Review

Information integration and multiattribute decision making in non-neuronal organisms

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Decision making is a necessary process for most organisms, even for the majority of known life forms: those without a brain or neurons. The goal of this review is to highlight research dedicated to understanding complex decision making in non-neuronal organisms, and to suggest avenues for furthering this work. We review research demonstrating key aspects of complex decision making, in particular information integration and multiattribute decision making, in non-neuronal organisms when (1) utilizing adaptive search strategies when foraging, (2) choosing between resources and environmental conditions that have several contradictory attributes and necessitate a trade-off, and (3) incorporating social cues and environmental factors when living in a group or colony. We discuss potential similarities between decision making in non-neuronal organisms and other systems, such as insect colonies and the mammalian brain, and we suggest future avenues of research that use appropriate experimental design and that take advantage of emerging imaging technologies.

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Many organisms, including humans, are continually faced with decisions about what to eat, with whom to mate and where to live. The enormous literature on decision making spans the disciplines of psychology, economics, behavioural ecology, ethology and neurobiology. However, given the fact that brainless (or non-neuronal) organisms comprise the vast majority of all known life, there have been a disproportionately small number of studies on their decision-making abilities. Although non-neuronal organisms lack the complex hardware of brained animals, they may live in environments that are no less complex. Hence, they face many of the same decision-making challenges as organisms with a brain: they must search for resources, choose between resources of varying quality, adapt to changing conditions and choose suitable microclimates to inhabit. We use the term ‘non-neuronal’ to describe those organisms that lack neuron-based information-processing systems. Non-neuronal taxa include the immense variety of organisms in the bacterial domain and plant, fungi and protist kingdoms, but exclude brainless animals such as the Crinaria which, although lacking a centralized nervous system, still possess neuron-based information processing in the form of a nerve net.

For the purposes of this review, we define the term ‘decision’ as follows: the action by an entity (individual organism or group) of selecting an option from a set of alternatives, based on characteristics of the alternatives that the entity can perceive. This definition does not make assumptions regarding the nature and complexity of the decision-making mechanism at work (i.e. the exact mechanisms by which the information on the different characteristics is integrated by the entity while making a choice). It relies only on the observable behaviour of the entity in question. A decision is considered made when the entity moves or points towards an option with a certainty level and repeatability greater than random. This makes possible the comparison of the decision-making capabilities of different entities regardless of their nature or level of complexity. The information relevant to the decision relates to one or more of each option’s ‘attributes’. Attributes are characteristics that describe an option, e.g. nutritive value of a food, humidity level of a shelter, presence/absence of conspecifics. The simplest decisions are ‘single attribute’, where the organism considers only one attribute. For example, cells of the bacterium Escherichia coli, when presented with five different concentrations of glucose, preferentially migrate towards the most concentrated glucose lure (Kim & Kim, 2010). In these experiments, the choice environment is deliberately simplified such that each food varies in only a single attribute: glucose concentration. Examples of non-neuronal organisms making single-attribute decisions include choosing...

Information relevant to the decision-making process is available to an organism both from external sources within the environment and from internal sources within the organism itself. External sources of information can include characteristics such as soil quality, food concentration and the presence/absence of competitors, while internal information can include the organism’s satiation level, memory or mating status. Information can be detected via multiple sensory channels and chemical and physical processes within the organism. The decisions that require the least processing power are those that can be reached using information detected via a single channel, and require only evaluation of a single attribute. Bacteria migrating towards a glucose lure, for example, need only process information on glucose concentration via a single receptor type (Wadhams & Armitage, 2004). However, many decisions in nature are multi-attribute, where each alternative can be characterized by an array of attributes, some or all of which the organism may take into account before making a decision. For example, an organism may need to simultaneously process information on a wide variety of relevant attributes such as the caloric value of a food, toxins in the food (McArthur, Orlando, Banks, & Brown, 2012), the risk of predation (Brown & Kotler, 2004) and suitability of the microclimate (Webster & Dill, 2006). Normative models of decision making assume that individuals make multiattribute decisions by assigning a value to some or all relevant attributes, calculating the sum of all attributes for each option and then selecting the option that has the greatest total value. The idea that an individual should choose whichever option yields the greatest benefit is encapsulated in the economics concept of ‘utility’ (Stigler, 1950). Decision making becomes sophisticated when the utility of available options can only be determined by combining information relating to multiple attributes. The ability to make multiattribute decisions by combining information from a variety of sources is called information integration.

