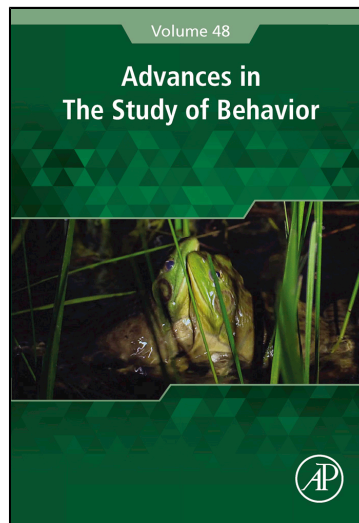


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Bridging the Gap Between Cross-Taxon and Within-Species Analyses of Behavioral Innovations in Birds: Making Sense of Discrepant Cognition—Innovation Relationships and the Role of Motor Diversity

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1. INTRODUCTION

Planet earth is undergoing unprecedented rates of environmental modification and destruction at global scales. Ironically, fast-paced environmental change provides a unique natural experiment with which to quantify environmentally induced phenotypical change in nonhuman animals and to identify the processes that mediate change. Behavioral plasticity plays a particularly important role in phenotypical change, as cross-generational hereditary genetic mutations are unlikely to occur fast enough for many species to keep pace with current rates of environmental change (Bell & Gonzalez, 2009; Lande, 1998; Reznick & Ghalambor, 2001).

Behavioral innovations, defined as the invention of novel behaviors or the use of preexisting behaviors in novel circumstances, are increasingly considered an essential source of behavioral plasticity. Although it is reasonable to assume that behavioral innovations probably arise in a variety of functional domains, including communication and reproduction, to date, much of what we know about animal innovations relate to the foraging domain. This is particularly the case for the work on birds. Following in the footsteps of research employing collections of behavioral anecdotes to test social intelligence hypotheses of brain evolution (Whiten & Byrne, 1988), Lefebvre and his coworkers (Lefebvre et al., 1998; Lefebvre, Juretic, Nicolakakis, & Timmermans, 2001; Lefebvre, Whittle, & Lascaris, 1997) initiated the study of innovative behavior in birds in the 1990s by surveying the ornithological literature and counting for each species the number of anecdotal reports of novel and unusual foraging behaviors in the wild. These “innovation counts” are often referred to as “behavioral flexibility” to avoid inferences about underpinning processes, but also to distinguish innovative behavior from behavioral plasticity, the broader umbrella term. Since the 1990s, innovation counts have been correlated with a number of morphological (eg, brain size), ecological (eg, migratory status), and evolutionary (eg, taxonomic radiation) parameters to gain insight into the ecological drivers and the evolutionary consequences of global innovation patterns. As a consequence of this body of cross-taxon comparative work, the benefits and evolutionary consequences of taxonomic level patterns of innovations

are considered to be relatively well established; foraging innovations facilitate invasion of new habitats (Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005; Sol & Lefebvre, 2000; Sol, Timmermans, & Lefebvre, 2002), survival in harsh (Sol, Lefebvre, & Rodríguez-Teijeiro, 2005) and changing (Shultz, Bradbury, Evans, Gregory, & Blackburn, 2005) environments, and accelerate taxonomic radiation (Nicolakakis, Sol, & Lefebvre, 2003; Sol, Stirling, & Lefebvre, 2005).

In contrast to this large body of knowledge regarding the function of foraging innovations in birds, much less is known about the mechanisms that underpin innovative behaviors. Central to the present paper is the well-publicized view that foraging innovation counts provide a measure of “general intelligence” in birds. Over the last nearly two decades, a body of cross-taxon comparative research has accumulated in both birds and primates in support of this interpretation. We begin by briefly reviewing that on birds as a backdrop for our discussion of experimental investigations of relationships between innovation and intelligence.

The aims of this piece are twofold. Our first aim is to draw attention to the high degree of inconsistency of empirical findings relating within species variation in innovativeness to within species variation in cognitive performance (ie, learning). Our second aim is to present a model that reconciles the possible (but perhaps controversial) existence of positive associations between cognition and innovation at the cross-taxon level with inconsistent associations at the within-species level. A key component of our model is the view that motor diversity might constitute a proximate link between diet generalism and innovativeness.



2. CROSS-TAXON COMPARATIVE ANALYSES OF INNOVATION MECHANISMS

Louis Lefebvre and his colleagues undertook the first large-scale comparative analysis of innovation counts. Two key studies revealed that avian taxa with more numerous innovation counts have larger brains relative to their body size (Lefebvre et al., 1998, 1997). Two further studies showed that brain size continues to correlate with innovation counts even when several potential confounds and explanatory variables are included in multivariate analyses, such as number of species per taxon, common ancestry, and mode of juvenile development (Lefebvre et al., 2001; Nicolakakis & Lefebvre, 2000). Based on the assumption that larger neural volumes support greater information processing power, these findings were

the first to point to the possibility of a link between cognition and innovation.

In order to investigate this possibility in more depth, a series of further correlational studies were undertaken over the next decade. First, avian innovation counts were found to be positively correlated with the volume of the mesopallium (Timmermans, Lefebvre, Boire, & Basu, 2000), a brain region involved in a diverse range of associative functions and the production of learned complex motor sequences (Cnotka, Güntürkün, Rehkämper, Gray, & Hunt, 2008; Güntürkün, 2012; Mehlhorn, Hunt, Gray, Rehkämper, & Güntürkün, 2010). Second, cross-species variation in innovation counts were positively correlated with cross-taxon variation in performance on standardized laboratory tests of learning (Timmermans et al., 2000). Specifically, the reversal learning performance of seven avian species from seven different taxa was ranked (Timmermans et al., 2000). That rank correlated positively with the innovation count rank of their taxon (Timmermans et al., 2000). Third, avian innovation counts were broken down into novel food innovations (ie, consumption of novel foods) and technical innovations (ie, novel searching and handling techniques). A multivariate model incorporating both measures as explanatory variables for brain size revealed that only technical innovations explained a significant amount of the variation in brain size (Overington, Morand-Ferron, Boogert, & Lefebvre, 2009). Drawing upon the technical intelligence hypothesis, which argues that the cognitive demands of technical skills, such as tool use, underpin the evolution of increased brain size (Byrne, 1997; Parker & Gibson, 1977), this finding together with the previous correlations was taken as strong evidence that innovations count are not only a correlate of intelligence, but in fact, represent a direct measure of intelligence.

The findings from one study are worthy of mention; however, because they challenge the idea that innovations are cognitively demanding. Using a tool use categorization system developed by previous authors and assumed to reflect increasing cognitive demands (references in Lefebvre, Nicolakakis, & Boire, 2002), Lefebvre et al. (2002) documented frequencies of borderline tool use (the use of objects that are part of a substrate, eg, anvils and wedges, assumed to involve “lower” cognitive demands) and “true” tool use in 104 avian species (tools that are detached from the substrate, eg, hammers and sponges, assumed to involve “higher” cognitive demands). Multivariate regression analyses were then undertaken to examine whether innovation counts predicted borderline or true tool use, and furthermore, which brain areas predicted borderline and true tool use. Innovation counts were found

to predict greater frequencies of borderline tool use, but not true tool use (Lefebvre et al., 2002, Table 2). True tool use increased with the volume of a neural area known as the nidopallium (Lefebvre et al., 2002, Table 2), thought to be the equivalent of the mammalian prefrontal cortex (Diekamp, Kalt, Ruhm, Koch, & Güntürkün, 2000; Kalenscher, Ohmann, & Güntürkün, 2006; Kalenscher et al., 2005; Rose & Colombo, 2005), whereas innovation counts have been found to increase with the volume of the mesopallium (Timmermans et al., 2000). These findings point to the possibility that true tool use and innovations might be two distinct behavioral phenomena involving different telencephalic structures. Correlations with borderline, but not true, tool use also raise the possibility that innovations might be less cognitively demanding than proposed. One way to reconcile this discrepancy is to reject the assumption that borderline tool use is cognitively less demanding than true use. Alternatively, technical innovations might need to be distinguished from novel food innovations, as done by Overington et al. (2009), to unmask a predictive relation between technical innovations and true tool use. To our knowledge, this analysis has not been done.

Putting aside the unexpected gap caused by the lack of a relationship between innovations and true tool use, the body of work reviewed above forms the basis for the inference that innovations provide a direct measure of cognition in birds (Lefebvre, 2011). In reality, however, correlational studies cannot determine whether innovation is a by-product of cognition or whether both phenotypes are coselected but mechanistically independent. As we will see, this distinction is critically important because it will determine the pattern of relations one should expect to find at the within-species level. Experimental paradigms in which innovative behavior is elicited experimentally provide the only research avenue that can disentangle the true relationship between these two behavioral phenotypes.



