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Instinct to insight: a variation-based framework to test hypotheses about how animals solve problems

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Opinion piece

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Problem-solving is an integral part of most animals' lives. There are generally four types of solutions animals may use: innate, learned previously, learned de novo or insightful. Identifying the types of solutions animals use can be difficult, especially with the trend of having increasingly difficult requirements to test hypotheses in this field. These requirements often amount to proving a negative, which may be impossible. Therefore, here we develop a novel framework for testing hypotheses that can help distinguish the types of solutions animals may use that does not require proving a negative. This framework is based on distinct patterns of *qualitative* and *quantitative* variation *between* and *within* individuals. Because this framework does not require knowledge of animal's prior history nor that the problem be evolutionarily novel, it can be used with a variety of animals, experimental designs and settings. We suggest this framework could serve as a valuable tool in expanding how we study animal problem-solving, especially in the types of animals studied. Studying problem-solving in a wide variety of animals would allow us to form a better understanding of the problem-solving abilities different brain sizes and structures confer and, more broadly, the evolution of those abilities.

1. Introduction: how animals solve problems

From removing a bit of dust off an eye to avoiding starvation, solving problems is an integral part of the lives of most animals [1,2]. By problem we refer to cases in which an animal finds itself in a situation where it must take action to change the situation in order to achieve its target (definition modified from [3]). The definition of a problem should be broad because problems can take a variety of forms [1]. Within each of these forms, problems can further vary according to the animal's natural history and behaviour, as can the ways in which animals solve them. Nevertheless, it is possible to classify the types of solutions animals may use into four general categories: innate, learned previously, learned de novo or arrived at through insight.

Innate solutions are encoded in an individual's genetics and do not require any form of learning [4–6]. For example, many spiders subdue prey using an innate solution of wrapping the prey in silk (figure 1). Recently, hatched spiderlings successfully execute this solution in their first attempt at capturing prey without any form of learning [8,9].

Learned solutions can be divided into two categories: learned previously or de novo. Previously learned solutions can be acquired by gathering information from personal experience [6]. For example, honeybees can use previously learned information (e.g. coloured markers) to solve mazes [10]. Previously learned solutions can also be acquired from observing the experience of other individuals [11–13]. For example, young *Sapajus libidinosus*

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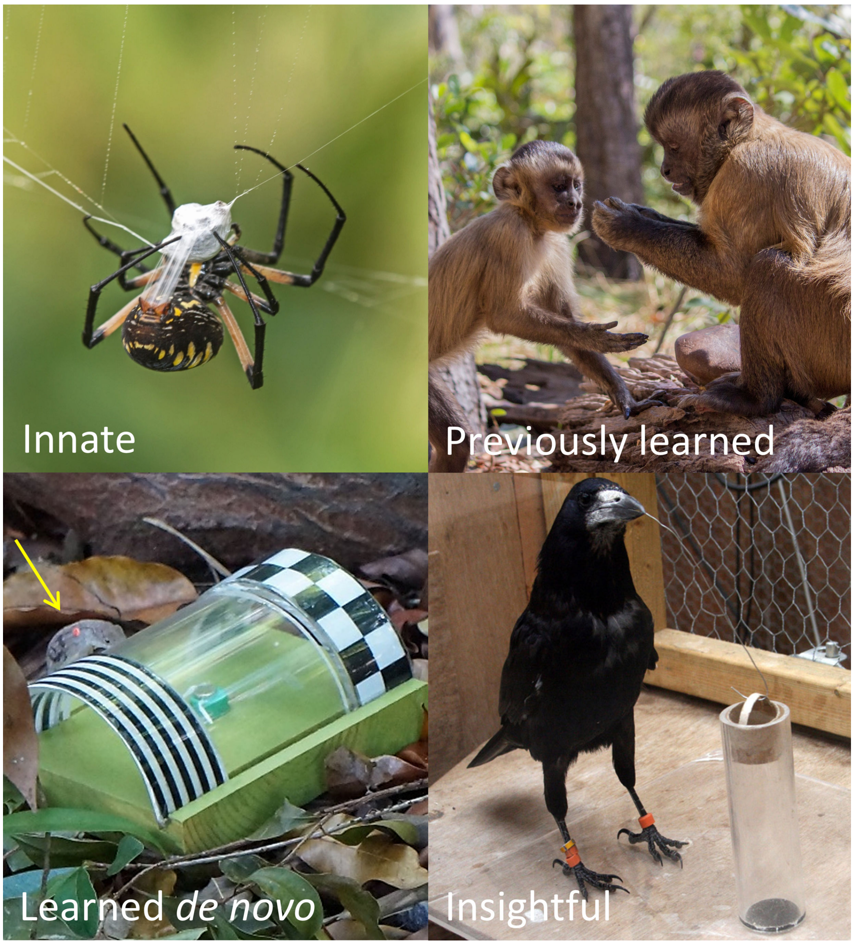

