

From the lab to the world: The paradigmatic assumption and the functional cognition of avian foraging

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Abstract Mechanisms of animal learning and memory were traditionally studied without reference to niche-specific functional considerations. More recently, ecological demands have informed such investigations, most notably with respect to foraging in birds. In parallel, behavioural ecologists, primarily concerned with functional optimization, have begun to consider the role of mechanistic factors, including cognition, to explain apparent deviations from optimal predictions. In the present paper we discuss the application of laboratory-based constructs and paradigms of cognition to the real-world challenges faced by avian foragers. We argue that such applications have been handicapped by what we term the 'paradigmatic assumption' – the assumption that a given laboratory paradigm maps well enough onto a congruent cognitive mechanism (or cognitive ability) to justify conflation of the two. We present evidence against the paradigmatic assumption and suggest that to achieve a profitable integration between function and mechanism, with respect to animal cognition, a new conceptualization of cognitive mechanisms - functional cognition – is required. This new conceptualization should define cognitive mechanisms based on the informational properties of the animal's environment and the adaptive challenges faced. Cognitive mechanisms must be examined in settings that mimic the important aspects of the natural environment, using customized tasks designed to probe defined aspects of the mechanisms' operation. We suggest that this approach will facilitate investigations of the functional and evolutionary relevance of cognitive mechanisms, as well as the patterns of divergence, convergence and specialization of cognitive mechanisms within and between species [*Current Zoology* 61 (2): – , 2015].

Keywords Functional cognition, Paradigmatic assumption, Informational properties, Avian foraging

1 Introduction

1.1 Mutual constraints versus genuine integration

Mechanisms of animal learning and memory were originally studied with little reference to species- or niche-specific considerations (Skinner, 1956). Somewhat ironically, the justifications for presuming that mechanisms of learning and memory would be identical across the animal kingdom came from an understanding of evolutionary principles (prior to the modern synthesis) that emphasized common descent at the expense of adaptive divergence (Bitterman, 1956). The animal's biology and ecology were presumed to be either irrelevant or, at best, a logistic inconvenience, to understanding the general processes of animal learning and memory. Early recognition that cognitive mechanisms potentially differed between species came from observations that ecologically congruent learning occurred (an increase in foraging behaviours when they were rewarded with food) while incongruent learning did not (no increase in grooming behaviours when they were re-

warded with food) (Shettleworth, 1973). This and similar observations were termed 'biological constraints' (Domjan, 1983). The emphasis on general rules of learning and memory persisted, while it was hesitantly acknowledged that in some circumstances species-typical biology constrained the way these otherwise general mechanisms operated (Logue, 1979).

Modern approaches to comparative cognition have largely moved beyond 'biological constraints' in favour of a more central role for ecology in the evolution of cognitive mechanisms (Dukas, 2004). The notion of constraints, though, has re-appeared as behavioural ecologists begin to recognise that the 'behavioural gambit' (the assumption that psychological mechanisms place no constraint on optimal behaviour, Fawcett et al., 2013) is not always appropriate (Dukas, 2002; Stephens, 2002). The norm in early behavioural ecology was to model the optimal solution to an ecological problem (that which maximizes fitness pay-offs) and to presume that animals will evolve mechanisms that produce that optimal behaviour. From this perspective, empirical devia-

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tions from optima have been attributed to hypothetical mechanistic constraints – failures of mechanisms to be capable of producing the otherwise optimal solution (Monaghan, 2014; Zuk and Balenger, 2014).

It is noteworthy that those focused on mechanism and function, respectively, no longer able to ignore the other aspect of behaviour entirely, initially viewed it as a mere constraint – a secondary factor that could add nuance to some of their predictions. A truly integrated approach to understanding behaviour recognizes that ecology does not place constraints on cognitive mechanisms, which would otherwise be free to operate in the same general manner across all species in all situations. Instead, ecology provides the framework within which cognitive mechanisms evolve. Without ecological selection pressures to learn, remember and use information in adaptive ways, there would be no mechanisms of learning and memory. Similarly, we must also recognize that mechanisms are the process by which behaviours occur. They do not constrain an animal such that it functions sub-optimally; they help determine what *is* optimal. Note that this is not the same as suggesting that mechanisms will produce optimal behaviour in every possible scenario. Cognitive mechanisms (instantiated in neural structure and function) allow animals to respond to environmental information. These responses (overt behavioural function) interact with the environment, producing selection pressures, which, in turn, act on the cognitive mechanisms. Thus, the mechanisms that are ultimately selected for are those that perform best across the life of the individual, within the range of typical environmental variation. When faced with novel environmental parameters, including in laboratory experiments, we should not *a priori* expect optimal behaviour to emerge.

Fawcett et al. (2013) have previously emphasised this tripartite relationship between selection, mechanism and function and the importance of placing mechanism and function on an equal, integrated footing, instead of each being studied in parallel, paying only lip-service to the other. Calls for greater integration between function and mechanism in the study of behaviour are not new (Bolles, 1985; Kamil and Roitblat, 1985; Kamil, 1994; Dukas, 2004; McNamara and Houston, 2009; Shettleworth, 2010; Vonk and Shackelford, 2012), nor do they enjoy universal acceptance within either camp (Bolhuis, 2005; Trivisano and Shaw, 2013; Zuk and Balenger, 2014). In spite of this skepticism, momentum appears to be building on this front. In fact, we acknowledge, and consider below, some key achievements already made

with respect to avian cognition and its role in foraging behaviour. We propose, however, that some of the most basic conceptualizations in comparative cognition – the presumed nature of the cognitive mechanisms that we study – need to be reconsidered to be more compatible with functionalist approaches. Only when this is explicitly recognized and addressed will a truly integrative study of animal cognition emerge.