3. EXPERIMENTAL INVESTIGATIONS OF INNOVATION

3.1 The Paradigm: Problem Solving

Since the advent of ethology in the 1930s, the scientific study of animal behavior has strongly advocated investigating animals in their natural environments performing behaviors that are relevant to their ecology. It is argued that the development, mechanisms, function, and evolution of any behavior can only be understood fully when placed in the ecological context

in which those behaviors evolved. This focus on understanding animals as they go about their daily lives was imported into the study of animal cognition in the 1980s with the advent of the ecological, also known as the synthetic, approach to the study of cognition (Kamil, 1988; Shettleworth, 2010). At this point in its history, the study of animal cognition branched out from being a field of science undertaken primarily by psychologists investigating animals as models for humans to a field of science undertaken by psychologists and biologists who were interested in understanding information processing in nonhuman minds in its own right. The ecological approach to the study of animal cognition has been a strong advocate of testing animals on problems that resemble those they are confronted with in their natural environments (eg, caching and relocating food, singing songs). This approach to the study of cognition has been very successful in revealing an extraordinary array of cognitive processes in nonhumans (Shettleworth, 2010).

However, the focus on ecological significance does not allow the researcher to investigate how animals deal with novel circumstances. Therefore, in stark contrast to methodologies established in the ecological approach to the study of animal cognition, most proximate analyses of behavioral innovations have drawn upon the experimental principle of presenting animals with novel problems they are unlikely to have encountered in their natural environment and measuring their propensity to solve them. Most often, these tests have been some kind of extractive foraging task that the animal needs to solve to gain access to food, but more recently, individuals have been required to interact with objects to gain access to their nest (Cauchard, Boogert, Lefebvre, Dubois, & Doligez, 2013) or to improve their sexual displays (Keagy, Savard, & Borgia, 2009, 2011a). In another line of novel problem-solving tests, animals are exposed to novel foods and their willingness to consume them is measured (eg, Martin, 2005; Sol, Griffin, & Barthomeus, 2012). This experimental principle of presenting animals with an unfamiliar problem, typically referred to as “innovative problem solving” or just “problem solving,” has now been applied in a large collection of single species and multispecies studies (eg, Boogert, Reader, Hoppitt, & Laland, 2008; Cole, Cram, & Quinn, 2011; Griffin, Diquelou, & Perea, 2014; Laland & Reader, 1999; Manrique, Völter, & Call, 2013; Morand-Ferron & Quinn, 2011; Sol et al., 2012). There has also been development of more complex, multistage problem-solving tasks (Auersperg, von Bayern, Gajdon, Huber, & Kacelnik, 2011; Auersperg, Kacelnik, & von Bayern, 2013; Taylor, Elliffe, Hunt, & Gray, 2010; Taylor, Hunt, Medina,

& Gray, 2009; Taylor, Medina, et al., 2010; Taylor, Roberts, Hunt, & Gray, 2009). Such tasks have enabled researchers to examine the involvement of causal reasoning and inference in problem solving (see [Section 3.6](#)).

One can wonder the extent to which experimental measures of problem solving and anecdotal reports of innovations in the wild measure the same phenotype. Comparisons of ranked performance on problem-solving tasks and innovation counts provide a first line of evidence that they might. [Webster and Lefebvre \(2001\)](#) found a striking parallel between the taxonomic distribution of innovation counts and innovation propensity measured using a problem-solving assay both in captive and free-ranging birds. Passerines, an avian family with high numbers of foraging innovations in the wild, significantly outperformed Columbiforms ([Webster & Lefebvre, 2001](#)), an avian family with almost no reports of field innovations ([Lefebvre, Reader, & Sol, 2004](#), p. 237). [Diquelou, Griffin, and Sol \(2015\)](#) recently found a similar overlap between species' innovativeness measured experimentally on free-ranging birds and the taxonomic distribution of innovation counts, with Australian ravens (*Corvus coronoides*), a true crow species, exhibiting the highest performance, followed by several Passerida. Once again, a Columbiform, the crested pigeon (*Ocyphaps lophotes*), never solved the foraging problem. In addition to taxonomic overlap between expression of problem solving at the species level and taxon level innovation counts, empirical work has demonstrated that task solving spreads through groups as one would expect were individual-level innovations to alter the phenotypical composition of populations ([Aplin, Farine, Cockburn, & Thornton, 2015](#); [Boogert et al., 2008](#)). These shared taxonomic patterns of expression and expansion provide some indication that the propensity to solve innovative foraging tasks is related to the tendency to forage innovatively in the wild.

In an attempt to develop an alternative approach to evaluating the ecological validity of problem-solving tasks, [Griffin and Guez \(2014\)](#) reviewed the problem-solving literature to determine whether the factors found to influence innovativeness overlapped with those found to influence problem solving. Their review revealed that problem solving has been linked consistently to motor variability and operant learning and is moderated by neophobia, all parameters known and predicted to influence innovations in the wild ([Greenberg, 2003](#); [Reader & Laland, 2003](#)). Thus, they concluded that problem-solving tasks provide a meaningful assay for measuring at least some of the processes that underpin variation in innovation propensity across individuals and across species in the foraging domain.

3.2 Problem Solving and Learning: Correlational Analyses

3.2.1 Background

As already mentioned, problem-solving tasks were in part developed to examine the psychological processes that underpin innovation, and in particular, whether cognition is a causal determinant of innovation. In practice, learning is used to operationalize cognition. The most common methodology for relating learning to problem solving has involved correlating individual performance ranks on innovation tasks (most often latency to solve a task) with individual performance ranks (typically acquisition speed or errors) on learning tasks to investigate whether more innovative individuals are also those that learn faster (reviewed by [Griffin & Guez, 2014](#)). Learning has been quantified in the context of tasks assumed to measure “general” learning abilities, including operant and classical conditioning, rather than learning abilities considered to be more modular, such as song learning and spatial learning. Thus, even though correlations cannot demonstrate causality, positive associations have typically been interpreted as evidence that problem solving is underpinned by a latent domain general cognitive process (sometimes referred to as “g”). For the most part, however, a small, but growing, collection of individual-level analyses of innovative foraging are revealing equivocal results regarding the association of cognition and problem solving contrary to expectations set up by the macroecological approach, whereby innovation propensity is quite clearly assumed to be attributable to higher order cognitive abilities.

3.2.2 Operant Learning

Two key studies have examined the association between problem solving and operant learning. In the first study, the number of task presentations it took individuals to solve the task for the first time was related to a measure of “learning efficiency”, namely the mean solving latency (in seconds) calculated across five subsequent task presentations. Carib grackles (*Quiscalus lugubris*) that solved faster the first time (ie, in fewer task presentations) learned more efficiently (ie, had a lower mean solving latency across five subsequent task presentations) [Overington, Cauchard, Côté, and Lefebvre \(2011\)](#). Using a slightly different measure of innovation performance (the number of times a bird was the first individual in a group setting to solve a task), [Boogert et al. \(2008\)](#) (for methodological detail, see [Boogert, Reader, and Laland \(2006\)](#)) showed that European starlings (*Sturnus vulgaris*) that were the first to innovate in a group setting progressed more rapidly

through successive stages of a shaping procedure to perform a novel foraging technique (ie, remove a lid from a container to access a mealworm reward). Each task presentation was capped at 10 min duration and a starling progressed from one stage to the next if it reached a learning criterion of reaching the food reward on two consecutive task presentations. These relationships have been taken to indicate that faster innovators are also faster operant learners.

In operant learning, one can think of one learning opportunity as being one body-to-task contact and one learning event as one action–outcome pairing (eg, action–food; action–secondary cue; see [Section 3.5](#)). The number of learning events provides a measure of learning rate while the number of learning opportunities provides a measure of effort (also referred to as motivation). To say an animal operant learns faster than another, one needs to be able to ascertain that that animal learns at a faster rate (eg, reaches a learning criterion in fewer action–outcome pairings) while ruling out any among-individual variation attributable to differences in the number of learning opportunities.

One important limitation of measuring operant learning within the context of acquiring a novel motor action (eg, flipping a lid on a box) is that the number of learning opportunities and the number of learning events are ill defined. This is particularly so if the dependent variable used to quantify operant learning performance is a mean latency to access a food reward across successive task presentations ([Overington et al., 2011](#)). Some individuals might have experienced several learning events while others might have experienced only some, but comparison of mean latencies does not factor in this variation because both uncapped (reward is accessed) and capped (reward is not accessed) latencies are included in the mean latency calculation ([Overington et al., 2011](#)). Among-individual variation in the number of learning events might also arise when quantifying operant learning using number of task presentations to reach a final stage of shaping ([Boogert et al., 2008](#)). For example, reaching mealworms on one, but not two successive task presentations (as required to meet the learning criterion) injects among-individual variation into the number of learning events experienced by each individual but this is not quantified.

In both the abovementioned studies, the number of learning events could be identified (and held constant) if every task presentation ended with a learning event (ie, accessing the food reward, ie, an action–reward pairing), but the number of learning opportunities would remain unknown. This is a serious problem because an animal that is reported to learn faster

(ie, in fewer task presentations) might have undergone in reality far more learning opportunities than an individual that appeared to have learned more slowly (Rowe & Healy, 2014). The learning rates of two individuals can only be compared fairly if they are given the same number of learning opportunities.

