

Innovating Innovation Rate and Its Relationship with Brains, Ecology and General Intelligence

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The classic paper discussed in this essay:
Lefebvre L, Reader SM, Sol D (2004): Brains, innovations and evolution in birds and primates. *Brain Behav Evol* 63:233–246.

In 2002, the three of us were working together at McGill University, brought together by our shared interest in animal innovation. We had begun to discuss writing a review on the different aspects of our work on behavioral flexibility, which we felt strengthened and supported one another. An ideal opportunity arose when then editor Walt Wilczynski devoted a special issue of BBE to a symposium on 'Ecology and the Central Nervous System', organized by Luc-Alain Giraldeau at the 2002 International Society for Behavioral Ecology congress in Montréal. In the paper we were able to discuss and review a new operational measure of cognition, innovation rate. Using innovation rate and related measures of behavioral flexibility, we provided evidence for convergent cognitive evolution in birds and primates, and for behavioral flexibility having important ecological and evolutionary consequences. Broadly, our contributions can be separated into three themes, and we discuss the genesis of each in turn.

(1) Encephalization and Innovation in Birds (Louis Lefebvre)

In 1985, Kummer and Goodall [1985] suggested that the study of behavioral innovations might be useful in understanding

the ecology of intelligence, while Wyles et al. [1983] had proposed that innovations, especially when they were socially transmitted, might serve as behavioral drivers of evolution, using the famous example of tits opening milk bottles. Around 1994, I started wondering whether there could be many more cases of innovations besides milk bottle opening hidden in the ornithology literature, and whether these cases could provide a valid quantitative estimate of cognition. The publication of McGill Biology colleague Rob Peters' influential book *The Ecological Implications of Body Size* [Peters, 1983] (currently 3,920 citations on Google Scholar) gave me a kind of 'quantification envy' that animal cognition could be as 'operationalizable' as body size and used in a similar manner in comparative analyses. Initially, the innovation project targeted taxonomic differences in socially acquired versus individually acquired innovations, predicting that, if the taxonomic distribution of the two modes of acquisition did not differ, this would be further support for the argument that social and individual learning are different sides of the same coin. The socially acquired category was soon dropped because too few cases were found in birds, but the data did show for the first time that a field-based quantitative measure of intelligence was positively correlated with relative forebrain size [Lefebvre et al.,

1997]. One aspect that initially helped us believe we had a valid measure was the fact that the coauthors of the 1997 paper, MSc student Patrick Whittle and the undergraduate team of Evan Lascaris and Adam Finkelstein, worked independently, but obtained very similar results from the UK and North American databases, respectively. Later papers showed that different ways of measuring both encephalization and innovation yielded similar results in birds, that the relationship between innovation rate and brain size was driven by technical innovations, but not new food types, and that the biases that might affect innovation rate could be removed in multivariate analyses without affecting the relationship with encephalization [Lefebvre et al., 2004; Overington et al., 2009].

(2) Innovation and General Intelligence in Primates (Simon M. Reader)

During my PhD, Kevin Laland and I had become increasingly interested in the issue of whether social and individual learning evolve together, feeling that resolution of this issue was important for theoretical models of the evolution of social learning. We had begun experimental work on the causes of individual variation in in-

novation rates in fish and, with the publication of Lefebvre et al. [1997], wondered if Lefebvre's comparative approach could be applied to primate innovation and to other potential indicators of behavioral flexibility, specifically social learning and tool use. The final push to begin the project resulted from an unusual chain of events. In late 1997, Indonesian forest fires had impacted air quality across Southeast Asia, where our fish supplier bred our experimental subjects, guppies *Poecilia reticulata*, in large outdoor pools. Soon, guppies were in poor health when they arrived in Cambridge, apparently due to the effects of the polluted air on rainwater, and experimental work was impossible. I thus turned to a project I could conduct in the library, and began to gather published data on primate innovation, social learning and tool use.

