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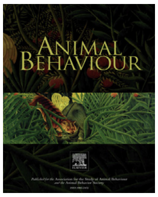

Noisy miners plan ahead: cryptic signalling of reward location impairs search for nectar, but not for invertebrates

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Noisy miners, *Manorina melanocephala* (Australian honeyeaters, Meliphagidae) feed on both nectar and invertebrates. The spatiotemporal distributions of these two food resources differ: nectar is a static, visually signalled resource, and invertebrates are cryptic and mobile. In the present study, we investigated whether birds would forage more efficiently if they could plan their search path through a 'patch' of feeders, than if they could not. We predicted that the ability to plan would only increase the efficiency of nectar foraging. Wild-caught captive birds were allowed to forage through arrays of feeders containing both nectar (sucrose) and invertebrate (mealworm) prey. When foraging for nectar, birds made more search errors if they were unable to plan their foraging route, while search efficiency for invertebrate prey was not affected in this way. These results suggest that noisy miners make use of the advertised locations of nectar to plan their search route. Such route planning may be a type of planning that does not involve anticipation of future motivational states.

As potential food sources for birds, nectar and invertebrate prey are distributed differently in the environment. Nectar is discontinuously distributed. It exists in discrete, visually advertised point locations (flowers) in space and is depleted and replenished on a predictable schedule: a single visit from an avian forager will typically deplete a flower (Collins, Newland, & Briffa, 1984; Kamil, 1978) and replenishment occurs after an extended period of time (Garrison & Gass, 1999; Gill, 1988). Invertebrate prey are often cryptic and mobile and so are potentially continuously distributed: a prey item could be at any location within a suitable microhabitat. Point locations at which a prey item is found may not remain reliably depleted for any length of time if the prey in question are mobile.

These different spatiotemporal distributions may have provided selection pressure for divergent cognitive mechanisms to maximize efficiency when foraging for the two different food types. Noisy miners, *Manorina melanocephala*, are Australian honeyeaters (Aves: Meliphagidae). They are omnivorous, feeding on both nectar and invertebrates (Pyke, 1980). In laboratory studies, noisy miners avoid discrete locations where they have recently found nectar (Sulikowski & Burke, 2007), as do other nectarivorous species (Burke & Fulham, 2003; Cole, Hainsworth, Kamil, Mercier, & Wolf, 1982; Demas & Brown, 1995; Healy & Hurly, 1995; Wunderle & Martinez, 1987; but see also Sulikowski & Burke, 2011a), in spite of being sensitive to reinforcement to return to them (Sulikowski & Burke, 2012). This 'win-shift bias' is not seen when birds are rewarded with invertebrates (Sulikowski & Burke, 2007) and may reflect an adaptation to the depleting nature of nectar. That a closely related honeyeater species reverts to a 'win-stay bias' after several hours (sufficient time for nectar to replenish) (Burke & Fulham, 2003) supports this interpretation.

Nectar foragers also appear to rely on memory for the specific locations that have and have not been searched to avoid unprofitable revisits (Sulikowski & Burke, 2010a, 2011b) when searching within a patch. Their performance does not suffer when their searching within a patch is briefly interrupted (Sulikowski & Burke, 2011b). When foraging for invertebrates in the wild, birds may rely on a variety of systematic movement rules (Robinson & Holmes, 1982; Smith, 1974). In the laboratory, noisy miners searching for invertebrates exhibit lateral movement biases: they tend to move left-to-right (or right-to-left) as they explore an array, with their search performance dropping to chance levels when their movement is interrupted. No such lateral biases were observed when noisy miners searched the same arrays for nectar rewards

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(Sulikowski & Burke, 2011b). Observations of wild hummingbird (*Selasphorus* spp.) foraging also suggest no correlation between the direction of successive movements from one inflorescence to another (Pyke, 1981).

