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From sensory to social: the information that impacts animal foraging decisions

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Foraging decisions reflect cost-benefit trade-offs. Costs arise from missed opportunities, ingestion (such as if prey are toxic), and acquisition (time and energy through exploration). Benefits arise from acquiring energy, nutrients and information. I present a collection of recent findings from vertebrates and invertebrates, demonstrating the breadth of information – sensory, social, nutritional, spatial and physiological, to name a few – that impacts animal foraging decisions. I also consider key challenges facing the study of foraging cognition, namely misgivings arising from observations of suboptimal foraging decisions in laboratory studies, and a lack of transferability between information use in the laboratory and that in the world. I conclude that an emphasis on custom experimental designs is key to continued empirical progress in the field.

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Introduction

Investigations of animal foraging decision-making are plentiful, and are energetically integrating approaches from experimental psychology with foraging ecology [1,2]. Experimental psychology has historically been focused on identifying the decision-making mechanisms (rules describing what information is used and how, during particular tasks), while foraging ecology has been primarily concerned with predicting the outcomes of such decisions, based primarily on optimality models. A flourish of recent reviews and syntheses focusing on the decision-making processes that underpin all kinds of diverse foraging modes and predator–prey interactions [3•,4–7] have emphasised the value of knowing how the function (outcomes) of animal decisions, define the selection pressures that shape the underlying mechanisms.

Recent empirical advances have also been numerous. The field of foraging decisions is currently characterised by a growing appreciation for the complexity of factors that impact on foraging decisions. This is reflected in current programs of research investigating mechanisms of simultaneous choice between competing options; how predators decide whether or not to attack potentially toxic or dangerous prey; the effects of social structure and personality on foraging decisions; and how foraging strategies differ for foods with different distributions and nutritional composition. The current review highlights recent empirical developments in these areas with the goal of capturing some of the extensive breadth of current research into animal foraging decisions. I also briefly review theoretical challenges facing the field and suggest that further advances rely on continued experimental innovation, with more attention paid to ensuring a close concordance between the experimental design developed and the specific theory of information use and utility being tested.

What makes a decision?

Decision-making reflects a trade-off between the costs and benefits of the chosen behaviour (and the non-chosen potential behaviours). These costs and benefits are affected by characteristics of the forager (both state and trait), the food (distribution and composition), and the current environmental state. Additionally, foraging behaviour functions not just to get food, but also to collect information [8]. Therefore, the costs and benefits of various options include the potential energetic costs of utilising information, and the value of the information gained while foraging [9••].

Choice-models of foraging decisions

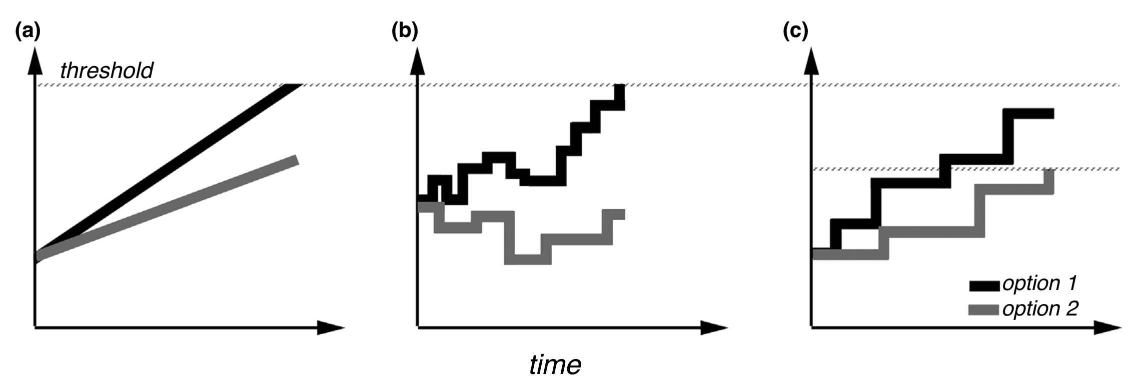
An animal faced with a choice between two options, could reasonably evaluate and compare the net benefits of each, and choose the option with the higher utility. However, simultaneous availability of options is rare [10], and decision-making mechanisms may be adapted to maximally exploit sequentially available options. For example, a single prey item is either pursued or ignored, based on a comparison between the perceived value of the item, and the predicted background opportunities in the environment. When simultaneous choices are encountered, each is considered independently and compared against the background in which it is typically encountered. The chosen option in simultaneous encounters is that which would elicit the briefest latency to pursue when encountered singly, as described by the Sequential Choice

Box 1 Accumulator models of decision-making.

