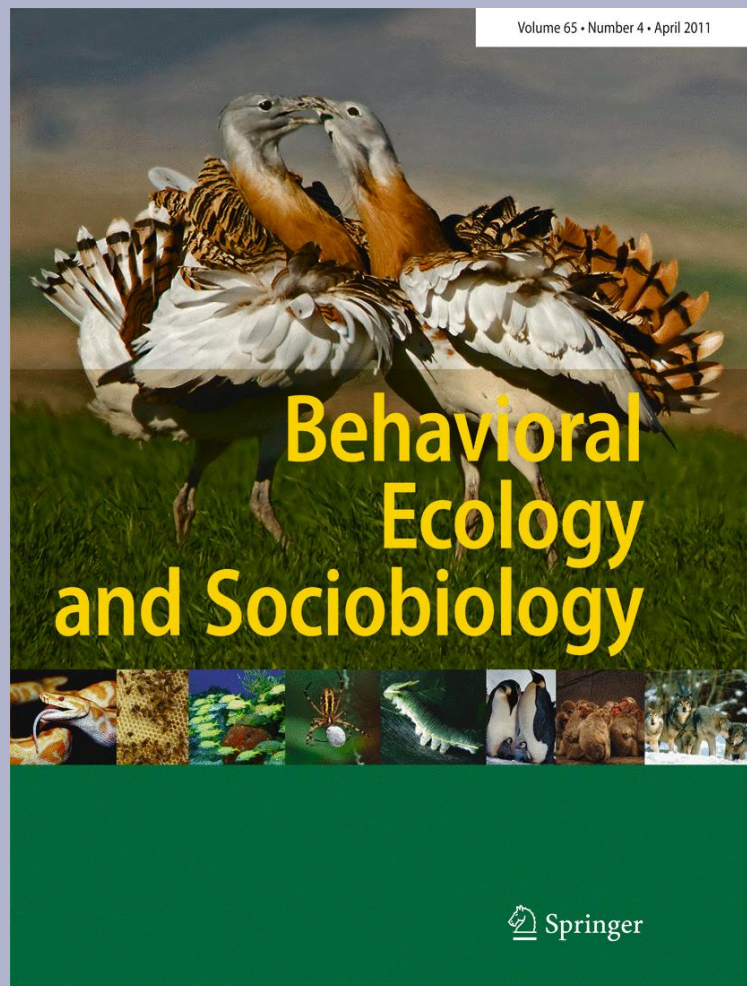
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Movement and memory: different cognitive strategies are used to search for resources with different natural distributions

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Abstract Recent attempts to integrate function and mechanism have resulted in an appreciation of the relevance of forager psychology to understanding the functional aspects of foraging behaviour. Conversely, an acknowledgement of the functional diversity of learning mechanisms has led to greater understanding of the adaptive nature of cognition. In this paper, we present data from three experiments suggesting that noisy miner birds use different cognitive strategies when searching for foods with different distributions. When searching for nectar, an immobile, readily depleted resource, birds spontaneously attend to fine-scale spatial information and use a spatial memory-based strategy that is efficient in a novel context and largely resistant to disruptions to movement. When searching for invertebrates, a mobile, clumped and cryptic resource, birds employ a strategy whose efficiency increases with increased task familiarity, is vulnerable to disruptions to their movement and may rely more on memory for movement rules than memory for location information. Previous reports of adapted cognition have reported performance differences between species (for example, better spatial cognitive performance in storing versus non-storing birds). Ours is the first study to demonstrate that differences in cognitive strategy (as opposed to just enhanced performance) occur within a single species in different foraging contexts. As

well as providing an example of how specially adapted cognitive mechanisms might work, our data further emphasise the importance of jointly considering functional and mechanistic aspects to fully understand the adaptive complexities of behaviour.

Keywords Function · Mechanism · Foraging · Resource distribution · Search strategy · Spatial cognition

Although behavioural ecologists often refer to the ‘optimal’ solution to a given foraging problem (Pyke 1984), it has long been recognised that animals rarely behave exactly optimally. Rather, they tend to approximate the optimal solution based on uncertain or limited information (McNamara and Houston 2009). It is frequently acknowledged that uncertainty can result from environmental stochasticity and incomplete knowledge, or interactions between the two—the more experience an animal has of individual stochastic events, the more accurate is the estimated mean and variance drawn from those events (Dall et al. 2005). Some authors (Bateson and Kacelnik 1998; Kacelnik and Brunner 2002; Kacelnik et al. 1990; Ydenberg 1998) have identified forager psychology as another source of uncertainty, referring to ambiguity in the psychological mechanisms used to perceive and process relevant information. Examples of such ambiguity arise from the systematic errors identified in the path integration mechanism of desert ants (Müller and Wehner 1988) and the psychological timing mechanisms such as those postulated by scalar expectancy theory (SET; Gibbon 1977). When SET is incorporated into optimal foraging (rate maximisation) models, replacing assumptions of perfect perceptions of time, it changes the predictions of those models (Kacelnik et al. 1990).

Kacelnik and Brunner (2002) take the role of forager psychology further by demonstrating that decisions made

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during foraging are not based on all the information available to the animal. Contrary to predictions of optimal foraging theory, the decision to stop foraging within a patch and the decision to move on to another patch are based on different information and so will not necessarily occur simultaneously (Kacelnik and Brunner 2002). In the current paper, we extend this aspect of forager psychology and investigate whether the same decision (where to search next) made in different foraging contexts (when foraging for different food resources) can be based on different information.

