

## Opinion piece

## Taxonomic counts of cognition in the wild

**In 1985, Kummer & Goodall pleaded for an ecology of intelligence and proposed that innovations might be a good way to measure cognition in the wild. Counts of innovation per taxonomic group are now available in hundreds of avian and primate species, as are counts of tactical deception, tool use and social learning. Robust evidence suggests that innovation rate and its neural correlates allow birds and mammals to cope better with environmental change. The positive correlations between taxonomic counts, and the increasing number of cognitive and neural measures found to be associated with ecological variables, suggest that domain general processes might be more pervasive than previously thought in the evolution of intelligence.**

**Keywords:** innovation rate; tool use; social learning; tactical deception; brain size; general intelligence

In the very first lines of their pioneering paper in 1985, Hans Kummer and Jane Goodall observed that ‘we almost completely lack an ecology of intelligence’, lamenting the fact that ‘no other dimension of behaviour has so systematically *not* been studied in the field’ [1, p. 203]. The ecological measure of intelligence that Kummer & Goodall proposed at the time was innovation, defined as ‘a solution to a novel problem, or a novel solution to an old one’ [1, p. 205].

Quantitative analysis of innovations in birds and primates started in the late 1990s [2,3]. Comparative analysis of anecdotal data on animal intelligence in the field had been pioneered a decade earlier by Byrne & Whiten [4,5]. Quantifying the concept of social intelligence, Byrne & Whiten collected several hundred reports of tactical deception from over 20 primate species. Taxonomic counts of tool use and social learning cases were added to innovation and tactical deception in 2002 [3,6].

Experimental and observational studies of cognition are important, as are other comparative approaches (e.g. [7]), but taxonomic counts offer a unique opportunity to test hypotheses on large comparative datasets covering a broad spectrum of animals. The counts are expressed on an interval scale that allows multivariate statistics to factor in confounding variables as well as alternative hypotheses, and they measure cognition directly, not through a trait thought to vary with it such as group size or diet. Through direct tests and/or studies using neural correlates like cortex and pallium size, taxonomic counts are providing important new insights into the ecology of intelligence,

as Kummer & Goodall had hoped. For example, innovation rate has been used to test the idea that enhanced behavioural flexibility helps animals cope with environmental change, whether in the form of climate variability [8,9], introduction to new countries [10] or seasonality in the habitats of non-migratory species [11]. These results are paralleled by those focusing on brain size as a correlate of cognition (climate variability: [12]; introduction to new countries: [10,13]; seasonality in the habitats of non-migratory species: [11]; response to recent habitat change: [14]).

Despite these successes, some critics [15] have argued that studies concerning taxonomic counts of cognition are too biased to be valid. They also object to the neuroanatomical measures used in the analyses, and suggest that the approach lacks integration into a coherent scientific framework. The critique on biases is surprising, given that at least 13 different ones have been addressed. For example, Byrne & Whiten [4] guarded against publication biases favouring positive results by not only asking their informants which species had been seen performing possible instances of deception, but also which species had *not* despite years of observation in the field. Research effort biases likely to inflate reports on well-studied species have been incorporated into statistical tests on primates [3,4,15] and birds [16,17]. Additional biases such as population size, likeliness to notice and report a case, and popularity of a species among observers, have all been controlled for in studies of avian innovation [16,17]. The effects of data collection method, origin of the cases, degree of human intervention, journal identity, geographical zone and historical period were also all controlled for in counts on both primates [3,4] and birds [1,16,17]. The anecdotal nature of the raw data in the taxonomic counts has been extensively discussed ([18]; see also open peer commentary to Whiten & Byrne [5]) and the inter-observer agreement in the classification of cases shown to be high (0.82–0.95: [3,16,17]).

In addition to potential biases, alternative hypotheses and confounding variables are routinely incorporated into multivariate analyses on taxonomic counts. For example, Sol *et al.* [11] examined six factors that could inflate or obscure the relations they were testing between innovation rate, residual brain size and migration: (i) mid-latitude of the distribution range, (ii) occurrence in buffered habitats (e.g. conifer forest in winter), (iii) use of temporally variable diet types, (iv) clutch size, (v) food storing, and (vi) gender dimorphism in body mass. Sol *et al.* [19] included 12 confounding variables in their study of avian brain size, innovation rate and introduction success: phylogeny, research effort, nest location, sexual dichromatism, migratory behaviour, clutch size, body size, diet, type of parental care, mode of juvenile development, presence or absence of human commensalism and number of introduction attempts per species. In a generalization of their earlier [19] study, Sol *et al.* [10] added a further four variables.

