Mapping Out the Landscape: A Multi-dimensional Approach to Behavioural Innovation

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Abstract

Transformations in the "behavioural innovativeness" of species—broadly, the capacity to generate new or novel behaviours—are often associated with significant evolutionary shifts in cognition. Whilst this assumption is intuitively and theoretically appealing, it lacks strong empirical support. One barrier to such support is the lack of a good measure of behavioural innovation. This paper offers a solution to this problem by breaking down innovation into its components and presenting a novel multi-dimensional framework for characterising and comparing putative cases of behavioural innovation.

Key words: Cognition, major transitions, innovation, insight, creativity, novelty

1. Introduction

In an evolutionary context the most successful individuals are those whose behaviour best suits their ecological niche, whether it be in outcompeting others for resources, being adept at avoiding predation, or so forth. Environments are rarely static, however, and as they change so too must the behaviour of the organisms within them if they are to remain well-suited to the challenges they face. One potent means via which organisms can maintain their behavioural adaptedness over time is via *behavioural innovation*: "the introduction of a new or modified learned behaviour not previously found in the population" (Reader & Laland, 2002, p. 14). Classic examples of innovation include the exploitation of a novel food source or the invention of a novel tool type, but the pool of possible behavioural innovations is almost endless. Whilst of obvious importance in driving individual adaptedness, behavioural innovation has been linked to larger scale evolutionary patterns in both morphology and culture (Arbilly and Laland 2017; Tebbich et al. 2016), such as the rapid diversification of the beaks of the Galapagos finches (Tebbich, Sterelny, and Teschke 2010). More proximately, comparative psychologists associate behavioural innovativeness with a range of cognitive capacities including insight, problem solving, causal cognition, and creativity (Reader and Laland 2003).

Despite the broad empirical and theoretical interest in behavioural innovation within various fields, what constitutes a behavioural innovation is not settled. There are multiple, conflicting definitions of the phenomena in the literature depending on research background and interest (table 1). For my purposes here, it is worth noting that these definitions tend to be binary (i.e., a behaviour is an innovation, or not; a cognitive mechanism is innovative, or not), and split regarding the question of whether innovation refers to a unique process[1] (as in definition (iii)), or type of behavioural product (as in definition (i)), or some mixture of the two as in definitions ((ii) or (iv)) (Reader and Laland 2003; Arbilly and Laland 2017).

That there are multiple definitions of behavioural innovation in the literature is hardly surprising given the broad interest in the phenomena. A non-trivial amount of ink has been spilt trying to establish a definition that suits all parties and reflects the biological realities of the phenomenon (Overington et al. 2011; Reader and Laland 2003; Ramsey, Bastian, and Van schaik 2007b; 2007c; Tebbich et al. 2016). Establishing what cognitive processes underlie behavioural innovation and its evolutionary implications, however, does not (and should not) require us to have a concrete and agreed definition from the outset. Rather, we can come to learn what is the best definition through broad enquiry about innovation aimed at better understanding the phenomena and refining our ontology as we go. It is in this spirit that the multi-dimensional framework for characterising and comparing putative cases of behavioural innovativeness presented in this paper has been developed. It is aimed at helping us to focus our investigations of the causes of behavioural innovation, the evolutionary role of innovation, and the evolutionary drivers of innovativeness within species. Significantly, this framework (inspired by Arbilly and Laland's (2017) discussion of the "magnitude of innovation") sits

[1] As in a process which is qualitatively distinct from related processes such as exploration and learning.

outside of the debate regarding the appropriate definition of innovation and its nature, acting as a tool for guided inquiry intended to help resolve such a debate.

Definition	Source
(i) "An innovation can be: a solution to a novel problem, or a novel solution to an old one; a communication signal not observed in other individuals in the group (at least at that time) or an existing signal used for a new purpose; a new ecological discovery such as a food item not previously part of the diet of the group."	(Kummer and Goodall 1985, 205)
(ii) "the introduction of a new or modified learned behaviour not previously found in the population"	(Reader & Laland, 2002, p. 14)
(iii) "the process that generates in an individual a novel learned behaviour that is not simply a consequence of social learning or environmental induction."	(Ramsey, Bastian, and Van schaik 2007a, 393)
(iv) "In the physical realm, a behavioural innovation is a new, useful, and potentially transmitted learned behaviour, arising from asocial learning (innovation by independent invention) or a combination of asocial and social learning (innovation by modification), that is produced so as to successfully solve a novel problem or an existing problem in a novel manner."	(Carr, Kendal, and Flynn 2016, 1515)

Table 1: Four prominent definitions of innovation in the literature of comparative psychology.

