



Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Innovation and problem solving: A review of common mechanisms

Andrea S. Griffin*, David Guez

School of Psychology, University of Newcastle, Australia

ARTICLE INFO

Article history:
Available online xxx

Keywords:
Behavioural flexibility
Cognition
Innovation
Problem solving

ABSTRACT

Behavioural innovations have become central to our thinking about how animals adjust to changing environments. It is now well established that animals vary in their ability to innovate, but understanding why remains a challenge. This is because innovations are rare, so studying innovation requires alternative experimental assays that create opportunities for animals to express their ability to invent new behaviours, or use pre-existing ones in new contexts. Problem solving of extractive foraging tasks has been put forward as a suitable experimental assay. We review the rapidly expanding literature on problem solving of extractive foraging tasks in order to better understand to what extent the processes underpinning problem solving, and the factors influencing problem solving, are in line with those predicted, and found, to underpin and influence innovation in the wild. Our aim is to determine whether problem solving can be used as an experimental proxy of innovation. We find that in most regard, problem solving is determined by the same underpinning mechanisms, and is influenced by the same factors, as those predicted to underpin, and to influence, innovation. We conclude that problem solving is a valid experimental assay for studying innovation, propose a conceptual model of problem solving in which motor diversity plays a more central role than has been considered to date, and provide recommendations for future research using problem solving to investigate innovation.

This article is part of a Special Issue entitled: Cognition in the wild.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

The last decade has seen a substantial increase in interest in animal **innovation**. Since **Reader and Laland's (2003a)** keystone contribution to the topic, **the ability to invent new behaviours, and/or use pre-existing ones in new contexts** has become central to our thinking of how animals may adjust to novel and changing environments. In an age of accelerating planet-wide environmental modification and destruction, there has never been a more pertinent time to investigate the psychological processes that underpin innovation, and the factors that influence its expression.

The first challenge to studying animal innovation has been to define it. As **Reader and Laland (2003a)** first pointed out, innovation may be defined as an end-product – “a new or modified learned behaviour not previously found in a population”-, or as a process – one “that results in new or modified learned behaviour and that introduces novel behavioural variants into a population's repertoire”. Even though the definition of innovation remains a matter

of debate (**Ramsey et al., 2007**), we do not attempt to tackle this issue once again here. Instead, we turn to another, closely related, challenge to studying innovation, namely its measurement.

Lefebvre and his co-workers (1997, 1998) were the first to crack the problem of quantifying innovation across taxa by surveying the ornithological literature and counting the number of anecdotal reports of novel feeding behaviour for each species encountered. More recently, attention has turned to quantifying intra-specific variation in innovation. Here, once again, in the context of inter-species comparative work on innovation, **Lefebvre and his co-workers** contributed to developing the methodologies that have become key to measuring intra-specific variation (**Webster and Lefebvre, 2001**). They compared the innovation tendencies of five different avian species by measuring their ability to open a puzzle box to gain access to food (**Webster and Lefebvre, 2001**). The experiment yielded a striking parallel between the taxonomic distribution of innovation counts, and innovation propensity measured using the problem-solving assay. Passerines, an avian family with high numbers of foraging innovations in the wild, significantly outperformed Columbiforms, an avian family with low numbers of field innovations (**Webster and Lefebvre, 2001**). This result suggested that problem solving provided an ecologically meaningful assay for measuring variation in innovation propensity (**Lefebvre**

* Corresponding author at: School of Psychology, University of Newcastle, Callaghan, 2308 NSW, Australia. Tel.: +62 02 4348 4393.
E-mail address: andrea.griffin@newcastle.edu.au (A.S. Griffin).

Table 1

Review of the methods used in studies of extractive problem-solving tasks to explore the effects of novelty responses, motor diversity, learning and necessity on problem-solving ability. Only studies published since 2000 and explicitly testing the processes underpinning problem solving and the factors influencing the expression of this ability were included in the review. In a few cases, the allocation of variables to a particular category does not correspond to the interpretation of the original authors (e.g. attempt rate as a measure of exploration re-allocated as a measure of persistence). Contact latencies were either categorized as a neophobia or a neophilia test depending on the details for the protocol (food deprivation or not, food reward available or not etc.) indicated under 'Task'. Further details of the headings (e.g. necessity) and tests (e.g. neophobia vs. neophilia) are provided in Section 3 of the main text.

Authors	Species	Experimental setting	Task	Problem-solving	Novelty responses	Motor diversity	Learning	Necessity
Aplin et al. (2013)	Blue tit, <i>Cyanistes caeruleus</i>	Wild-caught captive-tested in groups with a trained demonstrator	Tray of wells covered with lids; no habituation; food invisible; no food deprivation; alternative food available	Success; latency to solve (first contact to first solve)	NEOPHOBIA: task contact latency			COMPETITIVE RANK: sum of visits to a monopolizable feeder over three days; DOMINANCE RANK: agonistic interactions around a defensible food source; MOTIVATION: body condition
Benson-Amram and Holekamp (2012)	Spotted hyena, <i>Crocuta crocuta</i>	Free-ranging, tested preferentially alone, but also some group trials	Puzzle box; no habituation; visual and olfactory food cues available; no food deprivation	Success	NEOPHOBIA: task contact latency after entering a 5 m radius around task	Number of distinct motor actions		DOMINANCE RANK; MOTIVATION: body condition; PERSISTENCE: work time
Benson-Amram et al. (2013)	Spotted hyena, <i>Crocuta crocuta</i>	Free-ranging tested in natural groups; captive-held tested singly	Puzzle box; no habituation; visual and olfactory food cues available; no food deprivation; captive animals food deprived	Success	NEOPHOBIA: task contact latency after entering a 5 m radius around task	Number of distinct motor actions		DOMINANCE RANK; PERSISTENCE: work time
Biondi et al. (2010)	Chimango Caracara, <i>Milvago chimango</i>	Wild-caught captive-tested	Puzzle box; habituation; food visible; no food deprivation	Latency to solve (first contact to first solve); number of lids opened	NEOPHOBIA: neophobia test; task approach latency; task contact latency; NEOPHILIA: novel object approach latency; contact latency			
Bókony et al. (2013)	House sparrow, <i>Passer domesticus</i>	Wild-caught captive-tested	Four puzzle boxes, habituation, food visible, food deprivation	Latency to solve (first contact to first solve);	NEOPHOBIA: task contact latency			MOTIVATION: body condition
Boogert et al. (2008)	European starling, <i>Sturnus vulgaris</i>	Wild-caught captive-tested in groups	Six different puzzle boxes; no habituation; food visible; food deprivation	Total number of diffusion studies in which a bird was the first to solve	NEOPHOBIA: neophobia test; task contact latency; SPATIAL EXPLORATION: latency to feed in a novel space		Shaping of problem-solving (different task)	COMPETITIVE RANK: order of access to a preferred food following 1 h food deprivation; total time birds spent monopolizing a bathing dish
Bouchard et al. (2007)	Feral pigeon, <i>Columba livia</i>	Wild-caught, captive-tested	Puzzle box; no habituation; food visible; food deprivation	Latency to solve	NEOPHOBIA: neophobia test		Social learning of problem solving (same task)	COMPETITIVE RANK: total time spent feeding
Cauchard et al. (2013)	Great tit, <i>Parus major</i>	Free-ranging	String-pulling task blocking access to nest; no habituation	Latency to solve (first contact to first solve)	NEOPHOBIA: latency from landing on nestbox to first contact			MOTIVATION: nest provisioning rates; PERSISTENCE: number of task contacts

Table 1 (Continued)

Authors	Species	Experimental setting	Task	Problem-solving	Novelty responses	Motor diversity	Learning	Necessity
Cole and Quinn (2012)	Great tit, <i>Parus major</i>	Wild-caught captive-tested and field-tested	Lever-pulling task (details in Cole et al., 2011)	Success	EXPLORATION: novel room exploration			COMPETITIVE RANK: amount of time with sole access to a feeder in the wild; DOMINANCE RANK MOTIVATION: body condition
Cole et al. (2011)	Great tit, <i>Parus major</i>	Wild-caught, captive-tested	Lever-pulling task; no habituation; food visible; no food deprivation; alternative food available during test; repeat lever-pulling task; no habituation; food visible; food deprivation	Success	NEOPHOBIA: neophobia test; task approach latency; EXPLORATION: novel room exploration; SHYNESS: latency to feed after disturbance			
Day et al. (2003)	<i>Leontopithecus</i> , <i>Saguinus</i> , <i>Callithrix</i>	Captive-held tested in natural groups	Four puzzle boxes; no habituation, limited visual and olfactory food cues; no food deprivation	Latency to solve	NEOPHILIA: task contact latency			PERSISTENCE: number unsuccessful manipulations
Griffin and Diquelou (submitted for publication)	Noisy miner, <i>Manorina melanocephala</i> ; common myna, <i>Acridotheres tristis</i>	Wild-caught captive tested	Three tasks; habituation; food visible; food deprivation	Success; latency to solve (first contact to first solve)	NEOPHOBIA: neophobia test	Number of distinct motor actions		PERSISTENCE: number of attempts
Griffin et al. (in press)	Common myna, <i>Acridotheres tristis</i>	Wild-caught captive tested	Puzzle box; habituation; food visible; food deprivation	Success; latency to solve (first contact to first solve)	NEOPHOBIA: neophobia test	Number of distinct motor actions		PERSISTENCE: number of attempts
Keagy et al. (2011b)	Satin bowerbird, <i>Ptilonorhynchus violaceus</i>	Free-ranging	Barrier to be removed to access an aversive red object; red tiles attached to the ground to be covered; bower rebuilding	Latency to removal (first orientation to removal); area of a red tile covered after 24 h; bower rebuilding: handling time, flexibility, templating				MOTIVATION: latency to remove object after lifting barrier; distance a tile was moved in 4 h; latency to begin rebuilding
Keagy et al. (2009)	Satin bowerbird, <i>Ptilonorhynchus violaceus</i>	Free-ranging	Barrier to be removed to access an aversive red object; red tiles attached to the ground to be covered	Latency to removal (first orientation to removal); area of a red tile covered after 24 h				MOTIVATION: latency to remove object after lifting barrier; distance a tile was moved in 4 h
Kendal et al. (2005)	Callitrichid monkeys	Captive-held primates tested in natural groups	Seven tasks; no habituation; limited visual and olfactory access to food; no food deprivation	First to solve; frequency of successful manipulations	NEOPHILIA: task contact latency			PERSISTENCE: frequency unsuccessful manipulations
Manrique et al. (2013)	Orang-utan (<i>Pongo abelii</i>), chimpanzee (<i>Pan troglodytes</i>), bonobo (<i>Pan paniscus</i>), gorilla (<i>Gorilla gorilla</i>)	Captive-held primates in natural groups	One task with three variations, no habituation; food visible; no food deprivation	Success, latency to solve		Number of distinct motor actions		