The time spent, and distance travelled (energy expended), per unit of food (energy) consumed, is an indicator of foraging efficiency (Pyke, 1984). Nectarivores foraging for nectar on a single plant (assuming all flowers contain equal yield) can maximize their efficiency by minimizing the path length that takes them to each flower, while avoiding revisits. This is a variant of the travelling salesman problem (TSP) known as TSP-path: construct the shortest route possible that will take the traveller to all locations exactly once (Papadimitriou, 1977). The classical TSP includes the added constraint that the traveller must finish at the same location at which they began, a constraint that need not apply to nectarivores foraging on a plant. Critically, in this scenario, the most efficient place to visit next depends on the locations of all remaining places to visit. Bumblebees, *Bombus terrestris*, take shorter flight paths as they repeatedly forage on the same arrangement of flowers (Reynolds, Lihoreau, & Chittka, 2013) and incorporate newly encountered patches of flowers into their habitual foraging routes optimally (Lihoreau, Chittka, & Raine, 2010). If nectar-foraging birds, like bumblebees, are actively approximating TSP solutions as they forage, then we would expect them to rely, not just on memory for the specific locations already visited, but also on planning the order of future visits. Evidence of such route planning has been observed in wild foraging capuchin monkeys, *Cebus apella nigritus* (Janson, 2007; but see also Janson, 2014) and requires the animal to identify in advance a finite number of point locations it needs to search. For nectarivores, such planning is afforded by the visual conspicuousness of flowers.

When foraging for cryptic invertebrate prey the forager cannot solve the TSP as it cannot observe in advance the point locations to which it will need to travel to consume prey. Consider a bird gleaning leaves for insects or foraging along the ground: it moves through the patch visually scanning for a prey item, moving quickly to retrieve one when it is spotted. Having consumed a prey item, the forager's subsequent movements may tend to keep it in areas of relatively high prey density (Smith, 1974), or, after a period of no success, movements may take it to the boundary of the area it has been visually scanning, in order to begin a new scan (Robinson & Holmes, 1982). Therefore, unlike the system used for nectar, these foraging paths are not planned in advance, but dictated by where and when prey items are located. Therefore, we might expect that any cognitive mechanisms adapted for this type of invertebrate foraging would not have been selected to make use of advance knowledge of the location of individual prey items. The primary goal of the current study, therefore, was to determine whether knowing the point locations of food rewards in advance would facilitate within-patch foraging performance for nectar, but not for invertebrates.

We presented birds with arrays of feeders that contained a mixture of nectar and invertebrate rewards. In one condition the colour of the feeder indicated the reward to be found within, while in the other condition all feeders were the same colour. In the former condition birds could predict in advance which feeders would contain which reward and so knew the layout of the two reward types prior to searching, while in the latter the contents of each feeder were only known when that feeder was inspected and the reward consumed. We predicted that if birds do rely on advance knowledge of spatial layouts when foraging for nectar but not invertebrates, then they would retrieve nectar rewards more efficiently (with fewer revisit errors) than invertebrate rewards in the colour-coded condition. This would be consistent with all our previous findings where birds have always known what reward to expect and have always performed better with nectar (Sulikowski & Burke, 2007, 2010a, 2010b, 2011b). We predicted that in the condition that was not colour coded, however, where birds were deprived of prior knowledge of the spatial layout, information hypothesized to be important for nectar foraging but not invertebrate foraging, their performance with nectar would suffer and they would perform relatively better (make fewer revisit errors) when searching for invertebrates.

For the purpose of the above predictions we assumed that birds' foraging can be concurrently guided by both hypothetical sets of cognitive mechanisms at once. Although we have evidence of divergent cognitive mechanisms supporting foraging for these two foods, we have no knowledge of whether such mechanisms are sufficiently independent that they can function concurrently, with both influencing decisions within the same foraging bout. In the wild, omnivorous honeyeaters, such as noisy miners, tend not to forage on nectar and invertebrates at the same time, with nectar foraging occurring early in the day (Collins & Briffa, 1983) and invertebrate foraging occurring later (Timewell & Mac Nally, 2004). So noisy miners would not typically be required to engage both sets of hypothetical mechanisms at once. To help determine the extent to which one foraging system may be dominating over the other, we measured birds' lateral movement biases which we have previously observed to be strong when birds are foraging for invertebrates and absent when birds are foraging for nectar.

