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Chapter 5

FLORAL COGNITION: COMPARATIVE AND FUNCTIONAL PERSPECTIVES

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ABSTRACT

In this paper, I begin by presenting a detailed summary and discussion of work that has been conducted in my laboratory investigating how the cognitive mechanisms that underpin foraging may be adapted to maximally exploit resources of different distributions. My study species, the noisy miner (Aves: Meliphagidae, *Manorina melanocephala*) is a generalist forager that feeds on both nectar and invertebrate prey – resources with quite different natural distributions. Throughout this discussion I draw comparisons between the behaviour and cognition of noisy miners and other relevant species. These include the two other nectarivorous groups that have been the subjects of the most in-depth investigations of the cognition of nectar foraging: hummingbirds (especially rufous hummingbirds, *Selasphorus rufus*) and bees; and also several species of insectivorous birds.

I then consider how the different extant approaches to studying animal cognition lead researchers to ask different questions, apply different types of studies and ultimately draw quite different conclusions about the structure and function of cognitive mechanisms across the Animal Kingdom. In particular, I discuss the implications of these different approaches for interpreting the findings from avian nectarivores and for inspiring the directions of future research.

I finish by identifying some of the strengths and weaknesses of the research programs examined. I also suggest some potentially profitable future directions, including the development of more novel paradigms, and the use of formal modeling to guide quantitative predictions of behaviour.

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NOISY MINERS – A TALE OF TWO STRATEGIES

Noisy miners (Aves: Meliphagidae, *Manorina melanocephala*) are a species of Australian honeyeater. They are generalist foragers, feeding on nectar and invertebrates, which they capture using a variety of methods, including gleaning and hawking (Barker and Vestjens, 1984; Dow, 1977). Noisy miners also frequently feed on novel food sources in urban areas (personal obs.) including opening commercial sugar packets (Delgado-V and Correa-H, 2015). Aside from one recent investigation exploring problem-solving in noisy miners (Griffin and Diquelou, 2015), our knowledge of their cognition comes from a series of experiments conducted in our lab examining differences in how these birds use information while foraging for resources with natural distributions: nectar compared to invertebrates. In contrast to the majority of the work with hummingbirds described above, all of the research we have conducted in our lab with noisy miners has been conducted in captivity. Our subjects have all been adult noisy miners of unknown age and sex, although our samples are likely to be strongly male biased, mirroring the sex-ratio of these birds in the wild (Arnold, Griffith and Goldizen, 2001). For all of our studies, wild birds were trapped days (up to several weeks) prior to the experiments and banded and released shortly after. Banding birds prior to release allowed us to confirm that our experimental subjects successfully re-integrated into their social groups post-release (which we were able to observe was the case for the majority of birds), and also ensured that each sample of birds trapped was experimentally naïve.

While in captivity, all our birds are held individually in adjacent cages measuring 3m x 3m x 3m. All testing is carried out in each bird's home cage. The majority of our studies' designs have several features in common. Birds are required to search arrays of feeders presented, vertically, on the front wall of their home cage to locate rewards. In some cases, the number of feeders a bird was permitted to probe on any given trial was limited to the number of rewards available in the array, such that probing a non-rewarded feeder (or the same feeder twice) carried the cost of being unable to retrieve all available rewards. In most cases, however, the time a bird was permitted to search the array was ample to allow birds to retrieve all rewards, no matter how many 'incorrect' (unrewarded, or already visited) feeders a bird probed. Feeders are designed such that they are self-closing, so that after a bird has probed a feeder and moved on, the feeder closes again, making it visually indistinguishable from feeders the bird has not yet visited on that trial. To understand how noisy miners' cognitive strategies may have diverged to support efficient foraging on both nectar and invertebrate prey, birds in our studies were rewarded with either a 30% w/v sucrose solution (imitating nectar) or a mealworm (representing invertebrate prey). These food types were usually manipulated between-subjects.

Nectar is a resource with a reasonably well-defined distribution. It is found in visually conspicuous, discrete point locations in space (flowers), which are typically clumped (on plants). Thus, there are clear visual cues that indicate the potential locations of nectar and that define the locations and boundaries of patches of nectar. While invertebrates, as a category of prey items, is large and heterogeneous there are some generalisations that we can make about their distribution (at least with respect to the types of prey items that noisy miners typically consume). Unlike nectar, their point locations in space are not usually signaled prior to attack, as they are typically cryptic. They are also mobile. This means that, within the boundaries of a suitable 'patch' of microhabitat, invertebrate prey items are potentially continuously distributed (Benhamou, 1992). Only after some period of searching is a prey item located and then typically immediately attacked and consumed. Since the locations of prey are not signaled, a forager has only probabilistic information about the distribution of prey within a patch. If it searches and does not locate a prey item, this could be because prey items are currently at a low density, or it could be because the forager missed them. This can be contrasted with the analogous situation when foraging on flowers. If a forager visits a flower and does not find nectar, it can be certain that the flower does not contain nectar. While the profitability of a whole plant might need to be probabilistically estimated based on the yield from a subset of the flowers, at least the information gleaned from each flower is highly reliable.

There are also differences between nectar and invertebrates in terms of the effects of the forager's behaviour on the distribution of food remaining in a patch. A flower once visited by the forager will be reliably depleted, and so an unprofitable place to which to return for an extended period of time. After such time it will likely replenish and, unless visited by another forager, will again become a profitable place at which to forage. The mobile nature of invertebrate prey items, however, means that a point location at which an invertebrate prey item is located may not be reliably depleted for any length of time. Further, if the invertebrate prey are sparsely distributed, that point location in space may never contain another prey item again.

Therefore, the different distributions of nectar and invertebrate prey mean that different foraging strategies may be required to maximize foraging efficiency. It also means that different information becomes available to a bird as it forages on either food source. These two factors combined may have selected for noisy miners to evolve two divergent cognitive foraging systems[1]: one to support foraging on nectar and the other to support foraging on invertebrates. The other evolutionary solution to the problem of foraging on multiple resources with different distributions and different informational properties[2], is that a single generalist cognitive system could evolve that represents some optimal trade-off in efficiency between the two food types. Data collected in our lab suggest that the former outcome is the case.

