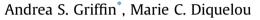
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Innovative problem solving in birds: a cross-species comparison of two highly successful passerines



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A R T I C L E I N F O

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Keywords: common myna comparative cognition competition innovation intelligence opportunism problem solving Macro-ecological comparisons have repeatedly demonstrated that the taxonomic distribution of foraging innovations coincides with the ability to adjust to novel and changing environments. We sought to obtain experimental support for the link between innovative foraging and opportunism by measuring the innovation abilities of two highly successful passerines on the east coast of Australia with very different success strategies. The ecological success of the introduced Indian myna, *Acridotheres tristis*, has been linked to its ability to occupy opportunistically an ecological niche that most natives cannot, whereas the native noisy miner, *Manorina melanocephala*, owes its success to its ability to aggressively outcompete other avian species. Indian mynas were significantly more neophobic than noisy miners. Yet, when tested on a range of innovative foraging tasks, Indian mynas consistently outperformed noisy miners. The ability to use the beak in a greater range of ways, and more flexibly, was highly repeatable in Indian mynas, and underpinned their superior problem-solving performance. We discuss the results in the light of potential methodological influences, but also the idea that necessity may facilitate innovation not only in less competitive individuals, as is documented in the literature, but also in species with less competitive lifestyles.

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The ability of birds to invent new foraging behaviours or use old ones in new contexts has been linked to invasion success (Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005a; Sol, Timmermans, & Lefebvre, 2002; Sol & Lefebvre, 2000), residency in winter environments (Sol, Lefebvre, & Rodríguez-Teijeiro, 2005b), occupation of urbanized landscapes (Møller, 2009; but see Kark, Iwaniuk, Schalimtzek, & Banker, 2007) and habitat generalism (Ducatez, Clavel, & Lefebvre, 2014; Overington, Griffin, Sol, & Lefebvre, 2011b). Foraging innovations are more common in avian taxonomic lineages with higher than slower rates of speciation (Nicolakakis, Sol, & Lefebvre, 2003; Tebbich, Sterelny, & Teschke, 2010). This body of comparative research provides strong evidence that foraging innovations are a source of behavioural plasticity and evolutionary change.

Increasing evidence that species and individuals differ in their propensity to adopt novel feeding behaviours has spurred a renewed interest in understanding the psychological mechanisms underpinning foraging innovations. Given that innovations are central to the study of animal intelligence and culture, and may facilitate species' adjustment to a rapidly changing planet, explaining how innovations arise is an important research endeavour. Within this context, innovative problem solving has become a particularly widespread experimental tool (Benson-Amram & Holekamp, 2012; Bókony et al., 2014; Cauchard, Boogert, Lefebvre, Dubois, & Doligez, 2013; Cole, Cram, & Quinn, 2011; Cole & Quinn, 2012; Keagy, Savard, & Borgia, 2011; Morand-Ferron, Cole, Rawles, & Quinn, 2011; Overington, Cauchard, Côté, & Lefebvre, 2011a; Sol, Griffin, & Barthomeus, 2012b; Soler et al., 2012; Tebbich, Stankewitz, & Teschke, 2012; Tebbich et al., 2010; Thornton & Samson, 2012). The most typical experimental assay involves measuring an animal's ability to open some kind of container to gain access to food. The use of innovative problem solving to study innovation draws its origins from the finding that the taxonomic distribution of anecdotal reports of novel feeding behaviours quantified in free-ranging birds overlaps with the pattern of species differences in innovative problem solving. For example, Webster and Lefebvre (2001) showed that among an array of five avian species, those most inclined to solve an innovative foraging problem belonged to taxa with higher numbers of foraging innovation anecdotes. A recent review showed that, more generally, the predictors of, and factors associated with, innovative problem solving are similar to those predicted to influence innovation in the wild (Griffin & Guez, 2014). These overlaps





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suggest that innovative problem solving provides an ecologically meaningful experimental assay for measuring innovative tendencies in birds, and exploring mechanisms underpinning the emergence and spread of novel foraging techniques (Lefebvre, Reader, & Sol, 2004; Lefebvre & Sol, 2008).

So far, research into mechanisms of innovation points to a role of both cognitive and motivational factors. Taxa with more foraging innovations have a larger relative brain volume, as well as larger relative multimodal integration areas (mesopallium in birds; neocortex in primates) broadly accepted to underpin higher order cognition (Lefebvre, Whittle, Lascaris, & Finkelstein, 1997; Lefebvre et al. 1998; Reader & Laland 2002; Cnotka, Güntürkün, Rehkämper, Gray, & Hunt, 2008; Mehlhorn, Hunt, Gray, Rehkämper, & Güntürkün, 2010; Güntürkün 2012). Species belonging to taxa with more innovations perform fewer errors on a reversal learning task (Lefebvre, Reader & Sol, 2004). Within species, innovative problem-solving propensity correlates positively with learning speed (Aplin, Sheldon, & Morand-Ferron, 2013; Boogert, Reader, Hoppitt, & Laland, 2008; Bouchard, Goodyer, & Lefebvre, 2007; Cole et al., 2011; Griffin, Guez, Lermite, & Patience, 2013a; Overington, Cauchard, et al., 2011a). Together, these findings have been taken to indicate that innovative behaviour, and its experimental proxy, innovative problem solving, offer an operational measure of cognitive ability (Cauchard et al., 2013; Cole, Morand-Ferron, Hinks, & Quinn, 2012; Keagy et al., 2011; Lefebvre, 2011; Soler et al., 2012) and focus is shifting to evaluating the relative contribution of associative learning and higher order learning processes, including transfer of abstract rules from familiar to novel foraging problems (Auersperg, Gajdon, & Bayern, 2012; Taylor et al., 2010; Thornton & Samson, 2012).