Figure 1. Examples of the various types of solutions animals may use to solve problems: innate, learned previously, learned de novo or insightful. Photo credits are as follows: innate—*Argiope aurantia* spider, Michael Q. Powell; previously learned—*Sapajus libidinosus* capuchin monkey, Luca Antonio Marino; learned de novo—*Anolis sagrei* lizard (yellow arrow), modified from Levi Stork and Manuel Leal; insightful—*Corvus frugilegus* rook, Bird & Emery, [7] with permission from the Proceedings of the National Academy of Sciences.

capuchin monkeys can observe adults using tools (e.g. rocks) and subsequently use that solution to access food in the future [14] (figure 1).

Solutions learned de novo are created through trial and error following the first encounter with a problem [7,15–17]. These solutions arise if an individual does not have a prior solution (either innate or learned previously) for a particular problem. For example, when *Anolis sagrei* lizards are first given a novel apparatus containing food, they do not know how to access the food (i.e. by going through a tunnel). Individuals are able to learn de novo how to access the food using trial and error [18] (figure 1).

Solutions arrived at through insight (henceforth 'insightful solutions') are created when an individual inspects a mental representation of a situation and uses that inspection to devise a novel solution without any trial and error [19–23]. As with de novo learned solutions, insightful solutions arise if an individual does not have a prior solution for a particular problem. An example of insightful solutions can be found in tool use. For example, *Corvus frugilegus* rooks can use insight to create functional tools to acquire food that would otherwise be unreachable [7] (figure 1). These birds did not need to observe another individual making a tool, nor did they repeatedly modify the tool after trying to acquire the food and failing (i.e. trial and error). The birds inspected the apparatus that held the food and bent a piece of metal to bring the food within reach.

Insightful solutions require some form of mental representation and an inspection of this representation. What an 'inspection of a mental representation' entails is still debated. Some have claimed it involves an understanding of causal relationships [20] and others claim it is more similar to a mental manipulation of the representation [7,22,24,25], which can even include something akin to mental trial and error [26,27]. Here, we do not assume what type of inspection is happening for our definition of insight, besides that there is some internal/mental process that is used to create a novel solution without learning.

2. Current difficulties in testing hypotheses about animal problem-solving

The study of how animals solve problems has a deep multidisciplinary history involving researchers with behaviourist, psychological, philosophical, neuroscience or modern Darwinian backgrounds, to name a few. Many researchers are interested in this topic because it has numerous implications. Understanding how animals solve problems allows researchers to understand the behavioural and cognitive abilities different animals possess. For example, this knowledge can inform our understanding of human psychology and neuroscience, ethical decisions in animal husbandry and how different behavioural and cognitive abilities evolved.

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Multidisciplinary research can be invaluable in forming a comprehensive understanding of topics. However, the confluence of such diverse perspectives also presents the opportunity for conflict when researchers with varying criteria for supporting and rejecting hypotheses converge. This can create challenges for synthesis and progress, as we have seen in the field of animal problem-solving. For instance, some researchers are proponents of learned solutions and tend to require a complete and detailed knowledge of an individual's prior history to identify the type of solution used [28–31]. Knowing an individual's history can be extremely helpful in identifying whether a solution was previously learned [1,9,32]. However, to know an individual's complete history practically requires that the individual be reared in captivity and continuously monitored. Not only can rearing individuals in captivity be impractical, it can also have unintentional impacts on behaviour that do not translate to natural settings [18,28,33]. For example, tool use in primates is vastly different in wild and captive populations [34]. Therefore, the requirement to know an individual's complete history to identify the type of solution used can restrict the way in which we test hypotheses about animal problem-solving.