In the laboratory, noisy miners spontaneously avoid (after a delay of 5 minutes) feeders that they previously visited which contained food rewards, in favour of feeders that did not contain rewards (Sulikowski and Burke, 2007). This behaviour, termed "win-shifting" (as opposed to "win-staying") or a "win-shift bias" is exhibited also by several other nectarivorous birds tested in the lab (Burke and Fulham, 2003; Cole et al., 1982; Wunderle and Martinez, 1987; although see also Sulikowski and Burke, 2011a), tested in the field (Healy and Hurly, 1995) and observed in the wild (Gill and Wolf, 1977; Kamil, 1978). Noisy miners exhibited this win-shift bias when rewarded with a sucrose solution (mimicking a nectar reward), but not when rewarded in an identical task with a mealworm. The most straightforward conclusion is that win-shifting is a nectar-specific behaviour that reflects a cognitive adaptation to efficiently exploit the depleting nature of flowers.

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[1] The term cognitive system is used here to indicate a collection of rules describing how the animal uses a subset of the information available in the world to make decisions in a particular context, such as foraging on a particular food type.

[2] In this paper, 'informational properties' refers to the different bits of information that are potentially available to an animal in its natural environment which are relevant to achieving the behavioural goal at hand. These can be contrasted with the 'computational requirements' of laboratory tasks, which refers to the way information must be used within the task to achieve the best possible task performance.

Not only did noisy miners not exhibit any significant bias to either avoid or return to locations where they had recently found a mealworm (after a five minute delay they were initially equally likely to search in locations that had been rewarded as in locations that had not been), they were also not particularly good at learning either of these basic rules. They barely performed above chance in either the win-shift, or the win-stay conditions, by the end of experiment (Sulikowski and Burke, 2007; see also Sulikowski and Burke, 2012). When rewarded with sucrose, however, birds reinforced to win-shift performed well above chance right from the first block of trials. This implies that birds foraging for nectar remember the locations where food has recently been found and use this information to guide subsequent foraging decisions. Birds rewarded with mealworms, though, did not seem to be able to use the point locations of previous prey items to guide decisions about where to search minutes into the future, even when being reinforced to do so. This observation inspired a series of studies (Sulikowski and Burke, 2010a, 2010b, 2011b, 2015a) designed to investigate how within-patch foraging behaviour and information use differed between the two food types[3].

When foraging within a patch of flowers, efficiency is increased if revisits to the same flower are avoided, irrespective of whether or not the flowers contained nectar when first visited. There is no reason to suppose that a forager would be better able to avoid already visited flowers that contained nectar, compared to already visited flowers that had been empty. Both are equally unhelpful places to which to return within that foraging bout. Neither will provide food, nor would they yield additional information about the current or future distribution of food in the environment. The same, however, is not true for a forager searching for invertebrate prey. In the wild, specific point locations within a patch of potentially continuously distributed invertebrate prey only become differentiated from the rest of the patch after a prey item has been found there. From this we predicted that a forager searching for invertebrate prey in the laboratory would be less effective at subsequently avoiding locations (feeders) it had searched that had been empty, than locations it had searched that had yielded food. The former would be less likely to be perceived as a defined location.

To test these predictions, we gave birds a series of search trials (Sulikowski and Burke 2010b). Each trial presented an array of 16 feeders, arranged in a four-by-four grid and presented vertically on the front wall of the bird's cage. Half of the feeders were randomly selected to be baited and the other half were empty on each trial. Food type was manipulated between-subjects, with half of the birds searching for 0.25ml sucrose solution in each feeder, and the remaining birds searching for half a mealworm in each feeder. Birds were allowed to freely search each array for 15 minutes (individual trials were spaced a day apart). This provided ample time for the birds to inspect all the feeders multiple times if they wished, with birds making upwards of 30-40 visits to the 16 feeders on some trials. Analyses examined the first eight visits that birds made to feeders that were originally baited and the first eight visits made to unbaited feeders. If birds made no search errors during these eight visits, then each visit would be to a unique feeder. If, within these first eight visits, birds re-visited a feeder they had already probed, this was considered to be a search error. The results were in line with our predictions. Birds foraging for nectar were equally likely to make search errors to baited as unbaited feeders, suggesting that they were equally adept at avoiding previously

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[3] To limit confusion, throughout my descriptions of these studies I will refer to birds ‘searching for’ or ‘rewarded with’ ‘sucrose’ or ‘mealworms’ when I am describing behaviour and information use within an experiment. When I wish to describe our interpretations for what this indicates about information use during wild foraging, I will refer to birds ‘foraging for nectar’ or ‘foraging for invertebrate prey’.

probed feeders, irrespective of whether the feeders had contained a food reward. Birds foraging for invertebrates, however, made more search errors to unbaited feeders than they did to baited feeders, confirming that they were better able to avoid revisiting a feeder if they had retrieved a food reward from it.

The differential pattern of search errors observed in the study described above (Sulikowski and Burke, 2010b) is best interpreted as an interaction between the cognitive strategies the birds employed while searching and the proximate demands of the artificial laboratory task they were given. We assume (the merits of this assumption are discussed in more detail below) that the birds in the respective food type conditions were engaging divergent cognitive mechanisms, differentially adapted to maximally exploit the natural distributions of nectar and invertebrate prey. If this is the case, then one of the first things to consider is that the distribution of food offered in this study (presented within 16 visually obvious, discrete feeders in fixed locations) maps more closely onto the natural distribution of nectar than onto the natural distribution of invertebrate prey. As previously described, while a forager may attend to the point locations at which invertebrate prey items are discovered (perhaps for the purposes of determining overall patch quality and/or delineating the boundaries of patches within their territory, Benhamou, 1992), the mobile nature of invertebrate prey means that we should not necessarily expect such a forager to spontaneously and systematically avoid such locations as it continues to search within that same patch. Birds foraging for nectar, on the other hand, would be predicted to spontaneously avoid all previously searched locations. Indeed, in similar studies where all feeders have been baited, we observe that birds searching for sucrose make fewer revisit errors overall than birds searching for mealworms (Sulikowski and Burke, 2010a; Sulikowski and Burke, 2011b – Experiment 1).