In addition, not knowing the number of learning opportunities seriously limits the interpretation of subsequent correlations with problem-solving performance. Learning opportunities are influenced by many factors including several not considered to be cognitive, including exploration, activity, responses to novelty and motivation. All these behaviors necessarily moderate the rate at which animals encounter learning opportunities, with increased exploration, activity and motivation, and lower avoidance responses to novelty undoubtedly increasing the rate of learning opportunities. Applying the same logic, an animal that is more motivated, more exploratory, more active, and/or avoids novelty less, is likely to encounter, and, more importantly, interact with a problem-solving task far more frequently. This animal will therefore encounter more innovation opportunities. Hence, positive correlations between individuals' innovation and operant learning performances (even if rates of operant learning were quantified properly) might be solely attributable to correlations between the numbers of learning and innovation opportunities. Unless learning and innovation opportunities are held constant across individuals, or at the very least, interindividual variation in these parameters is measured and accounted for statistically, associations of problem solving and learning performances cannot be used to infer that faster problem solvers are faster learners.

In a third key study of problem solving and learning, pigeons (*Columba livia*) that solved a problem-solving task faster required fewer social demonstrations to learn to perform an innovative foraging technique (Bouchard, Goodyer, & Lefebvre, 2007). In that design, performance was driven not only by the individual capacity to exploit social information, the key variable of interest, but also by the individual's own interactions with the task, each one of which constitutes a nonsocial learning opportunity, regardless of the social demonstration. Therefore, without recording the number of times each individual interacted with the task during the social learning experiment, we cannot exclude that associations between problem solving and social learning might be exclusively attributable to noncognitive factors.

Significantly faster solving (ie, significantly shorter latencies) on the second relative to the first solving of a problem-solving task have been found

in several species including common mynas (*Acridotheres tristis*) (Griffin et al., 2016; Sol et al., 2012), meerkats (*Suricata suricatta*) (Thornton & Samson, 2012), and house sparrows (Bókonyi et al., 2014). As a result, one final approach to examining the relation between innovation and operant learning has involved the correlation of innovation latencies (first solving) with the *change* in latency from the first to second solving. One concern here might be that an animal that has discovered it can reach a reward on the first solution might try more frequently to reach the reward the next time it is presented with the task (but see, Thornton & Samson, 2012 for other possibilities). Therefore, faster solving might be attributable to increased learning opportunities on the second solution. Correlating innovation latencies with the change in solving latencies from first to second solutions might be a method slightly more immune to ill-defined learning opportunities, however. This is because a correlation showing that faster innovators have a greater decrease in solving latency (ie, learn faster) could only be spurious (driven only by increased opportunities) if faster innovators try *disproportionately* more frequently on the second task presentation. Hence, it might be reasonable to interpret such associations as indicating that individuals that innovate faster learn faster.

Unfortunately, those studies that have employed this technique have found that changes in solving latencies are either unrelated (Bókonyi et al., 2014) or are positively related to initial solving times: in mynas, faster innovators show *smaller* decreases from first to second solution than slower innovators (Fig. 1). It is currently not clear whether this finding indicates that faster innovators learn more slowly or whether it is driven by a spurious numerical effect whereby changes in latencies from first to second solutions become smaller because initial latencies are already small.

We conclude this section by noting that motivation in its broadest sense is impossible to rule out as the underlying factor supporting problem solving—learning correlations. In other words, it is always possible to argue that an animal that shows faster learning rates and faster innovation latencies is simply more motivated (rather than more intelligent) than an animal that displays slower learning rates and longer innovation latencies. The best one can do is to quantify among-individual variation in specific operationalizations of motivation in *both* the problem-solving task and the learning task and account for these differences (eg, beak-to-task contacts as a measure of task-directed motivation; food deprivation times). A debate about the role of motivation without operationalization can only be sterile and should be avoided.

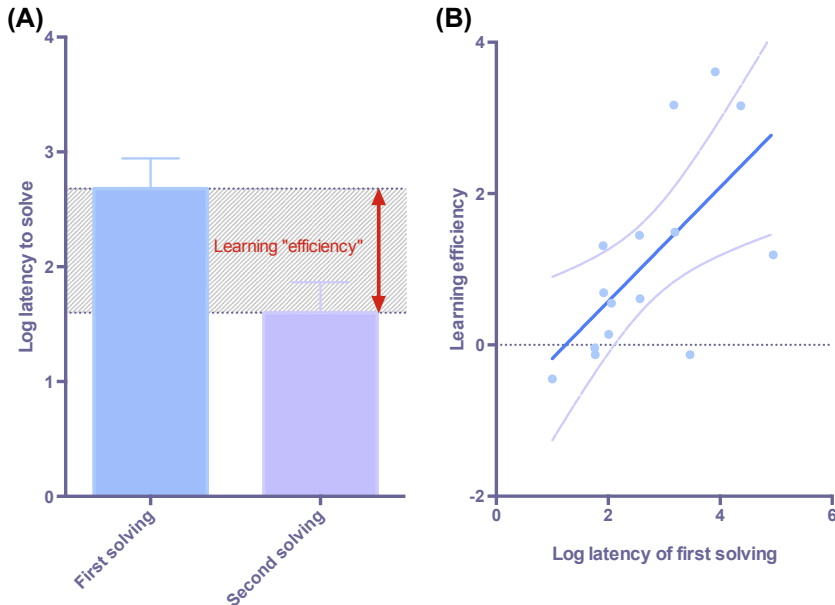


Figure 1 Learning “efficiency” in common mynas and its relationship to innovative problem-solving performance. (A) Learning efficiency can be calculated as the change in solving latency from first to second solving of a problem-solving task. (B) Learning efficiency is positively correlated with initial solving latency contrary to what one would expect if more innovative individuals are also those that operant learn faster.

3.2.3 Classical Conditioning and Learning Batteries

Two studies have avoided the difficulties of correlating innovation with rates of operant learning by measuring the extent to which problem-solving performance is associated with rates of classical conditioning. Contrary to operant learning tasks where the number of learning opportunities and learning events are ill defined, in a classical conditioning task, each learning opportunity is a learning event. For example, one presentation of two colored dishes from which the animal must chose the correct one to obtain a food reward constitutes a learning opportunity and the pairing of the animal’s choice and the outcome constitutes a learning event. Furthermore, every learning opportunity is controlled by the experimenter (rather than by the animal) and counted. Performance is then qualified as the number of times a choice is made until the animal reaches some predefined learning criterion or, alternatively, as the number of erroneous choices an animal makes until it reaches that criterion. Either way, the number of trials to criterion is a true measure of the number of times the animal has encountered a

learning opportunity and undergone a learning event. One can therefore reasonably assume that any interindividual differences are attributable to differences in the speed with which environmental information is learned (Griffin, Guillette, & Healy, 2015).

The two studies that have employed this approach yield inconsistent patterns of association between innovating and classical conditioning. Common mynas that learn a color discrimination task faster solve an innovative foraging task faster (Griffin, Guez, Lermite, & Patience, 2013). In carib grackles, individuals that learn a color discrimination faster solve a lid-removal task more slowly, whereas speed of discrimination learning is unrelated to latency to solve a stick-pulling task (Ducatez, Audet, & Lefebvre, 2014).

One last approach to investigating innovation–cognition correlations experimentally has involved quantifying innovation and then the rate of learning on batteries of tasks. Data reduction methods, such as principle components analysis, are then employed to determine whether problem-solving loads on the same component as do the learning performances on the task battery. Using this approach, one study has revealed that spotted bowerbirds (*Ptilonorhynchus maculatus*) tested on one problem-solving task and a variety of different learning tests produce innovation performances that load positively, but only weakly, on to the same principle component as do learning rates (Isden, Panayi, Dingle, & Madden, 2013).

3.2.4 Inhibition and Producer–Scrounger Strategies

Research methods have recently moved from measuring the rate of learning to measuring the rate at which animals switch from learned behaviors to new behaviors when those previously learned behaviors are no longer successful, an ability that falls under the multidimensional cognitive ability termed inhibition (Aron, Robbins, & Poldrack, 2014). To this end, associations of innovation performance and reversal learning have been measured. At a group level, mynas that have learned how to access a problem-solving task using two distinct motor actions have the capacity to alternate rapidly between two familiar solving techniques when one is blocked (Griffin et al., 2016). Although this finding suggests that mynas readily withhold from performing previously successful motor actions to use alternative ones, mynas that are faster to innovate learn a reversal-learning task more slowly (Griffin et al., 2013). This is the reverse of what one might expect based on the interpretation of comparative research that cognition facilitates innovation.