My analysis begins by introducing Arbilly and Laland's (2017) novel quantitative measure *the magnitude of innovation*—the degree to which an innovative behaviour is novel (§2.1) One of the advantages of employing such a measure is that it allows us to compare and contrast the impacts of different types of innovation in an evolutionary context. Using some paradigmatic examples of foraging innovation, I show, however that magnitude as construed by Arbilly and Laland (2017) has limited usefulness as a measure of innovativeness beyond the modelling context for which they developed it (§2.2). In the remainder of the paper (§3), I demonstrate how their simple magnitude measure can be further developed for broader use. I begin by using discussions of the wire-bending behaviour of Betty, the New Caledonian Crow to break down innovation into its components (§3.1). Although further evidence has now undermined this interpretation, Betty's behaviour was seen by many to be a paradigmatic case of animal innovation. Understanding why this was so and looking at why it is no longer considered as such, gives insight into the components or parameters of innovation. We can then represent these as a multidimensional space which allows us to represent variation between innovation along these different parameters (§3.2). This framework has several virtues (§3.3): it allows us to capture similarities and differences between cases of behavioural innovation that are frequently obscured in discussions of innovation, it allows us to identify commonalities within clusters of behavioural innovation in the tree of life that can then be empirically investigated, and it allows us to identify the impact of major transitions in cognition on the innovativeness of species. Untimely, it will allow us to test the idea that transitions in cognition generate transformations in behavioural innovativeness and other claims about the underlying causal history of novel behaviours of this type.

2. Magnitude of Innovation

2.1 Ordering innovations on a scale

Arbilly and Laland (2017) propose a novel quantitative measure *the magnitude of innovation* for use in modelling the evolution of behavioural innovation. They define magnitude of innovation as the degree to which an innovative behaviour is novel, the measure being quantifiable as the deviation of an innovation from the mean behaviour of the population.

Arbilly and Laland's (2017) measure offers a principled way of ordering innovations from low magnitude to high magnitude (see figure 1). They demonstrate, through a variety of models, the utility of the measure in thinking about the evolutionary implications of innovations of different degrees of novelty. Whilst this simple approach to measuring innovation is fit for Arbilly and Laland's (2017) purpose in modelling evolution, magnitude by itself is insufficiently nuanced for the further purpose of classifying different cases of innovation in the real world. In the next section I make these limitations clearer, before offering a more developed account of magnitude in Section 4 which overcomes these challenges.