Table 1 (Continued)

Authors	Species	Experimental setting	Task	Problem-solving	Novelty responses	Motor diversity	Learning	Necessity
Liker and Bókonyi (2009)	House sparrow, <i>Passer domesticus</i>	Wild-caught captive-tested in groups of 2 vs. 6	Tray of wells covered with lids; habituation; food invisible; food deprivation	Number of wells opened per individual	NEOPHOBIA: neophobia test			
Morand-Ferron et al. (2011)	Blue tit, <i>Cyanistes caeruleus</i> ; great tit, <i>Parus major</i>	Wild-caught captive-tested, and free-ranging	CAPTIVITY: lever-pulling task no habituation; food visible; no food deprivation; alternative food available; WILD: six lever-pulling devices	Success; latency to solve				MOTIVATION: fat score; PERSISTENCE: number of visits to wild feeder; duration of attempts to wild feeder
Overington et al. (2011)	Carib grackle, <i>Quiscalus lugubris</i>	Wild-caught captive tested	Puzzle box; no habituation; food visible; food deprived	Latency to solve (first contact to first solve)	NEOPHOBIA: neophobia test; task contact latency; EXPLORATION score: PCA analysis pooling neophobia, activity and exploration; SHYNESS: aggression in hand; latency to feed after disturbance		Shaping of problem solving (same task)	MOTIVATION: body condition
Sol et al. (2012)	Common myna, <i>Acridotheres tristis</i>	Wild-caught captive-tested	One task; habituation; food invisible; food deprivation	Success; latency to solve (first contact to first solve)	NEOPHOBIA: neophobia test; task approach latency; SHYNESS: latency to exit nest box			MOTIVATION: latency to feed during initial control and final control of the innovation task; PERSISTENCE: number of attempts
Tebbich et al. (2010)	Woodpecker finch, <i>Camarhynchus pallida</i> ; small tree finch, <i>C. parvulus</i> , medium ground finch, <i>Geospiza fortis</i>	Wild-caught captive-tested (except neophilia)	One task; no habituation, food visible, no food deprivation	Number of trials to solve	NEOPHILIA: mean time spent < 3 m of novel object (field data)		Discrimination learning followed by reversal learning on a colour discrimination	PERSISTENCE: frequency of task contacts
Thornton and Samson (2012)	Meerkats, <i>Suricata suricata</i>	Free-ranging tested in natural groupings	Three puzzle boxes; no habituation; food visible; no food deprivation	Success	NEOPHOBIA: task approach latency			DOMINANCE: number of aggressive interactions; PERSISTENCE: time spent manipulating the task
Webster and Lefebvre (2001)	Lesser Antillean bullfinch, <i>Loxigilla noctis</i> ; shiny cowbird, <i>Molothrus bonariensis</i> ; carib grackle; zenaida dove, <i>Zenaida aurita</i> ; common ground dove, <i>Columbina passerina</i>		Puzzle box; habituation; food visible; food deprivation	Success	NEOPHOBIA: neophobia; test task contact latency			

and Sol, 2008; Lefebvre et al., 2004). Since then, the experimental principle of presenting animals with a novel problem and measuring variation in the ability to solve it has been applied to a taxonomically broad array of species (e.g. Boogert et al., 2008; Cole et al., 2011; Griffin et al., 2014; Laland and Reader, 1999; Manrique et al., 2013; Morand-Ferron and Quinn, 2011; Sol et al., 2012; see Table 1 for more references). Most typically, tests involve presenting animals with an extractive foraging task that needs to be solved to gain access to food, but more recently, individuals may be required to interact with objects to gain access to their nest (Cauchard et al., 2013), or to improve their sexual displays (Keagy et al., 2011a, 2009). Although it may be said that the use of problem solving paradigms dates back to Thorndike (1898), Lefebvre and co-workers were nevertheless the first group to firmly anchor this methodology into modern-day research on animal innovation.

The extent to which variation in innovation propensity is associated with variation in cognition has been the focus of much attention. Across both avian and primate taxa (families in birds, species in primates), innovation counts increase with relative brain volume, as well as with the volume of multimodal integration areas (mesopallium in birds; neocortex in primates) broadly accepted to underpin higher order cognition (Cnotka et al., 2008; Güntürkün, 2012; Lefebvre et al., 1998, 1997; Mehlhorn et al., 2010; Reader and Laland, 2002). Although the brain size-innovation relationship may not occur at lower taxonomic levels in birds (Jönsson et al., 2012), this discovery forms the basis for the argument that innovation counts provide for the first time a field-based measure of inter-taxon variation in general-purpose cognitive abilities as opposed to specialized domain-specific cognitive abilities (Lefebvre, 2011). Through its link to field innovations, inter-individual variation in problem solving has also begun to be assumed to reflect inter-individual variation in cognitive capacity (Cauchard et al., 2013; Cole et al., 2012, 2011; Keagy et al., 2011a).

Here, we intend to sidestep the recent debates surrounding the issue of whether variation in innovation counts (Healy and Rowe, 2007) and in problem solving (Thornton and Lukas, 2012) reflect variation in cognitive ability. Instead, we focus on a question we see as more critical to the progression of innovation research. We ask whether variation in problem-solving ability provides a measure of variation in innovation propensity, as it was originally intended. There is some evidence that problem-solving ability is an individual trait that is stable across time (Cole et al., 2011; Laland and Reader, 1999; Morand-Ferron et al., 2011), and some contexts. There is a rapidly expanding literature unravelling the psychological processes underpinning problem solving and the factors that influence its expression. We suggest that now is a good time to pause and reflect on whether we can reasonably assume that those findings shed light on innovatory processes so thoughtfully discussed by Reader and Laland (2003b).

We attempt to answer this question by briefly recapitulating the predictions summarized by Reader and Laland (2003b), and echoed by others (Greenberg, 2003), concerning the processes that should mediate innovation, and then reviewing the current avian and primate literature on the processes that mediate problem solving in order to explore to what extent those processes that underpin problem solving are those predicted to underpin innovation. We review both inter-species and intra-specific data sets, as the processes that mediate innovation should operate at both levels of analysis. In addition, we review the current body of work on the factors that influence the expression of problem solving and examine to what extent these factors overlap with those predicted (Reader and Laland, 2003b), and found (Reader and Laland, 2001) to influence the expression of innovations in the wild. There have no attempts to analyse the factors that influence field innovations in birds, so our comparison is limited to those factors revealed in primates (Reader and Laland, 2001). Along the way, we review findings from our lab,

where we study the Indian (common) myna (*Acridotheres tristis*), a highly successful worldwide ecological invader and ideal model avian system for exploring problem solving behaviour and its correlates. Finally, we discuss the outcomes of the review in the light of a conceptual model integrating both underpinning processes and contextual influences on problem solving, together with recommendations for future research employing problem solving as a proxy for innovation.

2. Predictions

2.1. Innovation and novelty responses, learning and behavioural flexibility

Many authors have speculated independently about the various processes that should underlie innovation, but Reader and Laland (2003a) contributed the most succinct summary. The authors predicted that several different processes should be critical to innovation, including novelty responses, exploration, asocial learning, and behavioural flexibility. The authors also predicted that social processes, insight and creativity would underpin innovation, but as social processes were acknowledged to act in only a limited set of circumstances and insight and creativity remain ill defined in nonhumans, we do not consider them here. **Novelty responses and exploration determine the probability that animals will engage with a novel resource or encounter a novel context, around which an innovation can occur, while asocial learning determines the probability that the innovation will be repeated subsequently.** Behavioural flexibility, including the ability to change behaviour in response to environmental feedback, and **the ability to inhibit previously successful behaviour, determines the likelihood that new behaviours will emerge, and that pre-existing behaviours will arise in novel contexts** (Manrique et al., 2013). Hence, our review examines to what extent the above factors are associated with problem-solving performance.