2 The Paradigmatic Assumption: The Real Constraint on Studying Behaviour

When researchers (in comparative cognition) describe the different cognitive abilities that animals exhibit, discrete categories emerge that typically include such examples as spatial cognition, social cognition, episodic-like memory, categorization learning, associative learning, timing and planning (de Waal and Ferrari, 2010; Shettleworth, 2012). These categories of cognition derive primarily from the experimental paradigms designed to investigate them. For example, a task requiring an animal to make a choice based on the spatial locations of the available options (their locations relative to each other, or their absolute location in space) is presumed to be a test of the animal's spatial cognitive abilities. The apparently benign assumption that 'spatial memory tasks' test an animal's 'spatial memory ability' implies that there is a collection of closely related mechanisms, adapted to solve spatial cognitive problems, which are always engaged when such problems are encountered. Similarly, alongside such mechanisms and somewhat independent of them, ought to exist similar collections of mechanisms responsible for timing, planning, categorization learning and others. For example, a simple spatial cognition laboratory task can manipulate whether an animal must search in a specific location to retrieve a reward (the top-left location in a rectangular arena, a spatial cue), or whether it must search near a specific feature (whichever corner contains the blue object, a featural cue). These two cues can be placed in competition to determine whether an animal is more likely to rely on the spatial cue or the featural cue, when both have previously indicated the location of food. Several such studies are cited below in our discussion of the cognition of food-caching and Sulikowski and colleagues (2012) provide a brief review of this paradigm. Interpretations of such findings often assume a real functional and mechanistic distinction between 'spatial memory' and 'feature memory'. In this way, the structure

of cognition becomes indistinguishable from the structure of the tasks developed to study it. We have coined the phrase 'the paradigmatic assumption' to describe this ascension of laboratory paradigms and their reification into discrete cognitive abilities.

The paradigmatic assumption presumes a close correspondence between the laboratory tasks and the discrete cognitive mechanisms they supposedly investigate. Further, it assumes that the computational requirements of the task are all that determine the mechanisms engaged to do it. We argue that neither of these assumptions is likely to be valid when considered from first principles, nor are they borne out empirically. We consider each assumption in turn, below and then discuss the implications of the paradigmatic assumption for one of the early contenders of an adaptive specialization of cognition – preferential reliance on spatial versus colour cues in food-storing birds.

2.1 Assumption 1: Close correspondence between task and mechanism

Many of the laboratory tasks that are used (albeit in modified forms) to investigate animal cognition were not developed with the goal of investigating how cognitive mechanisms evolved to serve adaptive purposes. Rather, they were developed and applied across species with little consideration of any ecological relevance they may or may not have. Their inspiration came from a mixture of intuition about what the building blocks of higher mental processes in humans might be (to investigate whether rudiments of these processes existed in non-human animals; de Waal and Ferrari, 2010) and, later, a drive to identify the 'general processes' (presumed to be conserved, at least across vertebrates) of animal learning and memory (Papini, 2002). The likelihood that abstract tasks and paradigms developed under these conditions would happen to reflect the structure and divergence of adapted cognition across the animal kingdom must be vanishingly small.

Empirically speaking, such paradigms have had some success when used to test ecologically inspired hypotheses. This success, however, has been hit-and-miss, with the misses, we argue, reflecting discrepancies between the tasks used and the underlying adapted cognition. A recent study (Jelbert et al., 2014) subjected rufous hummingbirds *Selasphorus rufus* to an object-in-place discrimination-learning paradigm (developed by Gaffan, 1994, to probe apparent differences between humans and monkeys in object memory). Jelbert and colleagues found that rufous hummingbirds were able to select an appropriate experimental feeder when this

feeder was indicated by a combination of cues: the colour of the feeder, its relative location amongst the four options (at the top or the bottom) and the pattern on the board (the context) to which the feeders were attached (see Fig. 1). Birds were also able to perform the task when the visual context cue (board pattern) was replaced by a sequential timing cue – in this scenario a particular coloured feeder at the top of a board was correct the first time the board was presented, while the other colour at the bottom of the board was correct the second time the board was presented, in relatively quick succession. Such sequential timing cues are frequently used to examine the 'when' aspect of episodic-like memory (memories that supposedly incorporate what, where and when information). The authors predicted that as "hummingbirds use timing cues in their daily lives" they would readily integrate the sequential timing cue with the other cues and solve the task. Of all the cues in the task, however, the birds made the most errors with respect to the sequential timing cue, which the authors described as "somewhat surprising" noting apparent similarities between the sequential cue and trapline foraging (Jelbert et al., 2014).