Accumulator models have dominated speeded decision-making research in experimental psychology for several decades [47,48,but see also 49]. Many such models exist, and they vary in their complexity. Generally speaking, most models assume that (largely) independent evidence-accumulating processes exist for each option in a (typically binary) decision. These accumulators gather sensory evidence in favour of one of the options and race each other to a threshold level (Figure 1). When an accumulator reaches its threshold, the associated response is initiated, and at no time is the evidence in favour of the respective options ever directly compared.

While accumulator models dominate theories regarding speeded decisions, theories of heuristics and biases – which identify simple rules-of-thumb – are the dominant explanation for unhurried decisions in human psychology [38]. This is somewhat of a paradox, since one major reason given for the use of heuristics is their efficiency: it is faster and simpler to adopt a rule-of-thumb, than to consider all available evidence. One would imagine that in speeded decisions efficiency would be just as, if not more, important, and yet accumulator models account very well for both the decision ultimately made and the time taken to reach it. The extent to which accumulator-type models can also account for non-speeded decisions is an under-explored, but potentially fruitful arena.

Figure 1



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Accumulator models. In different models accumulators accrue information at constant **(a)** or variable (**(b)** and **(c)**) rates, can accrue information only for (a and c), or for and against (b) an option, and can race toward a single threshold (a and b) or toward different thresholds (c). The model proposed to account for high rejection rates of poor mimics [12••] is most similar to (c). If option 1 is 'attack' and option 2 'flee', then in this hypothetical example, the bird accumulates evidence more quickly in favour of attacking the mimic (perhaps because it does look more like a prey item than a predator), but because of the lower threshold on option 2, still ultimately decides to flee instead.

Model (SCM, [10]). Starlings presented (singly) with two food items of identical objective value, against divergent background contexts, will respond more quickly to the item with the highest value relative to the background. When the two items are then presented simultaneously, preferences for the item that previously elicited the shorter (single) latency are observed [11].

The SCM bears much conceptual similarity to accumulator decision models, which dominate in human cognitive psychology (see Box 1). Such models propose that separate accumulators govern each option in a binary choice task. Accumulators gather sensory evidence and their option is selected when evidence reaches a predetermined threshold. Castellano and Cermelli [12••] recently proposed an accumulator model to account for avian forager decisions to reject potential prey that mimic predators, such as caterpillars displaying eyespots to mimic snakes. Their model proposes that upon encountering a potential caterpillar/snake object, a bird accumulates perceptual evidence, independently, in favour of the caterpillar-appropriate response (attack) and the snake-appropriate response (flee), respectively. The optimal threshold for deciding the potential prey is a snake is much lower, however, than for deciding it is a caterpillar, since the cost of mistakenly attacking a snake is much greater than that of mistakenly fleeing a caterpillar.

Learning about toxic prey

The predator decision-making model described above has yet to be empirically verified, but could explain the existence of relatively unconvincing mimics (see Box 1). Interestingly, Kazemi *et al.* [13,14•] have demonstrated that mimics need only closely resemble their aversive models on one trait, while differing on several others, for avian predators to avoid them, a result replicated for human predators too [15]. It may be that reliance on detecting a single trait (as opposed decision-making mechanisms that may draw evidence from numerous traits) facilitates fast responses, alleviating speed/accuracy trade-offs in this potentially dangerous scenario [12••]. The choice of eyes (or eye spots) as the key trait would also contribute to the asymmetry of forager decisions: in the absence of perceptual errors a snake would never be attacked, at the cost of fleeing readily from harmless mimics. Given the asymmetry in costs – a false alarm costs the predator a meal, missing the eyes of a snake might cost him his life – this pattern of error management would be adaptive in most circumstances. The one circumstance in which the same may not be adaptive would be when the costs of foregoing a meal may be equivalent, or even greater (in terms of pending starvation) than the costs of potentially attacking a misidentified predator. Whether decision-making mechanisms are sensitive to current internal states, which would affect the cost-benefit matrix of the decision, is an empirical question, but there is reason to suspect they might be [16].