2.2. Innovation and motor diversity

Klopfer (1967) was the first to make a distinction between perceptual and motor stereotypy: whereas perceptual stereotypy referred to the tendency to respond to a narrow range of perceptual stimuli, motor stereotypy referred to the tendency to produce only a narrow range of motor actions to accomplish a given act. Greenberg (2003) elaborated on this concept further, proposing the concept of motor plasticity. Noting a relationship between high problem-solving abilities, innovative capacities and physical manipulation in the foraging context in primates (Boinski et al., 2000; Clarke and Boinski, 1995), Greenberg (2003) foreshadowed the role of this process in innovation. Central to innovation is the ability/tendency to express novel behavioural variants (novel or pre-existing ones in novel circumstances, Reader and Laland, 2003b). Applied to motor behaviour, this can occur either when a new motor action is invented or when a previously existing motor action (e.g. a foraging behaviour, a communication signal) is performed in a novel context. Hence, motor variability, including the number of different actions performed and their relative frequency of expression, should provide an important source of raw material for behavioural variants (Fig. 1). It makes intuitive sense that an animal that is more variable in its motor behaviour has more raw material to produce novel behaviours, or to use pre-existing ones in novel contexts, including social signals and/or foraging techniques, than an animal that is more stereotyped in its motor output. As such, we suggest that motor diversity is one source of behavioural flexibility.

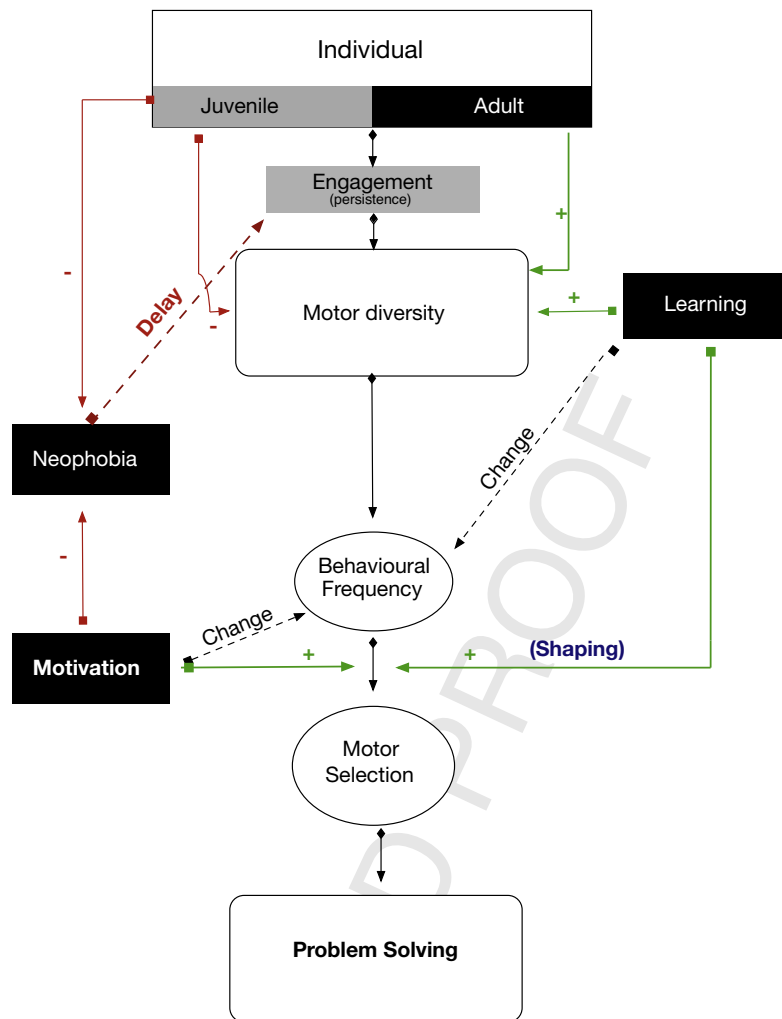


Fig. 1. Conceptual model illustrating the central role of motor variability coupled with learning of motor variability in problem solving. Red arrows indicate reducing factors, while green arrows indicate enhancing ones. Neophobia influences the likelihood of interacting with the environment and may delay engagement with the problem at hand. Motivation may influence engagement indirectly via neophobia (as indicated), but also directly (not indicated). Juveniles are predicted to be less neophobic than adults. But without motor variability, an animal will not problem-solve. Learning increases the frequency of successful motor actions (shaping) and can lead to an expansion of the motor repertoire. Motor variability increases interactions with the environment thereby increasing opportunities to learn object affordances, a source of goal-directed motor selection mechanisms, but also potentially facilitating other learning opportunities (Griffin et al., 2013a). We predict the same collection of mechanisms to operate in technical foraging innovations (Overington et al., 2009).

There is now indirect evidence that motor flexibility is involved in field innovations. Overington et al. (2009) classified avian innovations as either consumptions of novel foods or technical innovations, and demonstrated that technical innovations are a stronger predictor of residual brain size than consumptions of novel foods. Innovation counts correlate positively with tool use (Lefebvre et al., 2002; Reader and Laland, 2002) and with the quantity of physical manipulation while foraging (Boinski et al., 2000; Clarke and Boinski, 1995), pointing again to an association between motor actions and innovative behaviour. Hence, our review seeks to determine to what extent motor diversity facilitates innovative problem solving.

2.3. Innovation and necessity

Amongst the factors predicted to influence innovation is the idea that innovation should occur more readily in times of necessity (Clayton, 2004; Reader and Laland, 2003b). Consistent with this idea, macro-ecological comparative analyses have revealed that avian taxa with more frequent reports of innovation in the wild are more likely to survive in harsh and changing environments (Sol et al., 2005a, 2005b). At the intra-specific level, Reader and Laland

(2001) found that subordinate primates were generally more likely to innovate than were dominant individuals, providing evidence consistent with the prediction that innovation should be more common in subordinates than in dominants because subordinates tend to be excluded from resources and have a greater necessity to develop alternative strategies (Reader and Laland, 2003b). Hence, in our review, we seek to establish whether problem solving is more common in times of necessity by examining the effects of dominance and competitive ability on problem solving. Within this context, we also review the effects of motivation and persistence on problem solving, as well as their links to food deprivation, although we acknowledge that variation in motivation and persistence may not always be underpinned by necessity. Although macro-ecological analyses have revealed that innovations are more common in winter (Sol et al., 2005b), we know of no such analysis of seasonal effects on problem solving. Consequently, this factor is not considered here.

2.4. Innovation and age

A relatively widespread prediction is that innovative behaviours should be more common in juveniles than adults because the

former tend to be more exploratory than the latter (Benson-Amram and Holekamp, 2012; Greenberg, 2003; Heinrich, 1995; Reader and Laland, 2003b; Thornton and Samson, 2012). Contrary to this prediction, however, Reader and Laland (2001) found that adult primates had higher numbers of innovation reports in the wild than would be expected and juveniles had lower numbers than would be predicted by chance, a finding that was taken to reflect the possibility that innovation could build upon experience and competency (Hauser, 1988; Reader and Laland, 2001). Hence, in our review, we seek to determine whether problem-solving ability is greater in one age group than the other. Finally, some have predicted sex-dependent effects on the propensity to innovate (Reader and Laland, 2001). However, predictions tend to vary across species depending on which sex is more dominant more motivated to access resources. For this reason, we leave sex-dependent effects on problem solving aside.

3. Review of evidence

3.1. Problem solving and responses to novelty

3.1.1. How are responses to novelty measured?

Responses to novelty are not a uniform concept (Greenberg and Mettke-Hofmann, 2001; Russel, 1973) and the large range of protocols used to measure how animals respond to novelty most likely tap several independent motivations. For instance, Greenberg and Mettke-Hofmann (2001) suggested that neophilia (i.e. the attraction towards novelty) can vary independently from neophobia (i.e. the fear of novelty) and that different selective forces might shape these two behaviours. Neophilia could function to facilitate information gathering and is advantageous under high environmental variability, whereas neophobia could function to reduce the costs inherent to information gathering and is advantageous under high predation pressure (Greenberg and Mettke-Hofmann, 2001). Consequently, in considering how responses to novelty affect problem solving, it is important to examine the different ways in which such responses have been measured.

A survey of the literature reveals that three different types of experimental assays have been used for measuring responses to novelty within the context of research on problem solving (Table 1). These three types of assay include further variations as to whether animals are hungry or satiated during the test, whether approach latencies are calculated separately from problem-solving latencies, whether animals are given the opportunity to habituate to the problem-solving apparatus and/or associate it with food prior to attempting to solve it, whether novelty tests are conducted as stand-alone tests or as integral components of the problem-solving tests, and, finally, whether animals are alone or in social groups when tested (Table 1).