A simplified schema is provided in Fig. 1 that delineates the basic aspects of the decision-making process, and highlights the salient steps discussed in this review.

Strategies for dealing with multiattribute problems can be classified as either compensatory or noncompensatory (Pitz & Sachs, 1984). In noncompensatory decision making, a high value on one attribute always overrides all other relevant attributes. Noncompensatory decisions are usually highly context dependent. For example, a foraging organism might always choose the best quality food irrespective of the risk of predation, or it might always choose to avoid risky areas, irrespective of food quality. In these cases the organism can sense predation risk and food quality, but bases its decisions on only one of these attributes. Non-compensatory strategies have the benefit of being computationally simple, because the organism need only consider a single attribute, thereby disregarding information from all other attributes. In contrast, organisms using compensatory strategies must make trade-offs, so that high values in one attribute can sometimes trump values in the other attributes and vice versa. Compensatory strategies are thought to be computationally intensive, as they require the organism to compare options based on their relative

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**Figure 1.** Simplified schema for categorizing decision making in organisms.
differences, rather than whether one attribute simply exceeds a desired threshold.

In many environments, the ability to make trade-offs between different attributes could lead to improved survivorship and increased fitness. An organism that always chooses the highest quality food, regardless of the predation risk involved in acquiring the resource, would seemingly be at a disadvantage compared to an individual that could weigh up both relative risk and relative gain. However, the computational resources needed to make compensatory decisions might be lacking in brainless organisms, which might therefore be constrained to simple, noncompensatory forms of decision making. In addition, the lack of computational complexity in noncompensatory decision making may allow organisms to make decisions faster, which may be beneficial in some environments.

Here we review studies on information integration and multi-attribute decision making in non-neuronal organisms. In particular we ask: to what extent can non-neuronal organisms use and integrate information when making foraging decisions?

**DECISION MAKING DURING EXPLORATION**

Organisms living in patchy environments are faced with the challenge of locating new resources. Organisms can search their environment using specialized movement patterns, or by growing exploratory structures such as roots, hyphae or pseudopodia (Fig. 2). ‘Adaptive search strategies’ consist of two or more different patterns of movement that can be deployed under different circumstances. Many bacteria achieve chemotaxis by switching from a random walk to a biased random walk through slight adjustments in the frequency of their direction-altering ‘tumbles’. When tumbling, the bacterium pivots rapidly on the spot, randomly reorienting the direction it faces. When swimming towards an attractant, the foraging bacterium responds by decreasing the frequency of tumbles, biasing the direction of movement in the direction of the attractant (Alon, Surette, Barkai, & Leibler, 1999; Macnab & Koshland, 1972). Chemotaxis is widespread among bacteria, and at first glance seems a simple process involving a response to a single attribute of the local environment (the chemical gradient) at each time step. However, studies using *Escherichia coli* have shown that the decision about the direction in which to move requires the integration of internal, external and temporal information. Owing to their small size, *E. coli* cells are incapable of sensing a spatial gradient (Roth, 2013); two receptors spaced at maximal distance across the cell would still be too close to detect any local change in stimulus concentration. This means that the bacterium cannot discriminate between the chemical concentrations of two points in space at the same time, and so cannot rely on spatial information to inform its decisions. *Escherichia coli* adapts its search strategy based on temporal information, which requires a form of memory. The activity of the cell’s membrane chemoreceptors over the past 1 s in time is continually compared with the activity registered during the previous 3 s (Alejandra Guzmán, Delgado, & De Carvalho, 2010; Roth, 2013; Segall, Block, & Berg, 2003).
If receptor activity (corresponding to an increase in the chemical concentration) has increased in this time, the organism suppresses tumbling, and meanders towards the food source. To navigate away from repellent chemicals detected in the environment, the bacterium uses the same system, but increases tumbling frequency in response to a climbing gradient (Alon et al., 1999). These studies show that foraging E. coli integrate information from their present environment (current receptor activity) with information relating to their past environment (receptor activity over the previous 3 s) to decide which search pattern to employ. Several non-neuronal taxa are able to use information about previously searched areas when deciding where to search next. Advancing hyphae of basidiomycetous fungus deposit chemical inhibitors that prevent hyphae from searching the same area twice (Bottone, Nagarsheth, & Chiu, 1998). Cells of the amoeboid protist Physarum polycephalum similarly integrate information from chemical cues deposited in the environment to enhance both their foraging and navigation. During exploration, this slime mould leaves behind a thick layer of nonliving extracellular slime, which acts as a repellent to future local exploration (Reid, Beekman, Latty, & Dussutour, 2013; Reid, Latty, Dussutour, & Beekman, 2012). The memory of which areas have been searched is thus stored in the external environment. Physarum polycephalum is capable of discriminating between conspecific and heterospecific extracellular slime deposits, preferring to explore environments already visited by heterospecifics over those explored by conspecifics (Reid et al., 2013). A possible interpretation of this result is that the slime mould is attracted to the slime trail of heterospecific slime mould, perhaps in order to chase it down for consumption. However, when given a choice between virgin, unexplored territory and one coated in heterospecific deposits, P. polycephalum preferred the former (Reid et al., 2013). This choice hierarchy indicates that P. polycephalum is capable of eavesdropping on the foraging cues of other organisms, potentially enabling it to choose the less depleted of two partially exploited environments, as the diet of heterospecifics is unlikely to overlap completely with P. polycephalum’s diet. In contrast, an environment explored by conspecifics is likely to be stripped of useful resources. Such experiments show that P. polycephalum can integrate information relating to the current environment, as well as its own foraging history and that of other species, in order to make complex decisions in the search for food.