Generalising this logic, we could predict that foragers may tend to rely on a single trait, rather than multiple traits, to avoid dangerous, toxic, or otherwise aversive food items. Foragers who do so would then be expected to choose a trait whose absence indicates a very low probability that the food is aversive, even if its presence does not indicate with similarly high probability that the food is indeed aversive. Kazemi *et al.* identified colour as the cue upon which birds identified mimics of toxic prey, as opposed to pattern or shape. They attributed the reliance on colour to its greater visual salience. Further research should examine, however, whether the absence and presence of warning colour cues, more than pattern or shape cues, satisfy the diagnostic asymmetry described above. This could provide a functional explanation for the high salience of colour in this context.

Skelhorn *et al.* [3•] argue convincingly that when predators consume novel toxic prey, they are learning not just to avoid it, but are acquiring information about it (such as mean and variability of toxin levels and nutritional properties), which then informs future foraging decisions. This suggestion is supported by observations that birds will subsequently increase their consumption of familiar toxic prey when non-toxic prey becomes more difficult to attain [17], and when the nutritional value of the toxic-prey is artificially enhanced [18], and when prey items have constant, compared to variable, toxicity levels [19]. As Cuthill [20] points out, though, foraging decisions about any prey item, are influenced by an assessment of the costs and benefits of consumption, aided by information gleaned from previous foraging experience. The application of this fundamental principle of Optimal Foraging Theory [21] to consumption of toxic prey seems, perhaps, to be controversial only because of the apparent success of simple associative learning theories in accounting for the acquisition of prey avoidance behaviours [3•]. Such associative explanations have over-shadowed more complex functional explanations. The adaptive patterns of toxic prey consumption outlined above, however, imply that cost-benefit trade-offs involving quantitative estimations of the costs of ingesting the toxins drive these foraging decisions, and justify invoking more complex explanations.

Complexity of foraging decisions

Foraging decisions are influenced by a wide array of cues and factors, including the forager's personality; the presence and characteristics of other individuals; and the distribution and nutritional composition of the target food. Personality, (which, in animal behaviour, refers to any behavioural trait that differs across individuals, but is constant within an individual when tested at different time points or within different contexts) can affect foraging strategies with consequences for the utility of information. Great tits differing in exploration tendency also differed in tendencies to use a novel foraging technique (Exploration tendency is described as slow, medium or fast, which refers to the speed with which an individual move through a novel (laboratory) environment, in which they have been placed for the purpose of measuring exploration tendency). Fast and slow exploring great tits, relative to intermediate explorers, received a greater payoff from solving a novel foraging problem [22•]. Arvidsson and Matthysen [23] have also linked exploration tendency to information utility, with slow exploring great tits engaging in more patch-sampling (information gathering) behaviour than fast explorers, possibly indicating higher utility of the gathered information for the slow, compared to the fast, explorers fast. Social and personality effects on foraging decisions can also be contingent on the reliability of information the forager can observe firsthand. Foraging bumblebees will copy the flower choices of other bees when (artificial) distributions of nectar are highly variable and unpredictable [24]. Similarly, in wild chacma baboons, bold individuals are more likely to produce (locate and identify novel food patches) and shy ones more likely to scrounge (consume food from patches discovered by another individual), but only when the distribution of available food is unknown [25]. Social effects on foraging decisions can also be more complex than well-known social learning and producer-scrounger interactions. The addition of a single, extremely bold individual increased other spiders' participation in, rate, and success of hunts, and their survivability and mass gain, in a colony of social spiders *Stegodyphus dumicola* [26].