First, the relatively common 'neophobia' test involves measuring the latency of a typically food-deprived individual to feed next to a novel object relative to the latency to forage in the absence of a novel object (Greenberg and Mettke-Hofmann, 2001). At times, the latency to approach the novel problem-solving apparatus is used rather than a stand-alone neophobia test (Table 1). There is evidence that the two measures correlate, suggesting that they measure similar unpinning motivations (Boogert et al., 2008; Sol et al., 2012; Webster and Lefebvre, 2001). Neophobia latencies probably provide a measure of risk-taking in the presence of novelty when necessity is high given a state of food deprivation, or a need to access offspring (Cauchard et al., 2013; Griffin et al., 2014). It is noteworthy that risk taking in the presence of novelty is linked to risk taking in response to predators in some species (Bókonyi et al., 2012; Gabriel and Black, 2010) but not in others (Carter et al., 2012; Miller et al., 2006).

A second experimental assay (Greenberg and Mettke-Hofmann, 2001) involves presenting a typically satiated individual with a novel object and measuring the animal's willingness to approach and interact with the object. The neophilia test differs from the neophobia test in so far that approach is elicited in most instances by a novel object per se, and not by an extrinsic reward (e.g. food). Research to date suggests that high neophobia scores are not always coupled with low neophilia scores (Biondi et al., 2010; Mettke-Hofmann et al., 2005, 2002; Miranda et al., 2013). This finding supports the idea that neophobia and neophilia reflect differing motivations, with neophobia reflecting the ability to overcome fear of novelty by necessity, and a neophilia test reflecting an attraction to intrinsically rewarding novelty (Greenberg and Mettke-Hofmann, 2001).

Finally, a 'spatial exploration' task involves releasing an individual into a novel room and measuring how much of the room it moves through and/or how fast it moves through the room (Cole et al., 2011; Verbeek et al., 1996, 1994). The test is generally considered to reflect a mix of conflicting motivations between gathering information about novel spatial environments and the fear that novel environments generate (Hughes, 2007; Montgomery and Monkman, 1955; Renner, 1990), as reducing anxiety by treating animals with anxiolytics increases open-field exploration (Prut and Belzung, 2003). There is mixed evidence as to whether object and spatial exploration are linked (Fox et al., 2009; Verbeek et al., 1994).

3.1.2. Inter-taxon analyses of problem solving and novelty responses

Relatively few studies have quantified variation in problem solving across avian taxa or examined whether inter-species variation in novelty responses contributes to explaining inter-specific variation in problem-solving ability. For example, Tebbich et al. (2010) demonstrated inter-species differences in problem-solving ability in Galapagos finches, but did not report whether these are related to differences in novelty responses. Within those studies that have measured both inter-species differences in novelty responses and problem solving, there is little evidence to date that variation in one explains variation in the other (Table 2). In Webster and Lefebvre's (2001) comparative study of five avian species tested both in captivity and under free-ranging conditions, the species varied in their latency to feed near to a novel object but this variation in neophobia did not predict their problem-solving success. This finding is similar to that by Griffin and Diquelou (submitted for publication) who examined the effect of neophobia on problem solving in both a native Australian honeyeater, the noisy miner (*Manorina melanocephala*), and the introduced Indian myna. Although the native honeyeater was significantly less neophobic than the introduced myna, the latter was significantly more likely to solve an extractive foraging problem than the former and neophobia did not predict problem solving.

We found only one other interspecific study in another taxonomic group in which the authors compared variation in novelty responses with problem-solving performance. Day et al. (2007) quantified neophilia by measuring latency to approach a novel extractive foraging task and correlated this measure with the latency to solve the task across primate species from three different genera. The analysis revealed that latency to first contact predicted latency to first success. However, this significance of this finding is unclear because the latency to solve the task was confounded with the latency to approach the problem-solving task.

3.1.3. Inter-individual analyses of problem solving and novelty responses

There are substantially more studies examining the role of novelty responses in inter-individual variation in problem solving (Table 1). Our survey revealed substantial variability in the

Table 2
Summary of the findings of the studies reviewed in Table 1.

Authors	Conclusions – NOVELTY RESPONSES	Conclusions – MOTOR DIVERSITY	Conclusions – LEARNING	Conclusions – NECESSITY	Conclusions – AGE
Aplin et al. (2013)	NEOPHOBIA: no relationship			MOTIVATION: no relationship; COMPETITIVE RANK: no relationship; DOMINANCE: subordinate males and juvenile females most likely to solve	No relationship
Benson-Amram and Holekamp (2012)	NEOPHOBIA: latency to first contact predicts success	Motor diversity predicts success		PERSISTENCE: work time predicts success; DOMINANCE: no relationship; MOTIVATION: no relationship	Even though juveniles more exploratory, less neophobic, and more persistent, do not solve more; age does not predict success
Benson-Amram et al. (2013)	NEOPHOBIA: predicts success	Motor diversity predicts success		DOMINANCE: no effect; PERSISTENCE: work time predicts success	Captive juveniles less exploratory and more neophobic, and solve less often
Biondi et al. (2010)	NEOPHOBIA: neophobia predicts number of lids opened in juveniles, but not adults; NEOPHILIA: no relationship				Juveniles more successful, but not once greater persistence is accounted for
Bókony et al. (2013)	NEOPHOBIA: task contact latency predicts latency to solve on three of four tasks			MOTIVATION: no relationship	
Boogert et al. (2008)	NEOPHOBIA: no relationship; SPATIAL EXPLORATION: no relationship		Learning speed predicts problem-solving	COMPETITIVE RANK: predicts the number of studies which the bird is first to solve, but not when asocial learning included	
Bouchard et al. (2007)	NEOPHOBIA: predicts latency to solve			COMPETITIVE RANK: no relationship	
Cauchard et al. (2013)	NEOPHOBIA: solvers significantly less neophobic than non-solvers; solving latency unrelated to neophobia			MOTIVATION: no relationship; PERSISTENCE: solvers showed higher persistence than non-solvers; solving latency unrelated to persistence.	
Cole and Quinn (2012)				COMPETITIVE ABILITY: competitive ability in wild negatively correlated with problem solving in captivity	
Cole et al. (2011)	NEOPHOBIA: no relationship; EXPLORATION: no relationship; SHYNESS: no relationship			MOTIVATION: no relationship	No relationship
Day et al. (2003)	NEOPHILIA: latency to first contact positively correlated with latency to first success; latency to first contact negatively correlated with the frequency of successful manipulations				
Griffin and Diquelou (submitted for publication)	NEOPHOBIA: no relationship	Motor diversity predicts success		PERSISTENCE: number attempts predicts problem solving	No relationship in mynas (data not available for miners)
Griffin et al. (in press)	NEOPHOBIA: no relationship	Motor diversity predicts solving		PERSISTENCE: number attempts predicts problem solving	Juveniles more successful but not once greater persistence accounted for

Table 2 (Continued)

Authors	Conclusions – NOVELTY RESPONSES	Conclusions – MOTOR DIVERSITY	Conclusions – LEARNING	Conclusions – NECESSITY	Conclusions – AGE
Keagy et al. (2011b)				MOTIVATION: no relationship	No effect
Keagy et al. (2009)				MOTIVATION: no relationship	No effect
Kendal et al. (2005)	NEOPHILIA: no relationship				Adults have shorter latencies to first success than young individuals; age positively correlated with the number of successful manipulations; adults produce more successful manipulations than young individuals
Liker and Bókonyi (2009)	NEOPHOBIA: no relationship				
Manrique et al. (2013)		The ability to switch motor action predicted greater success			
Morand-Ferron et al. (2011)				PERSISTENCE: probability of solving increases with number of previous attempts and duration of attempts; MOTIVATION: no effect	Juveniles more likely to solve, but not once higher persistence was accounted for
Overington et al. (2011)	EXPLORATION: solvers significantly more exploratory than non-solvers; SHYNESS: no relationship		Problem-solving positively correlated with learning speed	MOTIVATION: no relationship	
Sol et al. (2012)	NEOPHOBIA: high neophobia predicts lower success			MOTIVATION: predicts shorter solving latencies	
Tebbich et al. (2010)	SHYNESS: no relationship. NEOPHILIA: Darwin's finches no more neophilic than other Galapagos finches.		No species differences in learning speed on initial discrimination; no species differences on reversal learning speed. Woodpeckers make significantly more errors than small tree finches in attaining criterion on the reversal task	PERSISTENCE: predicts shorter solving latencies PERSISTENCE: woodpeckers are more persistent than small tree finches	
Thornton and Samson (2012)	NEOPHOBIA: no relationship			PERSISTENCE: predicts solving latency; DOMINANCE: subordinate males are the most likely to problem-solve	Juveniles are more likely to approach and interact with the task, but were less likely to solve
Webster and Lefebvre (2001)	NEOPHOBIA: no relationship				

interaction of these two variables. First, we briefly review those studies that failed to find that low neophobia facilitates problem solving. We then turn to those that found evidence of such a relationship.

We found that, at least, in house sparrows (*Passer domesticus*; Liker and Bókonyi, 2009; but see below), starlings (*Sturnus*

vulgaris; Boogert et al., 2008) and blue tits (*Parus caeruleus*; Aplin et al., 2013) neophobia and problem solving are not correlated. We further identified only one published study investigating the relationship between neophilia and problem solving. That study found no evidence of a relationship between novel object exploration and problem solving in chimango caracaras (*Milvago chimango*),

a neotropical raptor (Biondi et al., 2010). Equally, Indian mynas show no evidence of a relationship between their propensity to explore novel objects and their ability to solve an extractive foraging task (Lermite, 2012). Finally, Morand-Ferron et al. (2011) found no evidence for a relationship between exploration of a novel environment and problem solving in great tits (*Parus major*).