Noisy miners (Aves: Meliphagidae, *Manorina melanocephala*), native Australian honeyeaters, exploit a variety of food resources with nectar and invertebrates both forming substantial parts of their natural diet (Barker and Vestjens 1984; Dow 1977). There is evidence that these birds use spatial information differently depending on which resource they are exploiting. Win-shifting, the tendency to better learn to avoid recently rewarding places (rather than learning to return to them), has been repeatedly demonstrated in a variety of nectarivorous birds (Burke and Fulham 2003; Cole et al. 1982; Wunderle and Martinez 1987) and in honeybees (Demas and Brown 1995). When foraging for nectar, noisy miners attend to fine-scale spatial information (discriminating locations that are less than 40 cm apart) spontaneously (Sulikowski and Burke 2009) and display a win-shift bias (Sulikowski and Burke 2007). When foraging for invertebrates, however, they use the same spatial information less effectively and do not display a win-shift bias.

The tendency of nectarivorous species to win-shift has been interpreted as an adaptation to the depleting nature of nectar (Cole et al. 1982)—a flower once visited will be an unprofitable place to revisit until sufficient time has passed for it to replenish. Therefore, as flowers are not mobile, a recently visited flower represents a reliably depleted point location in space. The same cannot be said of invertebrates. Whilst the distribution of invertebrates as a prey group can presumably be varied, it is largely true that invertebrate prey are mobile, clumped and somewhat cryptic. This means that a given point location, once visited by an insectivorous forager, will not necessarily be depleted, nor will it be likely to remain depleted, for a reliable length of time. Previous research shows that nectarivorous hummingbirds encode information about individual locations in space (Henderson et al. 2001, 2006). Data from birds foraging for invertebrates suggest less efficient use of available spatial information (Sulikowski and Burke 2009) and movement-based search strategies such as repeatedly turning in the same direction after subsequent prey captures to achieve area-restricted search in places of high prey density (Smith 1974).

Regular users of radial-arm mazes (Olton and Samuelson 1976) are aware that rats allowed to freely explore the maze

will often do so in a stereotypic way, visiting adjacent arms sequentially. Disrupting the rats' movement by temporarily confining them in the central chamber between arm visits breaks this stereotypy. Dubreuil et al. (2003) formally quantified this behaviour and showed that rats trained without confinement search the maze using movement-based strategies (such as sequentially visiting adjacent arms, known as clockwise serial search) and were unable to remember which arms they had previously visited when confinement was introduced in a test trial. In the current study, we apply this logic to an open-field maze (a radial-arm maze analogue, better suited to testing birds, where the goals are located in open space rather than at the ends of runways) to determine whether the reward type being searched for affects the extent to which noisy miners engage a movement-based versus a spatial memory-based strategy.

If the different distributions of nectar and invertebrates have adaptively shaped the cognitive mechanisms underlying foraging behaviour, then we would predict systematic differences in what and how information is used when exploiting these resources. When foraging for nectar, we predict that noisy miners will engage a spatial memory-based strategy with attention to point location information. When foraging for invertebrates, we predict a movement-based strategy to predominate, with less efficient use of point location information. In experiment 1, we presented birds with arrays of feeders to search for either nectar or invertebrate rewards. We predicted that birds searching for nectar rewards should perform more efficiently initially due to their propensity to spontaneously attend to and use fine-scale spatial information whilst foraging, whilst birds foraging for invertebrates are not predicted to perform as well. In experiment 2, we interrupted the movement of the birds as they searched the arrays, under the premise that such interruptions would only disrupt performance to the extent that that performance was dependent on a movement-based strategy. We predicted that birds foraging on invertebrates would be employing such a strategy whilst birds foraging for nectar would rely on a spatial memory-based strategy. In experiment 3, we further investigated the movement of birds foraging on nectar and invertebrates, respectively, to help determine the nature of the movement rules that might be guiding the birds foraging behaviour.

General methods

Twenty wild caught noisy miner birds (Aves: Meliphagidae, *M. melanocephala*) of unknown age and sex served as subjects in the experiments reported here. Noisy miners are dietary generalists, foraging regularly on both nectar and

invertebrate prey. During the testing periods, birds were held and tested individually in cages measuring approximately $3 \times 3 \times 3$ m and were maintained on a diet of commercial honeyeater food (Wombaroo© Lorikeet and Honeyeater Wet Mix). At the completion of testing, birds were released at the site of capture.

Prior to the experiments reported here, the birds had participated in social learning and colour learning tasks. None of the birds had previously participated in spatial learning or search tasks. Due to their previous experience, birds were familiar with how to open feeders used in these experiments so no pre-experimental training was required.

All procedures were approved by the Macquarie University Animal Ethics Committee and conducted under Animal Research Authority Numbers 2005/001 and 2007/035. All analyses reported were conducted using SPSS v16.0 for Mac (except Fisher's exact, completed using SISA online analysis software), and all means are quoted ± 1 standard error.

Experiment 1

Methods

Ten subjects were tested in four trials each. A maximum of one trial per day was conducted (in the morning before provision of the daily food), and each trial required birds to search for up to 10 min through an array of eight baited feeders. The feeders hooked onto the metal mesh front wall of the birds' cages from the outside and consisted of an opaque plastic well (approximately 1 ml capacity) with a metal flip top lid. The lids fell closed once a bird left the feeder, so feeders previously visited in a trial were visually indistinguishable from feeders not yet visited. Five of the subjects were searching these feeders for nectar rewards (0.3 ml of a 30% (w/v) sucrose solution), and five were searching for invertebrate rewards (half a mealworm, *Tenebrio molitor*, larva), a between-subjects manipulation.