Animals require combinations of protein and carbohydrate foods [27], which can differ in value and distribution. Foraging decision-making mechanisms across a variety of species (birds [28], bees [29•], ants [30] and fish [31]) appear differentially adapted to obtaining these nutrients. Noisy miner birds [32•] and bumblebees [33] given the opportunity to search simultaneously for protein (insects or pollen) and carbohydrate (nectar) rewards, will target the foods one at a time (consecutively), incurring efficiency costs if forced to search for both concurrently. These observations imply that the cognitive mechanisms supporting foraging for these two classes of nutrients are not just differentially adapted, but may be behaviourally incompatible. In laboratory tasks, miner birds use spatial information differently when foraging for nectar than for insects [5], while the integration of colour-cue associations in bumblebees differs between nectar and pollen rewards [29•]. For birds, this effect is predicted by the respective distributions of nectar and insects, and the decision-rules that would support efficient exploitation of each resource. The functional significance of this effect for bumblebee foraging is less clear and requires further investigation.

Simple foraging rules that approximate optimal solutions may be more likely to evolve, than the complex optimal strategies [34]. Substantial empirical evidence, however, suggests that some foraging decisions involve cognitive feats typically viewed as complex and advanced. Sulikowski and Burke [32•] demonstrated that noisy miner birds plan their foraging paths in advance when foraging for nectar, although not when foraging for invertebrates. Search performance for nectar rewards (only) was impacted when the capacity to plan ahead was compromised. Lihoreau *et al.* [35••] have also provided the first demonstration of simulated annealing, in an animal species, the bumblebee. Simulated annealing is a search optimisation algorithm (see Box 2), developed within the physical sciences and adept at differentiating a global maximum from multiple local maxima. There is also evidence of numerosity in wild bumblebees—keeping count of the number of nectaries they have probed as a strategy to limit the probability of re-probing an emptied nectary [36]. Perry and Barron [37] reported that honeybees were able to increase their overall foraging success in a visual discrimination task by choosing to opt-out of some trials (thereby avoiding the waiting period that would follow an incorrect choice), suggesting a form of metacognition: awareness of the level of uncertainty in their own knowledge about the state of the world.

Box 2 Optimization algorithms.

Optimization algorithms are sets of rules, heuristics and calculations to be used to find (or approximate) the optimal solution to a problem (with the optimal solution typically being that which maximizes some specific outcome variable, given sets of values of a number of input variables). In the simulated annealing algorithm the agent samples an undulating landscape looking for local maxima. At each iteration, the agent chooses whether to stay on the current maxima, or change to a neighbouring maxima (which need not be higher than the current one). Changes from one maximum to another permit scanning of large areas of landscape and, over iterations, the search area shrinks and the probability of switching to a lower maximum approaches zero. The agent finishes on a maximum that has a high probability of being the global landscape maximum [50].

The simulated annealing algorithm was developed based on the process of annealing (heating materials and then controlling their cool down, to create a uniform solid free of inconsistencies), and subsequently observed in foraging bumblebees. The search behaviour of animals has also been the inspiration for developing optimization algorithms. The artificial bee colony (ABC) [51], ant colony optimization (ACO) [52], cuckoo search [53], animal migration optimization (AMO) [54], and group search optimizer (GSO) [55] algorithms were all inspired by observations of animal search and foraging behaviour, and predator-prey interactions have inspired solutions to multi-objective optimization problems (where a set of optimal solutions, knows as the Pareto-set, rather than a single optimal solution is sought) [56]. Foraging behaviour-inspired optimization algorithms are an important application of studying foraging decisions and testament to the impressive array of decision-making mechanisms that have evolved under selection pressure to optimally exploit the environment.

Challenges facing the field of foraging decision-making

Observations of suboptimal behaviour in laboratory foraging studies have led some authors to question whether foraging decision-making mechanisms should be considered optimised [38], (and see Ref. [39]). Expecting mechanisms optimised for function in the world to always produce optimal behaviour in the lab, however, is too simplistic [40,41]. To understand whether decision-making mechanisms have been optimised to exploit information in the world, we must first discern how an animal is using information in the laboratory. We should then consider whether equivalent information use in the world would produce an optimal outcome. Discerning information use in the lab relies on carefully designed experimental paradigms and rigorous interpretation. It is problematic therefore that cognitive/decision-making paradigms, and the interpretations drawn from them have recently come under fire [1,42,and see Ref. 43]. One key criticism concerns the lack of concordance between many standard laboratory tasks and the real world. If it is critical to know how information use observed in the laboratory would function in the real world (and I argue that it is), then it is crucial that our laboratory tasks are structured such that the opportunities for information use they provide are transferable to relevant scenarios in the real world. For this to occur we should be less willing to use traditional laboratory paradigms off the shelf (which tend not to be high in ecological validity – a consequence of the a-biological roots of experimental psychology – [1]) and more ready to modify and re-design them to better suit our purposes [1,42]. Two cases where custom designed paradigms may have served the authors better than the traditional laboratory paradigms employed, in one case an object-in-place discrimination-learning paradigm [44], and in the other a geometric cues spatial task [45], have recently been discussed in detail [1,5] and the interested reader is directed there.