METHODS

Subjects

Subjects were 12 adult wild-caught noisy miners that were trapped and held in captivity for several weeks prior to testing. Birds were held and tested individually in outdoor cages measuring 3 × 3 × 3 m.

Ethical Note

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

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

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

Apparatus

The feeders were small round plastic wells (approximately 1 ml capacity) that hooked onto the front wall of the birds' cages from the outside. The square metal lids were hinged with tape and could be easily lifted. Once a bird had finished feeding, the lids of the feeders fell closed under gravity (see Fig. 1) so that visited feeders remained visually indistinguishable from yet to be visited feeders. Tape around the feeders and on the lids gave the feeders their black, white or grey colour. We chose these colours as they are relatively ecologically neutral, and we did not want the colours themselves to intrinsically elicit any particular kind of foraging behaviour.

The rewards used during testing were either 0.25 ml of a 30% w/v sucrose solution (per feeder, nectar rewards) or half a mealworm, *Tenebrio molitor* (per feeder, invertebrate rewards).

Procedure

Birds were first trained to open the experimental feeders by providing them with two such feeders on the front of the cage for several hours at a time so that the birds could freely explore them. During the birds' initial days in captivity the lids of the feeders were propped open and the feeders contained a few crumbs of cake. Once birds were reliably eating this cake each day, the feeder lids were closed. All birds readily learnt to open the feeders and retrieve the cake. The first time birds received either nectar or invertebrate rewards in the feeders was during the first trial of the experiment.

Each trial involved presenting a bird with an array of 12 feeders, six of which contained a nectar reward and six an invertebrate reward. The 12 feeders were placed in 12 of 16 possible locations defined by a 4 × 4 grid, with horizontal and vertical distances of 40 cm between each location (see Fig. 2). For six of the birds, all 12 feeders were grey, while for the other six birds, the colour of the feeder (black or white) indicated the type of food reward it contained (nectar or invertebrate, counterbalanced). The feeder locations (and food rewards they contained) were chosen randomly across each of the trials. The six birds in each condition (grey feeders and black/white feeders) completed the same sequence of trials (with feeders in the same locations).

Once the feeders were placed on the front of the cage, birds were given up to 5 min to begin exploring them. A trial was aborted if the bird did not open any of the feeders within this time, or if the bird failed to make at least 12 visits to feeders during the 10 min period. This typically occurred as a result of alarm calls (see below). Trials commenced when the bird first opened a feeder and lasted 10 min, or until the bird left the array if the bird happened to be at the feeders when the 10 min expired. Birds were free to search the feeders and consume the rewards during the trial period. All trials were video-recorded and subsequently scored (scoring procedure and dependent variables are described below).

Test sessions occurred in the morning and the afternoon (weather permitting), with half the daily food provided after each session. Each bird completed a maximum of one trial per test session. Not all birds completed a trial in every session; some sessions were interrupted by rain, others by alarm calls in response to predatory birds in the vicinity of the aviaries. Such alarm calls (from wild birds or from our captive birds) could render the captive birds

Figure 1. (a). An adult noisy miner feeding from one of the experimental feeders. (b) The lids of the feeders fall closed again once a bird removes its beak.

