

## Review

## Identifying animal complex cognition requires natural complexity

Christophe Boesch<sup>1,\*</sup>

## SUMMARY

**The search for human cognitive uniqueness often relied on low ecological tests with subjects experiencing unnatural ontogeny. Recently, neuroscience demonstrated the significance of a rich environment on the development of brain structures and cognitive abilities. This stresses the importance to consider the prior knowledge that subjects bring in any experiment. Second, recent developments in multivariate statistics control precisely for a number of factors and their interactions. Making controls in natural observations equivalent and sometimes superior to captive experimental studies without the drawbacks of the latter methods. Thus, we can now investigate complex cognition by accounting for many different factors, as required when solving tasks in nature. Combining both progresses allows us to move toward an “experience-specific cognition”, recognizing that cognition varies extensively in nature as individuals adapt to the precise challenges they experience in life. Such cognitive specialization makes cross-species comparisons more complex, while potentially identifying human cognitive uniqueness.**

## INTRODUCTION

Since the birth of philosophy, one of the main questions of humanity was to understand “what makes us humans?” and especially how human intelligence is unique in the animal kingdom. If this quest is often tainted by anthropocentric partiality, the comparative approach has been favored since Plato’s famous comparison of the human with a featherless chicken. If the comparison possibilities have originally been strongly limited, since science had no access to our closest living relatives in natural living populations, the aim of “comparing what is comparable” was central to many of the discussions (Allen, 2002; Bacon, 1960; Kuper, 1999). The reality being that different animal species live naturally in very different ecologies in different places on earth, the original solution was to remove those animals, whenever discovered, from their original habitat and to bring them to the scientists sitting in Europe (Buffon, 1812; Chaillu, 1868 [2002]). This approach was progressively presented as a scientific method, suggesting that captivity would allow for better observational conditions and without human disturbances (Hediger, 1969; Tomasello and Call, 1997). While such an approach, typical to experimental psychology, allows for more comfortable comparison in the laboratory, the question of the ecological validity has become a question of increasing debate.

The rise of field studies in the 1960s has forced a first revision of the experimental paradigm, as key human behavior patterns, such as tool use, tool making, hunting for meat, and meat sharing, were discovered in wild-living chimpanzees in Gombe National Park, in Tanzania (Goodall, 1963, 1964, 1968). As expected, these “uneasy” discoveries from an anthropocentric point of view were rapidly challenged (Clark, 2002; Power, 1991), but all subsequent studies with other wild chimpanzee populations confirmed these observations (Boesch and Boesch, 1981, 1984; Nishida et al., 1983; Sanz et al., 2004; Sugiyama and Koman, 1979). Similar cognitive abilities were likewise discovered in other primate species (orangutan: Schaik et al., 1996; baboons: Strum, 1981; capuchin monkeys: Visalberghi et al., 2007; macaques: Gumert and Ma-laijijitnond, 2013). Following the Gombe chimpanzee revelation, the main argument in favor of captive experimental studies became then that the presence of a certain behavior could be explained due to various factors of the natural environment. Consequently, one needed to study such behaviors in a controlled environment, the captivity, where the influence of different factors could either be eliminated or clearly controlled for (Povinelli, 2000, 2012; Tomasello and Call, 1997).

However, in recent years, this captive study paradigm has been criticized from three different and complementary angles: First, the rearing conditions of captive individuals are far from being representative to

<sup>1</sup>Max-Planck Institute of Evolutionary Anthropology, Leipzig, Germany

\*Correspondence: boesch@eva.mpg.de

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those experienced in the wild, and this needs to be considered before drawing any conclusions at the species level (e.g. [Boesch, 1993; 2007; Gardner, 2005; 2008; Leavens et al., 2019; Mettke-Hofmann 2014](#)). This parallels the main argument of cognitive ecology ([Healy and Braithwaite 2000; Healy et al., 2005; Hutchins 2010; Mettke-Hofmann 2014](#)) or embodied cognition ([Anderson et al, 2010, 2013; Clark 1999; Goldman 2012](#)). Second, the low ecological validity of the experiments proposed to captive subjects makes it difficult, even impossible, to reconcile with a valid evolutionary scenario for the evolution of cognition ([Boesch, 2007, 2012, 2020; Bräuer et al., 2020; Rosati, 2017; Rosati et al., 2014](#)). Third, existing populations' variability within species in cognitive performance were for too long ignored but became recently an important topic, as increasing information revealed how the bias introduced with incomplete population sampling distorted the conclusions ([Boesch et al., 2020; Webster and Rutz, 2020](#)). Psychological studies on humans included in 96% of the cases subjects originating from one specific subsample of the world human population, the so-called WEIRD (Western, Educated, Industrialized, Rich, Democratic), people that represent only 12% of the humanity ([Arnett, 2008; Atran et al., 2005; Boesch, 2007; Medin and Atran, 2004; Henrich et al., 2010](#)). This WEIRD population has now been shown to not be representative of the human species, being mostly an outlier ([Henrich et al., 2010](#)). Similarly, a large majority of the psychological studies have been done on BIZARRE (Barren, Institutional, Zoo, And other Rare Rearing Environments) chimpanzees, a sampling bias that ignores the many different living conditions experienced by chimpanzees throughout Africa ([Leavens et al., 2010](#)). It thereby threatens a fair representation of cognition achievements of our closest living relative ([Bard and Leavens, 2014; Boesch, 1993, 2007; Gardner and Gardner, 1989; Lyn et al., 2010; Racine et al., 2008](#)). More generally, [Webster and Rutz \(2020\)](#) have warned about the common trap of using unrepresentative samples of animal subjects in many behavioral and psychological studies. This STRANGE animal sampling has biased our conclusions as had been shown with human WEIRD samples ([Webster and Rutz, 2020](#)).