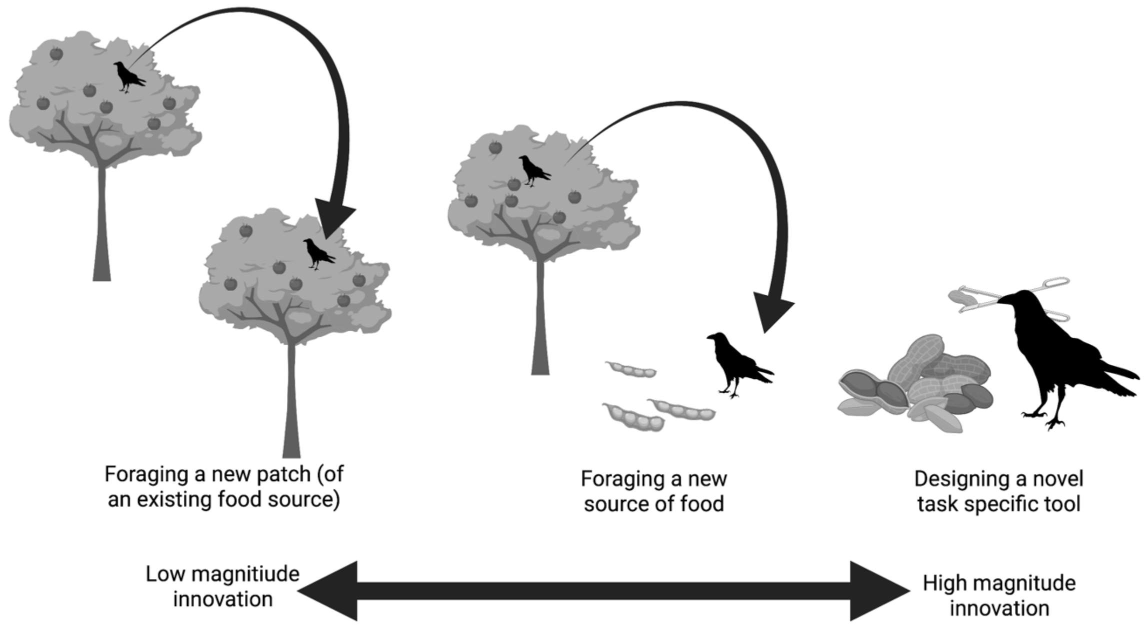

Figure 1: Magnitude of innovation as a way of ordering behavioural innovations according to the degree of novelty from the behavioural norm that they represent. The putative examples and ordering are drawn from Arbilly and Laland (2017). Created with biorender.com

2.2 Limits to magnitude

Ordering innovations from low to high magnitude is not straight-forward, particularly when we are looking at innovations in multiple species and across different domains (i.e., foraging versus predator avoidance). To illustrate, consider two highly cited examples of innovation:

(a) *Imo potato washing:* In the 1960s, primatologists studying in the behaviour of a troop Japanese macaques left sweet potatoes on a beach to entice the local macaques into the open to feed. To their surprise one young female Japanese macaque, Imo, was observed to spontaneously wash her sweet potatoes in the sea before eating them. Other macaques in the troop observed Imo's potato washing innovation and the practice subsequently spread rapidly throughout the population and was embellished upon (Kawai 1965). Imo's behaviour was startling because, while researchers had observed the macaques brushing dirt off their food, they had not observed any individuals washing food—this was a novel behaviour to the group, and a clear example of behavioural innovation.

(b) *British tit milk bottle opening:* First observed in the 1920s but ultimately seen to independently arrive over multiple sites in the 20th Century British tits (great tits and blue tits) have learned to peck the foil caps of milk bottles left on doorsteps to get drink the cream (Hinde and Fisher 1951; Fisher and Hinde 1949; Lefebvre 1995). Whilst neither the motor action itself (pecking), nor the context in which pecking occurs (foraging) are novel, the food source being accessed clearly is and hence why this is also considered a clear case of behavioural innovation.

With our cases clear, let us now consider how we should score them regarding magnitude.

Whilst both are foraging innovations, they differ along some dimensions. When potato washing, Imo employs a motor action (wiping) which is already part of the repertoire of her population. She also uses the action to solve a problem where that that motor action is typically used (to clean dirty potatoes). What is novel is that she is using the behaviour in a different context than is typically seen in the population (washing in water rather than brushing on land). In contrast, although the British Tits are also using an existing motor action in their repertoire (pecking), it is to access an entirely new food stuff (cream) found in an entirely novel context (milk bottles on doorsteps). Whilst both the milk bottle opening and potato washing would not be classed as high magnitude innovations on Arbilly and Laland's (2017) scale, neither falls neatly into the low magnitude category, and I struggle when trying to assess which is 'more innovative' than the other. This is because how exactly we quantify "deviation from mean behaviour of the population" is un-specified by Laland and Arbilly (2017)[2] and it is unclear how to integrate the varying degrees of novelty that the two innovations exhibit across the different dimensions of innovation into an overall measure. More is needed if we are to use the concept of magnitude in an empirical context.

In what follows, I offer an alternative approach which builds on the basic insight offered by Arbilly and Laland – that the deviation of an innovation from the mean behaviour of the

[2] This is not a criticism of their work; they do not need an empirically tractable specification for their purposes.

population can be used to order novelties—which is empirically tractable and useful. I begin by breaking down innovation into its basic dimensions in more detail.

3. The multi-dimensional alternative

3.1 Opening the black box: an analysis of a paradigmatic case of innovation

There are several dimensions of characteristic of the behaviours which are cited in the literature when talking about whether something is an innovation. The case of Betty the New Caledonian Crow, once classed a paradigmatic example of a high magnitude behavioural innovation, illustrates well what these are.