Although potentially interesting, we would argue that this study has fallen prey to the paradigmatic assumption – and the devil is in the detail. Hummingbirds are sensitive to the (manipulated) replenishment schedules of (artificial) flowers (Henderson et al., 2006; González-Gómez et al., 2011). However, exhibiting longer latencies between visits to flowers that take longer to replenish is not the same as recognising a relative temporal contingency that changes the meaning of another spa-

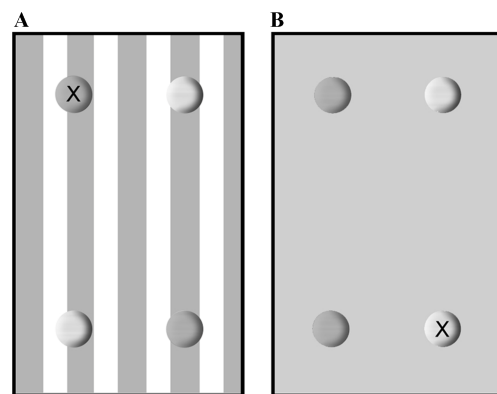


Fig. 1 The experimental set up used by Jelbert et al. (2014)

Against one type of background (A) the particular coloured feeder at the top of the array always contained food. Against the other background (B) the feeder of the other colour at the bottom of the array always contained food. Rewarded feeders could be either on the left or right.

tial/colour compound cue. The former maps very well onto the informational properties of the hummingbird environment (as we explain below), in an appropriate behavioural context – foraging for nectar. The latter does not. Hummingbirds defend territories within which are spatially distributed flowering plants, whose nectar replenishment rates may differ. Sensitivity to these different rates and the ability to time visits to different parts of the territory to coincide with replenishment would increase foraging efficiency compared to movement patterns that were not contingent on replenishment rates (González-Gómez et al., 2011) – the latter would lead to visits to flowers that were (still) empty (Cole et al., 1982) and/or to increased risk of theft by intruders if replenished flowers were left unattended for too long (Kamil, 1978). Therefore, based on ecological considerations, it makes *a priori* sense to expect that hummingbirds will possess cognitive mechanisms adapted for this task (we are not arguing here whether such mechanisms would be adapted only to this task or may underlie foraging and even territory defense more generally [González-Gómez and Vásquez, 2006] – just that there ought to be mechanisms whose functions include making use of these informational properties in this behavioural context).

With respect to the sequential timing cue, there is no corollary of those informational properties (of which we can conceive) in the bird's environment. The authors liken the task to traplining, but if a subset of flowers on each of two nearby plants is reliably producing nectar, the order in which the bird visits those two plants would have no bearing on which flowers yielded nectar. Instead of a meaningful relationship between the informational properties of the task and the animal's environment, the paradigmatic assumption has reified the 'timing' aspect of the task into a measurement of 'timing' mechanisms, which bear only semantic similarity to the cognitive sensitivity to time that hummingbirds have previously exhibited. As such, it is impossible to theorise about the nature of the actual cognitive mechanisms the birds relied on to decipher this sequential timing cue, including the informational properties of the environment that shaped them and the function(s) they serve.

A further example can be drawn from our own research. Sulikowski and Burke (2007) reported that noisy miner birds *Manorina melanocephala* exhibit a tendency to avoid locations where they have recently found nectar, but exhibit no such tendency with respect to locations where they have recently found invertebrates. Such "win-shift" behaviour is common in nectarivorous

birds (Cole et al., 1982; Wunderle and Martinez, 1987; Healy and Hurly, 1995; Burke and Fulham, 2003) and has long been hypothesised to represent a cognitive adaptation, guiding birds away from recently depleted flowers. Trials in this study included two phases. In the first phase birds were presented with four feeders, two of which contained a food reward and birds were allowed to visit all four feeders and consume the two rewards. After a retention interval of 5 minutes, the four feeders were presented in the same four locations. In this second phase either the same two feeders were baited as in the first phase or the other two were baited (see Fig. 2). This paradigm is known as a delayed spatial match (or non-match) to sample (hereafter, DSMTS) and ostensibly measures spatial memory ability. Birds foraging for nectar rewards performed much better in the non-match (compared to the match) version of the task, while for birds foraging for invertebrates, there was no difference in performance. We interpreted this finding as an adaptive bias in spatial memory that only occurs in response to nectar consumption, with no such bias affecting spatial memory for invertebrate prey. But just like Jelbert and colleagues, our readiness to conflate the task with the underlying mechanism meant that our interpretation was too simplistic.

We now have evidence that when noisy miners are foraging for invertebrates, their performance in a DSMTS task has little to do with traditional notions of spatial memory (Sulikowski and Burke, 2010a, 2011) – and so tells us little about their tendency to avoid, or otherwise, recently rewarded point locations in space.

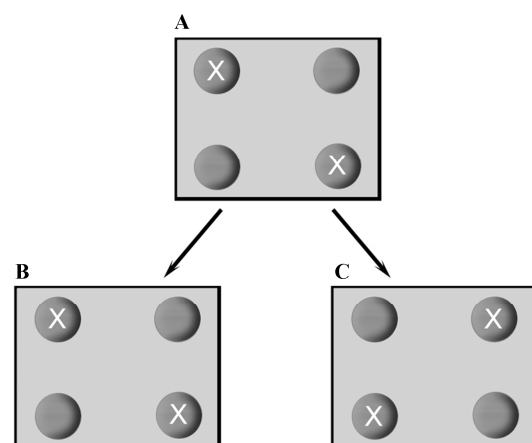


Fig. 2 The experimental set-up used by Sulikowski and Burke (2007)

Two of four feeders were baited in the first phase of the study (A). In the second phase, either the same two feeders were baited, the win-stay condition (B), or the other two were baited, the win-shift condition (C).