This debate has much reminiscence with the old nature-nurture debate, whereby some proposed that the environment, if it plays a role, is minimal, and studies removing animals from their natural environment are valid and tell us much about the behavior and cognition of a species ([Galef, 1990, 2004; Heyes, 1993, 1998; Povinelli, 2000; Tomasello, 1996](#)). Others, on contrary, argue that the influences of the environment on the cognitive development are essential and removing animals from their natural environment has strong detrimental effects on both the development of behavior and cognition ([Boesch 2020](#), see for reference [Table 1](#)). The more developed the learning abilities of a species are, the more negative will be the impact of growing up and living in artificial captive conditions. Animal welfare studies have convincingly shown that different species react differently strongly to captive conditions, with wide-ranging social species being affected negatively more strongly than less social species with smaller natural ranges ([Mason, 2010; Pomerantz et al., 2013](#)). So, it should be expected that a wide-ranging social species, like the chimpanzee, will be negatively affected by most captive conditions, and, therefore, the cognitive performance of captive individuals will not be representative to that of the wild-living chimpanzees.

In the following, I will discuss first the recent knowledge gained about the impact of living conditions during the upbringing and the role of daily practice on the development of the cognitive abilities and second, recent improvements in statistical methods allowing to control for multiple confounding factors in captive and natural studies. These allow us to have a newer fresh look at what cognition is and how it develops, thereby proposing a new model, strongly divergent from the "one cognition" model that has been prevailing much of the thinking of comparative psychologists over the last 4 decades (e.g. [Boesch, 2020; Bräuer et al., 2020](#)).

### Studying cognition within ecologies: ontogeny, environment complexity, and brain plasticity

The evolution of cognition has been proposed to be influenced by two main factors, the social and the ecological dimension. In an attempt to explain the proposed unique cognitive achievements of humans, a number of scholars have proposed the very special and complex social life of humans to be the explanation for our unique cognitive achievements ([Byrne and Whiten, 1989; Dunbar, 1988; Humphrey, 1976; Jolly, 1966](#)). At the same time, the importance of some aspects of the ecology for the evolution of cognition was stressed by different hypothesis, including the challenge of food extraction ([Gibson, 1986](#)), of finding dispersed food ([Milton, 1981](#)), or the challenge of the technical intelligence ([Byrne, 1997; Parker and Gibson, 1977](#)). If at first simple correlation analyses confirmed the role of some social factors, more recent and more complete analyses strongly supported the predominant role of the ecology on the evolution of cognition ([González-Forero and Gardner, 2018; MacLean et al., 2009; Sol et al., 2005; Sol, 2009](#)).

**Table 1. Summary of some of the data showing the effects on the development of brain structures and cognition of the socio-ecological environment during the ontogeny of physical practices at all ages and plasticity during adulthood.**

	Effects on brain structure	References	Cognitive effects	References
	During the ontogeny			
Maternal deprivation	<p>Growing with maternal deprivation early in life affects many areas of the brain:</p> <ul style="list-style-type: none"> <li>• Irreversible reduction of dentate gyrus granule cell number and density in adult female rats, as well as dentate gyrus neurons altered in dendritic arrangement.</li> <li>• Long-term alteration in hypothalamic-pituitary-adrenal axis activity, disturbance of auditory information processing, and neurochemical changes in the adult rat brain</li> <li>• Lifelong hypothalamic dysfunction, enlarged prefrontal cortex and cingulate cortex in rhesus monkeys</li> <li>• Lack of a secure attachment relationship in early years has detrimental long-term effects on health in rhesus monkeys</li> <li>• Decreased survival rate and lifelong effects on immune status in rhesus monkeys</li> <li>• Lifelong decrease of white-to-gray matter volume, in cortical folding and larger gray matter within cortical folds in nursery-reared compared to mother-reared chimpanzees.</li> </ul>	<p>Oomen et al., (2011) Feng et al., (2011), Spinelli et al., (2009) Conti et al., (2012), Lewis et al. 2000 Bogart et al., (2014)</p>	<p>Growing with maternal deprivation early in life leads to:</p> <ul style="list-style-type: none"> <li>• Deficits in association, social responsiveness, learning abilities, exploration, communication in primates,</li> <li>• Long-lasting increased cortisol response to stress with persistence of stereotypical behaviors after 3 y of normal social life in rhesus monkeys,</li> <li>• Impairment in spatial learning ability and reduced spatial working memory in adult rats,</li> <li>• In chimpanzees, shorter play bouts with more aggression outcomes in orphan compared to mother-reared ones.</li> <li>• Impaired spatial learning in adulthood in mammals</li> </ul>	<p>Novak and Harlow (1975), Suomi and Harlow (1972), Feng et al., (2011) Garner et al., (2007) Leeuwen et al. (2014) Pravosudov and Omanska (2005)</p>