Famously, Betty unexpectedly appeared to spontaneously bend a straight piece of garden wire in her enclosure into a hooked tool in order to lift a small food-bated bucket from a plastic well (Weir, Chappell, and Kacelnik 2002). Whilst New Caledonian Crows do manufacture and use twig and leaf tools in the wild (Hunt and Gray 2004), Betty had no experience with wire and appeared to be manipulating it in an innovative manner to solve a novel problem. In follow up studies Betty was also observed to manipulate another novel material (aluminium strips) in the same manner to make a hooked tool to solve similar problems (Weir and Kacelnik 2006).

Unsurprisingly, Betty's behaviour was lauded as a paradigmatic example of animal innovation and animal intelligence. Subsequent observations and experiments by Rutz et al. (2016) have taken some of the sheen off Betty's feats. Specifically, they show that the bending behaviour and particular motor actions observed in Betty are expressed by wild birds in bending their natural hooked stick tools so she may have simply been demonstrating a relatively stereotypical species-typical behaviour rather. This new evidence does not undermine the claim that Betty's wire bending is a behavioural innovation of some order (it is a novel solution to a novel problem), but it does undermine its status as an extreme example of animal intelligence and of a high magnitude innovation. Looking at the original descriptions of Betty's wire bending innovation (before more information about the baseline behaviours of the species were known) remains informative of what a paradigmatic behavioural innovation looks like.

Betty's behaviour was viewed as a maximal case of animal innovation—something very startling and special. Why? In the original paper describing the behaviour Weir et al. (2002, 981) state,

> "…at least one of our birds is capable of novel tool modification for a specific task. In the wild, New Caledonian crows make at least two sorts of hook tools using distinct techniques but the method used by our female crow is different from those previously reported and would be unlikely to be effective with natural materials. She had little exposure to and no prior training with pliant material, and we

> have never observed her to perform similar actions with either pliant or nonpliant objects."

Even in presenting evidence to counter the dominant analysis Rutz et al. (2016, 1), offer the following as reason why Betty's behaviour "shook the field of comparative cognition",

> "Although it was known at the time that these tropical corvids manufacture hooked foraging tools from forked twigs in the wild, Betty's wire-bending method appeared to be a spontaneous, innovative solution to a novel problem."

Drawing on both these quotes, three features of Betty's behaviour appear to have been particularly salient to the assessment of it as being a high magnitude innovation:

(i) Her apparent lack of experience with the wire (and other pliant material),
(ii) the apparently novel behavioural action (bending) which she performed, and
(iii) the novelty of the problem she solved.

Other features of the Betty case typically emphasised are:

(iv) spontaneity of the behaviour (i.e., that it arose without extensive trial and error), and
(v) that it was robustly repeated (i.e., suggesting that it was not accidental or undirected action).

Whilst not displaying analogues of all these features, Imo's potato washing and the British tit milk bottle opening display some of them. The potato washing innovation involved analogues to (iii), (iv) and (v). The tit milk bottle opening is similar with respect to (i), (iii)[3], and (v). In short, it appears necessary for something to be an innovation that it has at least some of these properties. In the next section, I use this insight to build my novel framework for thinking about and representing behavioural innovation.

3.2 A more nuanced approach: mapping behavioural innovation

The five different dimensions of innovation outlined in the previous section can be represented in simple a multidimensional space with simple orderings on the dimensions which draw on Arbilly & Laland's (2017) magnitude concept (figure 2). The centre of the space represents a complete lack of innovation (i.e., behaviours which do not deviate from the mean behaviour of the species in any respect, and entirely lack spontaneity and robustness). The further you move from the centre of the space along each of the dimensions (i)-(iii) the more novel the behaviour is in that dimension. Similarly, spontaneity and robustness increase along dimensions (iv) and (v) respectively. When we map behaviours in this space (as shown for Betty's behaviour as originally assessed in the darker line, and as assessed following revisionary evidence in the lighter line), we can represent overall magnitude of innovation. High magnitude innovations

[3] It is likely this behaviour arose through trial and error, rather than spontaneous innovation (Aplin, Sheldon, and Morand-Ferron 2013)

will produce mapping which tend towards the edges of the space along the various parameters (as for the original assessment of Betty's behaviour). Lower magnitude innovations will produce mappings which lie closer to the centre.