**DECISION MAKING DURING EXPLOITATION**

Once resources have been located, organisms are often faced with further decisions to make, such as deciding which is the best of multiple resources to exploit, and how to trade off conflicting attributes such as food availability and danger. The specific macronutrient composition of food items can also have a strong influence on an organism’s choice of food (Raubenheimer & Simpson, 1993). To maximize their growth, reproductive output or longevity, organisms need to balance their intake of two key macronutrients: protein and carbohydrates. The ratio that optimizes growth is known as the ‘intake target’, and varies between organisms. Individuals face the challenge of balancing their choice of food so that they reach their intake target. To investigate whether P. polycephalum slime moulds are able to actively influence their food intake so that they reach their intake target, Dussutour, Latty, Beekman, and Simpson (2010) presented slime mould amoebae with binary choices between food blocks that varied in their protein to carbohydrate (P:C) ratio. None of the food blocks on their own provided the amoebae with their ideal intake target (about 2:1 P:C), so in order to achieve their intake targets, amoebae needed to cover each food block with a precise amount of biomass through which they digested and absorbed the nutrients. On each of six food pairings, slime mould amoebae exhibited nutritional balancing by adjusting their biomass allocation in exactly the amounts needed to ensure uptake of the optimal P:C ratio. When simultaneously presented with a set of 11 diets that differed in their P:C ratios, amoebae selected the combination and coverage of food blocks that was closest to their intake target. The set-up of this foraging challenge resembles the combinatorial optimization problem known as the Knapsack problem. In the Knapsack problem, one is given a set of items that differ in their mass and ‘value’. The aim is to fill a container (the ‘knapsack’) to less than or equal to its weight limit with a combination of these items, while attempting to maximize the total value of the collection (Martello & Toth, 1990). In Dussutour et al.’s experiments (2010), amoebae were clearly able to integrate information about both protein and carbohydrate content and make a compensatory decision about how to ideally distribute their biomass to reach their preferred intake target.

Non-neuronal organisms can also take into account the varying strengths of different food cues. When a foraging P. polycephalum cell is given a choice between an oat-based food source and an egg yolk-based food source, it shows a strong preference for the egg yolk-based food (Reid et al., 2013). Reid et al. (2013) provided P. polycephalum amoebae with a choice between a region containing chemical cues of past exploration by conspecifics (which is repellent to the organism) that led to a highly attractive egg yolk-based food source and a region without such chemical cues but leading to a less attractive food source (oats). When the different food cues were detectable but somewhat weak (by placing them 4 cm from the amoeba), the slime mould avoided areas that had previously been explored by conspecifics and chose to consume the low-reward oat-based food. However, if the food cues were made stronger by placing the food sources closer to the organism (0.5 cm), it shifted its preference to ignore the extracellular slime and attain the highly rewarding egg yolk-based food (Reid et al., 2013). The slime mould thus makes a compensatory decision trading off whether an area has been explored and the strength of the different food cues.