Within the context of correlations between behavioral inhibition and innovation, one additional study merits a mention. Like several other species, the time that meerkats take to solve a problem decreases from the first to the second solving (Thornton & Samson, 2012). Detailed analyses of meerkat behavior revealed that decreased latencies were attributable to the animals' ability to inhibit behavior towards nonfunctional (ie, would not lead to solution) components of a task thereby ruling out that solving more quickly was merely a consequence of increased persistence (Thornton & Samson, 2012). In passing, persistence directed towards functional components did not increase (Thornton & Samson, 2012), as one might have expected, but this might have occurred because solving occurred too quickly once contact with functional components was made for the first time. Over and above this caveat, decreased solving effort towards nonfunctional components indicates that meerkats are able to retain task-related information during innovation and use it to solve the task the second time around. This finding does not speak to whether the capacity to innovate is associated with accelerated learning of task attributes, however. For this, one would need to know whether individuals that decreased their use of nonfunctional components the most were also those that innovated the fastest. Nevertheless, along with Griffin et al.'s (2013) work in mynas, this research does suggest that the relationship between innovation and behavioral inhibition is in need of further investigation.

A final body of work that might shed light on the relationship between innovation and learning is that on producing and scrounging, primarily in birds. Experimental analyses of producer—scrounger strategies have revealed that scroungers are poor at learning a food-producing foraging technique (Beauchamp & Kacelnik, 1991; Giraldeau & Lefebvre, 1987; Lefebvre & Helder, 1997; Munkenbeck Fragaszy & Visalberghi, 1990), a finding that confirmed the predictions of theoretical models that individuals should prefer to scrounge than learn to produce (Giraldeau & Caraco, 2000). If one considers producers to be conceptually equivalent to innovators and scroungers to be equivalent to noninnovators, this literature suggests that noninnovators learn more slowly. However, individuals engage in producer—scrounger strategies flexibly (Giraldeau & Lefebvre, 1986). For example, when producers were removed from the group, scrounger pigeons switched to producing and they switched back to scrounging when producers were reintroduced (Giraldeau & Lefebvre, 1986). Flexibility in individual strategies raises the possibility that failure of noninnovators to learn is not driven by a lower ability. Rather, that individuals attend to,

and learn about, different types of information depending on the costs and benefits of the situation.

3.2.5 Conclusions

In sum, we consider evidence for associations between problem solving and learning to be equivocal at the very least. Problems associated with how learning is measured and inconsistent findings, which might be expected given the small body of work available, nevertheless limit the strength of the conclusions. Future work is needed to investigate this relationship further. Assessment of individual differences in learning performance need to ensure that performance is measured using parameters that accurately reflect the number of learning opportunities and number of learning events subjects undergo. To this end, correlations with operant learning should incorporate the number of learning opportunities adequately or be abandoned altogether.

In addition, learning and innovation should be assessed on a variety of tasks, rather than just one, with the most sensible approach involving batteries of innovation and learning tasks, with performances then analyzed using data reduction methods. Thornton & Samson's (2012) and Griffin et al.'s (2013) behavioral experiments suggest that incorporating inhibition tasks rather than focusing on learning tasks would be a fruitful addition.

Finally, a broader variety of learning performance measures should be quantified. Learning rates measure the speed at which information is placed in memory, but other dimensions, such as how much information, both in terms of quantity and diversity, can be retained, how long it is retained and how accurate it is, might yield a richer description of relations between innovation and cognition.

By far the greatest limitation of existing work, one that no amount of future correlational work will address, is that correlations cannot be used to determine whether innovation is a by-product of cognition. Specifically, correlations cannot be used to determine whether inventing new behavior, or using preexisting ones under novel conditions, draws upon cognitive processes. It is to causal relations that we now turn.

3.3 Problem Solving and Learning: Causal Analyses

Rather than *infer* that cognition is involved in innovative foraging based on correlational evidence as in comparative macroecological and the vast majority of experimental research to date, a more powerful approach would involve demonstrating that cognition is a causal determinant of innovation.

Above, we focused on how operant learning might inculcate an innovative foraging technique across multiple solutions. This contribution of cognition to innovation is merely in the acquisition and retention of a successful motor action, not to innovation per se which should be limited to the first solving event (Reader & Laland, 2003). For cognition to be a causal determinant of innovation, operant learning must operate *during* the discovery of an innovative behavior leading to the first solving event.

Broadly speaking there are two possible ways in which cognition might facilitate innovation. First, animals might have the capacity to select particular motor actions in advance of attempting the new task based on prior knowledge. We discuss this possibility in the Section 3.6.

Another way in which cognitive abilities might operate during innovation involves a gradual “homing” in on the solution to a task within the first solving event, a learning process known as shaping (Thorndike, 1898). In this case, operant learning does not occur via a motor action—reward pairing but via a pairing of a motor action and a secondary cue that functions as an indirect cue for reward delivery. These secondary cues could be recognized largely independently from experience or learned through their own past pairings with reward delivery. For example, animals might learn that lifting or moving a leaf enables the capture of prey. In this case, the movement of the leaf predicts reward delivery. The learned significance of movement cues means the cues could then be used as a proxy for the reward, a process known as second-order conditioning (Rescorla, 2014). According to the principle of operant learning, pairing of a given motor action and a secondary cue causes the motor action that produced the secondary cue to be learned so that it can be repeated on a subsequent attempt. String-pulling, a behavior in which a suspended food reward is brought gradually closer to the body and studied in a variety of song birds species (Heinrich & Bugnyar, 2005; Obozova, Bagotskaya, Smirnova, & Zorina, 2014; Taylor, Medina, et al., 2010; Werdenich & Huber, 2006), is an example of a motor pattern in which intermediate reinforcers might act to reinforce partial solutions (the food is moved gradually closer to the body) to the final problem. In support of the idea that secondary cues facilitate innovation, Overington et al. (2011) have shown that carib grackles discover the solution to a foraging problem faster when they have access to movement cues than when these cues are blocked. An alternative possibility is that, rather than acting as a trigger for operant learning, movement cues increase persistence. In this scenario, secondary cues do not increase innovation performance by causing a specific motor action to be

learned so it can be repeated (ie, operant learning) but rather by increasing the likelihood that the animal will try again independent of which motor action is used.

One way to tease apart whether secondary cues trigger learning or increase persistence would be to undertake a detailed examination of the motor actions used by animals while trying to solve. Shaping should lead to gradual changes in the frequencies of motor expression with ones that produce secondary cues gradually becoming more frequent than those not paired with secondary cues. Persistence effects would be apparent if a movement cue elicited a sudden increase in the number of attempts without changing the relative frequencies with which different motor actions are expressed. To our knowledge, only one study has analyzed changes in behavior during the first solving event. [Overington et al. \(2011\)](#) showed that innovator carib grackles focused their pecking on areas of the task that produced movement cues gradually more and more in line with a shaping phenomenon, whereas noninnovators continued to peck at parts that did not produce movement.

3.4 Problem Solving and Motor Flexibility

3.4.1 Background

We now turn to another potential mechanism of innovation, motor flexibility. [Klopfer \(1967\)](#) proposed the concept of motor stereotypy to refer to an individual's tendency to produce only a narrow range of motor actions to accomplish a given act. He suggested that motor stereotypy, as opposed to motor plasticity and reflected by an inability to adjust movements in accordance with changes in the form of the substrate, might arise as a consequence of an animal's morphological features (eg, muscle attachments or shapes) and/or its central nervous system.

The possibility that motor flexibility facilitates problem solving has been gaining traction in recent years. [Greenberg \(2003\)](#) initially suggested that motor plasticity should be a key determinant of innovative foraging. Central to innovation is the ability/tendency to express behavioral variants (novel or preexisting ones in novel circumstances) that deviate from the individual's or the population's most common behavioral repertoire ([Reader & Laland, 2003](#)). Applied to motor actions, this occurs when a new motor action is invented or when a preexisting one (eg, a foraging behavior, a communication signal) is applied to a novel context. It follows that motor variability should contribute to producing behavioral variants. It makes intuitive sense that an animal that is more variable in its motor behavior has more raw

material to produce novel behaviors, or to use preexisting ones in novel contexts, including social signals and/or foraging techniques, than an animal that is more stereotyped in its motor output.

In line with this idea, motor variability has been found consistently to mediate faster and/or a higher probability of discovering the solution to a problem-solving task (Benson-Amram & Holekamp, 2012; Benson-Amram, Weldele, & Holekamp, 2013; Diquelou et al., 2015; Griffin & Diquelou, 2015; Griffin et al., 2014; Mangalam & Singh, 2013; Overington et al., 2011; Thornton & Samson, 2012). The reliability with which motor flexibility predicts faster/higher probability problem solving stands in stark contrast to the mixed patterns of results from research relating problem solving to learning.