Studies in other taxonomic groups have revealed that in meerkats, juveniles are more likely to approach problem-solving devices than adults, indicating that they are less neophobic, but they are also less likely to solve (Thornton and Samson, 2012). Furthermore, individuals that approached the task first were not always the first individuals to solve indicating that low neophobia does not facilitate problem solving in this species (Thornton and Samson, 2012). Similarly, a study measuring the effects of age on neophilia in seven species of callitrichids found that approach latencies were not related to problem solving as adults and juveniles were equally likely to approach the puzzle box, but adults were more likely to solve (Kendal et al., 2005).

In those species where relationships between low novelty responses and increased problem solving have been found (Table 2), the relationship appears to vary across contexts and individuals. A recent study in house sparrows has revealed that latency to approach the problem-solving device predicts problem-solving performance, but only on three of four problem-solving devices (Bókonyi et al., 2013). Juvenile chimpanzee caracaras that are more willing to feed in the presence of a novel object solve more containers when tested on an extractive foraging task, but adults are not (Biondi et al., 2010). In Indian mynas, inter-individual variation in neophobia predicts variation in problem solving (Sol et al., 2012), but this effect is not present once birds are habituated more extensively to the task (Griffin et al., 2014, 2013b). Benson-Amram and Holekamp (2012) showed that both wild and captive spotted hyenas (*Crocutta crocutta*) that took longer to approach an extractive foraging task were less likely to solve it (Benson-Amram et al., 2013). However, in wild hyenas, the inverse relationship did not hold. Even though juveniles were less neophobic than adults, they did not outperform adults on the problem-solving task (Benson-Amram and Holekamp, 2012). In pigeons (*Columba livia*) problem-solving latencies correlated significantly with approach latencies (Bouchard et al., 2007). However, because solving latency included the time to approach the task, the two variables were potentially confounded. Finally, Overington et al. (2011) found that responses to novelty and problem solving were linked in grackles (*Quiscalus lugubris*). However, novelty responses were measured using a compilation of activity and number of areas explored during a spatial exploration task, as well as the willingness to feed near a novel object, making it difficult to evaluate the relative contributions of activity, spatial exploration, and neophobia to the relationship.

We conclude with just two studies that have revealed straightforward relationships between novelty responses and problem solving. Captive juvenile hyenas are more neophobic and significantly less likely to problem solve than adults (Benson-Amram et al., 2013), and great tits that successfully remove an obstacle blocking access to their nest were significantly faster to make contact with the object after landing on their nestbox than birds that do not succeed in removing the obstacle (Cauchard et al., 2013).

3.2. Problem solving and learning

Work relating the learning performance of different species to their ability to solve extractive foraging tasks is scant. Our survey revealed only one inter-species comparative study, which found no relationship between problem solving and learning performance (Table 2). Tebbich et al. (2010) found that although woodpecker finches (*Camarhynchus pallidus*) significantly outperformed small

tree finches (*C. parvulus*) on an extractive foraging task, they were no faster to learn a colour discrimination task, and no faster to learn to reverse their choice of colour cue when the significance of the cues was reversed.

Our survey identified five studies that have examined this relationship at the intra-specific level, three of which have revealed a positive correlation between the ability to solve extractive foraging tasks and learning, and two of which suggest tentatively that problem solving is related to a more general learning capacity (Table 2). First, individual starlings that solved an extractive foraging task first in a group setting were those that acquired an asocial learning task faster even when the effects of competitive rank were accounted for (Boogert et al., 2008). Second, pigeons that solved an extractive foraging task faster acquired a social learning task faster even when inter-individual variation in neophobia had been accounted for (d). Third, carib grackles that solve an extractive foraging task faster acquired an asocial learning task faster (Overington et al., 2011). One limitation of these three studies is that learning was quantified by measuring decreases in solving time across repeated presentations of a problem-solving task, or by shaping the animals to solve a problem-solving task, where the task was either the same that had been used to measure problem solving, or a different one (Table 1). Consequently, problem solving and learning were measured within the same functional context and correlations in performance are more likely. However, there is some evidence to date that this correlation extends to learning within other domains. Individual Indian mynas' problem-solving latencies correlate positively with the speed at which they acquire a colour-discrimination learning task (Griffin et al., 2013a). In addition, recent research measuring problem solving as well as learning ability on several different learning tasks in spotted bowerbirds (*Ptilonorhynchus maculatus*), provides tentative evidence that problem-solving performance loads on to the same Principle Component as learning ability in other functional contexts (Isden et al., 2013).

3.3. Problem solving and motor diversity

A handful of recent studies have examined whether the ability to solve extractive foraging tasks is influenced by the range of motor actions an animal performs within the problem-solving context (Table 1). Motor diversity, defined as the total number of distinct motor actions expressed while attempting to problem solve, consistently explains variation in problem-solving performance (Table 2). Indian mynas express greater variation in the range of motor actions while attempting to solve than noisy miners, a native Australian honeyeater, and this variation was a significant predictor of their significantly greater problem-solving abilities (Griffin and Diquelou, submitted for publication). Amongst those studies that have explored the relationship between motor diversity and problem-solving ability at the intra-specific level, spotted hyenas that express a greater range of motor actions were more likely to solve a problem-solving device (Benson-Amram and Holekamp, 2012), while Indian mynas that express a greater range of motor actions are more likely to solve and have shorter solving latencies (Griffin et al., 2014). Finally, in primates, Manrique et al. (2013) have shown recently that both species and individuals that are more flexible in the range of motor actions they express are faster to solve problems.

3.4. Problem solving by necessity: effects of dominance, competitive rank, motivation and persistence

Just like responses to novelty, dominance is not a unitary concept and different methodologies are likely to tap different

dimensions of the behaviour. For example, the propensity to express aggression is typically measured by quantifying agonistic interactions during a 'dominance' test. The ability to monopolize critical resources is quantified by measuring the total time spent an individual has sole access to a defensible resource (Cole and Quinn, 2012), or the order in which animals access a defensible resource (Boogert et al., 2006). Dominance and competitive ability may (Cole and Quinn, 2012), or may not correlate (Boogert et al., 2006). Hence, we make a distinction between the effects of competitive ability on problem solving and those of dominance.

Competitive ability is not systematically related to problem-solving ability (Table 2). In starlings, more competitive individuals are the first ones to problem-solve within a group, but not when individual variation in asocial learning ability is accounted for, suggesting no direct relationship between competitive ability and problem solving (Boogert et al., 2008, but see Boogert et al., 2006 for methods). Similarly, in pigeons and in blue tits there are no relationships between competitive ability and problem solving (Aplin et al., 2013; Bouchard et al., 2007). In contrast, in great tits, individuals that problem solve in captivity are less competitive (i.e. monopolize a feeder for less time) in the wild than individuals that do not problem solve (Cole and Quinn, 2012). However, as problem solving in captivity does not predict problem solving in the wild in this species (Morand-Ferron et al., 2011), this relationship is difficult to interpret. In contrast to competitive ability, dominance influences problem-solving ability in blue tits, with subordinate males and juvenile females (also subordinate) being most likely to problem-solve (Aplin et al., 2013). Studies in other taxonomic groups have revealed that subordinate meercats (*Suricata suricatta*) are most likely to problem-solve (Thornton and Samson, 2012), whereas in spotted hyenas, there was no relationship between problem solving and social rank (Benson-Amram and Holekamp, 2012; Benson-Amram et al., 2013).

A range of methods have been used to quantify motivation, including morphological proxies, such as body weight, body fat, and body condition, and behavioural measurements usually collected outside the context of problem solving (Table 1). In contrast, persistence is generally measured by quantifying the extent to which individuals engage with the problem-solving device. Persistence is a measure of task-directed motivation, which may be linked to a variety of parameters including feeding motivation and the ecological relevance of the task for the species being tested. For example, in Indian mynas, the number of beak-to-task contacts, a measure of persistence, increases with food deprivation time (Griffin et al., 2014, but see Griffin and Diquelou, submitted for publication, for an example where it does not). It is important to note that persistence represents a measure of task-directed motivation but does not specify in what way the animal engages with the task. For example, an animal may be persistent, consistently using a single motor action when trying to solve a problem. In contrast, an animal may be persistent, yet express a large diversity of motor actions while attempting to solve a problem (Griffin et al., 2014).

The present survey revealed only one study examining the relationship between persistence and cross-taxon variation in problem-solving ability. Day et al. (2003) found that lion tamarins (*Leontopithecus* sp) made more successful attempts at solving an extractive foraging task than tamarins (*Saguinus* sp) and marmosets (*Callithrix* sp), but they also performed more overall attempts, indicating that their greater persistence underpinned their greater success. Although one additional study found results pointing to the possibility that cross-taxon variation in problem-solving ability could be linked to cross-taxon variation in persistence, this relationship was not tested formally. Tebbich et al. (2010) found that woodpecker finches were more successful in solving an extractive foraging task than small tree finches, and suggested that this might

be because woodpecker finches made many more attempts to solve the task.