The array of feeders consisted of a 4×4 square of 16 potential locations on the front wall of each bird's cage. Adjacent positions were spaced 40 cm apart. For each of the four trials, the actual locations of the eight feeders were chosen pseudo-randomly with the restrictions that every row and every column of the array contained at least one feeder, and over the four trials, each potential location contained a feeder exactly twice. The birds were able to access the feeders by clinging to the metal mesh wall of the cage beside the feeders (an activity the birds routinely engage in). All other branches and structures present (e.g. waterbath, bird box) were in the back half of the cages, well away from the arrays.

As a measure of motivation, we scored the total number of visits to feeders in the array each bird made in each trial. A bird was deemed to have visited a feeder if it opened the feeder lid with its beak. As a measure of performance, we scored the number of revisit errors (visits to feeders already emptied during that trial) birds made before finding all eight rewards. We also scored the number of feeder visits made during each search bout of a trial. A search bout ended if, during the trial, a bird left the array and flew to another part of the cage, and another search bout began if the bird returned to the array, before the 10-min time limit expired. A bird was deemed to have left the array if it perched somewhere in the cage outside the confines of the 4×4 array and from which location it could not reach the nearest feeder. A bird was deemed to have re-entered the array once it opened the lid of a feeder (so if a bird perched within the confines of the array but did not visit any of the feeders before leaving again, this was not counted as a search bout).

We also ran 64 random-walk simulations (16 on each of four test arrays) to estimate chance performance. In our model, the walker could step from feeder to feeder only, not to any of the eight empty locations. For each step, the walker stepped from its current feeder in one of the eight possible directions (up, down, left, right, up-right etc.), with equal likelihood as long as a move in that direction would encounter another feeder, not necessarily adjacently, a single step could move over an empty location to the next closest feeder. Steps in a direction that would lead the walker out of the array without encountering a feeder were not an available option. During testing, we observed that revisits to the most recently visited feeder (so from feeders A to B, then back to A again) were very rare. Our model walker, therefore, was also not permitted to move in the direction from which it had arrived at the present feeder (preventing A–B–A patterns of visits).

Results

The random-walk simulations estimated that birds would make an average of 12.73 ± 1.06 revisit errors before finding all eight rewards. They also revealed substantial right skew in this measure. Similar, but less severe, skew was observed in the collected data, so they were square root-transformed prior to all analyses.

Nectar-rewarded birds made significantly fewer revisit errors (2.80 ± 1.11) than invertebrate-rewarded birds (8.40 ± 1.44) in the first trial (independent samples *t* test: $t_8 = 3.427$, $P = 0.009 < 0.0125$, Bonferroni-corrected alpha), but performance of invertebrate-rewarded birds improved over the course of the trials until it was similar to that shown by nectar-rewarded birds (Fig. 1a). Performance was significantly better than chance in all trials for both reward

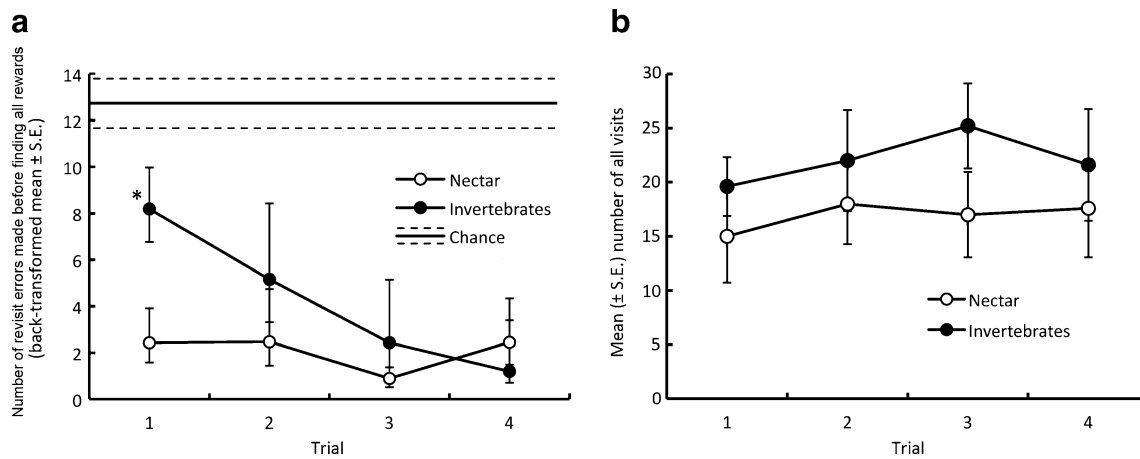


Fig. 1 Results of experiment 1. **a** The *y*-axis represents the mean \pm SE number of revisit errors (square root-transformed and back-transformed) that birds made before finding all the rewards. Invertebrate-rewarded birds made significantly more revisits than nectar-rewarded birds in the first trial (indicated by *asterisk*). Performance of invertebrate-rewarded birds then improved over the four trials until they were as efficient as nectar-rewarded birds. Both

reward groups performed significantly better than chance (as estimated by random-walk simulations, indicated by the *hard line*, with *dashed lines* representing one SE) from the first trial onwards. **b** The *y*-axis represents the mean \pm SE of all visits made to the array during a trial. Invertebrate-rewarded made more visits on average than the nectar-rewarded birds in each of the four trials, but there was no significant difference between the reward groups on this measure

groups, determined by one-sample *t* tests on the square root-transformed data against a test value of $\sqrt{12.73}=3.568$ (one-sample *t* tests: all $t_4 > 2.8$, all $P < 0.05$). A general linear model (GLM) ANOVA with trial (four levels, 1–4) as a within-subjects factor and reward type (two levels, nectar and invertebrates) as a between-subjects factor revealed a significant main effect of trial (ANOVA: $F_{3, 24}=3.844$, $P=0.022$) and a significant linear contrast effect of trial (ANOVA: $F_{1, 8}=9.509$, $P=0.015$). The invertebrate-rewarded group was largely responsible for these effects (as illustrated by a significant linear contrast interaction between trial and reward group, ANOVA: $F_{1, 8}=6.352$, $P=0.036$).