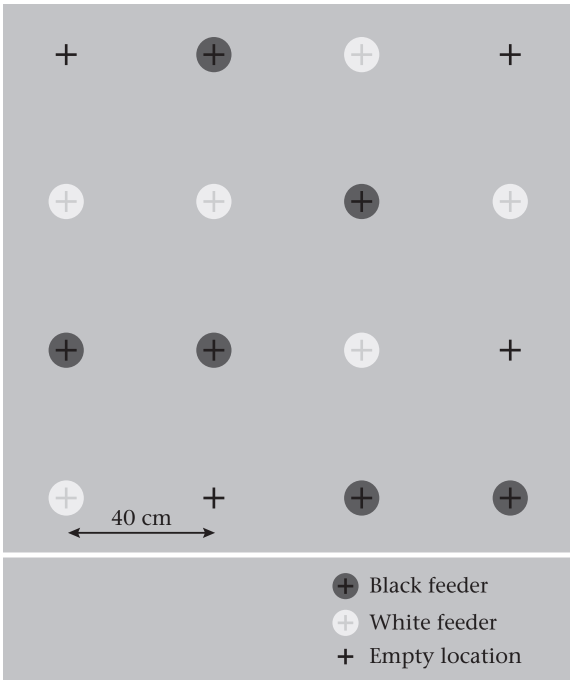

Figure 2. An example array. Whether black or white feeders contained nectar or invertebrate rewards, respectively, was counterbalanced across birds in the black/white condition. Birds in the grey condition searched the same arrays as birds in the black/white condition, but all their feeders were grey.

silent and still for an extended period, forcing an end to testing during that session, especially if the predatory bird in question remained in the general vicinity. Each bird completed its trials over 6–13 days (mean ± SD: 8.2 ± 1.2 days for grey condition, 8.5 ± 2.8 days for black/white condition). Four birds from each condition were tested in late summer (February–March) and two birds from each condition were tested the following winter (August, 2010). All birds were released within a few weeks of completing their trials.

Scoring

First, we examined how likely birds were to visit subsequent feeders offering the same reward type while they were searching. To do this we recorded, for each trial, every transition a bird made from one visited feeder to the next, without leaving the array in between. A bird was deemed to have left the array if it flew off the front wall and landed elsewhere in the cage, with the exception of the ground immediately below the array (which birds sometimes used to move between the bottom row of feeders, rather than skipping across the metal mesh cage). We classified each transition as ‘same’ (if both feeders offered the same reward) or ‘different’ (if the feeders offered different rewards) and then calculated a normalized same-different score: $(S - D)/(S + D)$, where S is the number of same transitions and D the number of different transitions. This same-different score was calculated for each bird for each trial.

Second, we examined the number of search errors birds made to locate the two food types. To do this we considered the six nectar feeders and six invertebrate feeders of each trial as two separate arrays. For each array we then scored the number of revisit errors: the number of times a bird revisited a feeder it had already emptied, prior to all six feeders of that food type being visited. As above, we calculated a normalized revisit errors score: $(N - I)/(N + I)$, where N is the number of revisit errors made to nectar feeders and I is the number of revisit errors made to invertebrate feeders. Therefore, if a bird made more revisit errors to nectar than invertebrate feeders this score was negative, and if more revisit errors to invertebrate feeders were made it was positive. This score was calculated for each bird for each trial and then averaged across the 12 trials.

Third, we examined the birds' movement patterns as they explored the arrays. We calculated the lateral movement bias of each bird for each trial as $(L - R)/(L + R)$, where L and R represent the number of movements (transitions from one feeder to another) that included a leftward and rightward component, respectively. This is the same measure that has previously revealed consistent biases in birds foraging for invertebrates and no biases in birds foraging for nectar (Sulikowski & Burke, 2011b).

RESULTS

To determine whether birds in the black/white condition were more likely to make subsequent visits to feeders containing the same food reward, we averaged the same-different scores of each bird across four blocks of three trials and conducted a mixed-effects ANOVA with block (four levels: 1–4) as a repeated measure and condition (two levels: grey and black/white) as a between-subjects factor. There was a significant effect of condition ($F_{1,10} = 8.604$, $P = 0.015$) as birds in the black/white condition made relatively more same than different transitions across all four blocks than birds in the grey condition (see Fig. 3).