The fact that birds rewarded with mealworms in the study described above (Sulikowski and Burke, 2010b) performed well above chance (if chance is defined as the number of revisit errors predicted by a random walk) may be explained in several (non-mutually exclusive) ways. Firstly, the demands of the task, where revisits to feeders were never rewarded, may have encouraged birds to avoid revisits. This reinforcement, coupled with the birds' greater tendency to attend to rewarded, compared to unrewarded, locations could have produced the observed pattern of errors. This combination of factors predicts that birds in the mealworm rewarded condition would reduce the number of revisit errors made across trials in these types of tasks (as the reinforcement shapes behaviour). This is also a pattern we have observed (Sulikowski and Burke, 2011b). Similarly, birds searching for mealworms in our studies also tend to change how they structure their search patterns over the duration of an experiment, organizing their visits to individual feeders into fewer search bouts of longer length (with a search bout defined as a string of visits to feeders made without leaving the array, Sulikowski and Burke, 2010a; 2010b). This is consistent with a search strategy that is adapting to the demands of the task. Birds searching for sucrose neither improve their error rates nor lengthen their search bouts over successive trials (Sulikowski and Burke, 2010a; 2010b; 2011b). We presume that this is because their nectar-foraging cognitive system spontaneously avoids revisits right from the beginning of the experiment, which suits perfectly the requirements of the task. So there is no scope for the differential reinforcement received between initial visits and revisits to shape the birds' behaviour.

If birds foraging for invertebrates truly have no spontaneous tendency to avoid specific locations where prey items have been located, we might expect that birds searching for mealworms in our within-patch studies to initially make many revisit errors, perhaps as many as predicted by a random walk. This is never the case. Even within the first trials of experiments, birds searching for mealworms tend to make more revisits than birds searching for sucrose, but make far fewer revisits than predicted by a random walk (Sulikowski and Burke, 2010a; 2010b; 2011b). One potential explanation is that birds searching for mealworms are employing a search strategy that does not specifically include remembering and avoiding particular locations, but nevertheless results in fewer revisits to feeders than predicted by a random-walk. Further analyses and a series of experiments were designed to test this possibility.

Movement analyses of birds as they searched the four-by-four array of 16 feeders (Sulikowski and Burke, 2010b; with results reported in Sulikowski and Burke 2011b – Experiment 3) reveal systematic differences in how birds searched the arrays as a function of whether they were searching for sucrose or mealworms. When birds were searching for mealworms they tended to move systematically through the array in either the leftward or the rightward direction. Different birds exhibited preferences for different directions but all birds were consistent with their chosen direction across trials. Birds that were searching for sucrose exhibited no such side-ways directional biases. A movement-based foraging strategy in which birds approach a potential patch of invertebrate prey at its edge and then move systematically through it, could result in the observed lateral movement biases when restricted to an experimental array. Such a movement rule would also make revisits to feeders less likely than predicted by a random walk, as already visited feeders would be behind the bird, and so less likely to be visited than the as yet unvisited feeders in front. A movement-based strategy could therefore explain how birds searching for invertebrates were able to perform well above chance (in terms of the number of revisit errors they committed) right from the first trial of our array-search studies (Sulikowski and Burke, 2010a; 2010b; 2011b), without explicitly remembering and avoiding previously visited feeders.

All birds tended to move downwards more often than upwards as they searched the arrays, but this is as likely to be an artifact of the experimental setup as it is to reflect an aspect of natural foraging. Wild birds foraging in the vertical plane (such as when collecting nectar from the flowers of a bush, gleaning the foliage for insects or creeping along the bark of a tree) may also tend to move downwards as this may be less energetically expensive than moving against gravity (also true in our experiments). The layout of our cages, however, meant that the perching furniture (in the top-back quarter of each cage) was much closer to the top of the arrays than to the middle or bottom of it, which no doubt influenced the birds to begin most of their searches of the arrays near the top. While foraging hymenopterans (bees and wasps) tend to move systematically in the vertical plane while emptying an inflorescence, their movement tends to be in the upwards direction, exploiting the lower flowers on an inflorescence first, as they are more likely to contain nectar (Pyke, 1979; although see also Corbet et al., 1981, where directionality of movement was linked to the insects' nectar retrieval posture and not to the gradient of nectar yield).

Recently, Flores-Abreu, and colleagues (2013; 2014) have examined differences in hummingbirds' (*Selasphorus rufus*) use of the horizontal and vertical dimensions to relocate goals. These studies illustrated that hummingbirds may make differential use of the vertical and horizontal components of a point location in space, defined in three-dimensions. Although, exactly how (and, therefore, why) their use of these components differs is not immediately clear. Flores-Abreu et al. (2014) reported that hummingbirds tended to be more accurate in the vertical dimension (compared to the horizontal dimensions) when relocating a single goal in three-dimensional space. This is consistent with previous observations that hummingbirds returning to the location of a (now removed) flower, arrive at a location that is closer to the original location of the flower vertically, than it is horizontally (Hurley, Franz and Healy, 2010). Flores-Abreu, Hurley and Healy (2013), however, reported greater accuracy to locate a goal flower along the horizontal axis, rather than the vertical one, and a preference to match the horizontal location of a flower in space when the limited options required them to choose between matching the horizontal component or matching the vertical component. Although there are small differences in methodology between these studies, potential reasons for the conflicting findings are not immediately apparent. Although contradictory, these findings nevertheless suggest that there may be differences in how nectarivorous birds relocate goals in the vertical, versus the horizontal, plane. Wolf, Roper and Chittka (2015) have also recently demonstrated that bumblebees (*Bombus terrestris*) readily used colour and pattern cues to differentiate feeders presented in the horizontal plane, but subsequently failed to use such cues as effectively to differentiate feeders presented in the vertical plane – further evidence that horizontal and vertical dimensions are not treated equally by nectarivores. For these reasons, it may be prudent not to too casually dismiss the systematic downward movement of birds searching for sucrose (Sulikowski and Burke, 2011b), exhibited in the absence of a systematic lateral movement bias, as an experimental artifact.

Further evidence that birds searching for mealworms in our arrays were relying on a movement-based strategy, and that birds searching for sucrose were relying on a strategy that involved remembering and avoiding the specific locations that had been visited, comes from a study inspired by Dubreuil et al. (2003). Dubreuil and colleagues systematically investigated the effects of central-chamber confinement on the behaviour of Sprague-Dawley rats in a radial arm maze. By confining rats to the central chamber of the maze for several seconds in between visits to each arm during, the authors were able to interrupt and eliminate movement-based search strategies (such as clockwise serial search). When central-chamber confinement was used to subsequently test the rats' memory for previously visited arms, those that had not experienced confinement during training (and were presumably relying on movement-based, rather than memory-based, strategies to solve the maze) performed poorly, as the forced confinement disrupted their movement.