Figure 1b shows the mean number per trial of feeder visits made by the nectar-rewarded and invertebrate-rewarded groups. The invertebrate-rewarded birds made more feeder visits in each of the four trials, but a GLM ANOVA with trial (four levels, 1–4) as a within-subjects factor reward type (two levels, nectar and invertebrates) as a between-subjects factor was not significant (ANOVA: $F_{1, 8}=1.742$, $P=0.223$).

Experiment 2

Methods

The same ten subjects as in experiment 1 (in the same reward conditions) were used in experiment 2. This experiment consisted of two series, baseline and test, of 12 trials each. The test trials were designed to test the extent to which performance by the birds in each reward group was underpinned by a movement-based search strategy. All birds

completed the 12 baseline trials first, followed by the 12 test trials. For this experiment, birds completed a maximum of two trials per day (one in the morning and one in the afternoon, with half the daily food provided after each testing session).

In the baseline trials, birds were presented with an array of eight baited feeders (the locations of each feeder chosen in the same way reported for experiment 1, but without restrictions on the number of times a particular location could contain a feeder over the course of the 12 trials). In these trials, birds were allowed to make a maximum of eight visits to the array before the feeders were removed. As the measure of performance, we scored the number of visits a bird made to unique feeders prior to making the first revisit error. We also scored the number of visits made during each search bout of a trial, as in experiment 1.

The test trials employed the same arrays in the same order as the baseline trials, and birds were also limited to eight visits. In the test trials, though, the experimenter stepped forward toward the front of the cage, forcing birds to leave the array after every second feeder visit. Most birds adapted quickly to this manipulation and readily re-approached the array once the experimenter stepped backward again. It was typically the case that birds were away from the array for approximately 3–20 s each interruption. Only one bird (in the nectar-rewarded condition) was persistently reluctant to re-approach the array and seven of its trials were abandoned (after a maximum of 15 min) and subsequently repeated. Analyses were conducted on the data from all birds, but as the behaviour of this one bird differed markedly from that of the other nine, Fig. 2b illustrates mean performance both including and excluding the data from this bird.

The number of feeders visited prior to making a revisit error was also scored for the test trials. We were most interested in the decrement in performance between the baseline and test trials and calculated this difference for each bird in each trial.

Results

As birds were limited to a maximum of eight visits to feeders during this experiment, performance was measured as the number of correct feeders a bird visited prior to making their first revisit error. Performance during the first 12 trials of this experiment (used as baseline measures, Fig. 2a) did not differ significantly between the reward groups as shown by a GLM ANOVA with block (mean score of three trials, four levels) as a within-subjects factor and reward type (two levels, nectar and invertebrates) as a between-subjects factor (ANOVA: $F_{1, 8}=0.064, P=0.806$). The mean score across a block of trials was adopted as the dependent variable rather than individual trial scores to help even out potential noise as a result of inter-trial variation.

There was no evidence that birds in either reward group improved their performance in response to the increased cost of making an error in the baseline trials of experiment 2. As these trials were limited to eight visits, we examined only the first eight visits of each trial of experiment 1 in order to validly compare search bout length between experiment 1 and the baseline trials of experiment 2. Invertebrate-rewarded birds significantly increased the length of the initial search bout of the trial from experiment 1 (5.3 ± 0.86 visits) to the baseline trials of experiment 2 (7.28 ± 0.53 visits, paired samples t test:

$t_4=3.272, P=0.031$). There was no change in length of the initial search from experiment 1 (6.90 ± 0.63 visits) to experiment 2 (6.74 ± 0.60) for nectar-rewarded birds.

To assess the extent to which performance may have been underpinned by a movement-based strategy, the performance decrement from the baseline trials to the test trials of experiment 2 (where birds' searching was interrupted after every second choice) was calculated for each trial for each bird (Fig. 2b). These difference scores were then analysed using a GLM ANOVA with factors as described above.

The analysis revealed a significant linear contrast effect of block (ANOVA: $F_{1, 8}=5.617, P=0.045$), which was largely attributable to an increase in performance in the invertebrate-rewarded group, as confirmed by a significant linear contrast interaction between block and reward type (ANOVA: $F_{1, 8}=6.412, P=0.035$). Moreover, the performance decrement for invertebrate-rewarded birds only was significantly greater than zero for the first two blocks (one-sample t tests: $t_4=3.586, 3.835, P=0.023, 0.019$), after which performance improved back to baseline levels. The overall performance decrement of nectar foragers (which did not increase or decrease over the 12 trials) was not significantly different from zero (one-sample t tests: $t_4=1.041, P=0.357$).