Inter-individual comparisons have pointed consistently to a central role of persistence in problem-solving ability, with those individuals that engage more with the task being more likely to solve and/or solving faster (Table 2). In both meercats and spotted hyenas, those individuals that spend the most time manipulating experimental tasks solve them most readily (Benson-Amram and Holekamp, 2012; Thornton and Samson, 2012). Similarly, the likelihood that great tits and blue tits solve problems increases with an increase in the duration of visits to the innovation device and the number of previous attempts (Morand-Ferron and Quinn, 2011; Morand-Ferron et al., 2011). In Indian mynas, those individuals that make more beak-to-task contacts are more likely to solve and are quicker to solve (Griffin et al., 2014; Sol et al., 2012). Recent work in great tits has revealed that solvers are significantly more persistent than non-solvers (Cauchard et al., 2013). The results from one study fall outside the consistent pattern. Spotted bowerbirds that are more persistent are no quicker to solve a problem (Isden et al., 2013).

In contrast to task-directed persistence, there appears to be little relationship between problem solving and alternative measures of motivation (Table 2). Keagy and his colleagues (2011b, 2009) found no relationship between the ability to access an aversive object (problem solving) and the latency to remove an aversive object once it had been accessed (motivation), or the latency to begin (motivation) and the ability to complete (problem solving) re-building a broken bower in satin bowerbirds (*Ptilonorhynchus violaceus*). Similarly, Cauchard et al. (2013) found no relationship between the latency of parents to remove an obstacle to access their nest (problem solving) and the rate at which they fed the nestlings (motivation) in great tits. Similarly, there is no evidence to date that any morphology-based measure of motivation, including body condition, body fat or body condition, correlate with problem-solving performance (Aplin et al., 2013; Bókonyi et al., 2013; Cole et al., 2011; Morand-Ferron et al., 2011; Overington et al., 2011).

3.5. Problem solving and age

Amongst those studies examining the effect of age on problem solving, most have revealed no effect of age on problem solving (Table 2). In raptors, great tits, Indian mynas, satin bowerbirds, hyenas, and meercats, there is no evidence that problem solving is more common in juveniles than adults, and this, despite juveniles being less neophobic and more exploratory than adults in several cases (Table 2). In some cases, including Indian mynas, blue tits and great tits, juveniles are more likely to solve, but not once their greater persistence has been accounted for (Table 2). Finally, in primates, age correlates positively with problem-solving ability (Kendal et al., 2005).

4. Innovation and problem solving: general conclusions

We reviewed the avian and primate literature on problem solving of extractive foraging tasks in order to better understand to what extent the processes underpinning, and the factors influencing problem solving, are in line with those predicted, and found, to underpin and influence innovation in the wild.

The first most compelling finding from this review is that problem solving of extractive foraging tasks requires motor variability. Hence, the number of different actions performed and their relative frequency of expression (Griffin et al., 2014) appears to provide an important source of raw material for behavioural variants (Fig. 1). More diverse manipulative skills may provide increased opportunity for learning of object affordances and their physical properties.

Such knowledge may in turn lead to more sophisticated goal-directed mechanisms for generating motor variation, which could complement motor variability in some systems (Auersperg et al., 2012, 2011; Huber and Gajdon, 2006; Taylor et al., 2009). The convergent evidence that behavioural variability is key to innovations in the wild (Boinski et al., 2000; Clarke and Boinski, 1995; Lefebvre et al., 2002; Overington et al., 2009; Reader and Laland, 2002) and to problem solving of extractive tasks (Table 2) provides a strong basis from which to assert that problem solving provides a meaningful experimental assay for studying innovation.

Our second most compelling finding is that problem solving is consistently associated with learning speed when learning involves the gradual acquisition of a motor technique. This finding suggests that problem solving is linked to operant learning, a form of associative learning in which behaviours that yield desired outcomes increase in frequency and those that do not decrease in frequency (Thorndike, 1905). This relationship suggests that once a motor variant is produced, operant learning ensures that successful variants are repeated, as predicted for innovation (Reader and Laland, 2003a). Standard learning assays typically measure how the frequencies of a given motor action (e.g. lever pressing, nose poke, key pecking) change in order to investigate how animals acquire associations between environmental cues (classical conditioning) and/or how they learn response–outcome contingencies (instrumental conditioning). In other words, in the vast majority of studies of associative learning, individuals are not required to vary their motor behaviour (but see Pryor and Chase, 2014). Problem-solving assays provide a relatively simple experimental assay, not only for measuring motor diversity, but further, for exploring how experience shapes the expression of motor behaviour and facilitates subsequent problem solving (Manrique et al., 2013; Overington et al., 2011; Von Bayern et al., 2009) (Fig. 1). It is important to note that despite the link between problem solving and operant learning, in our opinion the two behaviours should be considered as conceptually distinct and non-inter-changeable phenomena. Problem solving of the kind reviewed here relies upon the appearance of a behavioural variant, whereas operant learning underpins a subsequent change in frequency of expression of that behavioural variant as a function of experience (Fig. 1).

Problem-solving tests offer the opportunity for researchers to explore potential links between motor diversity (e.g. the ability to use a limb in multiple ways) and more general learning abilities (Griffin et al., 2013a; Isden et al., 2013). Such analyses provide a means of testing the idea that enhanced learning abilities have evolved within the context of an expansion of extractive foraging skills (Byrne, 1995; Gibson, 1986; Parker, 1974; Parker and Gibson, 1977). We have recently demonstrated that the sooner that Indian mynas solve a problem, the faster they learn that a cue predicts food, but the slower they change behaviour when the significance of the cue changes (Griffin et al., 2013a). The finding that problem solving is inversely related to reversal learning is at odds with the widespread assumption that innovation should correlate positively with behavioural flexibility. Tebbich et al. (2010) suggested that perseverance (i.e. the tendency to continue a behaviour even when it is not rewarded) may be a requirement of extractive foraging. We suggest, rather, that flexibility is most likely a multi-faceted concept, which encompasses the ability to inhibit a previously successful behaviour, the ability to invent a new behaviour in new circumstances, and the ability to perform an existing behaviour in a new context, amongst others. What's more, animals may be flexible in one domain (e.g. foraging) and not in another (e.g. predator avoidance). The common usage of 'behavioural flexibility' may represent an over-simplification of this complexity. Innovations in the wild may tap different facets of flexibility, some of which, we suggest, can be studied using problem-solving tasks, and some of which cannot.

Third, our review revealed compelling evidence that although neophobia represents a contextual factor that has some bearing upon whether animals interact with a novel situation or not, and therefore necessarily influences problem solving opportunity, neophobia does not co-vary with problem-solving ability (Fig. 1). Problem-solving ability was not linked to neophobia across species, and where relationships did occur intra-specific, effects typically varied across contexts, such as categories of individuals and tasks. Neophobia may be linked to problem solving because they are acted on in common by some underpinning process, such as feeding motivation (Fig. 1; Sol et al., 2012; Webster and Lefebvre, 2001) or stress. Overall, the contextual effect of neophobia on problem solving resembles the predicted effect of this variable on innovation (Greenberg, 2003; Lefebvre, 2000; Reader and Laland, 2003b; Webster and Lefebvre, 2001), suggesting once again that problem solving is a suitable assay for exploring innovation.

Fourth, the review revealed no evidence of a relationship with neophilia or spatial exploration propensity in birds and only one study indicating a positive relationship in primates. Greenberg (2003) reports little evidence of object neophilic responses in adult birds and Greenberg and Mettke-Hofmann (2001) note that this category of behaviour is only common in certain avian families (e.g. corvids and parrots). The general lack of object neophilia responses in avian taxa may explain why practically all published studies have focused on measuring neophobia (Table 1). More research is needed to ascertain to what extent neophilia influences problem solving in the way neophilia is predicted to influence innovation (Greenberg, 2003; Reader and Laland, 2003b), particularly in those avian families in which neophilia behaviour is thought to be more common (Auersperg et al., 2012, 2011; Huber and Gajdon, 2006).

Finally, we found mixed evidence that necessity systematically increases the likelihood of problem solving. There was no evidence that competitive ability predicted problem solving, and social rank was only occasionally associated with this ability (Table 2). Small details of testing protocols (e.g. availability of alternative food sources during problem solving; time of testing including peak vs. off-peak foraging times; Table 1) are likely to influence towards which resources dominant and subordinate individuals allocate their foraging efforts, and care needs to be taken to control, report and flag these details more carefully. In contrast, problem-solving ability was systematically related to persistence (Table 2), indicating that task-directed motivation is key to problem solving. As persistence has been linked to food deprivation time (Griffin et al., 2014), this finding indicates that necessity can facilitate problem solving. Perhaps surprisingly, motivation did not predict problem solving (Table 2). However, more research is needed to validate morphological (e.g. body size, body fat) measures of motivation (Table 1), by linking them to feeding motivation, for example.

Alternatively, it is possible that motor variability and motor skills are more central to problem solving than is motivation (Fig. 1). An animal that is exploratory and motivated to solve a problem may nevertheless be unable to do so, because it cannot perform a suitable motor action, either because it is not physically able to, or because its history of past experience has been such that it has not learnt to express a variety of actions within the functional context of the test. In Indian mynas, for example, motor variability matters over and above persistence (Griffin et al., 2014). Consistent with this idea, the present review revealed that problem solving is more common in adults than in juveniles in primates (Kendal et al., 2005), and that even in systems where younger individuals were less neophobic and more exploratory, juveniles did not solve more (Table 2). This pattern suggests that motor skills are key to problem solving and are consistent with the effects of age on innovation (Reader and Laland, 2001), suggesting once again that problem solving is a useful proxy for innovation.

