

## [Introduction] Cognition in the wild: exploring animal minds with observational evidence

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# Cognition in the wild: exploring animal minds with observational evidence

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Where a natural phenomenon can be brought under experimental control, either in the laboratory or the field, greater power of analysis is always achieved. But what of the phenomena that (so far) have not proved amenable to experiment? The answer for animal cognition has often been that analysis must in that case be reduced to the level of natural history description; cognitive science will have to wait until the crucial experiments can somehow be done. This black-and-white approach contrasts with that in the physical sciences, where experiments are often impossible (e.g. in astrophysics or plate tectonics) and carefully measured observations from the field are widely accepted and routinely used to build and test theories. Here, we argue that animal cognition is missing an important stream of evidence for cognitive modelling if it treats field data as second rate or preliminary: carefully recorded observations from the field can and should be used to build and test theories, and are necessary to enable appropriate, ecologically valid experiments to be designed where experimentation is subsequently possible.

In this special feature, we explore how observation and analysis of naturally occurring behaviour are already contributing to our understanding of animal cognition. Observational data may be necessary for several reasons: because certain types of behaviour, or certain species simply do not lend themselves to study in captivity; because certain questions, or certain settings do not allow the manipulation of variables necessary for experiments; or any combination of these problems. We shall illustrate how novel recording, statistical and analytical methods have led to advances in our understanding of several topics that cannot be fully understood with experiments alone. Specifically, we highlight: complex alliance formation in dolphins; gestural communication in apes; imitation of novel actions and pantomime; innovation in comparative perspective; the elaborate manual skills involved in chimpanzee tool use; elephant cognition; and the planning of travel routes and foraging decisions by primates.

The large brains of cetaceans, whether measured in absolute or relative terms, suggest that they will be significant for our understanding of the evolution of cognition. But cetaceans are relatively rare in captivity, with even fewer housed in dedicated research facilities; and as far as we know, no captive facility has the capacity to house these large-bodied mammals in social groups that match the size and spatial complexity of their natural environment. The analysis of alliance formation and social interactions of cetaceans is, therefore, one obvious area where observation of wild populations is necessary now and likely to be irreplaceable in the future. Here, Connor et al. [1] illustrate how observation of one wild population over several years has led to the rejection of previous hypotheses about the alliances formed between male bottlenose dolphins. Through computation of alliance coefficients, Connor et al. conclude that male bottle-nose dolphins form multi-level alliances of a hierarchical complexity not previously recognized.

Gestural communication in great apes is a second area where it is hard to imagine that experiments will ever answer all the key questions. Experiments have proved revealing; for instance, Cartmill & Byrne [2], using humans to control and manipulate variables, showed that orangutans are able to assess the degree of understanding of their gestures and modify further gesturing accordingly. But to study naturally occurring gestural communication, used within the species, observational data are

still necessary. Unlike vocalizations, where remote playback can effectively simulate communication, it is not clear whether apes would react to video gestures as 'real'; in any case, ape gesture is used normally in short-range or visual communication, where there is no way of simulating the gesturing ape. Nevertheless, cognitive theories have been put forward and tested, using observations alone: for instance, hypotheses about the ontogeny of gesture. Early suggestions that observational learning was the main means of acquisition were refuted by finding no local traditions of gesturing, and greater homogeneity within than between groups [3]. An alternative proposal was that repeated dyadic interactions during development served to condition relatively arbitrary actions to become understood as gestures, in a process called 'ontogenetic ritualization' [4]. In turn, this hypothesis has fallen short when confronted by recent data that have found the ape gestural repertoire to be essentially the same in widely separated populations (e.g. [5]): the repertoire is 'species typical'. Now, it seems most likely that great ape gesture types are guided by the genome, with the same latent potential in every member of the species; indeed, a recent comparative analysis has shown that many gestures are 'family typical', the same in Pan, Gorilla or Pongo [6]. Restricted-rearing experiments might have led to these revisions being made more quickly; but few ethics committees would allow such experiments nowadays, rightly.

Imitation of another's actions has long fascinated psychologists, and on the basis of laboratory experiments it has often been argued that imitation of arbitrary, novel actions lies beyond the capacity of non-humans. For two species, this has been refuted— by observational data, rather than experiment. Working with orangutans being 'rehabilitated' to the wild from illegal capture, Russon & Galdikas [7] recorded many compelling instances of elaborate copies of specifically human activities, such as chopping wood with an axe or lighting a camp fire with kerosene, copied by the orangutans with some fidelity. In the wild, Hobaiter & Byrne [8] took advantage of the 'natural experiment' of a snare-injured adult chimpanzee that had developed a novel, yet functional for him, way of scratching his body. They showed that this procedure was copied by several immatures for whom it offered no advantage, specifically those who spent prolonged periods in the same areas as the original model. In the special feature, Russon [9] returns to her data from rehabilitant orangutans to show that occasionally they use imitation to elaborate their intentions when gesture alone fails: apparently 'pantomiming' what they would like their target audience, usually a human, to do for them. The precise nature of pantomime in orangutans can now be explored experimentally, using humans to present challenges just beyond the capacity of ape subjects and then 'fail' to offer help to them. But would such experiments have been conceived at all if the observations of this fascinating behavioural phenomenon had not occurred? Understanding how cognition is used in everyday, natural circumstances may be critical to the design of experiments that are capable of properly assessing cognitive skills, whether in the laboratory or the field.