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	Effects on brain structure	References	Cognitive effects	References
Environment complexity	<p>Environmental enrichment experience in captivity reveals:</p> <ul style="list-style-type: none"> <li>• In rodents and primates, more complex environment results in increased number and volume of white and gray cells, in the number of synaptic connections, enhanced cell survival, increased neurogenesis, increase dendritic branching, and improved synaptogenesis and neurotransmitter expression</li> <li>• Enhanced length and complexity of dendritic tree, increase dendritic spine density and synaptic protein levels in hippocampus and prefrontal cortex in adult marmosets.</li> <li>• Continuous environmental enrichment promotes functional recovery after perinatal brain injury in mice.</li> </ul>	<p><a href="#">Praag et al., (2000)</a>, <a href="#">Mora et al., (2007)</a>, <a href="#">Hackman et al., (2010)</a>, <a href="#">May, 2011</a>, <a href="#">Voss et al., (2013)</a>, <a href="#">Gelfo et al., (2018)</a>, <a href="#">Kozorovitski et al. 2005</a>, <a href="#">Forbes et al., (2020)</a></p>	<p>Across taxa, decision-making, spatial and vocal learning, and discrimination are environment condition dependent.</p> <ul style="list-style-type: none"> <li>• Population of chickadees in harsher conditions exhibited faster problem solving, lower incidence of neophobic behaviors, and better spatial memory compared to populations in milder conditions.</li> <li>• In salmon, environmental enrichment enhanced the forebrain expression of NeuroD1 mRNA and improved learning ability assessed in a spatial task.</li> <li>• In chimpanzees, captive-born individuals presented long-term cognitive deficits compared to captive wild-born individuals associated with early impoverished rearing.</li> <li>• In human twin studies, hippocampal volume shows lower heritability than the frontal lobe volumes, indicating strong environmental influence on hippocampal development and consequently spatial abilities.</li> </ul>	<p><a href="#">Buchanan et al., (2014)</a>, <a href="#">Salvanes et al., (2013)</a>, <a href="#">Davenport and Rogers (1970)</a>, <a href="#">Davenport et al., (1973)</a>, <a href="#">Menzel et al., (1970)</a>, <a href="#">Peper et al., (2007)</a></p>

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	Effects on brain structure	References	Cognitive effects	References
Parental socioeconomic status	<p>Growing up in low parental socioeconomic status in humans is associated with:</p> <ul style="list-style-type: none"> <li>• Smaller gray matter volume in bilateral hippocampi, middle temporal gyri, left fusiform, and right inferior occipito-temporal gyri,</li> <li>• Lower cortical folding in anterior frontal regions,</li> <li>• Smaller cortical surface areas in the number of regions supporting language, reading, executive functions, memory, and spatial skills. This last effect is proportionally larger among children from lower income families than in those of higher income families.</li> </ul>	<p>Hackmann and Farah (2009), Jednorog et al., (2012) Farah et al., (2006), Noble et al., (2015)</p>	<ul style="list-style-type: none"> <li>• In humans, lower parental socioeconomic status is associated in humans with (1) lower literacy and verbal skills and (2) trends for lower memory and visuo-spatial processing.</li> <li>• Early stimulation for social and sensory interactions contributes to proper development of cognitive, affective, and psychosocial capacities in humans.</li> <li>• EE had a larger beneficial outcome on cognitive outcomes on infants with a larger hippocampus as neonates in humans</li> <li>• In chimpanzees, imitation training subjects show changes in white matter integrity and frontoparieto-temporal connectivity in the left hemisphere within the mirror system, which facilitated complex imitation learning abilities.</li> <li>• Orangutans more familiar with humans performed better in exploration and were less neophobic than those which had less exposure to humans.</li> </ul>	<p>Hackmann and Farah (2009), Jednorog et al., (2012) Schoentgen et al., (2020) Overfeld et al., (2020) Pope et al., (2018) Damerius et al. (2018)</p>
<b>Physical Practices at all ages</b>				
Foraging effort	<p>In humans and other animals, physical activity increases brain-derived neurotropic factor that supports neural survival, growth, and synaptic plasticity in the cerebellum and hippocampus.</p> <ul style="list-style-type: none"> <li>• In rodents, the number of dentate gyrus neurons of the hippocampus can double or triple with exercise.</li> <li>• Voluntary exercise and environment enrichment in adult mammals massively increase spine density and neurotrophins following two complementary pathways increasing neurogenesis</li> </ul>	<p>Voss et al., (2013) Praag (2008) Olson et al., (2006), Praag et al., (2000)</p>	<ul style="list-style-type: none"> <li>• The neurologic changes of voluntary exercise in adult mammals result in beneficial effects in spatial learning, odor discrimination, object exploration, and memory</li> <li>• Wild adult chickadees possess double so many new neurons important for the acquisition of new spatial memory within six weeks than those living in an aviary.</li> </ul>	<p>Olson et al., (2006), Gobbo and O'Mara (2004), Praag et al., (2000) Barnea and Nottebohm (1994)</p>

