



Innovative problem solving in birds: a key role of motor diversity



Andrea S. Griffin*, Marie Diquelou, Marjorie Perea

School of Psychology, University of Newcastle, Newcastle, Australia

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Foraging innovations are increasingly viewed as a key source of phenotypic plasticity and evolutionary change. Often thought to be associated with increased cognitive abilities, innovative foraging behaviour could potentially emerge as a simple consequence of being able to use a greater variety of motor actions in the foraging context. Here, we explored the role of motor diversity in the innovative problem-solving abilities of a highly successful ecological invader, the Indian myna, *Sturnus tristis*, using an extractive foraging task with multiple compartments. Consistent with findings from several other species, persistence predicted the latency to solve the first compartment. However, motor diversity was the strongest predictor of both solving latency of all further compartments and number of compartments solved. We suggest that motor diversity may facilitate innovation by increasing the ways in which objects can be handled, which in turn would allow for associative learning processes to enhance the expression of successful foraging behaviours.

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With natural environments changing faster than ever before, a multitude of species are faced with adjusting to these changing environments or disappearing (IUCN, 2013). Foraging innovations, that is, eating new foods or using novel foraging techniques (Lefebvre et al., 1998; Lefebvre, Reader, & Sol, 2004; Lefebvre, Whittle, & Lascaris, 1997), are associated with invasion success (Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005; Sol & Lefebvre, 2000; Sol, Timmermans, & Lefebvre, 2002), residency in winter environments (Sol, Lefebvre, & Rodríguez-Teijeiro, 2005), occupation of urbanized landscapes (Møller, 2009, but see Kark, Iwaniuk, Schalimtzek, & Banker, 2007), habitat generalism (Overington, Griffin, Sol, & Lefebvre, 2011) and increased speciation rates (Nicolakakis, Sol, & Lefebvre, 2003). These findings suggest that behavioural innovations provide a source of phenotypic plasticity and evolutionary adaptation (Nicolakakis et al., 2003). Behavioural innovations may hence provide an important means by which animals cope with environmental change.

Over recent years, there has been a substantial effort to understand the sources of cross-taxon, cross-species, cross-population and interindividual variation in innovative behaviour. In fact,

there is evidence that not all animals have an equal propensity to innovate. In both primates and birds, there are more anecdotal reports of novel feeding behaviours in some taxa than in others (Lefebvre et al., 1998, 1997; Reader & Laland, 2002). Studies quantifying interindividual variation in innovation propensity have also revealed that some individuals are more inclined to solve problems than others (Benson-Amram & Holekamp, 2012; Cauchard, Boogert, Lefebvre, Dubois, & Doligez, 2013; Cole, Cram, & Quinn, 2011; Cole, Morand-Ferron, Hinks, & Quinn, 2012; Keagy, Savard, & Borgia, 2009; Morand-Ferron, Cole, Rawles, & Quinn, 2011; Overington, Cauchard, Côté, & Lefebvre, 2011; Sol, Bartomeus, & Griffin, 2012; Thornton & Samson, 2012).

A large body of correlational work currently points to the possibility that cross-taxon variation in innovation propensity reflects cross-taxon variation in cognitive ability. This proposal rests primarily upon the finding that, across both primate and avian taxa, 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, Güntürkün, Rehkämper, Gray, & Hunt, 2008; Güntürkün, 2012; Lefebvre et al., 1998, 1997; Mehlhorn, Hunt, Gray, Rehkämper, & Güntürkün, 2010; Reader & Laland, 2002). These studies relating innovation to brain anatomy are complemented by cross-species comparative analyses relating innovation to performance on standardized laboratory tests of

* Correspondence: A. S. Griffin, School of Psychology, University of Newcastle, Callaghan 2308 and Ourimbah 2258, NSW, Australia.

E-mail address: andrea.griffin@newcastle.edu.au (A. S. Griffin).

learning. For example, Lefebvre et al. (2004) showed that among six avian species, those that made fewer errors on a reversal learning task belonged to avian parvorders with higher innovation counts. Similarly Webster & Lefebvre (2001) showed that among five avian species that learnt an extractive foraging task, those that did so most quickly belonged to avian parvorders with higher innovation counts. A similar series of studies suggesting that variation in innovation propensity is positively correlated with variation in learning exists at the interindividual level (Boogert, Reader, Hoppitt, & Laland, 2008; Bouchard, Goodyer, & Lefebvre, 2007; Overington, Cauchard, et al., 2011).

Innovation propensity is also influenced by persistence. Thornton and Samson (2012) showed that in meerkat, *Suricata suricatta*, groups the individual that solved an innovative problem-solving task first was the one that had spent the most time manipulating it. Similarly, Benson-Amram and Holekamp (2012) showed that spotted hyaenas, *Crocuta crocuta*, that spent more 'work time' on an extractive foraging task were the most likely to solve it, while in great tits, *Parus major*, and blue tits, *Cyanistes caeruleus*, the likelihood of innovative problem solving increased with an increase in the duration of visits to the innovation device and number of previous attempts (Morand-Ferron et al., 2011). Above persistence, studies of the influence of other behavioural traits (e.g. exploration and neophobia) on the expression of innovation have yielded far more mixed results. These divergences are probably due, at least in part, to the variety of methods used to measure these behavioural traits across studies (Aplin, Sheldon, & Morand-Ferron, 2013; Boogert, Reader, & Laland, 2006; Cole et al., 2011; Liker & Bókony, 2009; Overington, Cauchard, et al., 2011; Sol, Griffin, & Barthomeus, 2012; Sol, Griffin, Bartomeus, & Boyce, 2011; Tebbich, Sterelny, & Teschke, 2010; Webster & Lefebvre, 2001). As in the within-species studies cited above, whether variation in exploration, neophobia and persistence also underpin intertaxon variation in innovation propensity has been suggested (Tebbich et al., 2010), but remains untested to our knowledge.