3.4.2 Measuring Motor Flexibility

In most published data sets, motor diversity is conceptualized as a greater number of distinct motor actions or number of areas contacted. For example, in both spotted hyenas (*Crocutta crocutta*) and common mynas, individuals that express a greater range of motor actions are more likely to solve a problem-solving task than are individuals with a more restricted motor range (Benson-Amram & Holekamp, 2012; Griffin et al., 2014). More recently, Diquelou et al. (2015) and Griffin and Diquelou (2015) developed an index of motor flexibility based on the Shannon biodiversity index (Shannon & Weaver, 1949), which they applied to the analysis of problem solving in the highly invasive song bird, the common myna. Common mynas are more likely and faster to solve a problem-solving task than is the native Australian noisy miner (*Manorina melanocephala*). The higher motor index of flexibility of mynas depicted in Fig. 2 underpins this species difference (Griffin & Diquelou, 2015). A field-based species comparison in birds provided a taxonomically broader test of Griffin and Diquelou's (2015) index of motor flexibility on problem solving in birds (Diquelou et al., 2015). Of several urbanized avian species tested on a problem-solving task under free-ranging conditions, Australian ravens (*C. coronoides*) were by far the most likely and the quickest to solve the task. What differed strikingly between the highly innovative Australian raven and the other significantly less innovative species was not the number of techniques used (all species used several, both effective and ineffective), but rather the more balanced distribution of expression of motor actions, which stood in stark contrast to the highly skewed deployment of ineffective techniques in the other species (Fig. 3). Hence, it appears that a more even frequency of expression of

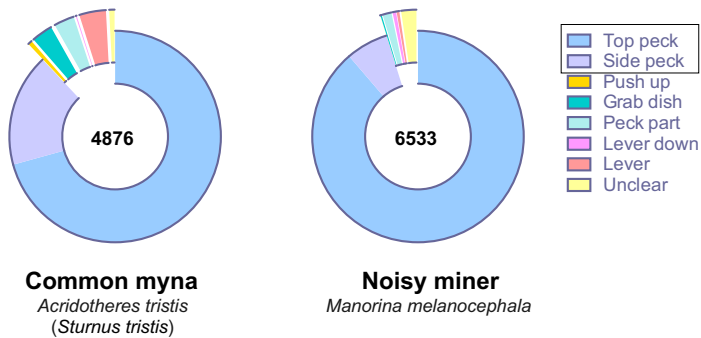


Figure 2 Motor flexibility in two species of Passerine when attempting to solve three different problem-solving tasks under captive conditions. The two motor actions most commonly expressed by both species (top peck and side peck) could not be used to solve. All others, made visible by areas protruding from the doughnut, could potentially solve the task. The total number of attempts recorded for each species is indicated in the center of each doughnut. Data based on Griffin, A.S. & Diquelou, M. (2015). *Innovative problem solving in birds: a cross-species comparison of two highly successful passerines*. *Animal Behaviour*, 100, 84–94.

motor actions might be more important to innovative foraging than is the total number of motor actions (Diquelou et al., 2015).

We suggest that motor flexibility is linked to animals' foraging patterns. Assuming that the relative frequency of foraging actions within an animal's repertoire tracks closely the frequencies of foods within an animal's diet, animals with more even motor repertoires should be those with broader diets, while those with more skewed foraging repertoires might be those with more specialized diets. Hence, skewed motor repertoires might be associated with diet specialization and more evenly distributed motor repertoires might be associated with diet generalism. We develop this point more fully in Section 4.

3.4.3 Modeling the Effects of Motor Flexibility

We have simulated the effects of motor flexibility on problem solving, focusing particularly on motor evenness (Griffin & Guez, unpublished). We built a computational model in which a hypothetical agent attempted to solve a problem-solving task by making repeated appendage-to-task (eg, beak-to-task) contacts using one of four possible motor actions within its repertoire (Griffin & Guez, unpublished). Only three of these could lead to a solution of the task (Griffin & Guez, unpublished). To model the effects of motor evenness, the probability of expression of each motor

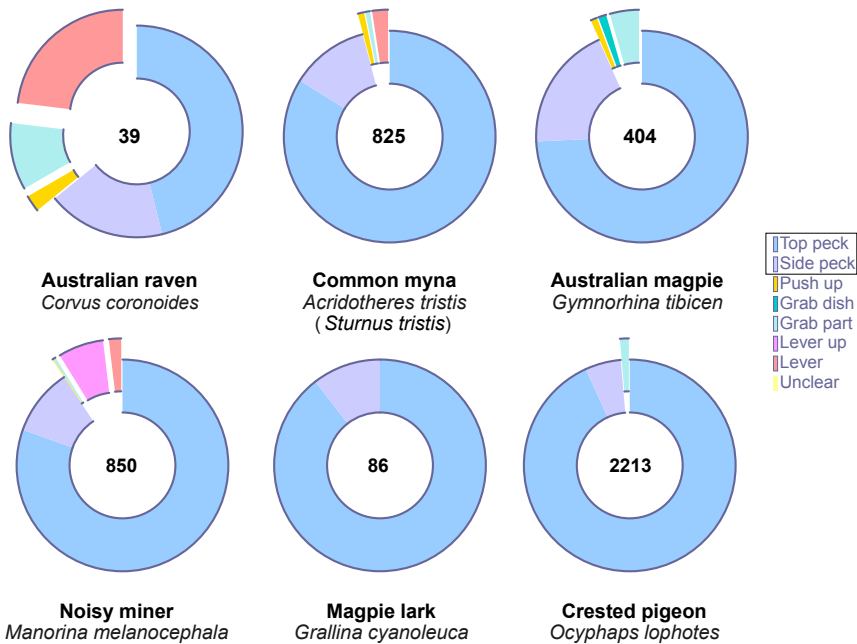


Figure 3 Motor flexibility of urbanized avian species when attempting to solve a problem-solving task under free-ranging conditions. The two motor actions most commonly expressed by all species (top peck and side peck) could not be used to solve. All others, made visible by areas protruding from the doughnut, could potentially solve the task. The total number of attempts observed for each species is indicated in the center of each doughnut. Data based on Diquelou, M., Griffin, A.S., & Sol, D. (2015). *The role of motor diversity in foraging innovations: a cross-species comparison in urban birds*. Behavioral Ecology.

action was either skewed towards preferential expression of the ineffective action or evenly distributed, such that each motor action had the same probability of expression on each attempt. Thus, we implemented computationally the behavioral differences we had observed in the field between motor specialists, such as the crested pigeons that attempted to solve our task using primarily one (ineffective) motor action, and motor generalists, such as the Australian ravens, that used a variety of different motor actions with more even frequencies of expression (Diquelou et al., 2015) (Fig. 3). In this simulation agents with a more even motor expression solved consistently faster than did agents that deployed motor repertoires skewed toward expression of an ineffective motor action (Griffin & Guez, in review). This effect occurred because motor evenness obviously raised the frequency of expression of effective motor actions

relative to ineffective ones. This model was then be used to examine the effects of learning and persistence of problem-solving performance (see [Section 3.5](#)).

3.5 Problem Solving: Motor Flexibility and Learning

So far, we have reviewed the literature indicating that problem solving is underpinned by operant learning ([Section 3.3](#)). We then reviewed evidence that problem solving is underpinned by motor flexibility ([Section 3.4](#)). Here, we briefly discuss the possibility that motor flexibility and operant learning act in conjunction with one another to yield the solution to a problem-solving task. Specifically, when an animal is faced with an unfamiliar foraging problem, motor flexibility might serve to generate random behavioral variants, either preexisting behaviors in novel circumstances or slight variations of existing behaviors, while operant learning might serve to reinforce those motor actions that elicit secondary cues (ie, movement). Once again, we turned to a modeling approach to simulate the effects of combining motor flexibility and learning on problem-solving performance.

We used the same model as we had used to examine the effects of motor flexibility, but modified the simulations to account for changes in the probability of motor expression as a consequence of the occurrence of secondary cues. We expected motor flexibility and learning to produce faster problem solving than motor flexibility on its own. Unexpectedly, comparisons of simulations in which the innovation performance of motor flexible individuals was compared with that of motor flexible individuals capable of learning revealed that the capacity to learn only rarely lead to faster problem solving (Griffin & Guez, in review). Only when learning opportunities (ie, secondary cues) were made to be extremely frequent in the environment and/or learning was fast (ie, the probability of expression of a given motor action went quickly from low to high) did learning improve problem solving. This outcome stood in stark contrast to scenarios in which we allowed secondary cues to trigger increases in persistence, which consistently increased the likelihood of solving even when secondary cues were rare. This is only a simulated finding, but it suggests that carib grackles encounter learning opportunities very frequently and/or learn fast as this species appears to show operant learning in response to secondary cues (see [Section 3.3](#); [Overington et al., 2011](#)). Models of this kind should help to stimulate future research investigating the relative roles of motor flexibility and persistence in explaining problem solving and innovative behavior more generally.

3.6 Problem Solving and Causal Reasoning

Having suggested that random motor variability might play an important role in generating innovative behavior, we should nevertheless not ignore the fact that the process of innovation might draw upon goal-directed mechanisms (Hills, 2006). Here, when attempting to solve a problem-solving task, animals select motor actions based on preexisting physical causal knowledge. Causal knowledge is highly generalizable across contexts because it is relatively independent of the perceptual attributes of objects (eg, “objects move along continuous surfaces”; “softer objects break when hit with a harder object”; “connected objects move together”).