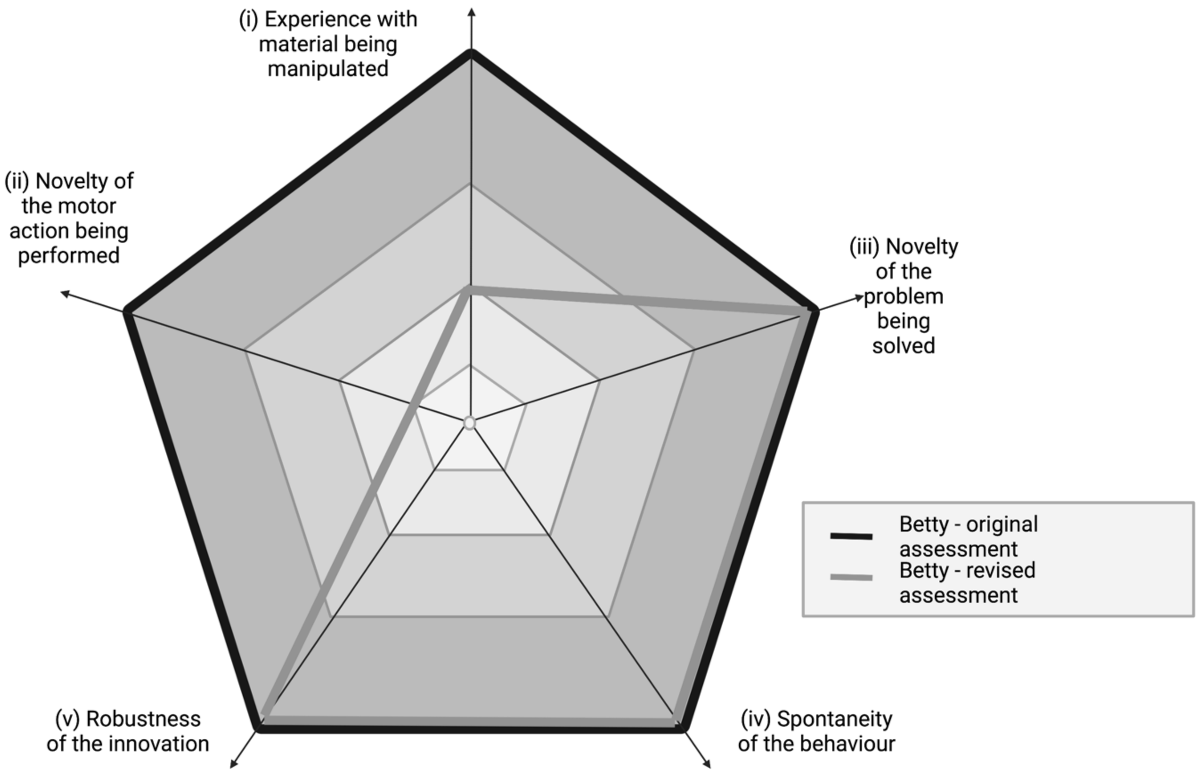

Figure 2: Comparing the original assessment of Betty's behaviour as a maximal innovation to the revised assessment which considers the evidence of tool bending behaviour in the wild. Created using biorender.com

Note that, for the purposes of simplicity of presentation here I have used a simple radial graph to represent the dimensions of innovation. In practice, a hyperdimensional space may be more objective. For example, representations within such a hyperdimensional space would not be sensitive to the arrangement of the dimensions in the way that they are in a two-dimensional radial graph. Whilst a reason to be cautious in use of the two-dimensional representation I think such a graph still has value (see following section). Turning now to the virtues of this overall approach.

3.3 Virtues of the multidimensional framework

There are several benefits to characterising behavioural innovations multidimensionally and representing those characterisations visually as I have here.