Experiment 3

Methods

Ten different birds (not used in experiments 1 and 2) served as subjects for experiment 3, five birds in each reward

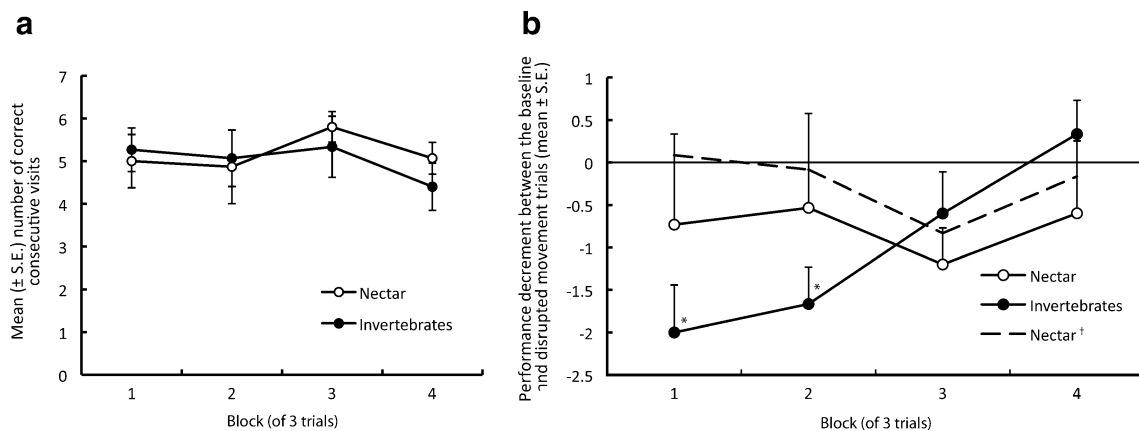


Fig. 2 Results of experiment 2. **a** Baseline trials. Mean \pm SE number of correct visits birds made to the array before making a revisit error (a maximum of eight visits per trial). There was no difference in performance between the reward groups and no suggestion of improvement over the course of the 12 trials. **b** Decrement from baseline to test trials. Again the measure of number of correct visits before making a revisit error is used, and the y-axis represents the difference in this measure from the baseline to the test trials. A negative score indicates a performance decrement from baseline to test. Performance of invertebrate-rewarded birds was significantly

below baseline during the first two blocks of the test trials (indicated by asterisk) but improved to baseline levels by the end of the 12 trials. Performance of nectar-rewarded birds did drop below baseline levels but not significantly so. †One bird in the nectar-rewarded group was reluctant to return to the array after being interrupted, and seven of 12 trials had to be aborted and subsequently repeated. The dashed line represents mean performance of the nectar-rewarded group when the data from this bird is excluded (for illustrative purposes only, analyses were conducted on all data inclusively)

condition. This experiment was designed to further examine the movement of the birds as they searched through arrays that, unlike those used in the previous experiments, were symmetrical. In each of the eight trials of this task, birds were presented with the full array of 16 feeders and were allowed 15 min to search freely. Of the 16 feeders, only eight contained baits and the locations of the baits were chosen in the same pseudo-random way as the locations of feeders were chosen in experiment 2.

As the birds searched the arrays, we recorded the leftward or rightward direction of each movement from one feeder to another (including leftward and rightward components of diagonal movements and ignoring purely vertical movements). We then calculated a lateral movement bias score for each bird for each trial using

$$(L - R)/(L + R)$$

where L is the total number of leftward movements made and R is the total number of rightward movements made.

Results

All five birds in the invertebrate-rewarded condition displayed a significant lateral movement bias over the eight trials (one-sample t tests against zero: all $t_7 > 2.5$, all $P < 0.04$; the bias of four of the birds remains significant when a Bonferroni-corrected alpha of 0.01 is applied). None of the birds in the nectar-rewarded condition displayed a significant lateral movement bias (all $t_7 < 1.7$, all $P > 0.14$, see Fig. 3a). There was a significant association between the presence of a significant lateral movement bias and the reward type (Fisher's exact test: $P = 0.048$, based on only four invertebrate-rewarded birds displaying a bias and using the two-sided sum of small p 's). An independent samples t test comparing the strength of the lateral movement biases of each reward group (absolute value of the mean lateral movement bias of each bird) also revealed that irrespective of the direction of the bias it was significantly stronger overall in the invertebrate-rewarded group (independent samples t test: $t_8 = 3.718$, $P = 0.006$, see Fig. 3b).

Motivational considerations

Methods

We used three separate measures to determine whether any of the differences in performance we found could potentially be accounted for by differential motivation for the two reward types. In experiments 1 and 2, we measured the latency to approach the array (number of seconds from when the experimenter left the front of the cage until the bird probed

the first feeder), the amount of time the birds actually spent in the array in each trial and the total number of visits made during this period. For both of these experiments, we did not include the latency to approach measure for the first trial for two reasons. Firstly, birds were not aware what reward they were foraging for in the first trial of these experiments and so any differences in these measures could not reflect differential motivation. Secondly, this initial latency was much longer and more variable than subsequent measures (not surprisingly, as the experimental situation was still novel at this stage), and its inclusion would have swamped any smaller systematic differences between the reward types. For experiment 2, where the birds were limited to eight choices in both the baseline and test trials, we measured latency to approach the array for each bird in each trial. As we report only movement differences, as opposed to more efficient learning or performance, for the groups in experiment 3, we will not include the motivational measures for these trials.