The informational properties of a DSMTS task correspond well with a nectar foraging scenario. A bird retrieving nectar from specific flowers within a patch, who, for some reason, is briefly interrupted, would do well to remember those flowers it had already emptied and avoid revisiting them (Gill and Wolf, 1977; Kamil, 1978). Furthermore, in order to exploit a patch of flowers efficiently, even without being interrupted, a bird would need to avoid revisits to flowers, and so remembering the specific flowers that have and have not been visited is expected (Sulikowski and Burke, 2010b), provided the neurophysiological costs of doing so do not outweigh the benefits.

The DSMTS task simply does not map onto the invertebrate foraging scenario nearly so neatly. Although potentially located in a functionally relevant micro-habitat patch, the point location in space where an invertebrate prey item is found does not afford the same information about future distributions as occurs for nectar and flowers. If prey items are mobile that spot will not be definitely depleted for any length of time and if prey is sparse, that precise point may never yield another prey item again. Not surprisingly then, subsequent studies have shown that while noisy miners can keep track of which feeders contained rewards while searching for invertebrates (Sulikowski and Burke, 2012) they only avoid revisits to feeders for a very brief period, if at all, compared to when foraging for nectar (Sulikowski and Burke, 2010a, 2010b). All of this has implications for interpreting the absence of a "win-shift" bias with respect to invertebrate rewards in our DSMTS. In that task, any memory that invertebrate foraging birds may have retained about the point locations of rewards was unlikely to influence subsequent search behaviour after the 5-minute retention interval. As a result we actually have no idea whether or not noisy miners find it easier to *learn* a win-shift than a win-stay rule when foraging for invertebrates. Sensitivities to such specific spatiotemporal contingencies were unrelated to invertebrate feeder choices in our DSMTS task (Sulikowski and Burke, 2007, 2012) and probably unrelated to within-patch foraging decisions made during natural foraging for invertebrate prey.

2.2 Assumption 2: Computational requirements alone dictate the mechanism used

In the laboratory, the cognitive tasks animals are

given are typically well-defined: there is a clear and limited amount of information available, the solution is unitary and unambiguous, and the outcome binary (a correct response entails a reward and an incorrect response, a punishment, or withholding of a reward). under these conditions the computational requirements^① of a task are clear and it is intuitively appealing to suppose that an animal presented with such a task would apply those cognitive mechanisms it has that best match the task's computational requirements, hence solving the task as well as the animal is able. the world in which cognitive mechanisms evolved, however, is rarely so well-defined. the information that is potentially available to an animal's senses far outweighs that which it can use (dukas, 2002). further, 'correct' solutions to cognitive challenges may not be fixed. theories of risk-sensitivity predict that optimal foraging decisions can be affected by the animal's current nutritional and motivational state (stephens, 1981; kacelnik and bateson, 1996). finally, the proximate outcome achieved from any decision the animal makes will not necessarily indicate whether the animal has made the appropriate choice. unlike the iterative trial-by-trial feedback a foraging bird receives in an experiment, a wild bird will forage in a particular patch, find some quantity of food, and will never know whether that was the least profitable or most profitable decision it could have made in that particular instance. from this perspective, it seems unlikely that the computational requirements of a hypothetical life-long optimal solution can act as the proximal cue that engages, or triggers, specific suites of cognitive mechanisms.

If the computational requirements of a laboratory task were all that determined the mechanisms engaged to solve it, then we ought to observe similar performance in tasks with the same computational requirements, across various contexts. while there are some examples of birds performing similarly in computer and real-world settings that present the same computational requirements (for example, brodbeck, 1994 and bordbeck and shettleworth, 1995; and cheng, 1989 and spetch et al., 1992), there are many instances in which this does not occur. different species, faced with identical cue-outcome contingencies, end up performing different species-typical, but irrelevant, behaviours (timberlake, 2001), some of which actually interfere with the animal achieving the desired outcome – a food reward (breland and

^① We distinguish between 'informational properties' of a task, which refer to all of the information that is potentially available within a given paradigm, and the 'computational requirements', which refer to the specific way in which some of the informational properties can be used to arrive at the correct solution.

breland, 1961). this cannot be driven by the computational requirements of the tasks, because they do not vary. similarly, rats (nocturnal foragers) learn to avoid the taste, but not the visual attributes, of foods that make them ill, whereas quail (visually-guided foragers), faced with the same arrangement, learn to avoid using visual rather than gustatory information (wilcoxin et al., 1971).