One elegant study illustrates both the value of carefully modified experimental designs, and the way suboptimal laboratory behaviour reveals the workings of mechanisms that produce optimal outcomes in the world. Vasconcelos *et al.* [46••] presented starlings with choices between outcomes with varying probability. For some choices starlings received immediate feedback as to whether or not they would receive the (delayed) reward, and for other choices they simply had to wait for the reward to be delivered (or not). When given the option to choose between these scenarios, starlings preferred to receive immediate feedback, even when this drastically reduced the available rewards. The authors reasoned that the starlings were valuing the feedback so highly as, in the real world (unlike the experiment), its use would maximise gains, permitting the birds to abandon unsuccessful foraging attempts earlier. A subtle modification to the procedure, providing the feedback immediately before the reward, meant that birds in both condition were effectively abandoning attempts as soon as they were signalled as unsuccessful. This reversed the starlings' irrational preferences.

Conclusions

Integration between functional and mechanistic approaches to behaviour is stimulating much exciting and fruitful research in animal foraging decision-making. Across a range of vertebrate and invertebrate species, studies involving laboratory experiments, real-world observations and experiments, and mathematical modelling are uncovering the complex and numerous influences on animal foraging choices. Continual refinement of the laboratory paradigms we use to investigate information use to better capture the nature and structure of information available in the real world, is key to understanding how information use in the wild facilitates adaptive foraging decisions.

Conflict of interest statement

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In this review, the authors present a series of findings demonstrating that predators do not simply learn to avoid noxious prey, but use information about the prey item's toxicity and nutritional value, to guide adaptive decisions about when to consume it. They rightly argue that our current knowledge of predator cognition in these circumstances is insufficient to properly understand the selection pressures acting on aposematic prey.

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The authors present an optimality model, demonstrating that the reproductive value of information gained from the environment ought to be proportional to the change in behaviour the information elicits. The model is applicable to range of behaviours across many species and contexts. By being able to quantify the value of the information an animal can gather, we can predict the cost it should be willing to pay to gain that information.

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The authors present a model of forager decision-making that accounts for high rejection rates of relatively poor Batesian mimics. The interest value of this paper cuts across a variety of disparate fields. It offers a model of animal speeded decision-making that is commensurate with empirically robust models of human speeded decision-making, provides testable predictions regarding proximate information use by a foraging predator, and offers an ultimate explanation for the success of poor Batesian mimics, in terms of exploitation of predator cognitive biases.

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The authors demonstrate that the salience of prey traits predict the extent to which those traits influence mimetic success of prey: mimics that match the model in a more salient trait, are consumed less often than mimics that match the model on a less salient trait. The authors suggest that prior sensory adaptation, or learning could determine which traits acquire higher salience for predators. A further possibility is that salience (for predators) is driven by traits of the model. A bird looking to avoid attacking a snakes head would do well to develop sensitivity to traits all snake's heads have in common: eyes, but would then be susceptible to mimics with eye spots. Thus, interactions between the predator, and the model (rather than the predator and the mimic) could maintain the visual sensitivities of the predator that the mimic then exploits.

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In this study, bumblebees demonstrated equal preference for two colours that had been reinforced sequentially with pollen-rewards. When reinforced with nectar rewards, however, the bees subsequently preferred the colour rewarded first, over the one rewarded second. The functional significance of this finding, in terms of nectar and pollen foraging, is not yet clear. This study is exciting, however, as it extends the robust differences in information use seen in miner birds when rewarded with carbohydrate- and protein-based foods, respectively, to a different group of foragers. This suggests that nutrient composition of food may be an important proximate cue determining information use while foraging, for generalist foragers across the Animal Kingdom.

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