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In Focus

Featured Articles in This Month's *Animal Behaviour*

The Food Search Strategies of Noisy Miners

Effective search strategies require the integration of different types of information. For example, it would be advantageous to an animal searching for food to have information not only about the location of the resource but also about the timing of its appearance. Episodic-like memory, which possibly links remembering the past with planning for the future, is the cognitive system thought to be sensitive to such information and other contextual details. Scientists hypothesize that the adaptive significance of episodic-like memory is to facilitate planning and therefore if an animal is capable of remembering events it should also be capable of planning and vice versa.

In the present issue (pp. 149–155) Danielle Sulikowski (Charles Sturt University, Australia) and Darren Burke (University of Newcastle, Australia) test whether noisy miners plan their foraging route. These Australian honeyeater birds feed on both nectar and invertebrates. Nectarivorous animals feeding on the same plant have to solve a variant of the classic travelling salesman problem (TSP), namely to use the shortest route that will take them to each flower only once. Indeed, earlier studies have demonstrated that bumblebees can integrate new information about flowers into their habitual foraging routes optimally in a way that approximates a TSP solution. This suggests that not only memory but also some form of planning must be involved and evidence of route planning has been shown in foraging capuchin monkeys. By contrast, when foraging for cryptic invertebrates, animals cannot use a TSP solution because they cannot see the location of their food before they have eaten it. Therefore, their foraging paths in this situation cannot be planned in advance but develop on the go depending on food availability. Sulikowski and Burke aimed to test whether noisy miners with advance information about the location of food are better at foraging when the resource is nectar but not when it is invertebrate prey.

The authors presented 12 wild-caught noisy miners (which successfully reintegrated into their groups after the experiments) with arrays of feeders containing both nectar and invertebrate food (Fig. 1). In one condition, feeders with white lids contained one food type and feeders with black lids contained the other, in a balanced design. In the second condition, the lids of all feeders were grey independently of whether they contained nectar or invertebrate food, which were allocated at random to the feeders for each trial. Therefore, in the former condition, birds could potentially plan their journey for a given food type while in the latter there was no such option. Half of the birds were exposed to the black/white condition and the other half to the grey condition. Each bird underwent 12 trials and was free to consume the food it had discovered. The birds in the two conditions were exposed to the same positions of the rewards within 12 locations of a 4×4 grid. The trials were video-recorded and the behaviour of each individual was scored from this record.

Sulikowski and Burke found that noisy miners made more transitions between locations with the same food in the black/white condition than in the grey condition. This demonstrates that these birds could use colour cues to guide their search for both nectar and invertebrate prey. As predicted by the authors, noisy miners in the black/white condition made more revisit errors for invertebrate than for nectar food while in the grey condition they made more revisit errors for the nectar food. These results suggest that noisy miners plan their search path when foraging for nectar and

Figure 1. A noisy miner; inset shows a bird from the study opening one of the experimental feeders. Photo: Danielle Sulikowski.

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depriving them of the opportunity to do this interferes with their ability to retrieve nectar, but not invertebrate food, efficiently. Therefore, the present study adds to earlier evidence that in noisy miners the cognitive mechanisms underpinning foraging for nectar are different from those underpinning foraging for invertebrates and to the notion that these different mechanisms could operate independently and concurrently within a single search bout. However, it is also possible that each individual has to choose which cognitive mechanism to engage and then searches for the other food only opportunistically. Future experiments are needed to address this.

Another avenue opened up by the present and earlier studies in this area is to establish the effectiveness of the noisy miners' solution to the TSP when foraging for nectar compared to that of invertebrates such as ants and bees. This would not only inform new heuristics for the computational solution of this hard optimization problem but also increase our understanding of the differences and commonalities between taxa in the underlying cognitive processes. The existence of planning abilities in nonhuman animals is controversial. There is a chasm between examples of planning in apes, monkeys and scrub-jays, on the one hand, and insects, on the other. The former examples focus on differences between current and future motivational states, while the latter do not involve motivational states in the first place. Sulikowski and Burke suggest that if episodic-like memory and planning evolved on the basis of preexisting neural architecture responsible for the spatial cognitive aspects of navigation (as independent neural evidence suggests is true), then the route planning demonstrated in their present study might be an evolutionarily older form of planning that does not entail a dissociation from the current motivational state.