Results

None of the motivational measures in any of the experiments revealed a significant difference between the reward groups. For experiment 1, there was no difference between the reward groups in mean latency to approach the array at the start of each trial (excluding the first trial, independent samples t test: $t_8 = 0.244$, $P = 0.813$) with latencies of 7.2 ± 1.8 and 8.1 ± 3.0 s for the invertebrate- and nectar-rewarded groups, respectively. There was also no significant difference (independent samples t test: $t_8 = 1.324$, $P = 0.222$) in the mean number of visits made to the array with invertebrate-rewarded birds making 22.1 ± 2.5 visits per trial and nectar-rewarded birds 16.9 ± 3.0 visits per trial. There was also no substantial increase or decrease in number of visits for either reward group over the course of the trials (Fig. 1b), and a Pearson correlation revealed no significant relationship between mean number of revisit errors and mean number of visits (Pearson correlation: $r = 0.423$, $N = 10$, $P = 0.223$). Birds also spent approximately equal amounts of time in the array per trial in experiment 1 (3 min 47 ± 35 s and 3 min 28 ± 37 s for the invertebrate-rewarded and nectar-rewarded groups, respectively, independent samples t test: $t_8 = 0.375$, $P = 0.717$).

For experiment 2, there was no difference between the reward groups in latencies to approach the array for either the baseline trials (5.4 ± 1.8 and 3.6 ± 0.8 s for the nectar- and invertebrate-rewarded groups, respectively, independent samples t test: $t_{5,352} = 0.904$, $P = 0.405$) or the test trials (6.3 ± 2.0 and 3.6 ± 0.9 s for the nectar- and invertebrate-rewarded groups, respectively, independent samples t test: $t_{5,594} = 1.246$, $P = 0.248$; an adjusted degrees of freedom was applied to both of these t statistics due to inequality of variances).

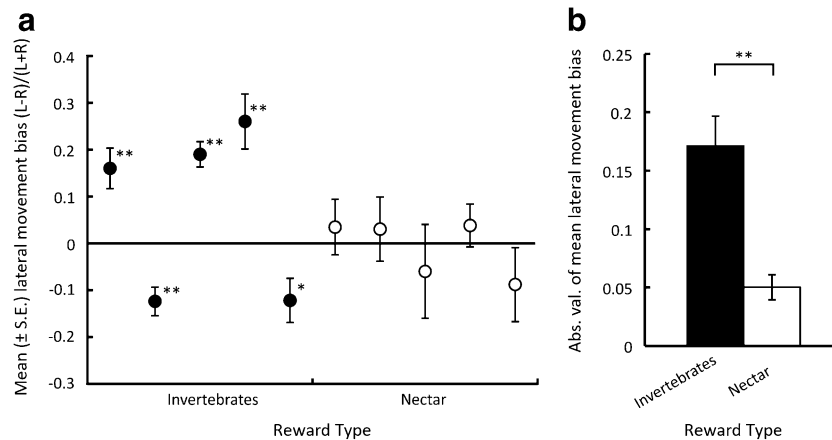


Fig. 3 Results from experiment 3. **a** Each data point represents the mean \pm SE lateral movement bias of one bird, over the eight trials. All invertebrate-rewarded birds displayed a significant lateral movement bias (indicated by *single asterisk*); for four birds, the bias remains significant when a Bonferroni-corrected alpha is applied (indicated by *double asterisks*). None of the nectar-rewarded birds displayed a

significant lateral movement bias (uncorrected alpha). There are no consistent patterns in the direction of the biases. **b** When the absolute value of each bird's mean lateral movement bias is taken, the invertebrate-rewarded birds display significantly stronger biases than the nectar-rewarded birds (indicated by *double asterisks*)

Discussion

Many authors have heralded the call for greater integration between functional and mechanistic approaches to understanding behaviour (Gibbon 1977; Kamil 1983; Shettleworth 1993; Timberlake 1993; Shettleworth 1998; Kacelnik and Brunner 2002; Gibson and Kamil 2009; Kacelnik et al. 1990; Freidin et al. 2009a) culminating in the advent of the 'Evo-mecho' approach (McNamara and Houston 2009), which calls for explicit investigation of not just *how* mechanisms produce behaviour but *why* those particular mechanisms have been selected. Our data further emphasise the importance of jointly considering functional and mechanistic aspects of behaviour. In the current study, we demonstrate that the information noisy miners attend to and use whilst foraging varies in ways predicted by the natural distributions of the foraged food.

In this study, we present evidence from three experiments that support the hypothesis that noisy miners engage different cognitive strategies in response to being rewarded with invertebrates or nectar in laboratory tasks. When rewarded with nectar, birds appeared to engage a spatial working memory strategy that involved spontaneous encoding of point location information independently of the birds' own movement. These findings are consistent with previous data (Sulikowski and Burke 2007; Sulikowski and Burke 2009) from this species and with reports of proficient spatial cognition in other nectarivorous birds (Hurly 1996; Henderson et al. 2001). When rewarded with invertebrates, birds relied on a strategy that was vulnerable to disturbances of their own movement patterns and displayed a tendency to move consistently in the same lateral direction. This behaviour is consistent with that

reported for other insectivorous birds that use movement strategies to concentrate their search in areas of high prey density (Smith 1974). As far as we are aware, this is the first study to demonstrate a within-species difference not just in cognitive proficiency but in the cognitive strategy employed to solve a task, as a function of natural, divergent reward distributions.

During the first trial of experiment 1, birds made fewer revisit errors when they were searching for nectar than when searching for invertebrates. Though there was no substantial cost to making an error in experiment 1 (there was sufficient time for all rewards to be recovered, irrespective of the number of errors made), the performance of invertebrate-rewarded birds improved over the course of the trials to be as efficient as that of nectar-rewarded birds. One possibility is that the invertebrate-rewarded birds learnt during the experiment to increase efficiency by engaging a spatial memory strategy. A second possibility is that the increased efficiency was achieved via a different strategy, one requiring a certain level of familiarity with the task. The results of experiment 2 support the latter interpretation.