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	Effects on brain structure	References	Cognitive effects	References
Training specific effects	<ul style="list-style-type: none"> <li>• In humans, expert pianists possess higher gray matter density and higher white matter integrity in the primary sensorimotor cortex and right cerebellum than novices.</li> <li>• Jugglers show bilateral expansion of gray matter in mid-temporal area and left posterior intraparietal sulcus.</li> <li>• Handballers possess increased gray matter volume in the right primary/secondary motor, bilateral cingulate motor area, and left intraparietal sulcus</li> <li>• Skilled golf players show larger gray matter in the fronto-parietal network including premotor and parietal areas.</li> </ul>	<p><a href="#">Han et al., (2009)</a>  <a href="#">Draganski et al., (2004)</a> <a href="#">Haenggi et al., (2015)</a>  <a href="#">Jaencke et al., (2009)</a></p>	<p>Physical training in captive setting leads to:</p> <ul style="list-style-type: none"> <li>• Enhance hippocampus-dependent spatial memory and pattern discrimination and the more so with harder cognitive tasks in rodents</li> <li>• Improves passive avoidance learning, spatial pattern separation, and novel object recognition in primates</li> <li>• Faster and more accurate spatial short-term memory performance and spatial learning performance in adult humans</li> <li>• Jogging and long jump are associated with cognitive information process and inhibitory control in humans.</li> </ul>	<p><a href="#">Voss et al., (2013)</a>, <a href="#">Praag et al., (2000)</a>  <a href="#">Erickson et al., (2009)</a>  <a href="#">Esmæilzadeh et al., (2018)</a></p>

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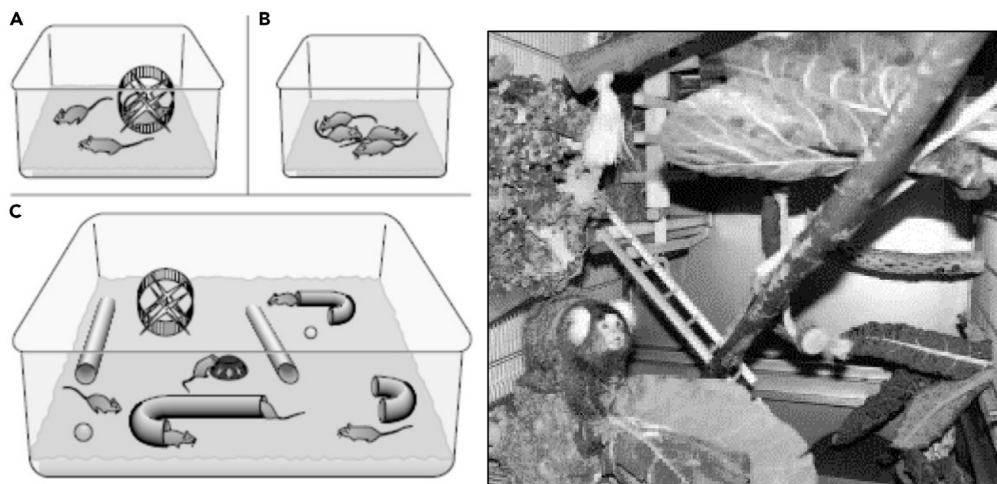
	Effects on brain structure	References	Cognitive effects	References
		Plasticity during adulthood		
Environment complexity	<ul style="list-style-type: none"> <li>In humans, ecology contributes to 60% of brain size increases, while cooperation accounts for 30% of brain size decreases.</li> <li>Populations of birds of the same species experiencing harder winter possess larger hippocampal volume, higher number of hippocampal neurons, and neurogenesis rate than the populations experiencing milder winters.</li> </ul>	<a href="#">González-Forero and Gardner, 2018</a> <a href="#">Pravosudov and Roth (2013)</a>	<ul style="list-style-type: none"> <li>Populations of birds of the same species experiencing harder winter have better spatial memory performances than the populations experiencing milder winters.</li> <li>Parrot species living in complex habitats showed shortest latencies in exploration test and longer duration in exploration.</li> <li>Bats living in greater ecological diversity learned complex rules flexibly quicker than those in homogeneous habitats.</li> <li>Rats from complex cities made more structured and extended movements than those from simple cities.</li> <li>Fish under EE conditions present overall higher exploratory behavior, spatial orientation, and learning capacities compared to those without EE.</li> <li>Pinyon jays that are highly social displayed lower error rates after reversal of reward contingencies for both spatial and color stimuli than the relatively solitary nutcrackers that are specialized for spatial memory and scrub jays which are ecologist generalists.</li> </ul>	<a href="#">Pravosudov and Roth (2013)</a> , <a href="#">Mettke-Hofmann et al., (2002)</a> <a href="#">Clarín et al., (2013)</a> <a href="#">Yaski et al., (2011)</a> <a href="#">Arechavala-Lopez et al., (2020)</a> <a href="#">Bond et al., (2007)</a> <a href="#">Bond et al., (2007)</a>