Data from our own lab provides compelling evidence that the behavioural context of the task, specifically the type of food for which the bird is searching, can engage food-specific cognitive mechanisms, in response to identical computational requirements. in noisy miners, we routinely observe (sulikowski and burke, 2007, 2010a, 2010b, 2011) that the proximal ingestion of either a mealworm or some sucrose solution produces markedly different search behaviour and sensitivities to different informational properties of a given task. these different responses are typically evident from the first trials of a task – as soon as birds are aware of the type of food contained in these feeders, they adopt food-specific cognitive strategies to find it (sulikowski and burke, 2007, 2011). furthermore, as we discussed above, the informational properties of our laboratory tasks typically correspond much better to the nectar than the invertebrate foraging scenario. as a result the birds' nectar-foraging cognitive strategies typically produce better performance (more efficient retrieval of more food rewards) than the invertebrate strategies (sulikowski and burke, 2007, 2010a, 2011). this is important because it means that birds in an invertebrate-rewarded condition in our studies are presented with a task whose computational requirements map very well onto cognitive mechanisms (for nectar foraging) that the birds possess, yet these birds persist in relying on other mechanisms (for invertebrate foraging) that match the food type found. this is especially strong evidence that the computational requirements of a task do not automatically, or even after some practice, evoke whichever of the animal's cognitive mechanisms are best suited to meeting them.

These observations suggest that it is not the computational requirements of a task that trigger specific cognitive mechanisms into action. rather it is the behavioural context in which the animal is seeking information that dictates what, and how, information is used. from this perspective, it follows that the proximate determinants of cognitive engagement should be closely linked to the proximate determinants of the behavioural function those cognitive mechanisms serve. somewhere in the mixture of internal and external factors that mo-

tivate an animal to begin foraging on a particular resource, courting a potential mate or defending their territory, must also lie the proximate cues that trigger the necessary cognitive mechanisms that support such behaviours. these considerations have important consequences for interpreting data from experimental cognitive tasks: if the context of the task does not induce the intended behaviour in the subject, then neither will it engage the cognitive mechanisms of interest, irrespective of how well the computational requirements of the task correspond to said mechanisms.

2.3 A case study of the paradigmatic assumption: Preferential reliance on spatial versus colour cues in food-storing birds.

Demonstrations that wild food-caching birds use memory to recover their caches (Cowie et al., 1981; James and Verbeek, 1985) stimulated investigation into whether food-caching birds possess an adaptive specialization of spatial cognition that underpins their cache-recovery behaviour. These early investigations were highly influential in positioning an animal's ecology as central to understanding its cognitive functioning. The emphasis in these early studies (during the 1980s and 1990s) was on between-species comparisons in laboratory performance on tasks of 'spatial cognition'. It was deemed necessary first to demonstrate that general cognitive mechanisms, conserved across species, and not adapted to any particular ecological challenge, could *not* account for a particular set of findings, before the idea of ecologically adapted mechanisms could be legitimately entertained. Species differences on identical tasks were an effective way to do this (Brodbeck, 1994). This presented a restrictive logistical problem – it is impossible to compare food-storing and non-storing birds on a laboratory cache-recovery paradigm, because non-storers will not cache and recover. Instead other cognitive tasks, reasoned to reflect some important cognitive aspect of cache recovery, were used (but see also Balda and Kamil, 1989; Brodbeck, 1994; Kamil et al., 1994).

One widely used paradigm examined whether food-storers were more likely than non-storers to rely on spatial (as opposed to featural) cues to locate food. The basic paradigm is illustrated in Fig. 3 and involved presenting birds with a feeder containing a food reward, only some of which the birds are permitted to consume. After a brief retention interval (usually 5–30 minutes) birds are allowed to search for the remaining food, but have a choice of feeders including one that was featurally the same as the original but in a different location, and one that was in the same location but a differ-

ent colour. Studies reported that food-storing birds were more likely to choose the feeder in the correct spatial location, while non-storers showed equal propensity to choose either the correct location or correct colour (Brodbeck, 1994, Clayton and Krebs, 1994a), but more recent studies have not always supported this difference between food-storing and non-storing species (Hodgson and Healy, 2005; LaDage et al., 2009; Feenders and Smulders, 2011). Herborn et al. (2011) have also questioned whether it is even appropriate to suggest that a given species has a general preference for either spatial or colour cues, as European greenfinches *Carduelis chloris* switched preferences, preferring the colour cue after a single exposure, but the spatial cue after repeated exposures.

Several aspects of these investigations are relevant to our arguments about the paradigmatic assumption and account for why a general preference for spatial over colour cues in storing, relative to non-storing, birds has not persisted as a reliable finding. Firstly, storing birds possess larger hippocampi than non-storers (reviewed by Pravosudov and Roth, 2013) and lesion studies implicate the hippocampus in cache recovery (Krushinskaya, 1966; Sherry and Vaccarino, 1989) and in spatial laboratory tasks (Hampton and Shettleworth, 1996), but also in non-spatial tasks (Cohen et al., 2013) and in episodic memory (Burgess, Maguire and O'Keefe, 2002). Also, when recovering stored food items, wild birds could rely on a multitude of local visual and spatial cues in the natural environment (Brodbeck, 1994). So even though successful cache recovery in the wild requires the bird to remember and revisit many different locations, and so presents a 'spatial' challenge in a real sense, it does not necessarily follow that cognitive mechanisms adapted for cache recovery should only be sensitive to spatial cues. To decide that cache recovery, as a spatial challenge, will be subserved by enhanced spatial