A few experiments have also shown that P. polycephalum can make sophisticated trade-offs between overall access to food and exposure to danger. All else being equal, slime mould amoebae prefer high-calorie foods over low-calorie foods (Latty & Beekman, 2010). Slime moulds are also particular about microclimate, and whenever possible will avoid light exposure, presumably to avoid the risk of dehydration associated with sunlight (Latty & Beekman, 2010, 2011a). Faced with a choice between a high-quality but illuminated patch, and a lower quality but darkened patch, slime moulds only select the illuminated high-quality patch when it contains food that is at least five times more concentrated than food present in the ‘safe’ alternative (Latty & Beekman, 2010).

The trade-off between reward and danger extends beyond the choice between risky food patches, to shape the structure of the organism itself. Slime mould amoebae connect food resources with transport tubules built from protoplasm, and these tubules are most likely to follow the shortest path between food items (Nakagaki, Kobayashi, Nishiura, & Ueda, 2004; Nakagaki, Yamada, & Hara, 2004; Nakagaki, Yamada, & Tóth, 2000; Tero et al., 2010; Reid & Beekman, 2013). When half of the region between two diagonally placed food sources was illuminated with a strong light source, the slime mould faced a trade-off between connecting the food sources via the shortest path and avoiding the lit region (Nakagaki et al., 2007). To solve this problem, the organism altered the course of its connecting tubule to minimize the amount of biomass that was exposed to light. Importantly, the slime mould did not simply avoid the light altogether, as this would have resulted in an overly elongated tubule. Rather, it calculated a path that was relatively short, while also keeping light exposure to a minimum: a successful demonstration of compensatory decision making applied to a path selection problem.
Like many other foraging organisms, the roots of a plant explore their environment in search of resources. Plant roots extend through the soil microenvironment, searching for soil regions with the most favourable combination of nutrients and moisture, while trying to avoid competition with neighbouring root systems. Hence, plant roots need to decide which soil patches to exploit and which to avoid. In general, roots avoid foraging in patches that have already been exploited by a competitor, and they preferentially exploit nutrient-rich soil patches over nutrient-deficient soil patches (Cahill & McNickle, 2011; McNickle, St Clair, & Cahill, 2009). For instance, when two *Abutilon theophrasti* plants were grown beside each other in soil with homogeneous nutrient availability, their root systems strongly avoided one another (Cahill et al., 2010). However, when a nutrient-rich patch was placed between the two plants, each plant’s root system overrode its usual avoidance behaviour, and root mixing occurred in the high-quality region (Cahill & McNickle, 2011; Cahill et al., 2010). In other species (Avena sativa), foraging roots employ the opposite strategy, ignoring the roots of heterospecífics under low-nutrient conditions, but expressing avoidance under conditions of homogeneously high resource availability (Litav & Harper, 1967). Foraging plant roots may choose to avoid neighbouring root systems to avoid searching depleted areas (Schenk, Callaway, & Mahall, 1999), or to minimize competition when the neighbouring root system is recognized as belonging to a closely related, nonself plant (Dudley & File, 2007; Murphy & Dudley, 2009). Alternatively, roots may proliferate around areas inhabited by competing root systems in order to pre-empt resources that would otherwise be available to the competitor (Bartelheimer, Steinlein, & Beyschlag, 2006), or they may ignore neighbouring roots altogether (Mommer et al., 2010). Multiple combinations of these strategies may be employed by the same species of plant depending on additive cues from the environment such as nutrient concentration, indicating that compensatory decision making is widespread in plants (Cahill & McNickle, 2011).

**MAKING DECISIONS TOGETHER**

When individual non-neuronal organisms group together to form colonies, they gain a new source of data to incorporate into their decision-making strategies: signals from their neighbours. This new channel of information can be integrated with that from their own internal physiology and from other external sources in their surrounding environment, to enhance the individual’s decision-making abilities, even beyond what they could accomplish alone.