It could be argued, however, that in all bird species studied to date juveniles are no worse at solving problems than adults (Table 2). Although it is possible that in this taxonomic group, problem solving does not require any experience-dependent motor skills, we suggest that age effects on problem solving may be less apparent in avian studies because juveniles are typically already experienced foragers when they are tested. The effects of inexperience may be more apparent in systems where maturation takes longer. Future research should attempt to test birds at younger ages, perhaps during stages where they are still foraging alongside their parents. For example, Indian myna fledglings are known to be less adept in their food handling skills than are adults (Cousilman, 1971).

In sum, our review revealed overlap in several of the factors influencing and processes underpinning problem solving and those predicted, and known to influence and underpin innovation. Hence our conclusion is that problem solving provides a meaningful experimental assay to study innovative tendencies. Problem-solving tests can be used to study how motor variability interacts with operant learning (Thornton and Lukas, 2012), but also other cognitive processes, such as transfer of causal rules from one situation to another (Taylor et al., 2009) to produce innovative behaviour. We conclude by suggesting that variations of problem-solving assays can be used not only to investigate the richness of mechanisms underpinning innovation (Auersperg et al., 2012; Manrique et al., 2013), but also their taxonomical distribution. This combined approach is likely to provide the most effective way of gaining a fuller understanding of which species will be able to use innovative behaviour to adjust to rampant environmental change.

Acknowledgements

We thank the University of Newcastle (Australia) for granting AG sabbatical funding, which lead to the writing of this manuscript. We thank Sabine Tebbich and two anonymous reviewers for helpful comments on an earlier version of the manuscript. We also wish to thank Thomas Bugnyar, Sue Healy, Kevin Laland, Lauren Guillette, and Dani Sol for discussions on the topic of innovation and problem solving, and Claudia Mettke-Hoffman for discussions on neophobia and neophilia.

References

- Aplin, L.M., Sheldon, B.C., Morand-Ferron, J., 2013. Milk bottles revisited: social learning and individual variation in the blue tit, *Cyanistes caeruleus*. *Anim. Behav.* 85, 1225–1232.
- Auersperg, A.M.I., Gajdon, G.K., Von Bayern, A.M.P., 2012. A new approach to comparing problem solving, flexibility and innovation. *Commun. Integr. Biol.* 5, 140–145.
- Auersperg, A.M.I., von Bayern, A.M.P., Gajdon, G.K., Huber, L., Kacelnik, A., 2011. Flexibility in problem solving and tool use of kea and New Caledonian crows in a multi access box paradigm. *PLoS ONE* 6, e20231.
- Benson-Amram, S., Holekamp, K.E., 2012. Innovative problem solving by wild spotted hyenas. *Proc. R. Soc. B* 279, 4087–4095.
- Benson-Amram, S., Weldele, M.L., Holekamp, K.E., 2013. A comparison of innovative problem-solving abilities between wild and captive spotted hyenas, *Crocuta crocuta*. *Anim. Behav.* 85, 349–356.
- Biondi, L.M., Bó, M.S., Vassallo, A.I., 2010. Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (*Milvago chimango*). *Anim. Cogn.* 13, 701–710.
- Boinski, S., Quatrone, R.P., Swartz, H., 2000. Substrate and tool use by brown capuchins in Suriname: ecological contexts and cognitive bases. *Am. Anthropol.* 102, 741–761.
- Bókony, V., Kulcsár, A., Tóth, Z., Liker, A., 2012. Personality traits and behavioral syndromes in differently urbanized populations of house sparrows (*Passer domesticus*). *PLoS ONE* 7, e36639.
- Bókony, V., Lendvai, A.Z., Vágási, C.I., Pátraş, L., Pap, P.L., Németh, J., Vincze, E., Papp, S., Preiszner, B., Seress, G., Liker, A., 2013. Necessity or capacity? Physiological state predicts problem-solving performance in house sparrows. *Behav. Ecol.* 25, 124–135.
- Boogert, N.J., Reader, S.M., Hoppitt, W., Laland, K.N., 2008. The origin and spread of innovations in starlings. *Anim. Behav.* 75, 1509–1518.

- Boogert, N.J., Reader, S.M., Laland, K.N., 2006. The relation between social rank, neophobia and individual learning in starlings. *Anim. Behav.* 72, 1229–1239.
- Bouchard, J., Goodyer, W., Lefebvre, L., 2007. Social learning and innovation are positively correlated in pigeons (*Columba livia*). *Anim. Cogn.* 10, 259–266.
- Byrne, R.W., 1995. Primate cognition: comparing problems and skills. *Am. J. Primatol.* 37, 127–141.
- Carter, A.J., Marshall, H.H., Heinsohn, R., Cowlshaw, G., 2012. How not to measure boldness: novel object and antipredator responses are not the same in wild baboons. *Anim. Behav.* 84, 603–609.
- Cauchard, L., Boogert, N.J., Lefebvre, L., Dubois, F., Doligez, B., 2013. Problem-solving performance is correlated with reproductive success in a wild bird population. *Anim. Behav.* 85, 19–26.
- Clarke, A.S., Boinski, S., 1995. Temperament in nonhuman primates. *Am. J. Primatol.* 37, 103–125.
- Clayton, N.S., 2004. Is necessity the mother of innovation? *Trends Cogn. Sci.* 8, 98–99.
- Cnotka, J., Güntürkün, O., Rehkämper, G., Gray, R.D., Hunt, G.R., 2008. Extraordinary large brains in tool-using New Caledonian crows (*Corvus moneduloides*). *Neurosci. Lett.* 433, 241–245.
- Cole, E.F., Cram, D.L., Quinn, J.L., 2011. Individual variation in spontaneous problem-solving performance among wild great tits. *Anim. Behav.* 81, 491–498.
- Cole, E.F., Morand-Ferron, J., Hinks, A.E., Quinn, J.L., 2012. Cognitive ability influences reproductive life history variation in the wild. *Curr. Biol.* 22, 1808–1812.
- Cole, E.F., Quinn, J.L., 2012. Personality and problem-solving performance explain competitive ability in the wild. *Proc. R. Soc. B* 279, 1168–1175.
- Cousilman, J.J., 1971. Some Aspects of the Behaviour of the Indian Myna, *Acridotheres tristis* (L.). The University of Auckland.
- Day, R.L., Coe, R.L., Kendal, J.R., Laland, K.N., 2003. Neophilia, innovation and social learning: a study of intergeneric differences in callitrichid monkeys. *Anim. Behav.* 65, 559–571.
- Fox, R.A., Ladage, L.D., Roth, T.C., Pravosudov, V.V., 2009. Behavioral profile predicts dominance status in mountain chickadees. *Anim. Behav.* 77, 1441–1448.
- Gabriel, P.O., Black, J.M., 2010. Behavioural syndromes in Steller's jays: the role of time frames in the assessment of behavioural traits. *Anim. Behav.* 80, 689–697.
- Gibson, K.R., 1986. Cognition, brain size and the extraction of embedded food resources. In: Else, J.G., Lee, P.C. (Eds.), *Primate Ontogeny, Cognition and Social Behaviour*. Cambridge University Press, Cambridge, pp. 93–103.
- Greenberg, R.S., 2003. The role of neophobia and neophilia in the development of innovative behaviour of birds. In: Reader, S.M., Laland, K.N. (Eds.), *Animal Innovation*. Oxford University Press, pp. 175–196.
- Greenberg, R.S., Mettke-Hofmann, C., 2001. Ecological aspects of neophilia and neophobia in birds. In: *Current Ornithology*, pp. 119–178.
- Griffin, A.S., Diquelou, M., Perea, M., 2014. Innovative problem solving in birds: a key role of motor diversity. *Anim. Behav.* 92, 221–227.
- Griffin, A.S., Guez, D., Lermite, F., Patience, M., 2013a. Tracking changing environments: Innovators are fast, but not flexible learners. *PLoS ONE* 8, e84907.
- Griffin, A.S., Lermite, F., Perea, M., Guez, D., 2013b. To innovate or not: contrasting effects of social groupings on safe and risky foraging in Indian mynahs. *Anim. Behav.* 86, 1291–1300.
- Güntürkün, O., 2012. The convergent evolution of neural substrates for cognition. *Psychol. Res.* 76, 212–219.
- Hauser, M.D., 1988. Invention and social transmission: new data from wild vervet monkeys. In: Byrne, R.W., Whiten, A. (Eds.), *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans*, pp. 327–343. Oxford.
- Healy, S.D., Rowe, C., 2007. A critique of comparative studies of brain size. *Proc. R. Soc. B* 274, 453–464.
- Heinrich, B., 1995. Neophilia and exploration in juvenile common ravens, *Corvus corax*. *Anim. Behav.* 50, 695–704.
- Huber, L., Gajdon, G.K., 2006. Technical intelligence in animals: the kea model. *Anim. Cogn.* 9, 295–305.
- Hughes, R.N., 2007. Neotic preferences in laboratory rodents: issues, assessment and substrates. *Neurosci. Biobehav. Rev.* 31, 441–464.
- Isden, J., Panayi, C., Dingle, C., Madden, J., 2013. Performance in cognitive and problem-solving tasks in male spotted bowerbirds does not correlate with mating success. *Anim. Behav.* 86, 829–838.
- Jönsson, K.A., Fabre, P.-H., Irestedt, M., 2012. Brains, tools, innovation and biogeography in crows and ravens. *BMC Evol. Biol.* 12.
- Keagy, J., Savard, J.-F., Borgia, G., 2009. Male satin bowerbird problem-solving ability predicts mating success. *Anim. Behav.* 78, 809–817.
- Keagy, J., Savard, J.-F., Borgia, G., 2011a. Cognitive ability and the evolution of multiple behavioral display traits. *Behav. Ecol.* 23, 448–456.
- Keagy, J., Savard, J.-F., Borgia, G., 2011b. Complex relationship between multiple measures of cognitive ability and male mating success in satin bowerbirds, *Ptilonorhynchus violaceus*. *Anim. Behav.* 81, 1063–1070.
- Kendal, R.L., Coe, R.L., Laland, K.N., 2005. Age differences in neophilia, exploration, and innovation in family groups of callitrichid monkeys. *Am. J. Primatol.* 66, 167–188.
- Laland, K.N., Reader, S.M., 1999. Foraging innovation in the guppy. *Anim. Behav.* 57, 331–340.
- Lefebvre, L., 2000. Feeding innovations and their cultural transmission in bird populations. In: *The Evolution of Cognition*. Academic Press, London, pp. 311–328.
- Lefebvre, L., 2011. Taxonomic counts of cognition in the wild. *Biol. Lett.* 7, 631–633.
- Lefebvre, L., Gaxiola, A., Dawson, S., Timmermans, S., Lajos, R., Kabai, P., 1998. Feeding innovations and forebrain size in Australasian birds. *Behaviour* 135, 1077–1097.