In the baseline trials of experiment 2, errors carried a greater cost relative to experiment 1, in that the number of choices birds were allowed was limited to the number of rewards present, so a revisit error prevented a bird from retrieving all rewards. In spite of this, neither reward group showed evidence of improvement over the 12 baseline trials nor was there a measurable difference in performance between the groups. The lack of a difference was likely due to both reward groups reaching an asymptote of performance in experiment 1 and transferring this to experiment 2. When the movement of the birds was interrupted (by causing them to fly away from the array after every second

visit), the performance of invertebrate-rewarded birds suffered significantly compared to the baseline trials, whereas the performance of nectar-rewarded birds was not significantly below that seen in the baseline trials.

There is evidence that hummingbirds are able to remember both the locations of artificial feeders and properties of those feeders, such as whether they have visited those feeders previously and when (Henderson et al. 2006), whether the feeders contained food (Hurly 1996) and whether the birds emptied the feeders or left some food remaining (Hurly and Healy 1996). We suggest that nectar-rewarded birds in our study may be using similar strategies. If birds encode the 'where' and the 'what' (whether or not visited) of individual feeders and update this information as they search, we would not expect a disruption to their own movement to affect their performance. Indeed, there is evidence from hummingbirds and honeyeaters that birds can retain and use this type of information up to several hours later (Healy and Hurly 1995; Burke and Fulham 2003) with foraging and other behaviours occurring in between.

The drop in performance when invertebrate-rewarded birds were interrupted suggests that the efficient performance of these birds (in experiment 1 and the baseline trials of experiment 2) is reliant upon the birds being able to progress, uninterrupted, from feeder to feeder and may not involve the specific encoding of individual feeder locations and properties. Rats allowed to search freely in a radial-arm maze tend to use a movement algorithm that involves them only needing to use one bit of information: the direction they need to travel in as they progress around the maze (Dubreuil et al. 2003). Disrupting the movement of these rats causes their strategy to fail, presumably because the rats are not attending to or encoding information about either their own location in the maze at any given time, or whether or not particular locations in the maze have been visited yet. When the rats' systematic movement is interrupted, they are, therefore, unable to recall which of the locations they have previously visited, nor can they simply pick up where they left off. We suggest that the performance of invertebrate-rewarded birds in our study may be underpinned by a similar movement-based strategy. Perhaps the major determinant of a bird's next feeder choice is the direction from which the bird approached the current feeder (so that it continues in the same direction) rather than a memory for specifically which feeders have or have not yet been visited. Such a strategy would avoid revisits by leaving visited feeders behind but would be vulnerable to interruptions, as a bird forced to leave the array would have no information to guide its first choice upon returning. A bird inclined to re-begin its search after each interruption at the same place within the array would be almost guaranteed to make errors upon its return. The

data from experiment 3 support this interpretation and are discussed further below.

Invertebrate-rewarded birds required some experience with the task to reach their maximum search efficiency whilst nectar-rewarded birds did not. Based on the theory that birds foraging for invertebrates are relying on movement-based strategies, we suggest that, for such strategies to work efficiently, some knowledge of the spatial layout of the area to be searched is needed. For example, a rat in a radial-arm maze would need to 'know' that arm entries are arranged sequentially before it could 'know' that clockwise serial is an appropriate strategy (such as stereotyped search strategies typically do appear gradually; Dubreuil et al. 2003). In our study, the maze was two-dimensional, so for uni-directional movement biases to produce efficient search, some knowledge of the boundaries of the search area are required. Birds relying on primarily leftward movement, for example, would need to know how much deviation from this direction is needed to cover the vertical extent of the array. On the other hand, if birds foraging on nectar achieve efficient search by spontaneously encoding the locations of individual food sources (with respect to stable surrounding landmarks), then knowledge of the array boundaries provides no extra useful information. If these interpretations are correct, then we predict that substantially changing the size of an array (once birds have become familiar with it) should have a detrimental impact on the performance of invertebrate foragers but not on performance of nectar foragers. Future experiments could explore this possibility.

The improvement of invertebrate-rewarded birds back to baseline levels by the end of experiment 2 can be interpreted in two ways. Firstly, birds may have incorporated their enforced retreat from the array into their movement patterns, perhaps by encoding the locations from which they left the array, and continued using largely the same strategy. Secondly, birds may have adopted another strategy that is robust to movement disruptions, perhaps similar to that used by nectar foragers. We are unable to say which interpretation is more likely at this stage.

Thus far in our interpretations, we have assumed that the behaviour we observed in our experiments is a reflection of how these birds may forage for these different food types in the wild. It is prudent, however, to consider the possibility that the experimental protocol has artificially produced these effects. Whilst we have evidence that the reward groups are using different strategies during the test trials of experiment 2, it does not necessarily follow that this was also happening during experiment 1. An alternative interpretation is that the reward groups were engaged in the same strategy during experiment 1 (whichever strategy that may be) and that limiting the number of search visits allowed during the baseline trials of experiment 2 caused

one of the reward groups to change their strategy. Indeed, the invertebrate-rewarded birds responded to this restriction by significantly increasing the number of visits they made to the array in the first search bout of a trial, completing all eight visits within one search bout on most baseline trials. We acknowledge that directly comparing the behaviour of the birds during experiment 1, where their performance was improving over trials and they were relatively unfamiliar with the task, with their behaviour in experiment 2, by which time their performance had apparently reached asymptote, is potentially problematic. Whilst familiarity with the task is confounded with the restriction on visit number applied in experiment 2, the change in bout length did appear abruptly and so we will consider the potential implications of this effect. Whilst this change in search structure could be seen as indicative of a change in strategy, it is also consistent with the view that performance of invertebrate-rewarded birds is based on a movement strategy, with birds electing not to interrupt their own movement during baseline trials where errors carried a cost. The data from experiment 3 suggest that the latter is the most likely interpretation and also support the view that differences in search strategy are not an artefact of the experimental protocol.