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	Effects on brain structure	References	Cognitive effects	References
Effort to reach food	<ul style="list-style-type: none"> <li>Chimpanzees' hippocampus is less asymmetrical and larger with more connectivity with other brain regions than in bonobos, possibly due to larger dependence on patchy fruit resources within large territories in chimpanzees.</li> <li>Frugivorous primates possess enlarged brain size compared to folivorous ones, presumably as a result from larger spatial information storage and retrieval due to higher cognitive demands of extractive foraging of fruits and seeds.</li> </ul>	<p>Hopkins et al., (2009) DeCasien et al., (2017)</p>	<ul style="list-style-type: none"> <li>Golden lion tamarins that range far to feed on insects and patchy fruits show more accurate spatial memory over longer time intervals than Wied's marmosets that are obligate gummivores in small home ranges.</li> <li>Lemurs with more complex diets show more sophisticated memory and inhibitory control capacities than more folivorous species.</li> <li>Lizards being active foragers are better at reversal tests than congeneric lizard being sit-and-wait foragers.</li> <li>Woodpecker finches in dry area with variable food availability were faster at reversal learning and more neophilic than conspecifics from cold forest where food abundance is stable.</li> </ul>	<p>Rosati (2017) Rosati et al., (2014), Day et al., 1999 Tebbich and Teschke (2014)</p>
Physical training	<ul style="list-style-type: none"> <li>In aging human adults, physical activity protects against age-related cognitive decline and brain atrophy</li> <li>In aged running mice, exercise increases the survival of newborn neurons.</li> </ul>	<p>Praag (2008)</p>	<ul style="list-style-type: none"> <li>In elderly humans, those who participated in high levels of exercise showed less cognitive decline in the following 5 years.</li> <li>In aged running mice, exercise improved acquisition and retention of the water maze task, contextual fear conditioning, spatial memory, and novel object recognition.</li> </ul>	<p>Middleton et al. (2008) Praag (2008), 2009</p>
Tool and technical innovation	<ul style="list-style-type: none"> <li><i>Macaques trained to use tools had increased gray matter in right superior temporal sulcus, right second somatosensory area, and right intraparietal sulcus, with less effect on the left. 17% increase within few weeks</i></li> <li><i>Chimpanzees' tool use result in marked leftward asymmetries in relative white matter of the perisylvian cortical regions,</i></li> <li><i>Tool-using birds have more folded cerebellar cortex but not a larger cerebellum than non-tool-using species.</i></li> </ul>	<p>Quallo et al. (2009) Cantalupo et al. (2009) Iwaniuk et al. (2009)</p>	<ul style="list-style-type: none"> <li><i>In primates and birds, absolute and relative brain size correlates strongly with tool use innovation and only weakly with non-technical innovation.</i></li> <li><i>In macaques, tool use training enhances performance in understanding spatial relations, causal cognition, numerosity, and causality.</i></li> <li><i>Wild capuchin monkeys consistently and immediately selected functional tools, regardless of conditions, outperforming captive capuchin monkeys tested in tool tasks.</i></li> </ul>	<p>Navarrete et al. (2016), Lefebvre et al. (2002) Tia et al. (2018) Schrauf et al. (2008), Visalberghi et al. (2009)</p>





**Figure 1.** Left: Classical environmental enrichment (EE) conditions as studied in many rodent studies in the laboratory (Praag et al., 2000). Interestingly, even the small EE improvements between (a) and (c) were enough to produce drastic differences on many measures both in the brain structure development and cognition. Right: A picture of an adult marmoset in a complex captive environment with branches, vegetation and objects used in a study documenting the positive effects on the dendrites spine length and branching in the hippocampus and the prefrontal cortex with increasing environmental complexity (Kozorovitski et al., 2005). The open question is of how much larger would the difference be if the EE would reflect the real complexity found in Nature?