In search of food on resource-limited substrates, colonies of the bacterium *Paenibacillus dendritiformis* take on a dendritic morphology reminiscent of a slime mould plasmodium or basidiomycetous fungus (Fig. 2d). This shape arises as the colony self-organizes to overcome a complex trade-off. The individual bacterium require a high density of neighbours to collectively generate a surface layer of lubricant through which they can swim; however, the resource-limited substrate contains insufficient food to sustain a dense population (Ben-Jacob & Levine, 2006). The bacteria solve this multiconstraint optimization problem by accurately adjusting the number of individuals within each branch such that a sufficient localized density for locomotion is reached, while not exceeding the carrying capacity of the substrate (Ben-Jacob & Levine, 2006; Harshay, 2003). This group-level search strategy is decided by individual cells each integrating information on local nutrient and lubricant levels. Individuals must make a compensatory decision about whether to join a branch, in which they balance the choice between increasing group size for maximal lubrication and limiting group size to prevent starvation and subsequent death of the branch.

Groups of Myxobacteria, such as *Myxococcus xanthus*, integrate information about individual and group-level starvation to make collective decisions. Myxobacteria use a surface-exposed protein called the C-factor to externally display information about their own internal physiological status (Ben-Jacob, Becker, Shapiro, & Levine, 2004). The bacteria use this information to perform different cooperative group behaviours depending on the group starvation consensus. At an advanced level of starvation, the cells aggregate and move in circular motions, both clockwise and anticlockwise, around a centre of rotation that will become the fruiting body, the site of sporulation (Koch, 1998). Under low levels of starvation, the bacteria move as roving groups of cells. The number of cells within the group must be high enough for their secreted lytic enzymes to digest prey bacteria in the surrounding environment (Koch, 1998). Deciding which group behaviour to undertake requires integration of internal and external information relating to starvation signals, a consensus decision based on the different starvation levels of all members of the group, and recognition of the group number exceeding a critical threshold.

**SIMILARITIES WITH OTHER DECISION-MAKING SYSTEMS**

Despite lacking the cognitive architecture typically associated with information processing, non-neuronal taxa are still capable of integrating information from multiple, disparate sources from within both their external environment and their own internal physiology. We have presented several examples of compensatory decision making by non-neuronal taxa and of unicellular organisms incorporating information from their neighbours when making their choices. Taken together, the body of literature strongly suggests that brains or even simpler neuronal networks are not prerequisites for complex decision making.

The mechanisms underlying the decision-making strategies of non-neuronal taxa may be strikingly similar to those observed in brained organisms. Evidence from slime moulds suggests that non-neuronal organisms may even be subject to the same cognitive constraints as humans. One study indicates that slime moulds are susceptible to the same kind of ‘irrational’ decision making previously only seen in humans and other animals (Latty & Beekman, 2011b). When given a choice between two options that varied in two competing attributes, in this case food concentration and light intensity, slime moulds did not show a strong preference for one option over the other. However, in the presence of a third option inferior to both original options (a decay), slime moulds changed their preference (Latty & Beekman, 2011b). Such behaviour is irrational, as the presence of an inferior option should not affect the organism’s original preference. A related study found that slime moulds, like humans, are subject to speed/accuracy trade-offs, but only when presented with a difficult task set (Latty & Beekman, 2011a). These similarities raise the tantalizing possibility that decision making in non-neuronal and neuronal organisms is based on the same underlying principles.

Decision making in brains has been modelled using a variety of approaches, most of which are based on the idea that evidence in favour of each alternative accumulates over time until some decision threshold is reached. In ‘tug-of-war’ models, decisions are based on the relative weights given to alternative options. Once sufficient information has accumulated, one option is chosen. Because such choice models require some sort of comparison between the different options, decision making becomes more difficult the more options there are or the closer the options are in value (Kacelnik, Vasconcelos, Monteiro, & Aw, 2010). An alternative decision-making model, coined the sequential choice model by Kacelnik et al. (2010), assumes no comparisons among different options. Instead each option is considered sequentially, and the first
that reaches the decision threshold is chosen (Bogacz, Brown, Moehlis, Holmes, & Cohen, 2006). The fundamental difference between the two decision-making models is the existence of a trade-off between decision accuracy and cost of evaluation in tug-of-war models, but not in the sequential choice model. Thus, when the number of choices increases, the tug-of-war model predicts that decision time will increase, whereas the opposite is predicted under the sequential choice model (Kacelnik et al., 2010).