New subjects (not experienced in laboratory spatial tasks) were used in experiment 3, and there was significant divergence in how birds from the different reward groups moved around the array. As well as providing further evidence that reward type influences search strategy, these data provide a clue as to which movement rules invertebrate-rewarded birds may be using to guide their search. Invertebrate-rewarded birds displayed significant lateral movement biases, indicating a tendency to move across the array from one side to the other as they searched. Just as rats exploring freely in a radial-arm maze can forage efficiently by moving consistently in the same direction around the maze, our data suggest that noisy miners may be using a similar directional rule to guide their search.

The data from all three experiments provide strong evidence that noisy miner birds employ different search strategies depending upon the resource they are exploiting. When searching for nectar rewards, birds appear to spontaneously attend to fine-scale spatial information and use a spatial memory-based strategy that is efficient in a novel context and largely resistant to disruptions to their movement. When searching for invertebrates, however, birds appear to employ a strategy whose efficiency increases with increased task familiarity, is vulnerable to disruptions to their movement and may rely more on movement rules than memory for fine-scale location information. These strategies are predicted from considerations of the natural distributions of nectar and invertebrates. They imply the existence of adapted cognitive mechanisms, capable of responding appropriately to different

foraging contexts, even when the spatial and temporal structure of the resources are identical, as in our experiments.

When animals respond differently to different rewards, it is important to rule out motivational explanations before other interpretations can be confidently accepted. In this study, we measured several variables that ought to reflect motivation levels including time spent foraging, latency to approach the test array and number of visits made to feeders in the array. On none of these measures was there a significant difference between the reward groups. It has long been known that fluctuating motivation levels are more reliably reflected in consummatory than in operant behaviours (Crespi 1942; Flaherty et al. 1978; Sastre et al. 2005; Freidin et al. 2009b). Since we found no evidence of differential motivation on two consummatory measures (time spent foraging in the array and number of visits to feeders), we conclude that it is highly unlikely that the differences in performance we report are a result of differential motivation between the reward groups. It is also worth noting that all of the motivation measures were slightly in favour of the invertebrate-rewarded group, when a motivational account would require the nectar foragers to be more motivated.

The baseline trials of experiment 2 also served as a sophisticated measure of the subjective value to the birds of the two food rewards. In these trials, the cost of making one revisit error was that the foraging bird missed out on one food reward. Presumably the performance of the birds in these trials is a reflection not of how well they could possibly do with maximum effort but a cost–benefit trade-off, with the extra cognitive effort required to find the last one to two rewards not worth the return. If considered from this perspective, the equal performance of the two reward groups across these baseline trials suggests that the birds were setting the subjective value of these two rewards at remarkably equal levels.

Furthermore, our experiments all employed between-subjects designs, meaning that the two rewards were never directly contrasted within an individual. Studies of incentive contrast phenomena have shown that groups of animals given rewards that differ in value (such that they will induce successive negative contrast effects) will often respond similarly to the different rewards if they have not yet experienced the contrast. For example, Pecoraro et al. (1999), in a successive negative contrast experiment, gave groups of rats either a 32% or 4% sucrose solution in a maze and recorded the amount of solution consumed, the time spent locomoting, the number of location changes and the bouts of orienting behaviour. When the 32% group were shifted to a 4% sucrose solution, all of these measures reported significant differences when compared to the group that had always been at 4%, demonstrating that the rats did experience the 4% solution as less valuable.

Critically, though, prior to the shift, there were no differences on any of these measures between the two reward groups, in spite of the obvious difference in absolute value of the two rewards. We suggest, therefore, that the differences we observed warrant explanation beyond that which could potentially be offered by considerations of differential motivation.

We also see no way that differences in motivation could logically explain the movement differences reported in experiment 3 since this behaviour does not reflect either consummatory or operant responses to receiving food but represents divergent patterns of search. With all of the above considerations, we feel confident in concluding that potential motivational differences are not responsible for the effects reported in this study.

Previous studies demonstrating evidence of adaptive specialisations of learning and memory have tended to report aptitude differences between species on relevant tasks, predicted by aspects of their ecology. For example, degree of dependence on stored food predicts performance on spatial cognitive tasks (Balda et al. 1997; McGregor and Healy 1999). Our study is unique in presenting differences within the spatial domain not just in aptitude but in the strategy used to solve the task. We have also demonstrated how cognitive mechanisms may be specially adapted within a single species. By presenting these differences within a species, we are able to rule out species differences in perception or temperament (or anything else) as contributing to the effects, adding significant strength to the adaptationist view of learning and memory.

To summarise, we present the data from three experiments that, when taken together, suggest that noisy miners tend to use a spatial memory-based strategy when foraging for nectar and a movement-based strategy when foraging for invertebrates. As well as providing an example of how specially adapted cognitive mechanisms might work, these findings add further weight to the argument that an appreciation of mechanism increases understanding of the functionality of behaviour. In agreement with others, we suggest that an assumption of omniscient information use (or simple rules-of-thumb) is not appropriate. A more detailed understanding of cognition is required if mechanism and function are to be meaningfully integrated.

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Ethical standards The experiments reported herein comply with the current laws of the State of New South Wales and the Commonwealth of Australia.

Conflict of interest The authors declare that they have no conflict of interest.

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