cognition, and then presuming that any spatial advantage in a laboratory task, including a preference for spatial over colour cues, reflects this enhanced spatial cognition is an example of the paradigmatic assumption. The cognitive mechanisms that subservise initial foraging may work differently from those engaged during cache recovery since only the latter can benefit from *a priori* knowledge of the food's precise location. In laboratory tasks that do not require an animal to cache food, it is not necessarily clear that mechanisms associated with cache recovery will even be engaged (Shettleworth and Krebs, 1986; Brodbeck, 1994). Further, some aspects of both types of mechanisms could be associated with the distributions of the food (Sulikowski and Burke, 2011, 2012), meaning that storers and non-storers exploiting foods with similar natural distributions could do so using similar cognitive mechanisms, whereas two storing species who create different distributions of cached food to recover (Balda and Kamil, 1989) could possess divergent cache-recovery mechanisms. Consequently, expecting a broad distinction between storers and non-storers on any single aspect of laboratory performance (such as a preference for the spatial over the colour cue in a particular laboratory paradigm) is too simplistic (Smulders et al., 2010).

Authors at the time recognized some of the issues we discussed above and addressed them with some success. Shettleworth and Krebs (1986) investigated similarities and differences in recollection of locations where birds had been allowed to cache food, compared to places where they had previously seen food, and Balda and Kamil (1989) designed elaborate cache-recovery tasks in which they compared food-storing species that differed in their reliance on stored food. Similarly, Clayton and Krebs (1994b) considered the possibility of separate initial foraging and cache-recovery mechanisms as an alternative to their main interpretation that food-storers possessed a more accurate spatial memory than non-storers. These authors also presented a delicate unpacking of potential interactions between: (1) the various hypothetical cognitive mechanisms storing (and non-storing) birds may possess; (2) the slight differences in methodologies used across studies; and (3) how well these different methods correspond to the informational properties of a food-storer's environment. The investigation of cognition in storing birds has been (and continues to be) an extremely fruitful endeavour, theoretically and empirically. As in all areas of comparative cognition, however, it has been hampered by too great a reliance on contrived laboratory paradigms to define the

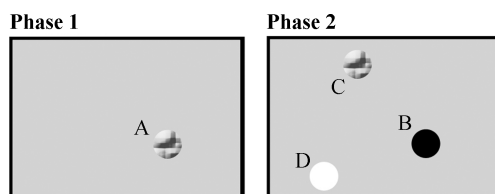


Fig. 3 A generic illustration of a task used to measure preferential reliance on featural versus spatial information. In Phase 1, the bird partially consumes some food from a feeder (A). In Phase 2 it searches for the remaining food. It can choose from a feeder in the same location but a different colour/pattern (B), a feeder in different location with the same colour/pattern (C), or a non-matching feeder (D).

cognitive mechanisms assumed to underpin behaviour (see Pravosudov and Roth, 2013, for a recent example).

3 The Long Journey from Selection Pressure to Laboratory Cognitive Performance

The paradigmatic assumption bridges the gap between laboratory task performance and evolved cognitive mechanisms via the following logic. Spatial memory is required to solve spatial challenges (such as recovering cached food), therefore evolution should have selected for better spatial memory (in food storers), and, if this is true, it will be reflected in performance in spatial memory laboratory tests. Thus it is implicitly assumed that the laboratory performance does not merely represent what an animal may be able to do in the wild, it is presumed to reveal the action of hypothetical selection pressures on cognitive mechanisms.

We are suggesting that the paradigmatic assumption is flawed for at least three reasons. Firstly, the underlying structure of cognition across the animal kingdom is unlikely to correspond to the different categories of cognition pre-supposed by traditional laboratory paradigms. Secondly, even to the extent that the computational requirements of laboratory paradigms may capture some important aspects of the cognitive mechanisms in question, if the context in which the task is administered does not elicit the intended behaviour in the animal, then it is also unlikely to engage the cognitive mechanisms of interest. Thirdly, it is generally unknown whether the neural tissue supporting any given cognitive mechanism serves only that mechanism (and its supposed function) or has been shaped by multiple functional outcomes. In pointing out the weaknesses in the paradigmatic assumption we are essentially advocating for a more considered and nuanced approach to developing both predictions about the nature and operations of cognitive mechanisms and the laboratory tasks used to test those predictions.

Smulders et al. (2010) have recently argued for such an approach, specifically with respect to investigating the cognitive mechanisms underlying cache recovery, outlining many of the same issues that we do with past approaches, including an oversimplification of how selection pressures derived from cache recovery may have impacted cognition, and the kinds of laboratory tasks expected to reflect these. These authors, however, stay within traditional conceptualizations of spatial memory when outlining the ways cache recovery may have

influenced cognition, nominating memory duration, capacity and spatial resolution as aspects of spatial cognition that may have been enhanced by selection pressure for efficient cache recovery. While we concur with the criticisms these authors raise, the solution to this problem is not simply to apply the paradigmatic assumption at a more fine-grained level of task-to-mechanism reification. If a given spatial memory task does not reflect general spatial memory ability, then the retention interval, for example, used in that task also cannot reflect the duration of this general spatial memory ability. In the absence of the paradigmatic assumption, therefore, several components of a more comprehensive approach are required to derive predictions about laboratory performance based on hypothesized selection pressures acting on cognitive mechanisms.