It rapidly became clear that the primate literature was a rich data source, and could be used, with appropriate caution, to examine the independence of social learning from individual learning processes, as well as links between cognition and brain enlargement. Our first major publication from the dataset [Reader and Laland, 2002] documented a link between executive brain volume and behavioral flexibility. Furthermore, the observed correlation between social learning and innovation suggested that these capacities had evolved together. The debate over the relative importance of social versus ecological drivers of brain evolution is not settled, nor is the debate over the independence of social and individual learning, but we were pleased to contribute to these debates, our data supporting the idea that social cognition could not easily be separated from other cognitive capacities. Together with Yfke Hager, we have since expanded the dataset and incorporated additional measures, again finding that a suite of cognitive traits have evolved together, and supporting a 'general intelligence' model of primate cognition [Reader et al., 2011]. Using this general intelligence measure, we found evidence that high cognitive abilities have evolved independently several times, just as in birds.

(3) The Ecology and Evolution of Innovation and Encephalization (Daniel Sol)

In 1997, while I was doing my PhD on invasion biology, I came across the Lefebvre et al. [1997] paper on feeding inno-

vations and forebrain size. I realized that the ideas in the paper could be applied to one of the most puzzling questions in invasion biology: what makes a species a successful invader? I felt that members of a species that can adjust their behavior to novel situations might be more able to survive and reproduce in a new environment compared to less flexible species that persist with their existing behavioral repertoire. I later learned that Ernst Mayr [1965] had proposed a similar idea over 30 years ago, a discovery that, for a young researcher, was more a relief than a disappointment! At the time I read Lefebvre et al. [1997], there was some pessimism about whether we would ever be able to predict the outcome of species introductions [Veltman et al., 1996]. A wide array of adaptations to succeed in novel environments had been proposed, but confidence in them was undermined by a perceived lack of empirical support. Indeed, Veltman et al. [1996] had just shown that, among birds introduced to New Zealand, their likelihood of establishment was not influenced by species characteristics such as clutch size and diet, but by the number of individuals released. However, we found a firm relationship between brain mass, innovation rate and colonization success in birds introduced to New Zealand [Sol and Lefebvre, 2000]. Over the following years, we were able to generalize these results using a global dataset of avian introductions and a new modeling technique proposed by Tim Blackburn and Richard Duncan to correct for phylogenetic and spatial nonindependence among introduction events [Sol et al., 2005]. Other more recent studies have reported similar evidence for mammals [Sol et al., 2008], amphibians and reptiles [Amiel et al., 2011], but not for fish [Drake, 2007]. Influenced by ideas from John M. Allman, Robert Deaner, Robert Ricklefs and Thomas Martin, among many others, I later started considering our findings in terms of cognitive buffer theory, the idea that large brains function to facilitate the construction of behavioral responses to unusual, novel or complex ecological challenges. Thus, my interests shifted to explore the assumptions and ecological and evolutionary implications of cognitive buffer theory, including the influence of brain size on life history, migratory behavior and evolutionary diversification [reviewed in Lefebvre et al., 2004; Sol, 2009].

Conclusion

Our paper's strength was, we feel, that it brought together several previously separate ideas. We had experienced some skepticism that innovation rate was a robust or relevant measure, and indeed had discussed and investigated these concerns ourselves in our publications. By providing evidence for parallel evolution in birds and primates, and linking innovation rate to survival in novel habitats, our paper increased confidence that innovation rate provided a useful comparative measure of behavioral flexibility. When conducting the analyses reported in figure 2 [Lefebvre et al., 2004] in particular, we were struck by the similarities when we put the data for birds and primates side by side. This correspondence suggested that birds and primates show similar, convergent relationships between innovation rate and relative forebrain volume, innovation rate and tool use, and innovation rate and individual learning. In turn, these positive relationships suggested that a common, general factor might underlie interspecific differences in animal cognition, an idea that is gaining ground [Deaner et al., 2006; van Schaik et al., 2012] after a period dominated by the concept of massive modularity.

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