I. A multidimensional approach allows us to make more accurate and nuanced comparisons of cases of innovation

Using a multidimensional approach to behavioural innovation allows us to compare examples of innovation and their degree of novelty without having to come up with an overall measure of novelty required for a magnitude assessment. As outlined in §2.2, whilst both Imo's potato washing and the British tit milk bottle opening fall somewhere in the middle of Arbilly and Laland's (2007) measure (both are foraging for new food), this tells us little about key features of the cases and tends to obscure important differences. When we focus merely on overall magnitude, for example, we lose sight of the fact that that British tit milk bottle opening innovation involves accident and trial-and-error, whilst Imo's behaviour is thought to have been far more directed in nature. This sort of difference can however be easily captured in this multidimensionally without obscuring that the cases are of similar magnitude at the coarse grain (see figure 3).

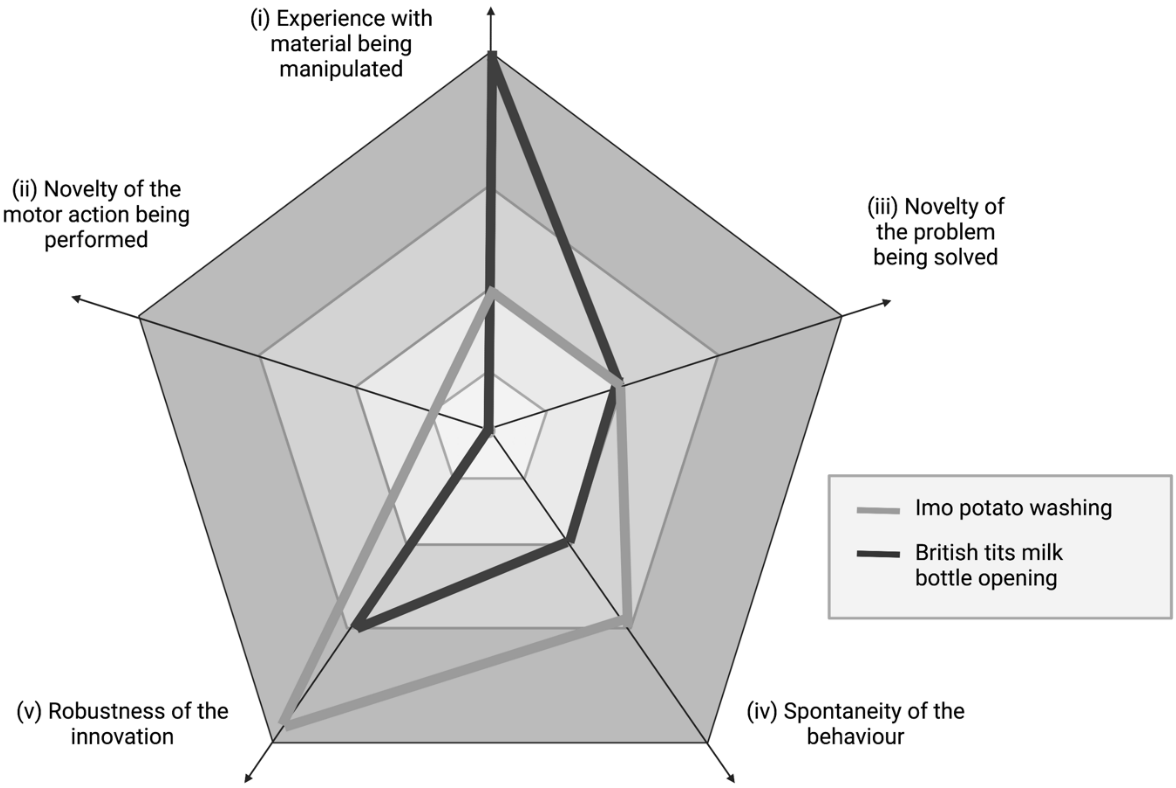

Figure 3: The multidimensional approach allows us to capture both magnitude (as the area within the mapping of a behaviour) and variation along dimensions of innovation. Created using biorender.com

II. The framework allows comparisons of innovativeness within species

Another virtue of the framework is that it allows us to both compare the features of different innovations and simply and easily look for patterns in those features and think about their significance. For example, within species we can explore the drivers of innovation by asking questions like: do macaque behavioural innovations typically produce a similar mapping? If they do, it seems likely that there are common mechanisms and constraints in their cognition of some sort. Similarly, we can look at how innovativeness changes over the lifetime of individuals within species and consider how this ties to life history. Do the innovations of younger individuals, differ from those of older individuals? Why? The novel framework outlined here provides a systematic way to respond to these questions because it makes it possible to easily and simply compare the innovativeness of individual macaques, and consider how their life history and experience influences the trait.