For example, New Caledonian crows (*Corvus moneduloides*) can extract functional properties of objects, store them to memory and apply them to subsequent problem-solving opportunities (Taylor, Hunt, et al., 2009; Taylor, Roberts, et al., 2009). Following extensive training on a trap-tube task, in which food needs to be extracted from one side of a tube to avoid it falling into a hole, birds solved a table-trap task, a perceptually very different looking task but one with the same functional properties (a hole in which food can get trapped) (Taylor, Hunt, et al., 2009; Taylor, Roberts, et al., 2009). It is also within the capacities of New Caledonian crows to solve metatool tasks, in which one tool must be used to retrieve another functional tool even when one tool has been systematically associated with an absence of reward (Taylor, Elliffe, Hunt, & Gray, 2010). Similar multistep sequential problem solving has been demonstrated in Goffins cockatoos (*Cacatua goffini*) (Auersperg et al., 2013), while kea, a New Zealand parrot, show a spontaneous attention to functional attributes of technical problems (Huber & Gajdon, 2006; Werdenich & Huber, 2006).

Although much of the research on physical causal reasoning has not been linked to the innovation literature (eg, Beckers, Miller, De Houwer, & Urushihara, 2006; Penn & Povinelli, 2007; Premack, 2007), one can assume that the ability to extract and store information relating to causation might assist in discovering new foraging opportunities. On the other hand, most demonstrations of inferential reasoning in nonhumans have been challenged by association-formation explanations and the most robust tests have failed to find such capacities (Maes et al., 2015). Furthermore, one cannot help but notice the apparent simplicity of many reported avian innovations. Even those classified as “technical innovations,” such as removing caps from milk bottles, catching insects on the wing, foraging for prey by artificial light or digging for prey in sand (Lefebvre et al., 1998, 1997; Overington

et al., 2009) bring to mind explanations based on exposure to, and motor variation in response to, novel stimuli.

These considerations lead us to suggest that it is unlikely that any substantial proportion of avian innovations draw upon inferential reasoning. In our opinion, it seems more likely that causal inference is more commonly involved in allowing individuals to create the opportunity for innovation (Tebich et al., 2016). For example, an animal might discover serendipitously that fish rise to the surface of a pond in response to floating foods and might then use a bait to elicit surfacing by other fish.

An alternative to abstract causal knowledge for generating goal-directed innovations is that animals might apply perceptual rules that guide their interactions with objects. Such perceptual rules might include making preferential contact with object edges, with areas of high visual contrast, or protruding surfaces, for example. Focusing solving effort on areas that produce movement cues, as discussed above, is another example. Such rules might be acquired as a consequence of experience of past pairings with rewards (eg, pecking the edge of an object is more likely to break/move it than pecking its center), in which case their use during problem solving would constitute a form of generalization (Kolodny, Edelman, & Lotem, 2015). Alternatively, recognition of such cues might be relatively hardwired. Such rules would remain tightly bound to the perceptual attributes of objects (Pearce, 1987), but would nevertheless assist animals in solving innovation tasks without requiring them to have any understanding of how solutions work (Hunt, Rutledge, & Gray, 2006; Maes et al., 2015).



4. INNOVATION AND COGNITION: A MODEL

Nearly two decades of comparative analyses in birds and primates spanning across taxonomic levels (order, family, species) have convincingly shown that innovation counts are associated with larger brains relative to body size (Lefebvre et al., 1998, 1997) and performance on a variety of cognitive tests (Reader, Hager, & Laland, 2011; Timmermans et al., 2000). In contrast, it appears not to be reliably true that more innovative *individual* birds are those with the higher performances on cognitive tasks. Hence, patterns of results from across taxa and within species appear to contradict one another. We ask how such a contradiction can arise given that interindividual variation provides the raw material for the evolution of cross-taxon variation.

Here, we propose a model of innovation that reconciles this apparent contradiction. The crux of our model is to consider whether the link between cognition and innovation is causal or correlational. Although, answering this question might seem to some to be a purely academic exercise, we suggest that understanding the nature of this relationship in the future will enable us to make predictions regarding the pattern of relations one should expect to find at the within-species level. Our model draws upon the findings from several bodies of research, including theoretical and experimental work on the evolution of behavioral plasticity and cognition, as well as empirical work on interindividual variation in cognition. It should also be noted that a premise of our model is that problem solving provides an ecologically meaningful measure of innovativeness both across and within species.

Theoretical and empirical research has converged on the conclusion that environmental variability is the most important evolutionary driver of behavioral plasticity (reviewed by [Snell-Rood, 2013](#)). One major contributor to behavioral plasticity is cognition. This is because cognition encompasses the psychological processes by which environmental information is acquired, processed, retained, and used to make behavioral decisions ([Dukas, 1998](#); [Shettleworth, 2010](#)). Hence, cognitive processes are the primary means by which animals adjust their behavior in response to spatial and temporal variation in their environment over the course of their lifetime. Ecological theories of brain evolution and intelligence bridge the gap between ultimate and proximate considerations by arguing that environmental variability is the primary driver of superior cognitive skills ([Byrne, 1997](#); [Clutton-Brock & Harvey, 1980](#); [Eisenberg & Wilson, 1978](#); [Gibson, 1986](#); [Parker & Gibson, 1977](#)). It is purported that higher-order cognition (eg, causal reasoning, analogical reasoning) allows animals to solve more complex ecological problems such as those involved in extractive foraging and managing and processing spatial and temporal information about varying resource availability. After several decades of research on social intellect theories, ecological theories of brain and cognitive evolution are back in the spotlight ([Parker, 2015](#); [Reader et al., 2011](#)).

In parallel with research on the evolution of behavioral plasticity and cognition, there is an increasing amount of work indicating that repeatable individual differences in cognitive abilities measured across batteries of standardized cognitive tests are underpinned by the existence of a general process factor referred to as a *general intelligence* factor, *g* ([Matzel et al., 2003](#); [Matzel, Sauce, & Wass, 2013](#); [Matzel, Wass, & Kolata, 2011](#); [Sauce](#)

& Matzel, 2013; but see Locurto, Benoit, Crowley, & Miele (2006)). This latent process explains between 30% and 40% of interindividual variation in performance and is typically operationalized by faster learning (Matzel et al., 2011; Wass et al., 2012). A substantial body of experimental work in rodents manipulating the processes that contribute to *g* has established that individual differences in *g* are related to enhanced selective attention, one component of working memory (Colas-Zelin et al., 2012; Light, Grossman, Kolata, & Matzel, 2011; Light, Kolata, Hale, Grossman, & Matzel, 2008; Matzel, Muzzio, & Talk, 1996; Matzel et al., 2011; Wass et al., 2013). The existence of a domain-general cognitive ability has been suggested to underpin cross-taxon variation in the performance of primates on standardized cognitive tests (Deaner, VanSchaik, & Johnson, 2006; Reader et al., 2011).

Although we are far from closing the gap between functional and proximate considerations of cognition experimentally, these parallel lines of research on evolution and mechanisms of cognition suggest that environmental variability has the potential to select for cross-taxon differences in a general intelligence factor. This is the starting point for our model because our analyses of innovation—cognition associations can be streamlined to ask whether innovativeness and *g* merely covary because they evolve under the effect of a common selective force (eg, spatiotemporal environmental variability), but remain mechanistically independent, or whether *g* is a causal determinant of innovation, as implied by some authors (Cole, Morand-Ferron, Hinks, & Quinn, 2012; Cauchard et al., 2013; Keagy, Savard, & Borgia, 2011b; Lefebvre, 2011).

This distinction is important because if *g* is a causal determinant of innovation then we should expect to find positive correlations at both the between and within species' levels of analysis. Specifically, species and individuals that, for example, learn faster should also be the most innovative. This is because any selection on *g* will have consequent downstream changes on innovativeness. For example, if selective attention increases, then innovation speed and probability should increase, whether across species or across individuals (Fig. 4A). If, in contrast, associations of *g* and innovation at higher taxonomic levels reflect mere covariation, then one should not expect to find any consistent pattern of correlations between innovation and cognition at the within-species level (Fig. 4B).