Consequently, recent years have seen a burgeoning of studies stressing the importance to consider the ecological validity of the tests used in experiments to understand the cognitive performance of animals (Bräuer et al., 2020; Healy et al., 2009; Janmaat et al., 2016; Smulders et al., 2010; Rosati, 2017). This specific aspect is the subject of another contribution to this special issue about natural behavior in this journal. However, in my view, an equally important aspect needs to be considered and that is what the individuals experienced during their ontogeny before they are tested. “Ontogeny” is too often thought as only a maturation period, neglecting the fact that it is also the period of life when the individuals acquire the specific skills needed in their environment to survive and strive as adults. All these early experiences in life are decisive for the future development of cognitive and physical skills (Davenport et al., 1973; Gardner and Gardner, 1989; Harlow and Harlow, 1962). As individuals mature in their environment, they develop the cognitive skills, knowledge, expectations, beliefs, and attitudes to cope with them, which will influence how they will attend, interpret, and organize new information and challenges (Clark, 1999; Frith, 2007; Mettke-Hofmann, 2014).

Classically, the brain, once mature, was proposed to be a very rigid organ with very limited regeneration potential in case of injuries (Kaplan, 2001; LaDage, 2015). Therefore, it came as a relative surprise that brains are much more plastic than anticipated and this, in humans, as well as in many other animal species (LaDage, 2015; Praag, 2009). Neuroscience has invested a large amount of work in understanding and explaining brain plasticity and its impact on cognition in humans, as well as in other animal species. This knowledge needs now to be integrated in the study of cognition in general and animal cognition more specifically.

Table 1 presents some examples of studies done on different animal species, including humans, in nature or in captivity, specifying the effects on the brain development and on cognition performance of the environment complexity and physical practices at different periods of the life span. Three important points emerged from this review: First, small variations in the complexity of the environment can lead to important and long-lasting improvements in the brain structures and in cognitive abilities (see Figure 1). Second, such improvements are observed in individuals of all age and sex classes and in many different animal species. Third, this brain plasticity is a special interest from a neurological point of view, as it opens the possibility to offset the effect of cognitive senescence due to aging, injuries, as well as to counteract the effect of neurodegenerative diseases, such as Alzheimer, and so on (Hackman et al., 2010; Sale et al., 2008).

The studies summarized in [Table 1](#) are relatively simple, as they tend to study the impact of one factor on both the brain and cognition. However, we should expect more complex interactions on both: for example, recently, it was shown that early infancy deprivation is associated with deficit in the adult brain structure, despite subsequent environmental enrichment ([Mackes et al., 2020](#)). Another interaction was found when maternal behavior was shown to be a fundamental mediator for environment enrichment to trigger a marked acceleration in the maturation of the visual system in the newborn mice ([Baroncelli et al., 2010](#)). Similarly, a longitudinal study of English and Romanian adoptees revealed that “Notwithstanding the resilience shown by some adoptees and the adult remission of cognitive impairment, extended early deprivation was associated with long-term deleterious effects on wellbeing that seem unsusceptible to years of nurturance and support in adoptive families” ([Sonuga-Barke et al., 2017](#)).

The vast majority of environmental enrichment (EE) have been done in a captive environment, and therefore, only a limited set of the spectrum of all the natural environmental variability could be tested ([Table 1](#)). If one looks at the level of complexity proposed to the individuals in such EE experiments (see [Figure 1](#)), it becomes obvious that the limitation of captivity prevents the study of the full range of environment complexity found in nature. This means we have yet only explored the effects of minimal EE but nonetheless found impressive positive effects on both brain structure development and cognition. Some of the examples I discussed above illustrate the more complex challenges encountered in nature and of the much more complex cognitive challenges encountered by animals.

Therefore, two questions arise: (1) how much larger would the effects of EE be when confronted to the complex environment found in nature? And (2) how much larger would these effects be if the whole ontogeny was spent under such conditions and not only during the short time of an experiment? These essential questions cannot be answered at present, but some facts underline their relevance to our discussion. The effects of EE complexity have been shown in many studies to be additional in the sense that the more complex the environment, or the longer the exposure to it, the larger the positive effects were measured ([Forbes et al., 2020](#)). The second aspect is that the more practice has been made in an environment, the larger the positive effects ([Haenggi et al., 2015](#); [Jaencke et al., 2009](#)). Third, the comparison of individuals in wild-living populations facing different levels of complexity shows clearly that an important effect exists in wild animals depending on the complexity of the challenges they are confronted with ([Clarín et al., 2013](#); [Arechavala-Lopez et al., 2020](#); [Pravosudov and Roth, 2013](#); [Mettke-Hofmann et al., 2002](#); [Yaski et al., 2011](#); See [Table 1](#)).