III. The framework allows comparison of innovativeness across species and clades.
Phylogenetic comparisons are a key source of evidence for hypothesising about the role of cognitive evolution in transitions in innovativeness. Without a clear way of representing innovativeness and differences in innovativeness between species, such phylogenetic comparison is difficult. The multidimensional framework offers a means to make such comparisons in a systematic way by allowing us to look for types of mappings which are exemplified by a particular lineage or clade (see hypothetical example in figure 4). For example, if there are no innovations observed involving novel motor action within a lineage (as in the uppermost three lineages in the phylogeny in figure 4), this seems reasonable reason to believe that there is some sort of constraint acting on innovation along this dimension. In a similar way, the presence of lots of innovations which involve engagement with novel materials, might imply an important role for neophilia in innovation in that lineage.

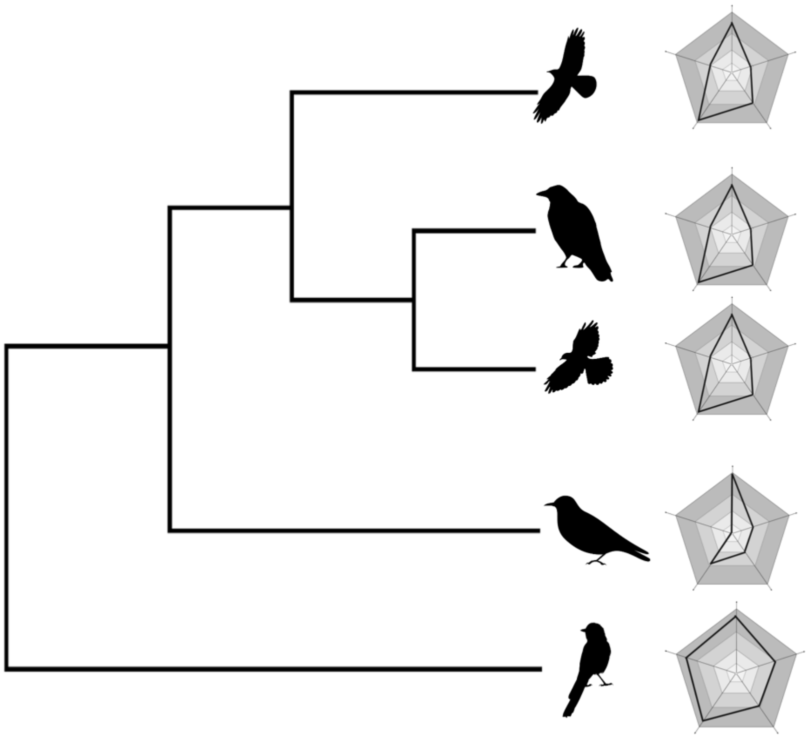

Figure 4: Looking at the distribution of mappings in a phylogenetic context can be telling of the underlying mechanisms and their evolutionary history.
Created using biorender.com

Using the multidimensional framework, we can look not only at clusters in types of innovation within the tree of life but also at patterns in how innovation changes over evolutionary time. For example, there are phylogenetic patterns in the mappings we would expect to see if transitions in innovation have been driven by transitions in cognition (assuming those transitions are marked in the way that transitions in biological organisation are). Specifically, we would expect to see that there are apparent path dependencies in the mappings (you only get mapping *x* evolve, after mapping *y*).

4. Conclusions

The multidimensional framework for measuring, representing, and theorising about innovation presented in this paper is novel for its focus on capturing the heterogeneity of the many different types of novel behaviours which fall under the umbrella of *behavioural innovation*. This heterogeneity is key to understanding both the many ways in which innovations arise, but also the role of innovation in evolution. Whilst a valuable and informative way to represent and think about innovation, the framework is only a first step in a broader endeavour. As we learn more about innovation, the dimensions within the framework may change, interdependences between the dimensions may become apparent, and scales will be refined. The framework offered here allows us, however, to begin to answer these questions in a way that existing definitions cannot and in this way is a significant contribution to the literature.

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