The criticisms of inappropriate neuroanatomical measures and lack of integration into a coherent framework are also surprising. Specialized, domain-specific cognitive modules such as spatial memory for food stores, filial imprinting and imitated song may well be associated with dedicated, anatomically localized

neural centres, e.g. the hippocampus [20], the left intermediate medial mesopallium [21] and nuclei such as HVC and robust nucleus of the arcopallium [22]. However, innovation, tool use, tactical deception and social learning are less likely to be modular. For one, Chiappe & MacDonald [23] have argued that the repeated encounters over evolutionary time that are needed for specialized modules to evolve are unlikely to characterize the constantly changing situations where innovations, which are by definition novel, are used. Second, resource defence theory predicts that the spatial and temporal unpredictability of food should drive social and ecological intelligence in similar directions [24]. This argues for concerted selection on multiple cognitive domains rather than strict modular specialization.

Comparative work provides further evidence that the cognitive processes measured by taxonomic counts are positively correlated across taxa. Reader & Laland [3] report phylogenetically independent positive correlations between species-level counts of social learning, innovations and tool use; the taxonomic distribution of tactical deception cases is also similar to that of the other three counts of cognition. In birds, counts of tool use and innovation are positively correlated at the level of the parvorder [6], while reversal learning performance correlates with innovation in both birds and primates [25]. Experimental tests also yield positive correlations across primate genera [26] and individuals [27].

These correlations suggest that many aspects of cognition might be better understood in terms of general processes (also termed *g*) rather than modules. This is not to say that some cognitive processes are not specialized and domain-specific, but the idea that all cognitive and neural systems are necessarily modular is increasingly being criticized as oversimplified [28,29]. Brain imaging studies in humans suggest that distributed networks of multiple interconnected areas are active during cognitive tasks with a high *g* loading [30–32]. Even tool use, which requires specialized motor skills, has been linked to increased activity in at least eight areas of the cortex in humans, plus areas in the cerebellum and basal ganglia [33], and 10 areas in macaques [34]. The non-human with the most sophisticated form of tool manufacture and use, the New Caledonian crow, has recently been shown to have a larger allometrically corrected brain [35] than other corvids and passerines, as well as a larger mesopallium, striatopallidal complex, septum, tegmentum and nidopallium [36]. The idea that changes in a single dedicated brain area can suffice to understand the evolution of cognitive processes like tool use, innovation, social learning and tactical deception, is thus at best naive.

This implies that the search for neural correlates of cognitive divergence should focus either on the distributed networks or the large divisions of the brain that include these networks. In higher vertebrates, encephalization occurs via a disproportionate increase in the relative size of structures such as the avian pallium and mammalian cortex. As a consequence, the allometrically corrected size of pallial and cortical structures can be closely predicted by the size of the telencephalon

(99.5% of the variance in birds; 98.5% in primates), which can be closely predicted by the size of the whole brain (98.5% in birds; 99.2% in primates). This is not the case for more specialized structures like the hippocampus (11.5% in primates). This implies that tests of modular abilities at broad neuroanatomical levels would be inappropriate, but that tests of general cognition would probably not be. Comparative analyses at these broad levels are very robust to technical differences between studies. For example, the use of one versus several combined datasets or the use of fresh brains versus endocranial volumes (a method that controls for changes in fresh brain mass over an individual's lifetime, as well as problems of freezing, desiccation or perfusion that can affect fresh brain samples) has no effect on conclusions [37].

Far from a 'bewildering deluge' lacking any 'attempt to integrate the diverse results into a coherent scientific framework' [15], the recent increase of comparative work on intelligence is providing valuable ideas and data. General cognitive processes grounded in distributed neural networks and analysed with multivariate statistics incorporating alternative hypotheses will probably be more useful than strict modular views in integrating the many correlations between ecological, neural and cognitive measures.

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