Based on these findings, Sulikowski and Burke (2011b) developed an analogous paradigm to determine the effect of disruptions to the birds' movements while searching through arrays. We predicted that, to the extent that search for mealworms was movement-based and search for sucrose was nectar-based, interruptions during search, which forced the birds to physically leave the array, would have a greater detrimental effect on their ability to avoid revisit errors when searching for mealworms, compared to when searching for nectar. This is precisely the pattern of errors we observed. There was no measurable difference in performance for birds searching for sucrose when they were permitted to search for eight uninterrupted visits to an array of eight feeders, compared to when their search was interrupted after every second visit (Sulikowski and Burke, 2011b – Experiment 2). For birds searching for mealworms, however, the same interruption regime reduced their search performance to chance levels – that is with as many revisit errors as predicted by a random walk. The fact that performance was not just impaired but reduced to chance levels – below that which is typically seen, even in the earliest trials when searching for mealworms in these types of tasks (Sulikowski and Burke, 2010a; 2010b and 2011b – Experiment 1) – further supports the notion suggested above that initial above-chance performance when searching for mealworms in these tasks is the result of systematically biased movement, and not recollection and avoidance of previously visited locations.

The use of a movement-based strategy for birds foraging on invertebrates is not a novel proposition. Area-restricted search (Tinbergen, Impekoven and Franck, 1967), observed in captive (Zach and Falls, 1976) and wild foraging ovenbirds (*Seiurus* aurocapillus, Zach and Falls, 1979) and wild blackbirds (*Turdus* merula, Smith, 1974), describes a scenario where a moving forager is more likely to remain within the immediate vicinity after it captures a prey item, than at other times along its search route (achieved through fewer subsequent steps, and/or successive turns). Wild foraging ovenbirds have also been observed to move in a consistent direction through a patch (Zach and Falls, 1979), mirroring the movement biases of noisy miners searching for mealworms in our arrays. The movement strategies that insectivorous birds may adopt while foraging are many and varied (Holmes and Recher, 1986; Robinson and Holmes, 1984) owing to the varied nature of "invertebrates" as a group, and also to habitat structures (such as the shape and density of foliage) that influence bird movement (Holmes and Recher, 1986). While there are, therefore, precedents for movement-based foraging strategies in insectivorous birds, studies of the movement patterns of wild foraging noisy miners would be needed to see whether their natural foraging paths, when searching two-dimensions, lead to a consistent drift in a particular direction.

The use of a memory-based strategy, that affords remembering and avoiding the specific locations of already visited flowers, has been thought to support the foraging of both avian (Cole et al., 1982; Healy and Hurly, 1995) and hymenopteran (Brown and Demas, 1994) nectarivores for quite some time. The above studies provide evidence that noisy miners searching for sucrose not only perform above chance on a laboratory spatial task, but confirm that they are not relying on movement-based strategies to achieve this performance (as can be the case in some laboratory spatial studies, Dubreuil et al., 2003). The absence of a lateral movement bias while searching for sucrose is consistent with wild foraging bumblebee behaviour (Zimmerman, 1982). In spite of the aforementioned tendencies of bees to move upwards along an inflorescence following a decreasing gradient of nectar yield (Pyke, 1979), bumblebees (*Bombus bifarius* and *B. flavifrons*) foraging on dense patches of flowers for pollen exhibit directionally random movement, avoiding revisits by visually recognizing avoiding flowers depleted of pollen. Hainsworth, Mercier and Wolf (1983) have examined the search behaviour of captive hummingbirds (*Eugenes fulgens* and *Lampronis clemenciae*). Consistent with noisy miners, they reported no obvious systematic movement strategies being used by the hummingbirds to avoid revisits when searching an array. These authors did, however, use a mixture of two-dimensional arrays (as did we) and three-dimensional arrays. They found that, in terms of minimizing revisit errors, hummingbirds performed better in the three-dimensional arrays. The greater differentiation of spatial locations afforded by a three-dimensional, compared to a two-dimensional array, may have facilitated memory for the individual locations. This suggests that future experiments wishing to capture, as closely as possible, the relevant informational properties of real world, should consider using three-dimensional arrays that mimic the arrangement of flowers on a bush.

The visually conspicuous nature of flowers affords nectar foragers another opportunity for information use that birds foraging for invertebrate prey do not have – planning their search route in advance. To forage efficiently within a patch of flowers, a bird must not only avoid revisits to flowers already probed, but should visit flowers in an order that minimizes the search path length. Path-length minimization can be facilitated by planning a route in advance, as opposed to making independent decisions about which flower to visit next based on a simple nearest-neighbour (or similar) rule. A forager seeking invertebrate prey, especially mobile, cryptic prey, however, cannot know the locations of prey in advance of consuming it. Unlike the flowers on a plant, there is nothing to define a finite number of specific locations as the places within the patch to search. So a route that minimizes travel distance to retrieve the available food items cannot be planned.

To investigate whether foreknowledge of the specific distribution of food rewards facilitated searching for nectar rewards (while not affecting searching for mealworms), Sulikowski and Burke (2015a) presented birds with arrays of feeders containing either sucrose or mealworms, with both food types contained within the one array. Half of the birds were given arrays in which the colour of the feeders (black or white) reliably indicated the food reward located within. The remaining birds searched identically shaped arrays, but the feeders were all the same colour (grey) and so the birds could not predict the contents of a feeder prior to probing it. Birds in the colour-coded condition, therefore, were able to plan a specific foraging route to retrieve their nectar rewards (if they chose to do so). Birds in the noncolour-coded condition could not plan a nectar-specific search path. We predicted, therefore, that birds in the colour-coded condition, who had all the information available to forage independently on each reward, would make fewer revisit errors to feeders containing sucrose, compared to feeders containing mealworms. This is consistent with all our previous observations of more revisit errors committed when birds are searching for mealworms, compared to birds searching for sucrose (Sulikowski and Burke, 2010a; 2010b; 2011b). Critically, however, all previous observations of the effect of food type have been observed between-subjects. This study (Sulikowski and Burke, 2015a) was our first opportunity to observe this effect within-subjects.

We further predicted that birds in the noncolour-coded condition would make more revisit errors to sucrose feeders than to mealworm feeders, due to the removal of a key informational property necessary for efficient nectar retrieval – *a priori* knowledge of the locations of nectar rewards. This was also a critical prediction in the context of our broader program of research. In all previous studies, our predictions about differential performance as a function of food type, had always favoured birds searching for sucrose to perform better – primarily due to the closer match between the computational requirements of our tasks and the informational properties of the world facilitate nectar foraging, compared to those that facilitate foraging for invertebrate prey. The consistent direction of these predictions (and results)- potentially opened our findings up to an alternative explanation – differential motivation. Although we had previously demonstrated that appetitive behaviours neither differed between the birds searching for sucrose and mealworms, respectively (Sulikowski and Burke, 2010a; 2011b) nor did they correlate with performance measures (Sulikowski and Burke, 2011b), the best way to refute explanations appealing to differential motivation is to reverse the performance advantage as a function of the computational requirements of a task.