An ecologically inspired, functional approach to animal cognition would not begin with the assumption that a base unit "spatial memory" (for example) mechanism exists and has been adapted in different species for different purposes. Rather, the theoretical start point ought to be an analysis that jointly considers the functional goals of behaviour (for example, foraging in a manner that maximizes energy intake, optimizes nutrient intake and minimizes time and energy costs) and the informational properties of the environment that could facilitate those goals. Hypotheses about the operation of cognitive mechanisms should refer to how information in the environment might be used in specific ways, to optimize behavioural outcomes.

Predictions about an animal's behaviour in a contrived laboratory setting ought to be based on a hypothetical understanding of how the relevant cognitive mechanisms should operate in that controlled environment. Given that this setting, like all experimental environments, will contain limited information and restricted behavioural options, it will not always be the case that the behaviour predicted in the experiment will correspond to the behaviour these same mechanisms are theorized to support in the natural, information-rich and flexible world (Houston, 2009). This is a key benefit of replacing the paradigmatic assumption with a more nuanced approach. Hypotheses derived via the paradigmatic assumption can only predict better performance on the laboratory task that supposedly represents the cognitive ability of interest – which explains why food-caching birds were always predicted to perform better on so-called spatial tasks and always predicted to attend preferentially to the spatial cue. In contrast, a sophisticated theory of the nature of a given cognitive mecha-

nism, based on real-world informational properties and theoretically optimal outcomes, could permit different predictions in different controlled settings, each constrained in different ways. For example, using two similar experimental paradigms that were both, ostensibly, tests of spatial working memory, we have recently demonstrated (Sulikowski and Burke, 2015) better search performance for nectar (than for invertebrates) in one paradigm and better search performance for invertebrates (than for nectar) in the other paradigm. If we assume that spatial working memory tasks simply reflect spatial working memory ability, it is difficult to reconcile how birds can simultaneously possess better memory for both food types. On the other hand, consideration of the informational properties of each task (specifically, whether or not a search route could be planned) and those available when foraging for each food type in the wild (flowers afford route planning for nectar, while search paths to retrieve cryptic invertebrate prey cannot be planned in advance) can account for the differential performance in the two tasks.

Cognitive mechanisms will have evolved to bring into alignment the informational properties of the environment and the relevant behavioural goals of the animal. As previously discussed, the ways in which this alignment is achieved are unlikely to be adequately captured by the discrete cognitive categories traditionally adopted by researchers. As a result, the traditional experimental paradigms used will need to be replaced by customized paradigms inspired by the specific coupling of the behavioural goal and informational properties under investigation.

As well as reflecting the environment's informational properties, an appropriate paradigm must sufficiently mimic the context in which the mechanisms of interest naturally operate to ensure that they are engaged. This is, of course, easier said than done. Those aspects of the natural context that need to be mimicked may not be apparent, and it will not always be clear whether the context has been sufficiently mimicked. If null or unpredicted results are obtained, for example, it is difficult for a researcher to determine whether their predictions were flawed or whether they failed to provide the appropriate context. Even if the predicted results are obtained, this does not necessarily mean that the laboratory context affects the study organism in the same way as the corresponding natural context. In our own laboratory studies with noisy miners, for example, we simply manipulate the type of food (sucrose solution or mealworms) with which the birds are rewarded. This

has proven sufficient to reveal marked differences in subsequent performance and behaviour, as predicted by the natural distributions of nectar and invertebrate prey. Considering the context of wild foraging, however, it is unlikely that proximal ingestion of a particular food type is necessary to engage the associated cognitive mechanisms, since one might expect such mechanisms to operate when the bird commences foraging, before it has found or consumed anything.

The consequences of this kind of disconnect between the laboratory and the real world are not immediately clear. There may be aspects of the relevant mechanisms that this approach, or any one approach, is unable to reveal. Systematic manipulations, designed to capture various aspects of the natural context, are needed to thoroughly investigate any set of cognitive mechanisms and to ensure that null or unexpected results are not due to a mismatch between the laboratory context and the real world.

Although the current paper is primarily concerned with the theoretical and methodological issues surrounding laboratory investigations of cognition, laboratory experiments alone are not sufficient to fully understand the evolution and function of cognitive mechanisms. Thorough analyses of the informational properties of the environment will help develop appropriate hypotheses to test, while field observations and experiments are also important to corroborate laboratory findings. While field settings offer less stringent control of extraneous factors, they may be more likely than laboratory settings to provide the appropriate context. Field studies are also especially important for testing theories about the selection pressures shaping cognitive mechanisms. They allow for investigations of relationships between cognitive mechanisms and specific environmental factors (Pravosudov and Roth, 2013) and can help uncover the fitness consequences of individual differences in cognition (Cole et al., 2012; Cauchard et al., 2013; Niemelä et al., 2013; Morand-Ferron et al., 2015).