Thus, I think, the discussion, in addition of being about the ecological validity of the experiment, should concentrate on the experiences lived during the ontogeny and the daily life of the “individuals prior to the experiments”. All the evidence available presently points to a strong detrimental effect of artificial and simple environment, and in my eyes, the unescapable conclusions are that studies of cognition should be performed on individuals within their natural complex environment.

### **Identifying complex cognition in the wild: how statistical improvements made it possible to reveal new dimension of animal cognition?**

When one follows a chimpanzee in the forest as he is searching an anvil to crack some nuts, one will notice that this decision implies constantly to consider and evaluate sometimes varying and conflicting aspects that will determine whether efficient nut cracking will be at all possible. These aspects concern, e.g., the selection of a suitable hammer, depending on the local availability of hard materials, their weight, shape and distance to an anvil, the species of nuts, and their present state of maturation and abundance. Further, the social dimension in terms of the number of competing group members present needs also to be considered. This multitude of factors makes the study of the decision to crack nuts very complex, but at the same time, it is the natural context under which chimpanzees base their daily foraging decisions.

Therefore, controlling for many confounding factors may sound important, but at the same time, it creates an artificial simple context that chimpanzees in the forest never encounter. When I first published in 1984 an analysis of the hammer transport for Panda nuts ([Boesch and Boesch, 1984](#)) and suggested that the cognitive capacities upon which chimpanzee select their hammers equal what has been observed in 9-year-old children, our results were ignored. One reason for this could be that, we used a simple Chi-square test after binning the hammer weight and transport distance in categories. This was at the time the best method was

available, but it could be viewed as too simple and unable to control for the potential confounds mentioned at the beginning of this paragraph.

Reanalyzing the same data with modern statistical methods, including a mixed model, improved the control of many possible confounds, while still confirming the results of the original analysis (Mundry, 2019; Figure 3 p. 33). Recently, Giulia Sirianni analyzed the hammer selection by chimpanzees for Coula nuts (Sirianni et al., 2015) by using a generalized linear mixed model (GLMM) approach. She could include 5 different factors like the weight of the hammer, the hardness and type of the material, the distance to the anvil, the position of the anvil, as well as the chimpanzees' interactions. At the same time, she controlled for the chimpanzee identity, the GPS location in the forest, the hardness of the nut measured by the day in the nut season, the hammer selection episode, and the number of available hammers (see Sirianni et al., 2015 for more explanation of the analysis). Such an elaborate analysis allowed not only to exclude many of the possible confounding factors we knew could have played a role but also to analyze the potential interactions between the many factors that were critical for the chimpanzees. This approach allowed us to identify a complex conditional selection process, whereby the chimpanzee select the weight of the hammer as a function of the distance they need to transport it, the hardness of the hammer, and the location of the anvil (Sirianni et al., 2015): lighter and harder hammers are selected, the longer the distance of transport to the anvil is. Thus, a hammer selection analysis using modern GLMM technique not only confirmed our original result from 1984 but also revealed a much more complex and flexible selection process in chimpanzees. In other words, contrary to what experimental psychologists suggested when studying captive chimpanzees, Tai chimpanzees never think of weight in isolation but always in combination with hardness, shape, and context (see Figure 2).

The statistician Roger Mundry (2019) wrote that *"the statistical modeling techniques available today, with their ability to account for various sources of variation in a response, can help to bridge the gap between randomized experimental studies and correlational studies. In fact, using the appropriate statistical models can be expected to largely remove the biases and distortions of effects, which are common in classic analyses and tests, and bring the validity of observational studies much closer to those of experimental studies"* (p. 41).

Importantly, such a complex statistical analysis allowed to reveal that chimpanzees in the natural environment do not make decisions based on only one or two factors but that their decision process follows an optimization process by which, depending on the present contextual situation, the tool is always selected by including up to 5 different factors related to the tool itself and to the varying context at the time of selection (see Figure 2). Such a level of flexibility and complexity would never have been identified in captive experiments, simply because the captive context has been purposefully simplified to isolate one or two factors assumed to be important for the subjects. In other words, the controlled environment of the laboratory prevents researchers to address the type of complex cognition that animals need to apply to solve tasks in their natural environment.

Similarly, cognitive complexity should be expected in spatial skills, as the dense African rainforest strongly limits visibility on the ground, which represents a distinct challenge for an animal species ranging daily over 10 kilometers (Janmaat et al., 2013a, 2013b; Normand et al., 2009). Yet, in contrast to this, spatial skills in chimpanzees have been studied extensively in the laboratory by proposing an environment drastically less challenging than the wild one, with the aim to understand their ability to conserve length and distance, to rotate objects in landscape or to plan in the future and remember object locations (e.g. Beran et al., 2005; Call, 2003; Newcombe, 2019; Poti, 1996; Poti and Langer, 2001; Premack, 2007; Premack and Premack, 1983). Such experiments generally required from the captive chimpanzees sitting to follow invisible displacements of grapes or sweets hidden under cups that are moved or not or place miniature houses or cars in landscape oriented differently in space, and the scientists tend to agree in finding limitations in chimpanzees both in the vertical and horizontal displacements. This could have been expected, considering that the bare environment experienced by captive chimpanzees for years do not select much for spatial skills when looking for food or a sleeping place (Figure 2).