We then compared the mean number of revisit errors birds made while searching. As predicted, birds tended to make fewer errors when foraging for nectar in the black/white condition than in the grey condition ($t_{10} = 2.067$, $P = 0.033$, one-tailed), with no such difference apparent when foraging for invertebrates ($t_{10} = 0.583$, $P = 0.573$, two-tailed; see Fig. 4a). We then compared the mean normalized revisit error score (which was negative if more revisit errors were made to nectar feeders and positive if more revisit errors were made to invertebrate feeders) between the two conditions. An independent-samples t test confirmed a significant effect of condition ($t_{6.2} = 3.636$, $P = 0.010$, adjusted degrees of freedom applied due to unequal variances, Levene's $F_{1,10} = 6.143$, $P = 0.033$), with birds in the grey condition making relatively more errors to nectar feeders and birds in the black/white condition making relatively more errors to invertebrate feeders. One-sample t tests comparing the mean score from each condition to 0 (the null value indicating equal propensity to make revisit errors when searching for either food) confirmed that birds in the grey condition made significantly more errors to nectar than invertebrate feeders ($t_5 = 3.600$, $P = 0.016$), while birds in the black/white condition

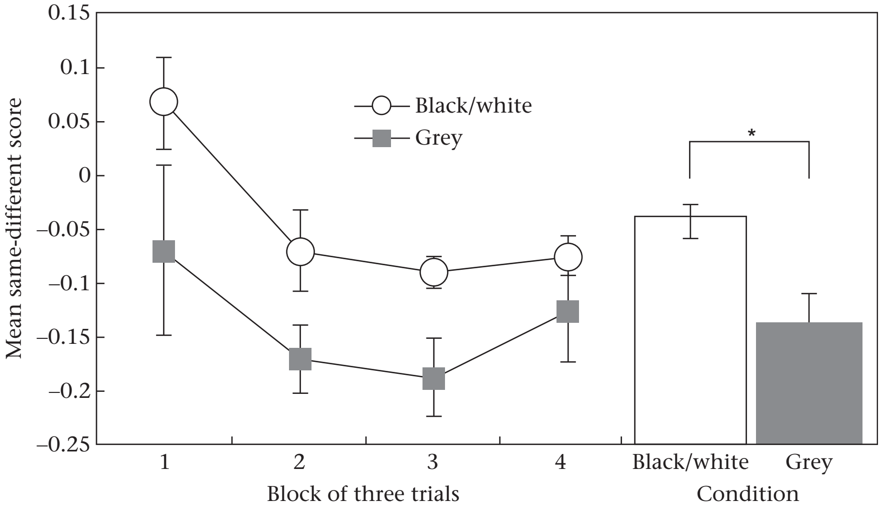

Figure 3. Mean ± SE same-different score, calculated as a normalized score: $(S - D)/(S + D)$, where S (D) denotes the total number of same (different) feeder transitions, i.e. consecutive visits to feeders containing the same (different) food type. In the black/white condition the colour of the feeder indicated the reward type inside; in the grey condition all feeders were the same colour. Scores are shown across all four blocks of the experiment and overall for the two conditions. *$P = 0.015$, mixed-effects ANOVA.