4 Functional Cognition: What Would A Truly Integrated Approach Look Like?

Replacing the paradigmatic assumption with more sophisticated empirical and theoretical approaches to studying cognition requires substantial changes in how researchers define and investigate cognitive mechanisms. If such changes were to occur this would essen-

tially create a new research program for avian cognition (and comparative cognition more generally), with a new set of core, guiding principles (Lakatos, 1970). There are some examples of current research projects that already embody some aspects of the approach we outlined above, suggesting that this new research program is already emerging.

Research developing and testing the sequential choice model (SCM) by Kacelnik and colleagues (Shapiro et al., 2008; Freidin and Kacelnik, 2009; Kacelnik et al., 2011) provides one such example. The SCM reconsiders the presumed comparisons that animals make between simultaneously presented options, a key feature of many experimental paradigms, as independent comparisons made between the value of each option and the value of background alternatives in the wider environment. An option that fares poorly compared to potential future alternatives would be rejected in the wild (Charnov, 1976). In the laboratory, where behavioural options are restricted, relatively poor options tend to be accepted with longer latencies, rather than being rejected completely. So, when two options are presented simultaneously in a laboratory experiment, the option with the highest value is chosen not because it is directly compared to the alternative, but because it elicits the shortest latency to consume. The key insight of this model, therefore, is the realization that mechanisms that may result in rejection of a prey item in the wild result in delayed consumption in the laboratory. The strengths of this work, in terms of the approach we are advocating here, lie in the development of a formal model of a cognitive mechanism, based on the informational properties of the foraging environment, and the use of customized laboratory paradigms to test the model.

Our own work on foraging in noisy miners has demonstrated food-type-dependent differences in laboratory cognition. These differences were predicted by joint consideration of the behavioural goals (efficient foraging) and the informational properties of the environment. When searching for nectar within a patch of experimental feeders, noisy miners appear to plan a route through this patch that effectively avoids revisits and their search performance is robust to repeated interruptions, suggesting that they keep track of where they are up to. When searching for invertebrates, they are unable to pick up where they left off after an interruption, adopt systematic movement biases rather than a planned route, and are subsequently less able to avoid re-visiting feeders they have already emptied.

Although our previous work encompasses several

aspects of the functional cognition approach we are advocating, there are weaknesses in our research program that require attention. We have not yet adequately measured or modelled the informational properties of the environment, especially with respect to the distribution of invertebrate prey. We have also not yet undertaken any formal field manipulations or observations to verify our laboratory findings. Finally, although we have recently become somewhat more creative in our experimental designs and interpretations (Sulikowski and Burke, 2015), we have not yet attempted to create a laboratory scenario that provides equivalent informational properties to those present during wild invertebrate foraging. So even though our own research program has provided valuable insights into foraging cognition and has strived for the sensitivity to nuance and detail for which other authors have previously called (for example, Smulders et al., 2010), it is still only scratching the surface of the kind of integrated approach that we argue is required to properly understand animal cognition.

5 Final Remarks

Fawcett, Hamblin and Giraldeau (2013) have conceptualized evolved cognitive mechanisms as "multi-purpose rules which are capable of providing effective solutions to a wide range of problems." McNamara and Houston (2009) also recently advocated a shift from considering complex (mechanistic) models of behaviour in un-realistically simplified environments, to modelling the evolution of simple mechanistic rules in more complex environments. We would argue that what might need to be modelled are complex cognitive mechanisms operating in complex environments. Artificial neural network modelling has revealed several instances where simple (shape and size discrimination; Beer, 2003; Williams et al., 2008) and more complex (decisions predicted by optimal foraging theory; Niv et al., 2002) cognitive feats can be performed by circuits with fewer than 10 neurons. This implies that surprisingly small amounts of neural tissue may be required for any given cognitive task, allowing brains to instantiate a multitude of potentially very complex cognitive mechanisms.

While some cognitive rules may operate similarly across species in a variety of scenarios (the sequential choice model described above is one potential candidate for such a rule, as is the phenomenon of peak shift; Lynn et al., 2005), we note that the physical instantiation of cognitive mechanisms is neural and the ways in which neurons manifest cognition (beyond localizing certain cognitive mechanisms to gross brain regions) are

poorly understood (Chittka et al., 2012). Concurring with the argument of Chittka and colleagues, it is possible, or even probable, that the same cognitive rule applied across different contexts could be subserved by independent context-specific neural structures. This would permit subsequent subtle divergence and adaptation of these neural structures to their own unique task. We should therefore expect even general mechanisms to be overlaid by subtle adaptive tweaks. At the next layer of analysis, we should expect these minor adaptive changes to produce similar nuances in different species solving similar tasks – in other words, convergence. At the other end of the generalist/specialist continuum we should also expect to see as much variation between species in cognitive mechanisms as we do in other aspects of behaviour and morphology. There is no *a priori* reason to suppose that the brain and cognition should be any less susceptible to evolutionary change than other categories of phenotype. In short we should see the full gamut from generalist (divergent and convergent) to highly specialist, even unique, examples of cognitive mechanisms across animals and the extent to which generalization or specialization proves to be the rule or the exception will likely vary across taxa and across behavioural contexts. Cross-species comparisons that consider both ecology and phylogeny will be required to elucidate these patterns of divergence and convergence. We see no reason, however, to pre-suppose that cognitive divergence across the animal kingdom will be adequately captured by a relatively small number of general heuristics and rules-of-thumb.

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