In addition to knowledge of an animal's history, some researchers require further experimental evidence to show the solution was not learned [30,31,35,36]. This additional evidence can include designing experiments to prove that the animal was never rewarded for behaviours similar to the solution (i.e. shaping [37]); that the solution was not a result of an automatic chain of behaviours (i.e. chaining [36]); or that the solution was not previously learned under a different context (i.e. generalization [38]). This is not to say that providing sufficient evidence against alternative explanations is a bad thing, rather, the amount of evidence required to prove learning has never occurred can become exorbitant.

The primary alternative for proponents of learned solutions is to present animals with evolutionarily novel problems, i.e. one that the individual nor any individual in their evolutionary lineage has ever encountered [18,30]. Solving an evolutionarily novel problem inherently eliminates certain types of solutions (e.g. innate or previously learned) without needing to know an individual's prior history. However, it is nearly impossible to be certain that a given lineage of animals has never encountered a particular kind of problem. For instance, some problems that are generally considered evolutionarily novel (e.g. needing to throw stones into a pitcher or pull a string to bring a reward within reach) are featured in ancient fables [39] or have been documented as early as AD 23–79 [40]. This suggests that 'novel' problems may have been encountered by some individuals in an animal's lineage in repeated generations over some thousands of years. Finding a truly evolutionary novel problem that is still relevant to an animal's life history would drastically limit the types of problems researchers can use when studying animal problem-solving. Presenting animals with truly evolutionarily novel problems therefore restricts the ways in which we test hypotheses in this field.

Requiring complete knowledge of an animal's prior history or that animals be presented with evolutionarily novel problems amounts to proving a negative. In the former case, proving learning has never occurred, and in the latter, proving the problem has never been encountered before by the animal's lineage. Providing sufficient evidence for either of these negatives, or any negative in general, may be impossible and has severely restricted the ways in which we can test hypotheses in this field.

We therefore propose a novel framework that can help distinguish the types of solutions animals may use that does not require proving a negative. This framework instead offers testable predictions that can be applied in a variety of settings without requiring knowledge of an animal's history nor that the problem be evolutionarily novel.

3. A new variation-based framework for testing hypotheses

Here, we develop a framework that can help distinguish the types of hypothesized solutions animals may use. This framework is based on distinct patterns of *qualitative* and *quantitative* variations *between* and *within* individuals when they repeatedly encounter the same problem (table 1, figure 2). Importantly, this framework does not require knowledge of an animal's prior history nor that the problem be evolutionarily novel. We propose that studying variation in how animals solve problems could be a valuable tool in advancing this field because it can expand the experimental designs, animals and settings (e.g. field or lab-based studies) in which we study problem-solving. We outline the rationale for the patterns of variation and the corresponding predictions below.

(a) Predictions for innate solutions

Innate solutions are 'pre-programmed' responses, such as fixed action patterns, that evolve under selection due to repeated encounters with the same problem [5,41,42]. These solutions are thus likely to be widely shared among conspecifics and show little *qualitative* variation *between* individuals. For example, we would not expect one web-building spider to subdue prey by wrapping it in silk and another spider of the same species to actively hunt and wrestle it. We see this variation across species (e.g. orb weavers versus jumping spiders), but we would not expect such qualitative variation in these solutions within species. We acknowledge that innate solutions could have polymorphisms or polyphenisms. Even in those cases, we expect that each of those variants could be recognized as an innate solution, as each would behave similarly to a single innate solution and would therefore still follow our predictions. There may, of course, be some additional variation in innate solutions as a result of genetics, neural imprecision or plasticity [43,44]. But we would expect any variation due to these processes to constitute continuous differences, rather than discrete qualitative solutions.

We would also expect relatively little variation in innate solutions *within* individuals (*qualitative* or *quantitative*) across repeated encounters with the same problem. In other words, we would not expect an individual to have qualitatively different innate solutions. We would also expect any plasticity to be reduced, if not eliminated, if individuals are presented with the same

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Table 1. Predictions for patterns of variation regarding the hypothesized types of solutions animals may use to solve problems. Each hypothesis posits a distinct pattern of qualitative and quantitative variations between and within individuals when they repeatedly encounter the same problem. Both innate and insightful solutions may be modified by learning. We outline predictions for those cases as well.

hypotheses	predictions		
	total number of qualitative solutions (between individuals)	variation in qualitative solutions across trials (within individuals)	quantitative improvement across trials? (within individuals)
innate	1[a]	no	no
learned previously	≥1	no	no
learned de novo	≥1	no	yes
insight	≥1	yes	no
innate × learning	1[a]	no	perhaps
insight × learning	≥1	no	yes

[a]We are excluding any variation due to processes like genetic variation, neural noise, or polyphenisms (see text).

problem [43]. Note, however, there may be more *quantitative* variation *within* individuals if they learn to improve their innate solution (see §3e).