Why should this be the case? With a higher *g*, species not only benefit from being able to track a broader range of spatiotemporally variable environmental stimuli (eg, predation risk; replenishing foods), they also incur the

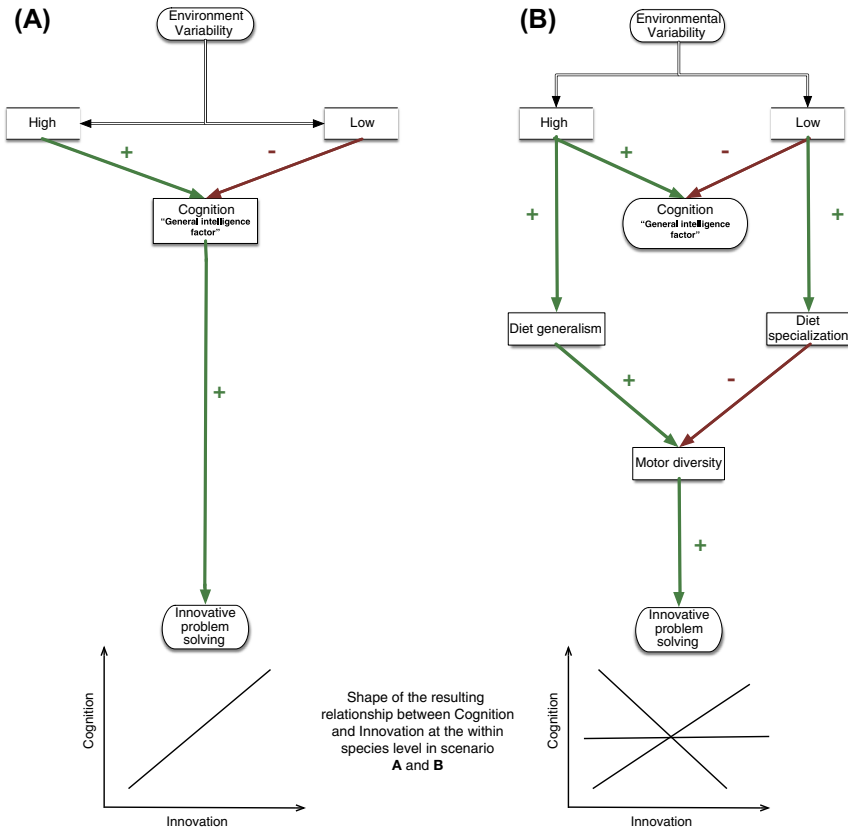


Figure 4 Possible relationships between environmental variability and innovativeness as measured by problem-solving performance. (A) In one case, innovation is a by-product of cognition, while in the other (B) innovation is a product of motor flexibility, itself a consequence of diet diversity, and is not causally linked to cognition.

costs of reduced behavioral efficiency and high attentional load (Dall & Cuthill, 1997; Tosh, Krause, & Ruxton, 2009). As a consequence, we predict that individual specializations will arise, whereby individuals within populations adopt different behavioral strategies. For example, we have recently demonstrated that fast innovators can be fast (ie, they learn a discrimination fast), but not flexible (ie, they reversal learn slowly) learners. This finding appears to contradict consistently positive associations between brain size, cognition, and innovation at the cross-taxon (family/species) level. The latter would lead one to expect that innovative individuals should be both fast *and* flexible learners. These findings can be reconciled, however, by proposing that at least two (perhaps overlapping) individual phenotypes

exist at the species level: some individuals are innovators, while others are flexible learners (Fig. 5). Although each phenotype reflects a distinct behavioral strategy, both are linked to the computational power of the species (eg, residual brain weight or brain organization (Roth & Dicke, 2005; Smaers & Soligo, 2013)). Based on these hypotheses, one would find reliably positive correlations between problem solving and learning at the cross-species level, but not at the within-species level (Fig. 5).

Reflecting on the lack of consistent relationship between learning and problem solving at the within-species level (see Section 3.2), we suggest that the most likely scenario is that innovation and cognition are associated, but not causally linked (Fig. 4B). In other words, in most avian innovations, neither taxa, nor species, nor individuals bring to bear their cognitive abilities when innovating. For this reason, we do not expect future research to find

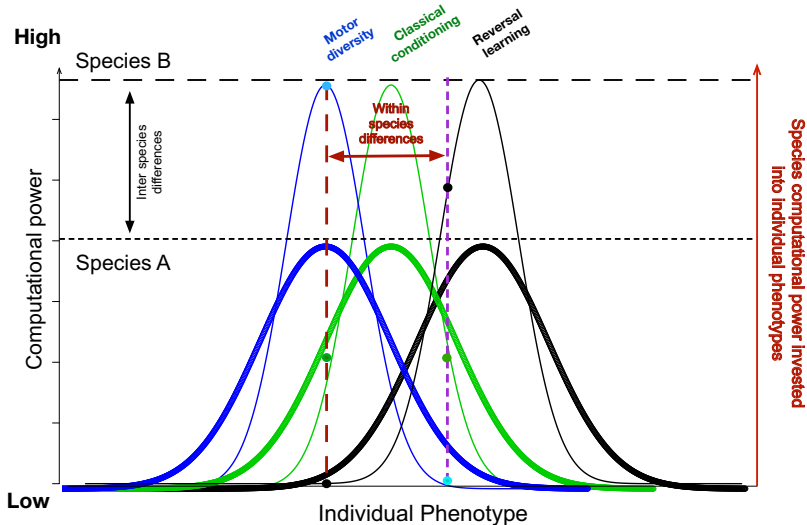


Figure 5 Speculated relations between phenotypical composition of species with differing brains if the link between cognition and innovation is correlational and not causal as depicted in Fig. 4B. Each species benefits from a given computational power (left y axis) that is in turn distributed to different abilities at the individual level (right y axis). It can be understood from this diagram that macroecological approaches in which species level traits are measured, will yield positive correlations across abilities (ie, species B will perform higher on all abilities relative to species A). In contrast, within-species comparisons, which test the same individual on multiple tasks, will yield no systematic correlations between abilities. This is illustrated by the two *dashed lines*, which represent two individuals of species B. Their intersection with the blue (dark gray in print versions), green (light gray in print versions), and black curves (three abilities) defines their respective phenotypes reflecting different within-species ecological strategies.

any consistent relationship between innovation and learning performances at the within-species level. Relationships will be necessarily paradigm-specific (eg, they will differ across learning and inhibition).

Reflecting on the consistent relationship between motor diversity and problem solving at the within-species level (see [Section 3.4](#)), we suggest that environmental variability drives the evolution of behavioral plasticity, cognition, and learning, as explained above, but also diet generalism ([Macarthur & Levins, 1967](#); [Moldenke, 1975](#)), which in turn, generates more flexible motor repertoires (with more even frequencies of motor expression). It is these more flexible motor repertoires, and not cognition, that cause (see [Section 3.3](#)) the first occurrence of novel behaviors ([Fig. 4B](#)). We suggest this is why species with higher innovation counts have recently been found to be those with more diverse diets ([Ducatez, Clavel, & Lefebvre, 2014](#); [Sol, Sayol, Ducatez, & Lefebvre, 2016](#)).

A simple way to think about how the relationship between cognition and innovation can differ at different levels of analysis is to envisage that increased computational power (eg, residual brain weight or brain organization; [Roth & Dicke, 2005](#); [Smaers & Soligo, 2013](#)) is a shared derived character in the last common ancestor of two sister species ([Sol, Duncan, et al., 2005](#)). Diverging dietary needs among daughter species would then explain why one species becomes a dietary generalist and therefore innovative, while the other remains a dietary specialist and less innovative. Diversification of individual strategies within the dietary generalist species then diversifies the types of relationships (ie, positive, negative, zero) that can be found between performance on specific learning tasks and innovation.

Consistent individual differences in innovativeness ([Griffin & Diquelou, 2015](#); [Morand-Ferron, Cole, Rawles, & Quinn, 2011](#)) might form part of a more general behavioral phenotype ([Réale et al., 2010](#)). For example, increased innovativeness, with high persistence and little attention to changing circumstances ([Griffin et al., 2013](#)), might form part of a proactive phenotype, whereas a lower inclination towards innovativeness, with less persistence and more attention to changing circumstances, might fit into a more reactive phenotype ([Carter, Marshall, Heinsohn, & Cowlshaw, 2013](#); [Coppens, de Boer, & Koolhaas, 2010](#); [Griffin et al., 2013](#); [Kurvers, van Oers, et al., 2010](#); [Kurvers, Prins, et al., 2010](#); [Réale et al., 2010](#)). This hypothesis would explain why one finds more innovations in species with a larger brain than in species with smaller brains. If flexible learners are also more prone to using social information, as suggested by recent empirical work ([Kurvers, van Oers, et al., 2010](#); [Kurvers, Prins, et al.,](#)

2010), then the frequencies of innovations will be more readily amplified through social learning, making it more likely that an innovation will be frequent enough to be noticed by an ornithologist (Fig. 5).

Finally, we wish to mention the body of work measuring cross-species variation in motor diversity and that relating motor variation to brain space. A substantial amount of effort has been allocated to quantifying motor diversity in some taxonomic groups. For example, Parker (1974) used data from 74 primate species to determine over 500 object manipulation patterns and their taxonomic distribution. She concluded that taxonomic groups differed substantially in the size of their motor repertoire, with primates such as lemurs having the smallest repertoire and cebus monkeys and apes having the largest. More recently, Changizi (2003) quantified the repertoire size of 24 mammalian species. Developing similar measures of repertoire size of foraging repertoires for birds and relating it to diet diversity and innovation counts would shed light on the relationships as proposed in our model.