The motivational factors influencing innovation most researched so far include responses to novelty and persistence (reviewed by Griffin & Guez, 2014). Conclusions regarding the link between responses to novelty and innovative problem solving vary substantially across studies, perhaps because of the wide variety of methods used to measure this behavioural trait within that literature (reviewed by Griffin & Guez, 2014). Some have demonstrated that low fear of novelty is associated with improved problem solving, whereas others have found no such relationship, or that the relationship is only present in certain age categories (Aplin et al., 2013; Boogert, Reader, & Laland, 2006; Cole et al., 2011; Liker & Bókony, 2009; Overington, Cauchard, et al., 2011a; Sol, Griffin, et al., 2012b; Sol, Griffin, Bartomeus, & Boyce, 2011; Tebbich et al., 2010; Webster & Lefebvre, 2001). In contrast, persistence, a motivational measure of task-directed engagement, consistently improves problem solving. In meerkats, Suricata suricatta, and spotted hyaenas, Crocuta crocuta, individuals that spend the most time manipulating experimental tasks solve them most readily (Benson-Amram & Holekamp, 2012; Thornton & Samson, 2012). Great tits', Parus major, and blue tits', Cyanistes caeruleus, likelihood of innovative problem solving increases with an increase in the duration of visits to the innovation device and the number of previous attempts (Morand-Ferron et al., 2011; Morand-Ferron & Quinn, 2011).

Another potential process underpinning innovative problem solving is the ability to produce a variety of motor actions. Several recent studies have demonstrated that individuals that express a more diverse range of motor behaviours are more successful problem solvers (Benson-Amram & Holekamp, 2012; Griffin et al. 2013b, and Griffin et al. 2014; Mangalam & Singh, 2013; Overington, Cauchard, et al., 2011a; Thornton & Samson, 2012). Cross-taxon analyses of innovation propensity also point towards a central role of motor processes in innovations observed in the wild. Overington, Morand-Ferron, Boogert, and Lefebvre (2009) classified avian innovations as either consumption of novel foods or technical innovations, and demonstrated that technical innovations are a stronger predictor of residual brain size than consumption of novel foods. This finding suggests that innovations in the wild may be associated with increased ability to use the beak in a variety of ways, an idea consistent with Huber and Gajdon's (2006) proposal that birds may have evolved the ability to use their beaks as a 'Swiss Army knife'.

Here, we extended the primary focus of earlier work on mechanisms of intraspecies variation in innovative problem solving (but see Tebbich et al., 2010; Webster & Lefebyre, 2001), by conducting a cross-species comparison of innovation propensity and investigating underpinning processes. The selected species are highly successful in Australian urbanized landscapes, but rely upon very different success strategies. Noisy miners are a native Australian species of honeyeater, which aggressively defends colony territories (Lowe, Taylor, & Major, 2011; Parsons, Major, & French, 2006). Noisy miners are the most common native avian species in suburban areas of Newcastle (Sol, Bartomeus, & Griffin, 2012a), benefiting largely from the abundant availability of suitable vegetation in gardens (Parsons et al., 2006). Overabundance of noisy miners has been linked to the decline of numerous small avian species and the species is considered a reverse keystone species (Grey, Clarkei, & Loyn, 1998; Maron & Kennedy, 2007; Piper, Catterall, & Forest, 2003). By contrast, Indian mynas are an introduced species that is the most common species in urban areas of Newcastle (Sol, Bartomeus, et al., 2012a). One of only three bird species to be listed in the top '100 World's Worst Invasive Alien species' by the International Union for the Conservation of Nature (IUCN), Australian public opinion considers it the most significant pest (http://www.abc.net.au/tv/wildwatch/results/award.htm) and it is the target of ongoing pest control measures. Although the species has been reported to aggressively defend its nest (Pell & Tidemann, 1997), it is becoming increasingly clear that it owes much of its ecological success to its opportunistic nature that allows it to occupy niches that most natives are unable to invade owing to their greater dependence upon natural habitats for breeding (Grarock, Tidemann, Wood, & Lindenmayer, 2013; Lowe et al., 2011; Parsons et al., 2006; Sol, Bartomeus, et al., 2012a). Several recent studies have shown that it is most often the recipient of aggression around food sources and it is no more aggressive than would be expected on the basis of its occurrence (Haythorpe, Burke, & Sulikowski, 2013; Lowe et al., 2011; Sol, Bartomeus, et al., 2012a).

We compared the innovation propensity of wild-caught, captive-held noisy miners and Indian mynas. Based on macroecological analyses linking innovation to opportunism (Ducatez et al., 2014; Overington, Griffin, et al., 2011b) and invasion of novel habitats (Lefebvre & Sol, 2008), we predicted that Indian mynas would show a significantly higher innovation propensity than noisy miners. We also aimed to identify the mechanisms that underpinned species differences in innovation focusing on the relative contribution of neophobia, persistence and motor diversity.

METHODS

Subjects and Husbandry

Subjects were 23 wild-caught noisy miners of unidentified age and sex and 25 wild-caught Indian mynas, including 15 males (four adult, 11 subadults) and 10 females (three adults, seven subadults). Subadult mynas could be identified by their premoult brown plumage. We have no means of determining whether the sex ratio and age structure of the noisy miner and Indian myna samples differed. However, a recent review found no evidence to date for age differences in problem-solving performance in birds once the greater persistence of young individuals is accounted for (reviewed by Griffin & Guez, 2014), and in Indian mynas problem-solving Download English Version:

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