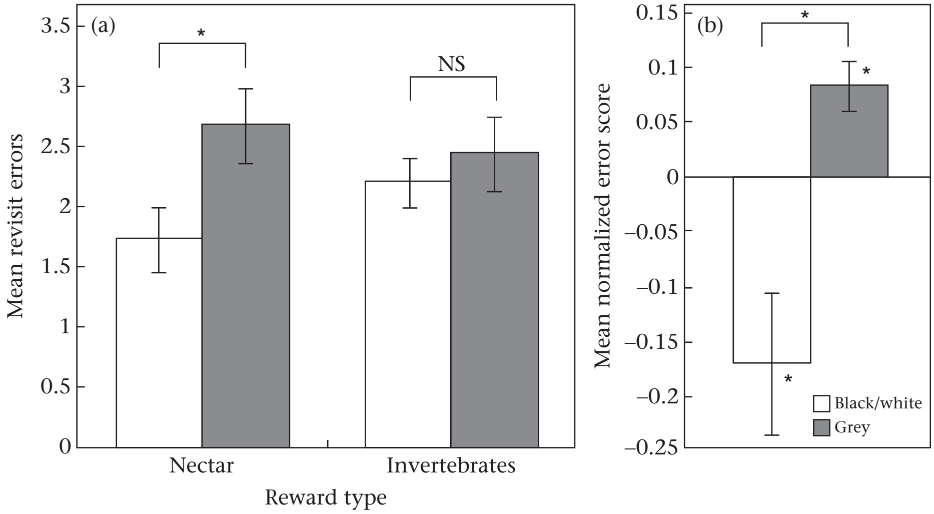

Figure 4. (a) Mean ± SE number of revisit errors birds in either condition made when foraging for nectar and invertebrate rewards and (b) the mean normalized error scores (calculated as $(N - I)/(N + I)$, where N is number of revisit errors made to nectar feeders and I is the number of revisit errors made to invertebrate feeders) for both conditions. * $P < 0.05$, mixed-effects ANOVA.

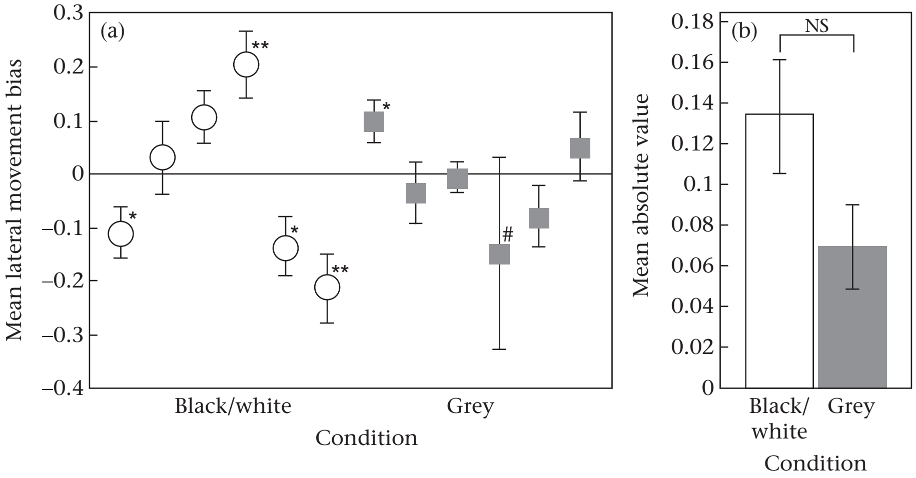

Figure 5. (a) Mean ± SE lateral movement bias of individual birds (calculated as $(L - R)/(L + R)$, where L is the number of movements that contained a leftward component and R is the number of movements that contained a rightward component) and (b) mean ± SE strength of the bias across birds in the black/white and grey conditions. *Bias is significantly different from zero at $P < 0.05$, one-sample t tests; **bias is significantly different from zero at $P < 0.01$, one-sample t tests. # This bird exhibited strong lateral biases within individual trials, but was the only bird to substantially change the direction of its bias across trials.

made significantly more errors to invertebrate than nectar feeders ($t_5 = 2.594$, $P = 0.049$; see Fig. 4b).

When we examined the lateral movement bias scores of each bird (averaged across the 12 trials, and compared to a null mean of 0) we observed significant lateral biases for five of the 12 birds (a sixth bird exhibited lateral biases that changed direction from trial to trial; see Fig. 5a). When the absolute value of the mean lateral movement bias was compared across conditions (to assess the relative strength of the bias, independent of the direction), there was a tendency for birds in the black/white condition to exhibit stronger biases ($t_{10} = 1.845$, $P = 0.095$; see Fig. 5b).

DISCUSSION

We demonstrated that birds used colour cues to guide their search for nectar and invertebrate rewards. When these colours cued the spatial layout of each food type, birds made fewer revisit errors to nectar feeders than to invertebrate feeders. In the absence of these cues the spatial layout of each food type was cryptic and birds made relatively more revisit errors to nectar, than invertebrate, feeders. These results provide evidence of a new difference in the cognitive mechanisms that underpin foraging for these two food types: route planning.