In slime moulds, biomass is transported through tubules that widen when in contact with resources. It has been argued that competition between biomass flows may be analogous to the build-up of ‘evidence’ thought to occur in human brains (Latty & Beekman, 2011a). Although the specific mechanism is different (neuron firing rate versus biomass flow rate), the underlying principles appear to be the same. A similar idea was proposed by Marshall et al. (2009), who showed that positive feedback could underlie decision making in systems as dissimilar as ant colonies and human brains. Similarly, Nicolis, Zabzina, Latty, and Sumpter (2011) argued that positive feedback could account for the irrational behaviour observed in both slime moulds (Latty & Beekman, 2011b) and ant colonies (Sasaki & Pratt, 2011). We suggest that decision-making processes in brains (Usher & McClelland, 2001), slime moulds (Nakagaki et al., 2000) and social insects (Pratt, Mallon, Sumpter, & Franks, 2002; Seeley, 2010) are all based on the accumulation of information and positive feedback. Whether these similarities are purely superficial or whether they point to a deeper principle underpinning decision making and information processing in biological systems remains to be tested.

CHALLENGES AND FUTURE

The Principal challenge facing future behavioural studies of non-neuronal organisms lies in appropriate experimental design. The long history and extensive literature relating to information processing, memory, learning and problem solving in neuronal animals should provide the scaffolding for the design of experiments investigating these phenomena in non-neuronal organisms. This approach has proven fruitful with the labyrinth maze, first used to explore the mental processes of rats (Small, 1901), and recently successfully applied to slime moulds (Nakagaki et al., 2000; Reid & Beekman, 2013) and fungal hyphae (Hanson, Nicolau, Filipponi, Wang, & Lee, 2006). Similarly, the mechanisms of problem solving and decision making in slime moulds have been explored using the classical Y-maze choice set-up (Reid et al., 2013, 2012), the U-shaped trap maze used in robotics for testing autonomous navigation (Reid et al., 2012), and the protocols used to study choice and irrationality in animals and humans (Latty & Beekman, 2009, 2011b). The difficulty and importance of appropriate experimental design are illustrated by the history of research seeking to demonstrate learning in the protozoan Paramecium caudatum. A host of studies stretching back to 1911 have claimed to demonstrate discrimination learning and the learning of tube escape behaviour in P. caudatum. For each of these studies, however, there exists a slew of counter-studies demonstrating that the original evidence resulted from artefacts (recounted in Minge & Armus, 2009). Artefacts are difficult to avoid when studying the behaviour of unicellular organisms, because the environmental scale at which they function is so removed from ours. Researchers studying the behaviour of brained animals take care to minimize familiar confounding factors such as distracting visual, auditory and olfactory stimuli, seasonal changes and the animals’ past experience. It is intrinsically more difficult to account for such minute and unfamiliar factors as surface ion accumulation or homogenous culture mixing: environmental factors pivotal to unicellular functioning, yet overlooked in past experiments purporting to demonstrate unicellular learning (Minge & Armus, 2009). One solution to this problem is to work with non-neuronal organisms that function at a scale closer to our own, which perhaps explains the disproportional success of behavioural experiments using macroscopic slime mould rather than microscopic unicellular model systems.

Innovative design of experimental apparatus and techniques offers another avenue for successful research. Where the challenge is a question of spatial scale, live cell imaging technologies, which have progressed dramatically over the last decade, can be of great use. Tools such as atomic force microscopy, traction force microscopy and total internal reflection microscopy have found wide application in cellular and subcellular research, especially where the molecular dynamics and mechanical properties of individual cell movements are investigated. These tools have the potential to uncover the underlying functional mechanics of unicellular decision-making behaviour, in the same way that neurobiology informs animal behaviour. We suggest that these established and powerful tools designed for detailed observation of cell activity should be incorporated into future unicellular behaviour experiments.

The studies reviewed here clearly demonstrate the capacity of non-neuronal organisms to make complex decisions. The most important area of future study is to prove the potential adaptive significance of this decision-making behaviour. The study by Latty and Beekman (2009) is one of the few to attempt this, by demonstrating that P. polycephalum amoebae had greater foraging success (measured by weight gain) when grown in environments with patchy food distribution, and gained less weight in more uniformly distributed foraging environments. Since the number of spores that can be produced by a plasmodium is directly related to plasmodium mass, weight gain is an excellent proxy for reproductive fitness in plasmodia. Future studies should follow this example, and be specifically designed to quantify adaptive outcomes of certain decision-making behaviours in non-neuronal organisms.

Acknowledgments

This work was funded by Australian Research Council grants to T.L. (DP140103643 and DP110102998) and M.B. (FT120100120 and DP140100560).

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