Across species, larger motor repertoires, defined as the number of behaviors in published ethograms and obtained for 24 mammalian species, as well as the number of muscle types, computed across eight mammalian orders, both increase with increasing encephalization (Changizi, 2003). A similar relationship exists in bats (Ratcliffe, Fenton, & Shettleworth, 2006). Within species, starting with the organization of the primary motor cortex, it has long been known that the amount of brain matter devoted to any particular body part represents the amount of control that the primary motor cortex has over that body part (Penfield & Rasmussen, 1950). Larger amounts of brain matter are associated with an increase in the degree of precision of movement that body part can achieve (Penfield & Rasmussen, 1950). There is evidence that the primary motor cortex is developmentally highly plastic in terms of its organization (Sanes & Donoghue, 2000). This plasticity might extend to the amount of brain matter devoted to a given set of movements. For example, comparative studies suggest that the premotor and motor areas of professional musicians have larger gray matter volume than do those of amateur musicians (Gaser & Schlaug, 2003). There is similar evidence for developmental plasticity of motor areas in nonhumans. In canaries, the RA, a brain nucleus involved in the production of bird song, expands and shrinks seasonally as the birds learn new and different song repertoires on successive years (Nottebohm, 1981), suggesting that amount of relevant neural tissue increases and decreases along with the song repertoire size. This body of work creates unambiguous links between motor capacities and areas of the brain known to be involved in motor control. We suggest

that future research relating innovations to neural volumes should focus more specifically on these motor areas.



5. BEHAVIORAL VARIABILITY: A GENERAL SOURCE OF INNOVATIVE BEHAVIOR

We have presented a model in which we suggest that foraging innovations are attributable to variation in foraging behavioral repertoires, which itself is a consequence of dietary generalism. We have pitched our model against the backdrop of foraging innovations in birds, first because it is based on research on problem-solving tasks, which typically involve working to obtain food, and second, because the bulk of research to date, supported and spurred along by research by Louis Lefebvre and his colleagues, has been on innovations in the foraging domain. Our model is anchored in the empirical literature demonstrating that high motor diversity consistently improves problem solving. Here, we discuss whether one should expect to find innovations in other functional domains and how behavioral variability more generally might be considered a potential causal variable. It is not our intention to assert that behavioral variability is the only mechanism by which all instances of innovative behavior can be generated. Indeed, we have discussed a range of other mechanisms elsewhere (Tebbich et al., 2016).

Kummer and Goodall (1985) proposed that behavioral innovations should arise in a variety of functional domains, including ecological, technical, and social. For example, the authors described how a female chimpanzee interrupted an aggressive encounter with an adolescent male by holding the branch with which he was hitting her and on another occasion tickling him (Kummer & Goodall, 1985). The subsequent research focus on foraging innovations both in terms of adaptive significance and underpinning mechanisms is probably a practical one. Ornithological journals publish reports of novel feeding behaviors that can be counted and related to life history, and it is experimentally straightforward to motivate animals to seek to obtain food contained inside extractive foraging tasks. As suggested by other authors, there is little reason not to assume that animals have the capacity to invent new behaviors in other functional domains, including in the context of antipredator/antiparasite defense and reproduction. Some examples include Galapagos finches rubbing their feathers with a plant-based mosquito repellent (Sabine Tebbich, personal communication) and deer lying down in the thick vegetation to avoid human hunters, a behavior that would cost them their lives in the face of their natural predators

(Thomas, 2009). Unfortunately, such published reports of behavioral innovations outside the foraging context appear to be too uncommon for large-scale comparative analyses of their mechanisms and ecological drivers.

One interesting exception is nesting innovations. In an exhaustive review of 30 years of ornithological literature, Nicolakakis and Lefebvre (2000) put together a database consisting of 176 anecdotes of nesting innovations across 21 avian taxa (orders, suborders, or infraorders). Such innovations included reports such as “nest cup composed of polythene”; “nesting in a commuter station”; “seen excavating nest,” etc. (Nicolakakis & Lefebvre, 2000). The goal of this comparative study was to test the prediction that nesting innovations would not show the significant correlation with relative brain size found with foraging innovations despite sharing similar confounds (eg, research effort, biased reporting of anecdotes). This prediction was based on the assumption that nesting behavior is generally thought of as relatively inflexible and immune to experience-dependent influences. As predicted, multiple regressions revealed that forebrain size fell short of being a significant predictor of nesting innovation counts. However, as pointed out by the authors, the correlation between forebrain size and nesting innovations was positive, albeit nonsignificant, and the partial correlation for forebrain size on nesting was not significantly different from that for forebrain size on foraging. One might conclude that nesting behavior is not as inflexible and experience-independent as once thought, a possibility in line with emerging research demonstrating that learning is an important facet of nest building (Muth & Healy, 2014).

As for foraging innovations, however, one should remain cautious when taking such correlations to infer causality. Do nesting innovations involve cognition or do they, as we have suggested for foraging innovations, rely upon motor flexibility in the nesting domain? Contrary to foraging innovations, there is no research to date examining the role of motor flexibility in nesting and so any discussion of this possibility remains speculative. Whereas in foraging innovations, one can identify diet generalism as the factor facilitating diversification of motor actions involved in foraging, it is not clear how motor variability in the nesting domain would evolve. One possibility is that environmental variability might select for greater nesting generalism directly. In environments where nesting opportunities vary spatially and/or temporally both in terms of where to nest and what materials to use, one can assume that this fluctuation will select for more open-ended nesting behavioral patterns. With more handling of a greater variety of nesting materials, motor diversity might also increase. An alternative possibility is

that motor variability in one functional domain might be transferable to other functional contexts. For example, an animal that has a diverse feeding repertoire might be capable of performing a variety of motor actions when building nests. Nicolakakis and Lefebvre's (2000) analysis revealed that regressing nesting and foraging innovation counts, respectively, against the number of species per taxon yielded residuals that were significantly correlated across nesting and foraging domains, indicating that taxa with higher numbers of feeding innovations also had higher numbers of nesting innovations. This finding indicates that foraging and nesting innovations go hand in hand providing the only evidence to date to the best of our knowledge that innovative behavior might transfer across functional contexts.

More generally, we suggest that larger and more evenly distributed motor repertoires should be considered a possible cause of innovations in a variety of domains for the same conceptual reasons that have led us to link motor flexibility in the foraging context with foraging innovations. For example, greater variation in song repertoires provides a broader basis from which to generate new vocal variants that can then be retained or lost depending on their effect on intruders and/or females. The same should apply to gestural communication and antipredator/antiparasitism responses.

Recent research has revealed that animals rewarded to produce new behavioral variants become behaviorally more variable (Jensen, Miller, & Neuringer, 2006; Kuczaj II & Eskelinen, 2014; Pryor & Chase, 2014). Dolphins reinforced for producing new behavioral responses produce significantly more new behaviors (Pryor & Chase, 2014), as do pigeons (Jensen et al., 2006). There is emerging evidence that intraindividual variation in behaviors, such as activity, is repeatable (Biro & Adriaenssens, 2013), suggesting it might have the potential to undergo selection. Together these findings suggest that the raw material for the evolution of enhanced behavioral variability and its genetic assimilation exist. Hence, we suggest that the contributing role of behavioral variability to innovative behavior more generally warrants more attention.



6. GENERAL CONCLUSIONS

The starting point for our paper is the view that avian innovation counts provide a direct measure of cognition (reviewed by Lefebvre, 2011, 2013). We have reviewed the literature relating cross-taxon variation in innovativeness (operationalized by field innovation counts) on the one

hand, and within-species innovativeness (operationalized by problem solving) on the other, to cognition. Although cross-taxon associations yield consistent patterns, within-species associations do not. We have discussed several ways in which future research on within-species variation in innovativeness and cognition can tackle this question using more robust and a more diverse array of research methods.

In an attempt to reconcile apparent contradictory patterns of findings at different taxonomic levels of analysis, we have presented a model in which motor diversity is the primary process by which innovative behaviors arise. Although innovative orders and species might have on average a higher cognitive capacity, in our model, these capacities are not applied to novel innovation opportunities. As suggested by several other authors (Auersperg et al., 2011; Auersperg, Gajdon, & Von Bayern, 2012; Greenberg & Mettke-Hofmann, 2001; Reader & Laland, 2003), we envisage that innovations are contextually facilitated by object manipulation and spatial exploration tendencies, as well as play (Tebich et al., 2016), but that these factors operate on innovation by simply increasing encounter rates with novel opportunities and object affordances, leaving information processing speed (eg, learning rates) unaffected. In other words, innovators do not learn environmental information more quickly, they simply encounter it more frequently. We also envisage that motor variability can be expanded exponentially via morphological adaptations such as using both the beak and the feet to manipulate objects (Tebich et al., 2016). Finally, we suggest that environmental variability selects for both enhanced cognitive abilities and diet diversity. However, it is diet diversity, via its effects on motor diversity, which drives innovativeness, and not enhanced cognition.

In conclusion, behavioral innovations are an important source of behavioral plasticity. Findings from macroecological comparative analyses strongly suggest that the capacity to innovate will facilitate persistence in rapidly changing ecosystems worldwide. Understanding the behavioral and cognitive processes that allow animals to innovate is key to predicting which species are likely to persist and which ones are likely to go extinct. In coping with rampant environmental modification and destruction, the costs associated with innovations that draw upon higher-order cognitive mechanisms—large brains, long ontogeny, delayed reproduction, low reproductive rates, larger amounts of neural tissue—might well counteract the benefits associated with innovating. Those innovations that draw upon motor variation, coupled with associative learning of successful outcomes, presumably avoid some of those costs, thereby providing greater net payoffs.

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