Ana Sendova-Franks
Executive Editor

Handsome Is as Handsome Does

In a species with biparental care, for a female the choice of a mate is not so simple. If she can choose a very handsome male, her sons may inherit the advantage of increased reproductive success both by attracting a top quality mate and through extrapair opportunities. On the other hand, this handsome mate may shirk his fatherly duties in pursuit of these opportunities leaving the female to pick up the slack, or not. From the male's perspective, his attractiveness is expected to have an effect on the trade-off between his parental effort towards the current offspring and his future or additional opportunities; however, it is unclear exactly how his attractiveness will affect his parental behaviour. On the one hand, attractiveness and care could be negatively correlated because of the trade-off and the increased opportunity for extrapair matings (parental–mating trade-off hypothesis) or because the male's mate will be more willing to pick up the slack if he is attractive (positive differential hypothesis); on the other hand, they could be positively correlated because his attractiveness provides an honest signal to a mate that he will be an attentive father (good parent hypothesis).

Working with blue-black grassquits, *Volatinia jacarina*, Pedro Diniz, Desirée Ramos and Regina Macedo of Universidade de Brasilia investigate how male attractiveness affects both male and female parental care (pp. 109–117). Previous studies exploring this relationship have provided mixed results. Commonly they have considered only one or a subset of multiple attractiveness signals. These grassquits have multimodal sexual traits and these signals may convey different, redundant or emergent messages especially about individual quality. Diniz et al. propose that understanding their adaptive functions and plasticity may facilitate an understanding of the covariation of attractiveness and parental effort.

Male grassquits have striking blue-black plumage and perform an energetic leap display that shows off their white underwing patches (Fig. 2). A stereotyped short song often accompanies this display. The authors measured the coverage and spectral characteristics of the male's blue-black plumage and white underwing patch. Reflectance indicates body condition and parasite load. Most plumage traits vary within individuals and may indicate condition and age whereas UV chroma varies between individuals and may be a better indicator of intrinsic genetic quality. For the leap display, which correlates with pairing success, the authors measured the display duration, number of wing beats and amount of rotation (proportion of displays in which the tail reached the highest point). They also measured the vocal output (songs/min), which correlates with territory quality, and characteristics of the buzz subunit and song consistency.

Male grassquits provide extensive parental care, helping to build the nests and provision young. Cameras recorded the rate of feeding visits to the nest by each parent. Male and female feeding rates were positively correlated with each other but only the female's rate was positively influenced by her partner's rate. Provisioning rates of socially paired males and females were influenced by different properties of the male's plumage. The UV chroma of the male's blue-black feathers negatively influenced his feeding rate and the female's feeding rate was positively influenced by the male's blue-black coverage. No other plumage trait influenced male or female provisioning rates. Neither were male or female provisioning rates influenced by any measure of vocal performance or any measure of the male leap display.

The major finding that bluer males (those with plumage shifted towards higher levels of UV and blue reflectance) provided less

Figure 2. A male blue-black grassquit performing a leap display. Photo: Pedro Diniz.

food to their offspring supports the hypothesis that there is a trade-off between a male's parental effort towards the current offspring and his future opportunities. Previous studies on grassquits have shown that UV reflectance correlates positively with age, coverage of blue-black plumage and body condition, and is highly repeatable across years, which may indeed signal genetic quality. Thus very attractive males may derive more fitness benefits from extrapair courtships than from caring for their social offspring. Furthermore, there is some evidence that females paired with males with more blue-black coverage invest more heavily in offspring but they do not compensate for reduced care by attractive mates, which does not support the positive differential hypothesis. From the female's perspective, plumage characteristics may be an honest indicator of parasite load, condition and immune response and females do invest more in offspring when mated to males with greater blue-black coverage, which supports the hypothesis that females will invest more in offspring fathered by attractive males (positive differential hypothesis).

No characteristics of either the songs or the dramatic leap displays predicted parental effort. It is challenging to explain why some male ornamental traits predict parental effort and others do not. One might think that the ability to perform energetic displays would be an honest indicator of quality but that did not seem to be the case in this study. However, these results point to the need to examine the whole suite of sexually selected male traits when making predictions about their possible effect on male parental effort.

Michelle Pellissier Scott
Executive Editor