Both of our predictions were upheld (Sulikowski and Burke, 2015a), providing evidence that that noisy miners may indeed plan their search route in advance when approaching a patch containing a clearly visible number of finite flowers to visit. This suggests a further refinement of the notion that noisy miners remember (and avoid) each of the specific locations they have previously visited while foraging within a patch, allowing them to continue to avoid such feeders, even if their foraging is interrupted. The same outcome could be achieved if the bird simply knows the route it planned to take and the single location it was up to when it was disturbed. The possibility that search paths for nectar may be planned in advance is consistent with the observations of Henderson and colleagues (2001) that rufous hummingbirds are aware of the locations of flowers that they have previously seen but had not visited, and differentiated between these flowers and newly presented flowers when re-visiting an experimental array in the field. It is also consistent with recent observations that hummingbirds tend to reuse the same routes when revisiting experimental patches (Tello-Ramos, Hurley and Healy, 2015), even as these patches are incrementally increased in size.

The habitual routes (traplines) used by bumblebees are frequently the shortest distances possible and so constitute solutions to the Travelling Salesman Problem (TSP, Reynolds, Lihoreau and Chittka, 2013). This is an important observation because the hypothesized benefit of route-planning is that it has the potential to provide shorter routes than would a series of independent decisions made after visiting each flower (Ouaarab, Ahiod and Yang, 2014). It remains to be seen how closely noisy miners (or any other avian nectarivore) is able to approximate solutions to the three-dimensional TSP, but their use of planning in this context suggests that they may be quite successful at this task. Given the animal behaviour-inspired algorithms that have already been developed to approximate solutions to this computationally challenging problem (including the cuckoo search algorithm, Ouaarab et al., 2014; and the ant colonies optimization algorithm, Dorigo and Gambardella, 1997) – quantitative investigations of noisy miner behaviour with regards to the TSP are likely to be fruitful.

In summary, our research suggests that noisy miners engage differential cognitive systems when foraging on nectar and invertebrates, respectively. As a direct consequence of differences in the natural distributions of nectar and invertebrate prey, the hypothesized cognitive systems differ in the information to which they are sensitive, how this information is subsequently utilized to guide behaviour, the overt behaviour produced and, as a result of these behavioural differences, the information to which the forager is subsequently exposed. We summarise how each of these systems uses information during a single foraging bout within a patch as follows. Birds foraging on nectar, approach a patch and begin by assessing the number and arrangement of flowers that it must visit and plans a search route. It is able to keep track of where along this search route it is up to as it forages, such that interruptions do not affect its ability to avoid revisiting the same flowers. Birds foraging for invertebrates become sensitive to the point locations of prey items only after they are detected and consumed. Locations at which the birds search but do not locate a prey item are not differentiated from the rest of the patch. The point locations at which prey items are located may be used to identify patch quality and patch boundaries of continuously distributed prey (although we have yet to directly test this notion) but do not seem to readily inform subsequent decisions about where to search within a patch. Birds avoid searching the same areas repeatedly by employing a drifting search that moves them systematically through a patch.

The extent to which these different patterns of information use are considered to represent genuinely specialized cognitive mechanisms, may depend on the notion of cognition that one adopts. If cognition is broadly defined as the collection of mechanisms that mediate the relationship between environmental information and animal behaviour, and these mechanisms are described by the specific rules of the relationships between the information and the resulting behaviour (see discussion of ‘functional cognition’ below), then, almost by definition, the cognition of noisy miner foraging meets the definition of divergent adaptive systems. Other conceptualizations of adaptive specializations of cognition, however, emphasise the importance of identifying experience-independent adaptive patterns. This is to help rule out the possibility that the adaptive patterns of information use have not simply been learned over the animal’s lifetime via general process (non-adapted) learning mechanisms (Macphail and Bolhuis, 2001; Papini, 2002). Although the implausibility of the nature-nurture dichotomy has been articulated repeatedly (for example, Lickliter and Berry, 1990; Stotz, 2008; Lewkowicz, 2011), the contrasting of evolved (“innate” or “hard-wired”) origins of behaviours and abilities with learned or experiential (“acquired”) origins still occurs in both human (Davey, 1995; Schaal, 2012) and comparative (Healy et al., 2009 pg. 289; Roussel, Padie and Giurfa, 2012) psychology.

Many proposed adaptations of cognitive mechanisms to species ecology have focused on aspects of ecology that are unusually specialized (such as cache recovery, Pravosudov and Roth, 2013, and brood-parasitism, Guigueno, et al., 2014). With respect to the noisy miner, however, we are proposing adaptations of cognitive mechanisms as a result of more mundane selection pressures – those resulting from the need to forage efficiently on multiple resources with differing distributions. The case of generalist foraging resulting in a multiplicity of foraging strategies may be common across the Animal Kingdom. Individual honeybees (*Apis mellifera*) and bumblebees (B*ombus spp.*) within a colony will tend to specialize on either nectar or pollen collection (Brian, 1952; Hunt et al., 1995). Honeybees also exhibit spontaneous flower constancy (a tendency to forage on the same species of flower, even if other types of profitable flowers are available (Hill, Wells and Wells, 1997)). Desert ants (*Cataglyphis spp.*, Wehner, 1987; and *Melophorus bagoti*, Muser et al., 2005) exhibit sector fidelity, where individual foragers continually forage within a small sector of the available landscape. Individual ants (*M. bagoti*) may also specialize on insect prey compared to plant-sourced foods (Muser et al., 2005). There is also evidence for potential divergence of search strategies in *M. bagoti* when collecting protein compared to carbohydrate food sources. Schultheiss and Cheng (2013) provided ants with feeders containing either mealworms (protein) or cookie crumbs (carbohydrates). Ants visited these feeders repeatedly, learning their distance and location from the nest. The feeders were removed and the ants’ search paths in the vicinity of the feeders’ original locations examined. The search paths surrounding the protein feeder were more dispersed than those surrounding the carbohydrate feeder, mirroring differences in the natural distributions of protein (primarily dead insect bodies which are sparsely distributed) and carbohydrates (plant sourced foods that are typically clumped) on which these ants typically forage (Schulteiss and Cheng, 2013).

