



## 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.

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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 & Hurlly, 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 nigrurus* (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  $3 \times 3 \times 3$  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

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