- Lefebvre, L., Nicolakakis, N., Boire, D., 2002. Tools and brains in birds. *Behaviour* 139, 939–973.
- Lefebvre, L., Reader, S.M., Sol, D., 2004. Brains, innovations and evolution in birds and primates. *Brain Behav. Evol.* 63, 233–246.
- Lefebvre, L., Sol, D., 2008. Brains, lifestyles and cognition: are there general trends? *Brain Behav. Evol.* 72, 135–144.
- Lefebvre, L., Whittle, P., Lascaris, E., 1997. Feeding innovations and forebrain size in birds. *Anim. Behav.* 53, 549–560.
- Lermite, F., (MSc thesis) 2012. Innovation in Indian Mynahs (*Acridotheres tristis*): A Behavioural Syndrome Dependent Upon Social Context? University of Paris 13.
- Liker, A., Bókonyi, V., 2009. Larger groups are more successful in innovative problem solving in house sparrows. *Proc. Natl. Acad. Sci. U. S. A.* 106, 7893–7898.
- Manrique, H.M., Völter, C.J., Call, J., 2013. Repeated innovation in great apes. *Anim. Behav.* 85, 195–202.
- Mehlhorn, J., Hunt, G.R., Gray, R.D., Rehkämper, G., Güntürkün, O., 2010. Tool-making New Caledonian crows have large associative brain areas. *Brain Behav. Evol.* 75, 63–70.
- Mettke-Hofmann, C., Ebert, C., Schmidt, T., Steiger, S., Stieb, S., 2005. Personality traits in resident and migratory warbler species. *Behaviour* 142, 1357–1375.
- Mettke-Hofmann, C., Winkler, H., Leisler, B., 2002. The significance of ecological factors for exploration and neophobia in parrots. *Ethology* 108, 249–272.
- Miller, K.A., Garner, J.P., Mench, J.A., 2006. Is fearfulness a trait that can be measured with behavioural tests? A validation of four fear tests for Japanese quail. *Anim. Behav.* 71, 1323–1334.
- Miranda, A.C., Schielzeth, H., Sonntag, T., Partecke, J., 2013. Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? *Glob. Chang. Biol.* 19, 2634–2644.
- Montgomery, K.C., Monkman, J., 1955. The relation between fear and exploratory behavior. *J. Comp. Physiol. Psychol.* 48, 132–136.
- Morand-Ferron, J., Cole, E.F., Rawles, J.E.C., Quinn, J.L., 2011. Who are the innovators? A field experiment with 2 passerine species. *Behav. Ecol.* 22, 1241–1248.
- Morand-Ferron, J., Quinn, J.L., 2011. Larger groups of passerines are more efficient problem solvers in the wild. *Proc. Natl. Acad. Sci. U. S. A.* 108, 15898–15903.
- Overington, S.E., Cauchard, L., Côté, K.-A., Lefebvre, L., 2011. Innovative foraging behaviour in birds: what characterizes an innovator? *Behav. Process.* 87, 274–285.
- Overington, S.E., Morand-Ferron, J., Boogert, N.J., Lefebvre, L., 2009. Technical innovations drive the relationship between innovativeness and residual brain size in birds. *Anim. Behav.* 78, 1001–1010.
- Parker, C.E., 1974. Behavioural diversity in ten species of nonhuman primates. *J. Comp. Physiol. Psychol.* 87, 930–937.
- Parker, S.T., Gibson, K.R., 1977. Object manipulation, tool use & sensorimotor intelligence as feeding adaptations in early hominids. *J. Hum. Evol.* 6, 623–641.
- Prut, L., Belzung, C., 2003. The open field as a paradigm to measure the effects of drugs on anxiety-like behaviors: a review. *Eur. J. Pharmacol.* 463, 3–33.
- Pryor, K.W., Chase, S., 2014. Training for variability and innovative behavior. *Int. J. Compar. 27.*
- Ramsey, G., Bastian, M.L., van Schaik, C., 2007. Animal innovation defined and operationalized. *Behav. Brain Sci.* 30, 393–407, discussion 407–32.
- Reader, S.M., Laland, K.N., 2001. Primate innovation: sex, age and social rank differences. *Int. J. Primatol.* 22, 787–805.
- Reader, S.M., Laland, K.N., 2002. Social intelligence, innovation, and enhanced brain size in primates. *Proc. Natl. Acad. Sci. U. S. A.* 99, 4436–4441.
- Reader, S.M., Laland, K.N., 2003a. *Animal Innovation*. Oxford University Press, Oxford.
- Reader, S.M., Laland, K.N., 2003b. Animal innovation: an introduction. In: Reader, S.M., Laland, K.N. (Eds.), *Animal Innovation*. Oxford University Press, Oxford, pp. 3–35.
- Renner, M.J., 1990. Neglected aspects of exploratory and investigatory behavior. *Psychobiology* 18, 16–22.
- Russell, P.A., 1973. Relationship between exploratory behaviour and fear: a review. *Br. J. Psychol.* 64, 417–433.
- Sol, D., Duncan, R.P., Blackburn, T.M., Cassey, P., Lefebvre, L., 2005a. Big brains, enhanced cognition, and response of birds to novel environments. *Proc. Natl. Acad. Sci. U. S. A.* 102, 5460–5465.
- Sol, D., Griffin, A.S., Barthomeus, I., 2012. Consumer and motor innovation in the common myna: the role of motivation and emotional responses. *Anim. Behav.* 83, 179–188.
- Sol, D., Lefebvre, L., Rodríguez-Teijeiro, J.D., 2005b. Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. *Proc. R. Soc. B* 272, 1433–1441.
- Taylor a, H., Hunt, G.R., Medina, F.S., Gray, R.D., 2009. Do New Caledonian crows solve physical problems through causal reasoning? *Proc. R. Soc. B* 276, 247–254.
- Tebbich, S., Sterelny, K., Teschke, I., 2010. The tale of the finch: adaptive radiation and behavioural flexibility. *Philos. Trans. R. Soc. B* 365, 1099–1109.
- Thorndike, E.L., 1898. Animal intelligence: an experimental study of the associative processes in animals. *Psychol. Monogr. Gen. Appl.* 2, 1125–1127.
- Thorndike, E.L., 1905. *The Elements of Psychology*. Seiler, A.G., New York.
- Thornton, A., Lukas, D., 2012. Individual variation in cognitive performance: developmental and evolutionary perspectives. *Philos. Trans. R. Soc. B* 367, 2773–2783.
- Thornton, A., Samson, J., 2012. Innovative problem solving in wild meerkats. *Anim. Behav.* 83, 1459–1468.
- Verbeek, M.E.M., Boon, A., Drent, P.J., 1996. Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour* 133, 945–963.
- Verbeek, M.E.M., Drent, P.J., Wiepkema, P.R., 1994. Consistent individual differences in early exploratory behaviour of male great tits. *Anim. Behav.* 48, 1113–1121.
- Von Bayern, A.M.P., Heathcote, R.J.P., Rutz, C., Kacelnik, A., 2009. The role of experience in problem solving and innovative tool use in crows. *Curr. Biol.* 19, 1965–1968.
- Webster, S.J., Lefebvre, L., 2001. Problem solving and neophobia in a columbiform–passeriform assemblage in Barbados. *Anim. Behav.* 62, 23–32.