(b) Predictions for previously learned solutions

Learned solutions (whether learned previously or de novo) offer the possibility for individuals to vary in whether they had the opportunity to learn how to solve a given problem. Thus, it may not be uncommon to observe some individuals to fail to solve a given problem initially.

Learned solutions also offer the possibility for individuals to learn qualitatively different ways to solve a given problem. Deciding what is qualitatively similar/different can be subjective. In addition to solutions that appear different, we would also consider solutions that require distinctive behaviours or behavioural sequences as 'different'. Because individuals may vary in their prior experiences, learned solutions are more likely to vary *qualitatively between* individuals than innate solutions. For example, in some jumping spider species, different individuals can learn different ways to escape from a confinement problem [45]. Note that the number of qualitative solutions may depend on the type of problem presented.

Once an individual has learned a solution, we would expect that individual to continue to use it [46]. We would therefore expect little *qualitative* variation *within* individuals. In addition to reusing the same solution across trials, we would expect little *quantitative* variation *within* individuals. This is because learning, and therefore most of the quantitative improvements to the solution, has already happened.

(c) Predictions for solutions learned de novo

In addition to the qualitative predictions that are true for both types of learned solutions, solutions learned de novo may show relatively high *quantitative* variation *within* individuals as they improve their solution through further experience. Of course, another key distinctive feature of learned de novo solutions is that researchers will observe the animal learning the solution de novo through trial and error (as described in §1). Because this solution is novel to the individual, it is not uncommon for many individuals to fail to solve the problem initially [15,45,47].

(d) Predictions for insightful solutions

For insightful solutions, the literature emphasizes that the animal may face an 'impasse' when first confronted with the problem and that the animal then solve the problem without a phase of trial and error [19,36,48]. The initial impasse indicates that the animal cannot solve the problem upon first encounter—it has neither an innate nor a previously learned solution for the problem. The subsequent solving of the problem without trial and error indicates that the animal analysed its mental representation of the situation, devised a solution and executed it. The literature also suggests that it is common for many individuals to fail to solve the problem using insight [48–50].

To these predictions, we add the following: insightful solutions are creative by nature [51] and could therefore show a high level of *qualitative* variation *between* individuals. These discrete qualitative solutions naturally could lead to *quantitative* variation *between* individuals as well. Once an individual that previously arrived at an insightful solution encounters the same problem, it may use that prior solution (if the solution was learned) or may create a new insightful solution (see §3e). Without learning, we may expect individuals to create a new insightful solution each time the problem is presented. This would create both *qualitative* and *quantitative* variations *within* individuals. Unfortunately, there is little evidence for qualitative variation in insightful solutions in the literature. Most studies have focused on the presence or absence of insight and use experimental