Due to their eusocial nature, foraging specialisations at the individual level within the Hymenopterans, still permit the entire colony to exploit all types of available resources from all areas of the surrounding territory. In non-eusocial generalist foragers, however, divergence and specialization of foraging strategy, if it is to occur, needs to do so within the one individual. In order for such divergent mechanisms to evolve, the net benefits (in terms of increased foraging efficiency resulting ultimately in increased fitness benefits) of having specially adapted cognitive systems (relative to the foraging efficiency that a single all-purpose mechanism could achieve) must exceed the (physiological) costs of developing and maintaining two systems. Attempts to quantify these costs and benefits with respect to the proposed cognitive systems identified in the noisy miner are yet to be carried out.

COMPARATIVE COGNITION – A COMPLEX ENTERPRISE

Much work in comparative cognition is chiefly concerned with demonstrating whether or not an animal possesses a particular cognitive ability, often focusing on abilities thought to be unique or specially advanced in people (Shettleworth, 2012). Often times, the focus is on whether one group of animals outperforms, or can match another, on some cognitive ability. This is true for research examining potential adaptations to foraging ecology (Barkley and Jacobs, 2007; Shettleworth and Hampton, 1998), sociality (Seyfarth and Cheney, 2013; Whiten, 2013), or tool use (Emery and Clayton, 2009), as well as investigations of animal cognition that are not so closely tied to species ecology, such as those into numerosity (Scarf et al., 2011) concept formation (Zentall et al. 2008), or planning (Emery and Clayton, 2004; Osvath and Osvath, 2008).

This approach characterizes much research in comparative cognition. Many studies offer, as their rationale, a desire to investigate whether the animal exhibits a specific cognitive ability: Do rhesus monkeys recognize themselves in the mirror (Rajala et al., 2010)? Do finches understand physical causation (Teschke and Tebbich, 2011)? This approach also describes some of the work on hummingbird cognition. Do hummingbirds use visual beacons (Hurly et al., 2010)? Can they learn abstract spatial relationships (Henderson et al., 2006)? Are they sensitive to geometric cues (Hurly et al., 2014)? Although sometimes interpreted in ecological terms, the existence, or otherwise, of such abilities are not strictly predicted by identifying the specific functional advantage they would offer the bird, beyond such general observations that the clustered distribution of wild flowers in a cluttered environment could make learning abstract spatial relationships between goals and landmarks useful.

A more ecologically driven approach characterizes most research investigating potential adaptations of cognition to foraging behaviour. Based strongly on Kamil’s (1994) synthetic approach and the modular approach described by Shettleworth (2002), most studies of animal cognition identify (often unusual) aspects of a species’ ecology, and derive hypotheses about how their cognition may be specially adapted to meet the demands of these challenges. The most famous body of work in this vein would surely be investigations into species differences in laboratory spatial cognition tasks as a function of reliance on scatter-hoarded food (Balda et al., 1996; Shettleworth, 1990; Pravosudov and Roth, 2013). Generally speaking, birds that rely more on scatter-hoarded food (which they must retrieve from many hundreds or even thousands of locations) are expected to exhibit better performance in laboratory tasks of spatial memory than closely related species that do not cache (Clayton and Krebs, 1994), or who rely less on cached food (Balda et al., 1996). Another notable example of this approach includes the identification of win-shift biases in nectar foraging birds (Cole et al., 1982; Healy and Hurly, 1995; Sulikowski and Burke, 2007) and bees (Brown and Demas, 1994; Demas and Brown, 1995) – a potential adaptation to the readily depleting nature of nectar. Authors have also observed better performance by female brown-headed cowbirds (compared to male brown-headed cowbirds) on a spatial memory task (Guigueno, et al., 2014) – explained as the result of sex-specific selection on females, as only they are required to locate and monitor potential host nests (although see also Guigueno, MacDougall-Shackleton and Sherry, 2015).

More nuanced than simply wishing to demonstrate whether an animal possesses a particular cognitive ability, the ecological approach, presumes that animal cognition is structured as a series of more or less discrete and independent cognitive abilities (sometimes referred to as modules, Shettelworth, 2002). Irrespective of whether research questions are motivated by implicit (or explicit) comparisons with humans, or by species-centric ecological considerations, the prevailing view sees animal cognition as comprising a series of basic mechanisms (such as associative and discrimination learning, categorization, memory) and/or a collection of more function-specific mechanisms (such as spatial cognition, timing, problem solving, planning, etc.) which may or may not be adaptively shaped across species (Shettleworth, 2012).

Conceptualising cognition as a collection of discrete abilities is, almost by necessity, a judgmental process. Species A will be seen as more intelligent, or at least as having better-developed cognition than Species B in the relevant domain, if Species A exhibits evidence of a cognitive ability and Species B does not (for example Emery and Clayton, 2004, p. 1903). This is similarly true if Species A outperforms Species B on a specific cognitive task (for example Balda et al., 1996 p. 40; Pravosudov and Roth, 2013, pp 178-179). Different cognitive abilities are frequently ranked relative to each other based on the supposed complexity, sophistication and/or flexibility of the mechanisms underlying them (for example Healy and Hurly, 2003, pg. 347; Call and Tomasello, 2008). For example, episodic-like memory (Clayton and Dickinson, 1998), so labeled when an animal shows evidence of simultaneously recalling multiple aspects of an event (typically what, where and when,) is considered to be the non-human version of episodic memory (the subjective experience of consciously recalling a specific event). Episodic-like memory is considered to be a highly advanced cognitive ability among non-human animals (Clayton et al., 2001). Along with other supposedly advanced traits, such as planning and theory of mind, evidence for episodic-like memory is highly sought after and much celebrated when found. Criticisms of such studies typically focus on the extent to which the findings may be explicable via less impressive, simpler cognitive abilities (for examples see Penn and Povinelli, 2007; van der Vaart, Verbrugge and Hemelrijk, 2012). This is because these simpler, lower abilities (such as associative learning mechanisms) are presumed to be widespread throughout the animal kingdom, whilst the advanced abilities are presumed to exist only in a very restricted number of animals – the modern day adherence to Morgan’s Canon (Morgan, 1894, pg. 53; see also Burke, 2014 for an alternative perspective on the apparent conservation of associative mechanisms across species).