Among the body of empirical work described above, the contribution of motor processes to innovation propensity has been largely overlooked. This is surprising for three reasons. First, Overington, Morand-Ferron, Boogert, and Lefebvre (2009) classified innovations as either consumption of novel foods or technical innovation, and demonstrated that technical innovation is a stronger predictor of residual brain size than consumption of novel foods. Second, the most common experimental test of innovation propensity involves measuring an animal's ability to manipulate a container (extractive foraging task) until it 'opens' the container and obtains a food reward confined within it (Boogert et al., 2008; Morand-Ferron et al., 2011; Overington, Cauchard, et al., 2011; Sol, Griffin, et al., 2012; Tebbich et al., 2010; Thornton & Samson, 2012). Success in solving this foraging task may involve performing a variety of motor actions (e.g. pecking, grasping, sliding, etc.) until one (or a subset) of motor actions yields a solution. Third, innovation counts have been shown to correlate positively across species with tool use (Lefebvre, Nicolakakis, & Boire, 2002) and the evolutionary antecedents of tool use may be an increased variation in motor actions that allow for objects to be manipulated in a variety of ways. Together, these considerations point to a pivotal role of motor processes in innovation. An individual that is neophilic, perseveres, explores and learns fast may nevertheless be a low-probability innovator if it is unable to perform more than one motor action, either because it is not physically able to, or because its history of past foraging experience has been such that it has not learnt to express a variety of actions in the foraging context. Hence, motor diversity may limit the emergence of innovative behaviours both within and across species. Yet, to our knowledge, only one study system has investigated the role of motor diversity in innovation.

Benson-Amram and Holekamp (2012) and Benson-Amram, Weldele, and Holekamp (2013) demonstrated that spotted hyaenas that expressed a more diverse range of exploratory motor techniques (e.g. biting, lifting, flipping) were more likely to solve an innovative foraging task. To our knowledge, there is no similar analysis of motor diversity in birds. Although a handful of studies have investigated the role of exploratory behaviour in avian innovation, exploration tendency has typically been quantified using object exploration assays, which do not differentiate between morphologically different motor actions (Sol, Griffin, et al., 2012; Webster & Lefebvre, 2001), or by using spatial exploration assays (Cole et al., 2011; Overington, Cauchard, et al., 2011).

Here, we explored the role of motor diversity in innovative problem solving in an ecologically highly successful avian invader, the Indian myna, *Sturnus tristis* (formerly classified as *Acridotheres tristis*, Christidis & Boles 2008). We investigated whether increased motor diversity increased the likelihood of an individual solving problems, and to what extent solving the task was influenced by other documented sources of interindividual variation in innovation, including neophobia and perseverance.

METHODS

Subjects and Husbandry

Subjects were 39 wild-caught Indian mynas. These included 22 males (12 adult, 10 yearlings), and 17 females (seven adults, 10 yearlings). Yearlings were birds born that year identifiable by their premoult juvenile brown plumage. Birds were captured in the Newcastle region (NSW, Australia) using a walk-in baited trap specifically designed to trap this species (Tidemann, 2006). A detailed description of the trap can be found in Griffin (2008). Dog pellets were used as bait. Upon capture, mynas were transported to the Central Animal House at the University of Newcastle. Before release into an outdoor group aviary (4.4 × 1.25 m and 2.25 m high), each individual was individually identified using plastic coloured leg bands. The aviary contained numerous perches and nestboxes, a large water bath and a large feeder. Mynas were left undisturbed for at least 7 days to acclimatize to captivity. Birds had access to water and dog pellets ad libitum, except during tests that required short periods of food deprivation. For 2 full days prior to testing, birds were offered a variety of foods as part of a study on diet diversity, the results of which are not presented here. During tests mynas received mealworms, a highly preferred food type. At the time of testing, no bird used here had participated in any other experiment. However, at the end of testing birds were returned to group holding aviaries to take part in other studies. Mynas are classified as a pest species in Australia, and are the target of extensive pest control and it is illegal to re-release them into the wild following capture. For this reason, all birds were euthanized as described elsewhere (Griffin, 2008) once they were no longer required for research. As mynas are not sexually dimorphic, this allowed us to sex each bird by post mortem analysis of sexual organs. All animal care and experimental procedures were in accordance with the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes and were approved by the University of Newcastle Animal Ethics Committee (protocol A-2011-154).

Apparatus

The innovation task consisted of a Plexiglas box (25 × 10 cm and 6 cm high) with two drawers and two petri dishes attached to the top (Fig. 1). The task was designed to encourage birds to use a variety of motor techniques to solve it and presented rewards in four different compartments (see legend to Fig. 1 for details). To reduce

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