The existence of planning abilities in nonhuman animals is controversial (Suddendorf & Corballis, 2010; de Waal & Ferrari, 2010). Examples of planning in apes (Osvath & Osvath, 2008), monkeys (Naqshbandi & Roberts, 2006; Visalberghi et al., 2009) and scrub-jays, *Aphelocoma californica* (Raby, Dickinson, & Clayton, 2007; reviewed by Raby & Clayton, 2009) focus on autonoetic aspects, as evidenced by behaviours that are independent of current motivational states, but serve future, expected motivational states. The current study offers evidence of planning that does not hinge on differences between current and future motivational states. Based on overlap of neural mechanisms, Pastalkova, Itskov, Amarasingham, and Buzsáki (2008) suggested that episodic-like memory and planning exapted neural architecture that originally evolved to support spatial cognitive aspects of navigation. If true, the movement-based planning seen in the current study could be the type of planning that first evolved, not requiring a dissociation from the current motivational state to be adaptive.

If noisy miners plan their foraging paths, other nectarivores may do the same. Wild rufous hummingbirds, *Selasphorus rufus*, concurrently monitor several artificial nectar sources, matching their visits to various replenishment schedules (Henderson, Hurly, Bateson, & Healy, 2006). While this is not unequivocal evidence of planning, the birds in this study routinely declined to visit feeders that were not yet replenished, in spite of being within their vicinity. This is at least suggestive of an expectation of future opportunities to forage at those flowers.

Hummingbirds also integrate different cues into ‘episodic-like memories’ (Jelbert, Hurly, Marshall, & Healy, 2014), as do scrub-jays (Clayton & Dickinson, 1998). Although the equivalence of episodic memory in humans and episodic-like memory in other animals is not certain (Rattenborg & Martinez-Gonzalez, 2013; but see also Salwiczek, Watanabe, & Clayton, 2010), there are neural processes common to remembering the past and imagining, or planning for, the future. Evidence of this comes from co-morbidity of deficits in these areas among people with amnesic brain damage (Hassabis, Kumaran, Vann, & Maguire, 2007; Klein & Loftus, 2002; Williams, Ellis, Tyers, & Healy, 1996) and from neuroimaging studies of healthy human (Okuda et al. 2003; Szpunar, Watson, & McDermott, 2007; reviewed by Schacter, Addis, & Buckner, 2007) and rodent (Pastalkova et al. 2008) brains. One function of episodic memory, therefore, may be to facilitate planning for future similar events (Schacter & Addis, 2007). If the adaptive significance of episodic(-like) memory is to facilitate planning, we would expect planning and episodic(-like) memory to co-occur within species. This suggests that, like hummingbirds, noisy miners and honeyeaters (Meliphagidae) in general may be candidate species for episodic-like memory investigations.

Route planning may be energetically efficient if it allows search paths to be minimized (Lihoreau et al. 2012) and it may also be cognitively efficient if it means that a bird or insect does not actually have to remember, separately for each individual flower, whether it has been visited or not, but simply needs to know its planned route, and where along that planned route it currently is. This cognitive efficiency may explain why route planning and memory for point locations searched are interdependent: in the current study depriving birds of the opportunity to plan a route impacted their ability to avoid previously rewarded locations. This implies that route planning, afforded by prior knowledge of the spatial layout, is an important cognitive step that, in turn, facilitates the more effective memory for point locations where nectar has been found, compared to those where invertebrates have been found.

For all previous studies we have conducted with noisy miners we have predicted, and observed, better performance when searching for nectar than when searching for invertebrates in various laboratory tasks (Sulikowski & Burke, 2007, 2010a, 2010b, 2011b). Greater motivation to search efficiently for nectar rewards (due to a general preference for sucrose over mealworms) could, therefore, have explained these effects. We have previously argued that this alternative explanation cannot adequately account for the variety of food type effects that we have reported, as these effects extend to behaviours that do not affect performance (such as movement biases in search patterns, Sulikowski & Burke, 2011b), but do not extend to behaviours that should change under appetitive motivation (such as latency to begin searching once feeders are presented, Sulikowski & Burke, 2010a). This is the first instance in which we have contrived a laboratory scenario in which performance when foraging for nectar was predicted (and observed) to be poorer than when foraging for invertebrates. This reversal in performance makes it highly unlikely that food type effects on cognition are the result of a general preference for sucrose solution over mealworms.