Such ranking of cognitive traits, wherein the human versions of such complex abilities are implicitly placed at the top, can lead to an anthropocentric view of comparative cognition (discussed by Shettleworth, 2012). Demonstrations of complex cognitions, previously supposed to be unique to humans are heralded with much more fanfare than similarly robust demonstrations of subjectively less impressive patterns of information use. Consequently, research efforts may become more focused on demonstrations of these advanced cognitive feats and less focused on asking species-centric questions about what, and how, information is used to support certain behaviours.

Recently, Sulikowski and Burke (2015b) have outlined the ‘functional’ approach to comparative cognition. This approach shares features with the ‘bottom-up’ approach recently outlined by de Waal and Ferrari (2010), the ‘ecology and natural history’ approach advocated by Smulders, Gould and Leaver (2010), the ‘phylogenetic comparative psychology’ approach (MacLean et al., 2012), and ‘Evo-mecho’ (McNamara and Houston, 2009). It focuses less on asking whether an animal possesses some particular cognitive ability, but instead asks how the animal exploits the informational properties of the environment to achieve adaptive behaviour. One key difference between the functional approach and approaches within comparative cognition is that the functional approach seeks to identify the rules that describe how animals use the information in the environment to guide their behaviour. The predominant synthetic (Kamil, 1994) and modular (Shettleworth, 2002) approaches seek to describe and evaluate the animal's cognitive abilities. I will use the example of reversal learning (Bitterman, 1972) to illustrate what this difference means in practical terms.

Reversal learning requires animals to learn that one stimulus (S+) is associated with reward and another is associated with no reward (or a punishment, S-). After this contingency has been learnt it is reversed and the time taken for the animal to extinguish its responding to the previous S+ and acquire a response to the previous S- is taken as the measure of reversal learning (Bitterman, 1972; Ben-Shahar et al., 2000). Serial reversal learning repeats the acquisition – extinction – acquisition cycle several times (Mackintosh et al., 1968). Progressively faster acquisition and extinction over successive reversals is typically seen as indicative of intelligent cognitive/behavioural flexibility (Bond, Kamil and Balda, 2007). A functional approach to this task, however, does not necessarily presume that faster extinction and acquisition necessarily indicates better, more flexible cognition. Rather, it would view the probability of responses to the two stimuli at any point in time as a function of two factors. Firstly, the extent to which an animal tends to integrate conflicting information from multiple time points to guide behaviour would predict the speed of extinction and re-acquisition. Animals attempting to integrate information about the contingencies across reversals would tend to extinguish more slowly, while animals relying purely on the most recent information would extinguish and reverse very quickly. Secondly, with respect to serial reversal learning, the extent to which animals perceive the successive changes as a reliable pattern, in addition to the immediate pattern of contingencies, should determine the rate of increase in speed of extinction and acquisition over successive reversals. The way these two factors influence the behaviour of any given animal in these tasks would be viewed as a complex interaction between the cognitive mechanisms of the animal, the informational properties they are shaped to respond to and the motivational context in which the task is conducted.

The functional approach to comparative cognition was chiefly inspired by attempts to avoid the paradigmatic assumption – which is the assumption that there is a sufficiently close correspondence between cognitive mechanisms and the experimental paradigms we use to study them, to justify conflating the two (Sulikowski and Burke, 2015b). The potential problems with conflating spatial memory tests, for example, with spatial memory mechanisms are discussed in detail by Sulikowski and Burke (2015b), but the two main issues are outlined briefly below.

Firstly, the diversification of cognitive mechanisms across the Animal Kingdom are unlikely to map onto the diversification of experimental paradigms that comparative psychologists use. This is at least partly because the former have radiated and adapted in response to functional needs, while the latter were primarily developed to investigate mechanisms that were either assumed to be conserved across vertebrates (Papini, 2002); or in other cases to search for human-like traits in non-human animals (de Waal and Ferrari, 2010). As a result the majority of experimental paradigms employed to study animal cognition are simply not designed to capture the specific informational properties of the world that particular species likely exploit to achieve adaptive behavioural goals (although see also arguments offered by Timberlake 2002; and Timberlake and Hoffman, 2002, pp 342-3, for reasons to expect some level of paradigm/mechanism correspondence).

Secondly, even to the extent that there is some meaningful correspondence between the computational requirements of a laboratory task, and the informational properties of the world that the cognitive mechanisms of interest have evolved to exploit (discussed by Timberlake, 2002), there is no guarantee that these are the mechanisms the animal will engage to solve the task. If this were the case we would not see animals exhibiting different performance on the same task (presenting the same computational requirements) presented in different contexts. Yet this is frequently observed with noisy miners' performance changing as a function of food type (Sulikowski and Burke, 2007, 2015a). This may be because in the real world, unlike the laboratory, cognitive challenges are poorly defined (Schraw, Dunkle and Bendixen, 1995) and the information an animal could potentially use (that which is available to its sensory apparatus), far exceeds that which it can actually use (Dukas, 2002). Thus, the computations required to maximise foraging efficiency are not directly perceptible. The behavioural goals of the animal, dictated by its current motivational state are much more likely to determine the cognitive mechanisms engaged to solve a task, than the computational requirements of the task itself (Sulikowski and Burke, 2015b).

These two issues could potentially compromise different types of studies in different ways. The first issue presents a challenge to comparative studies employing traditional laboratory paradigms, as opposed to those studies that develop paradigms *de novo*, which are explicitly designed to capture specific informational properties of the animal's environment. The second is more of a concern for laboratory studies than it for field studies. I will discuss each of these in turn.

Studies that employ previous laboratory paradigms that were not designed with the specific cognition of the current species in mind may be compromised by a poor correspondence between the computational requirements of the paradigm in question and the cognitive mechanisms of the study species. When considering such potential mis-matches the devil is in the detail, and so I will provide just a single example. Recently, Hornsby et al., (2014) applied the well-worn geometric cues laboratory paradigm to free-living rufous hummingbirds. This paradigm requires the animal subject to locate a food reward in one of the corners of a rectangular enclosure/array (Cheng, 1986). Animals frequently commit search errors by visiting the diagonally opposite corner and this is considered to reflect use of geometric cues (where a corner is defined by the relative positions of the adjacent long and short walls (Cheng et al., 2013; also see Cheng, 2008). Hornsby and colleagues (2014) trained hummingbirds to find a sucrose reward in one corner of a rectangular array of four feeders, that we linked by dowel to create a geometric rectangle. This corner was differentiated from its diagonal opposite by a featural cue (one adjacent piece of dowel was painted blue). When tested with the featural cue shifted or removed, hummingbirds nevertheless returned to the rewarded flower – demonstrating that they were not using the featural cue to locate the sucrose. But they also failed to make a disproportionate number of errors to the diagonally opposite corner that use of the available geometric cues would have predicted (Hornsby et al., 2014). This is in spite of previously being trained to retrieve rewards from two diagonally opposite corners of an array without the featural cue (without any dowel).