Where rare behaviour types may be significant, one approach is to 'data mine' a large corpus of existing observations, collected ad libitum in the course of other work. This was used to study tactical deception in primates [10]. The tactics seemed mostly to be learnt from natural opportunities, but in the case of the great apes, there was evidence that individuals were to some extent able to appreciate the mental states of others, and monkeys showed the ability at least to appreciate others' physical viewpoint. These hypotheses were not tested experimentally for a decade, though when they were, the results were generally confirmatory [11]. But data mining can be used deliberately to suggest and ground innovative experimentation. Elephants have a popular reputation for intelligence but until recently, experimental studies provided far from inspirational results, implying that elephants were slow to learn and lacked even the basic components of social knowledge [12]. Data mining of the long-running study at Amboseli suggested the possibility that wild elephants might have more powerful cognitive abilities, which led to a series of novel field experiments and some quite surprising results. Thus, we now know that African elephants distinguish the bones and tusks of long-dead elephants from those of other megafauna, even when

cleaned of all possible olfactory cues [13]; they categorize people along tribal lines, when this matches the level of risk to themselves, and identify these risk categories by olfactory and visual cues separately [14]; they recognize specific individuals on the basis of olfaction alone, and they keep track of the relative locations of up to at least 17 other adults with whom they are travelling but often out of sight, suggesting remarkable working memory capacity [15].

When it comes to taking a 'wide-angle' perspective on animal cognition, comparing across a taxonomically broad range to explore common traits, use of data-mined observations is usually the only way to proceed: limiting to experimental data will not work because experiments have not yet been conducted on a wide enough range of animals. Here, Lefebvre [16] argues for the utility of such taxonomic overviews, using innovation as one type of behaviour that indicates cognitive specialization. Of course, captive animals can be innovative too and experimental tests of innovation should be easy to set up; comparative overviews of the kind presented here will allow selection of appropriate species and tests in the future.

Studies of tool use in chimpanzees likewise stand to benefit from an improved understanding of the challenges presented by their natural environment and the solutions that they generate. There have been many experiments aimed at investigating chimpanzees' understanding and use of tools, most in captivity but some in natural settings; but all analyse behaviour in terms of binary choices: pull/twist, lift/drop, probe/sponge, etc. In the Goualougo Triangle of Congo, however, chimpanzees exhibit a suite of skills in which two different tools, each made to a specific design, are used in different ways to gain insect food [17]. Here, Sanz & Morgan [18] analyse the individual elements involved in termite gathering, one of the most elaborate of these two-tool tasks, revealing impressive complexity. Moving away from the binary to this more detailed level of analysis has also helped to explain the puzzling abilities of captive gorillas, performing as well as chimpanzees on artificial tool using tasks, when in the wild they show no tool use [19]. Recording the details of gorillas processing challenging leaf foods has revealed multi-stage, hierarchically organized behaviour [20]: although gorillas do not use tools, they structure behaviour in similar ways to Goualougo chimpanzees using tools. This finding points to a need to separate tools per se from the cognitive challenge of dealing with physical problems; intriguingly, Seed et al. [21] have found that chimpanzees tackle physical problems more insightfully when they do not need to use tools, even though in the wild they are the species that uses tools the most.

For most primates, feeding may present a particular cognitive challenge: lacking complex stomachs to harness bacterial aid in digestion, yet missing the balanced nutrition provided by eating meat, they must 'food combine' to maintain an adequate diet. Efficient food-finding in large-scale space answers this challenge, but studies of cognitive maps usually require environments larger in extent and complexity than any captive facility could offer (though for an exception, see [22]). Nevertheless, fieldwork has made progress towards understanding the cognitive resources that primates can bring to this challenge. At one site, baboons set off at dawn for out-of-sight resources that are rich but can be readily depleted by competitors, by-passing other attractive foods—not at risk in the same way—to which they return and feed upon later in the day [23]. Evidently, they are able to use their memories of what is found where, and when it may be lost when they make route-choice decisions. By using encounters with larger baboon groups as 'natural displacement' experiments, the structure of this knowledge was investigated in more detail [24], and found to lack the distinctive signs of Euclidian, vector-map properties. The cognitive maps of baboons, then, are no more 'map like' than those of people navigating in familiar environments [25]. Monkeys' understanding of timing was also high-lighted in studies of the decisions mangabeys make, as to whether to check a fruiting tree that on a previous visit had held unripe fruit [26]. When the intervening days (not just the day of return) had been warmer and sunnier, the monkeys were more likely to revisit; this applied not only to fruit that might potentially give off a scent plume, but also to

ripening fruit that was eaten for the insect larvae it contained. It seems that monkeys remember the weather over the course of several days and can, like fruit-growers, take into account the effect of good weather on fruit ripening.

One of the problems confronting those using natural observations to understand the planning behind route choice in animals is that the human eye readily identifies patterns in mapped routes, attributing possible goals and intentions to travel: but the human brain is poor at statistical evaluation of whether such patterns are real. A new statistical procedure, the change-point test (CPT) promises to help make these judgements objectively [27]. The test has already been used to show that gibbons travel in a goal-oriented way between high quality resources, far more efficiently than they could do on the basis of opportunistic random search [28]. Here, Joly- Radko & Zimmerman [29] apply it to a nocturnal mouse lemur, which forages over an area of about 100 m from its sleeping site.

We hope that the articles in this special feature will help re-focus attention on the productive ways in which naturalistic observations and appropriate experimentation can work together to extend the scope and power of cognitive analyses of animal behaviour. The days of partitioning—between natural history and behavioural ecology, on the one hand, and the cognitive capacities that underlie animals' natural behaviour, on the other hand—are, we hope, numbered.

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