In the black/white condition we observed longer strings of visits to feeders containing the same rewards than in the condition that was not colour coded. So an alternative explanation for the observed effects of food type in the two conditions is that longer strings of uninterrupted foraging successes better facilitate performance when searching for nectar than when searching for invertebrates. Two previous findings suggest that this is not the case. First, when birds forage freely within arrays containing either nectar or invertebrate rewards, but not both, birds foraging for invertebrates organize their visits into fewer search bouts of longer visit lengths than birds foraging for nectar (Sulikowski & Burke, 2010a). As invertebrate search bout length increased over trials in that study, so too did performance. Second, experimentally limiting search bout lengths to two visits drastically impairs search performance for birds foraging for invertebrates but does not impact search performance for nectar (Sulikowski & Burke, 2011b). In neither of these studies did we conclude that there was likely to be a direct causal relationship between search bout length itself and performance, but even if our theoretical explanations were incorrect and such a relationship did exist, it would have predicted a relative decrease in revisit errors to invertebrate feeders in the colour-coded condition, rather than the condition that was not colour coded: the exact opposite of what we found.

From this and previous studies, we are accumulating evidence that different cognitive mechanisms guide behaviour when foraging for nectar and invertebrates, respectively. The extent to which such mechanisms operate independently, and potentially concurrently, is not known. In the current study, birds performed reasonably well with both food types, in both conditions. The relatively fewer search errors towards invertebrates in the grey condition and nectar in the black/white condition is consistent with the notion that both cognitive strategies can operate concurrently, within a single search bout. If birds were engaging just one of the two strategies and applying it equally to all feeders, then, irrespective of which birds chose which strategy, we would not have expected any effects of food type within each condition, let alone opposite effects across conditions.

It is conceivable, however, that individual birds faced with the dilemma of which cognitive mechanism to engage could have engaged just one of these, concentrated their efforts on feeders that contained the congruent reward and only opportunistically checked other feeders as their search path led to/passed them. Such a scenario could have produced the effects of food type we observed within each condition, but only if birds in the black/white condition were predominantly applying a nectar strategy and birds in the grey condition were predominantly applying an invertebrate strategy. This would have resulted in a stronger lateral movement bias in the grey condition, relative to the black/white condition. The opposite trend was observed, however, with some birds in both conditions exhibiting significant movement biases (previously associated with invertebrate foraging) and other birds exhibiting no such bias (previously associated with nectar foraging).

Research should now directly examine how effectively birds solve the TSP when foraging for nectar compared to invertebrates. The TSP is an NP-hard optimization problem (Arora, 1998), which means it is among the hardest computational problems to solve. There is currently no algorithm for definitively solving the TSP (Ouaarab, Ahiod, & Yang, 2014) although many attempts have been inspired based on animal search behaviour, including the cuckoo search (Ouaarab et al. 2014; Yang & Deb, 2010) and ant colonies optimization (Dorigo & Gambardella, 1997) algorithms. Work with bumblebees (Lihoreau et al. 2012; Reynolds et al. 2013) has also inspired an iterative improvement heuristic model that provides efficient solutions to TSP-like problems. There is, therefore, potential scope for further algorithms to be developed based on the foraging behaviour of avian nectarivores.

Conclusion

The current study provides evidence that noisy miners plan their search path when foraging for nectar, but not when foraging for invertebrates. This type of planning does not involve a dissociation from the current motivational state and may represent a cognitively more rudimentary type of planning than the behaviours that typically earn that label in nonhuman animals. The divergent search strategies employed when noisy miners search for both nectar and invertebrates represent potentially independent cognitive strategies, which may operate concurrently.

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