Aside from the general contention that hummingbirds rely heavily on visually mediated spatial memory when foraging (Hornsby et al., 2014, p. 138), no specific cognitive mechanism (a rule or description about how hummingbirds use a specific type of information while foraging) is hypothesized that would predict that hummingbirds should use such geometric cues. Throughout the training phase of this study, the array was repositioned and turned after every visit to ensure that hummingbirds could use only geometric or feature cues to locate the sucrose rewards (and not extra-array landmarks or features in the environment). Hummingbirds may well use the position of flowers relative to each other to help relocate especially rewarding flowers (Henderson et al., 2006), since wild flowers, even on the same plant can differ in the amount of nectar they produce (Pacini and Neppi, 2007). However, by repeatedly repositioning the array, the authors may have been simulating the appearance of different patches of flowers within the birds' territory. The spatial arrangements between flowers and how these may indicate an especially rewarding flower (for example, the flower to the top left of a set of four), may be stable within a patch, but would not be expected to generalize between patches in the wild. So while the repeated repositioning of the array during training is an experimentally robust technique to isolate the geometric cues and try to ensure that only these cues are used, in the context of this study, the procedure simply created a cue that doesn't map well onto the informational properties of the hummingbird world (there probably are no reliable patterns to be detected across spatially disparate patches in how the relative arrangements of flowers indicate reliable differences in flower quality). Given this, it is perhaps, not so surprising that the hummingbirds appeared to use neither featural nor the geometric cues during this task, but instead appeared to rely on subtle (unintended) differences between the different feeders presented at each corner of the array (which were not rotated during training; Hornsby et al., 2014).

Confirming that the mechanisms that one wishes to study are also the mechanisms that are determining behaviour during laboratory tasks is not necessarily straightforward. When animals are tested in laboratories their current motivational state determines their behavioural goals, and therefore, the mechanisms driving that behaviour. This likely makes it very difficult to study the mechanisms that underpin behaviour not easily elicited in the laboratory. This could, for example, explain discrepancies reported in the direction of sex differences observed in brown-headed cowbirds (*Molothrus ater*) completing laboratory spatial tasks (Guigueno et al., 2014; Guigueno, MacDougall-Shackleton and Sherry, 2015). While the studies in question were motivated to examine a potential female advantage in spatial cognition (since only females face the challenge of locating and monitoring multiple host nests), the two studies report opposing sex differences (the former, a female advantage and the latter a male advantage). In both studies, birds were motivated by food rewards and were not engaging in behaviour associated with nest-monitoring or reproduction, so it is not necessarily clear that sex differences in either task should be assumed to relate to whatever cognitive mechanisms underpin host nest choice in these birds.

While providing an animal with food rewards inevitably creates some sort of a foraging context, it does not follow automatically that this context is sufficient to elicit all appropriate foraging behaviours and decisions. In our laboratory studies of noisy miners for example, we have successfully identified several differences in information use purely as a function of the type of food reward with which birds are provided (sucrose or mealworms). In the wild, however, proximal ingestion of food is unlikely to be the cue that triggers the relevant cognitive strategies, since these must presumably be involved in the decision to begin foraging, before any food is located or consumed. It is likely then that the motivational and physiological state of the animal plays an important role in its decision-making and information use. By housing birds in captivity on a standard commercial diet, we are ensuring that birds in our studies are deprived of neither protein nor energy. The consequences this could have for how information is used during foraging are not clear. It could well be that food-type associated differences would be even larger, or qualitatively different, if birds in our studies were appropriately physiologically motivated to seek their specific food reward.

A further consequence of captive studies is that we are greatly limiting the range of behaviours that birds could exhibit. In one sense this a feature of captivity, in that it permits control over what the animal can possibly do. However, wild foraging birds must make decisions about whether or not to forage, where (on a large scale) they should forage, when to leave a patch and forage elsewhere and when to cease foraging. Our investigations of within-patch foraging cognition have deprived birds of the opportunity to make these decisions. If within-patch foraging decisions are independent of other decisions, such as when to leave a patch, then this may not be a serious issue. However, to the extent that such decisions interact, we may be getting a somewhat limited or compromised perspective on how wild foraging miners make search decisions within patches.

One of the key strengths of the research on free flying wild hummingbirds (Healy and Hurly, 2003) is that is immune to these criticisms. The wild hummingbirds are engaging in exactly the behaviour whose underpinning cognitive mechanisms the authors wish to study and they are doing so against a background of real life interruptions and complexities. As well as foraging in the tasks provided by researchers, they are simultaneously monitoring other food sources within their territory, their own physiological state, potential intruders to their territory and any other aspect of life that affects a wild hummingbird. So while field experiments may not exhibit quite the control of laboratory tasks, their potential importance to understanding the cognition that underpins natural behaviour cannot be overstated.

FINAL THOUGHTS

A full realization of the functional approach to cognition, as applied to foraging, would entail:

1. examination of the informational properties of the world that might assist foraging efficiency/effectiveness;
2. the design of experimental tasks whose computational requirements capture the relevant informational properties;
3. the development of formal quantitative models that predict how cognition might be optimized to achieve the dual goals exposing the animal to useful information in the environment and then using this information in adaptive ways to guide foraging efficiency; and
4. a combination of field and laboratory empirical studies to test the models' predictions.

With respect to nectarivorous species, aspects of this approach are already being realized. Some studies of both hummingbirds (Tello-Ramos et al., 2015) and noisy miners (Sulikowski and Burke, 2011b, 2015) have adopted novel paradigms, designed explicitly to capture informational properties of the real world, although formal models quantifying the verbally described cognitive mechanisms are still lacking. Such quantitative models describing cognitive strategies have been used effectively, however, to predict various aspects of search behaviour in bees (for example, Reynolds et al., 2013). Field and laboratory experiments examining the cognition of nectar foraging in both birds and bees are also amassing at an impressive rate. The true potential of the functional approach to comparative cognition to illuminate adaptations of cognition to resource distribution will be realized when all of these aspects are combined and coordinated within the one program of study.

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