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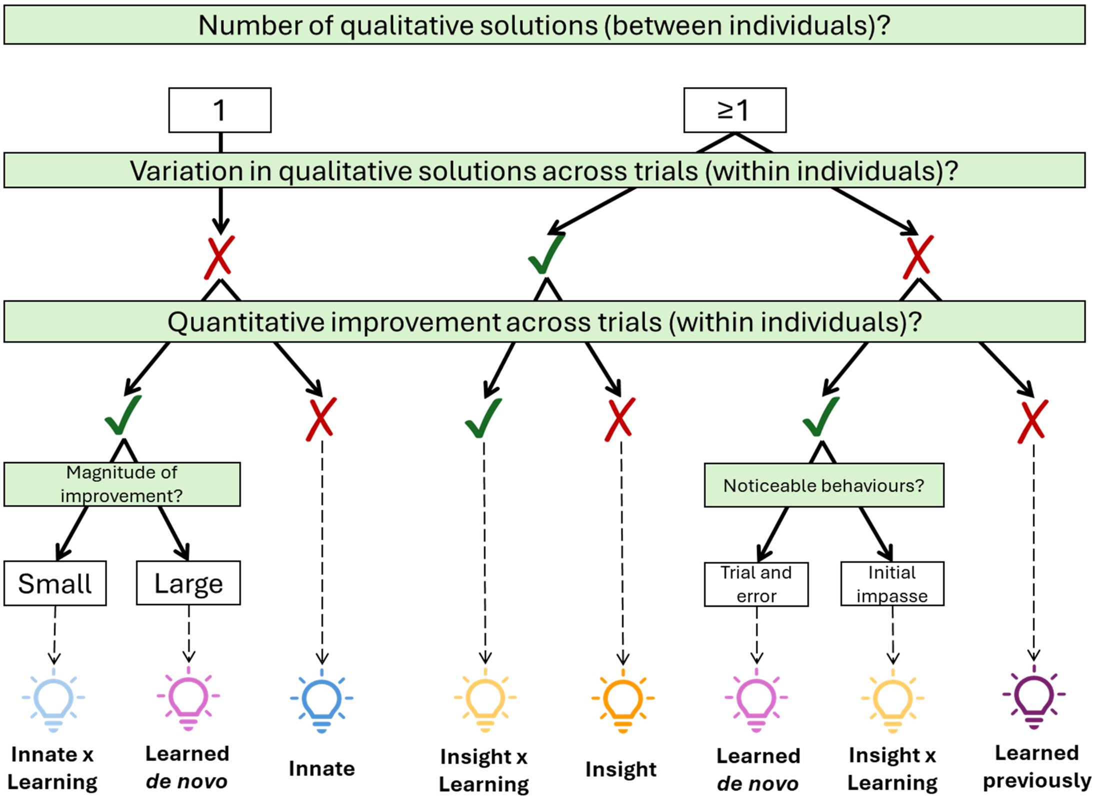

Figure 2. Flowchart depicting how the proposed variation-based framework can be used to help decipher the types of solutions animals may use to solve problems (innate, learned previously, learned de novo or insightful). The different types of solutions are shown with colour-coded light bulbs; similar colours indicate similar solutions.

designs that restrict the number of solutions that can be used to solve it [52]. We therefore believe that this lack of evidence is not due to a lack of existence but rather a lack of attention to natural behaviour.

(e) Predictions for modifications by learning

We previously mentioned that innate solutions do not require learning, but that does not mean the solutions cannot be improved through learning. For example, honeybees have an innate solution to communicate information about the location of available resources, i.e. the 'waggle dance' [53]. Although the waggle dance itself is innate, the accuracy of the dance can be improved through social learning [54]. We therefore propose that if individuals learn to improve innate solutions, we may expect some *quantitative* variation *within* individuals as the solution is improved. We would still, however, expect that there would be relatively little *qualitative* variation *between* and *within* individuals in the innate solution.

It is also possible for learning to impact insightful solutions. Arriving at a solution via insight does not require learning, but it does allow for the solution to be influenced by learning. If an individual arrived at a solution through insight and learned that solution, we would expect little *qualitative* variation *within* that individual. In other words, individuals should reuse the same insightful solution upon repeated encounters of the same problem. Individuals may also learn to improve upon that insightful solution. We may therefore also expect some *quantitative* variation *within* individuals.

4. Concluding remarks

Here, we synthesize the types of solutions animals may use to solve various problems. We highlight current constraints on how we test hypotheses in this field and provide a potential solution. We propose that studying variation in how animals solve problems could be a valuable tool in deciphering the types of solutions animals use that do not require knowledge of an animal's prior history nor that the problem be evolutionarily novel (figure 2). Although this framework relieves some constraints on how we test hypotheses regarding animal problem-solving, this framework has its own limitations. For example, this framework requires that animals be repeatedly tested with the same problem and a detailed attention to behavioural variation. These limitations prevent this framework from being applied to many previously published papers. Moving forward, we propose that this framework serves as a call to attention to behavioural variation and can be easily implemented to aid in our understanding of animal problem-solving. Additionally, the versatility of this framework may allow researchers to expand the settings in which we investigate the problem-solving abilities of animals. Broadening our understanding of how animals solve problems can reveal the cognitive abilities different animals (with different brain sizes, brain architectures and natural histories) possess and subsequently the evolution of those abilities [55,56].

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Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. This article has no additional data.

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. M.A.R.: conceptualization, funding acquisition, visualization, writing—original draft, writing—review and editing; R.L.R.: conceptualization, supervision, writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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