In nature, the situation is dramatically different, as chimpanzees need to find the ripe fruits they consume within a territory of at least 20 km<sup>2</sup> in which fruiting trees are widely scattered, their production is highly seasonal, the visibility is limited to about 30 meters, and where individuals are regularly alone or in small



**Figure 2. Chimpanzee using hammers in captive experiments (above) and in nature (below)**

Precisely controlled captive experiments tend to simplify to the extreme the context in which chimpanzees use hammers in nature to better control for the one factor under study: The study on the upper left intended to study the notion of weight in chimpanzees (Matsuzawa et al., 2006) and the one upper right studied the hitting movement of chimpanzee (Bril et al., 2009, 2012). In both cases, only one single type of flat hard anvil with round very hard hammers is provided. In nature, animals have to make decisions in a context where many factors differ in space, time, and for each task. The two pictures below illustrate the natural nut-cracking context, where chimpanzees have to select a branch as a hammer among the many found on the forest floor and then transport it to a selected root as an anvil both with varying hardness, orientation, shape, size, and, for the hammer, also weight (Boesch and Boesch, 1981, 1984; Sirianni et al., 2015).

groups when searching for food. The challenge of finding trees full of ripe fruits should not be underestimated, as the likelihood to find a fruiting tree during a walk in straight line has been estimated to be one for every 10 to 21 km walked (Janmaat et al., 2016; Pontzer and Wrangham, 2004). Knowing that a chimpanzee eats fruits daily from about 8 different species of fruits and travels daily a minimum of 2–4 km, the selective pressure to improve spatial skills in the forest is massive. This is further complicated by the fact that fruit production is very seasonal and irregular: trees bear ripe fruits at most for a month, and, within a same species, fruit production can vary extensively among individual trees, across season and years (Janmaat et al., 2016). Thus, in wild chimpanzees, detailed spatial knowledge to select and reach trees from all possible directions needs to be combined with long-term memory, botanical knowledge, and long-term planning of movements (see Normand and Boesch, 2009; Normand et al., 2009; Janmaat et al., 2013a, 2013b, 2014, 2016).

Thanks to the progress of the statistics, we were not only able to explore the complexity of the spatial knowledge, by including a large number of factors into the model (between 4 and 6), but also able to control for the contextual dimension, by including a number of control variables (up to 7) (Ban et al., 2016; Janmaat et al., 2014). It is only with such a complex model that we could identify the level of complexity of the chimpanzees' spatial skill when searching for ripe fruits in such high diversity and low visibility forest. Detecting such level of cognitive complexity is presently out of reach in captive studies and has only

become possible thanks to the important progresses of model complexity in statistics. In a review of the challenge to find fruits through the African tropical forest, the authors concluded *"In short, ecological intelligence involves much more than solely remembering the spatial location of a number of food trees within a large home range. We conjecture that successful foraging depends on a combination of cognitive skills, especially an ability to obtain, store and retrieve knowledge on temporal availability of food in individual trees. Here, we hypothesized on the existence of a suite of cognitive strategies that chimpanzees can employ to maximize food finding efficiency in periods of scarcity by using individual and species-specific information on the predictability of their food in individual trees."* (Janmaat et al., 2016, p. 15).

Sharing food has often been proposed to be a uniquely human trait, as chimpanzees in captivity are, according to different procedures used to test this, not especially active food sharers (Herrmann et al., 2007; Warneken et al., 2007). However, food sharing does not make much sense in a captive setting, where all individuals are provided with large amounts of food on a daily basis. The situation is radically different in nature where food has to be found and extracted, requiring sometimes much effort. Therefore, food sharing has a very different value for the individual and is perceived differently in wild chimpanzees. I studied meat sharing some 25 years ago in the chimpanzees of the Taï forest (Boesch, 1994) and found that hunters obtained more meat than bystanders and this observation supported the notion of cooperation within chimpanzees. At the time, it was not possible to control for potential confounding factors, like the intensity of begging for meat, the identity of the individual, its rank and sex, or group size. Since cooperation and food sharing was not observed in captive chimpanzees, some concluded that I was misled due to insufficient controls in my natural observation (see for example Tomasello, 2009; Tomasello and Call, 1997, 2008). A more recent study of meat sharing in the same chimpanzee population using a GLMM and controlling for multiple confounders (Samuni et al., 2018) confirmed my observations that hunters receive more meat than bystanders but could also show that this observation is a function of the sex of the individuals and the relative rank of the two individuals. Furthermore, they could exclude some alternative hypotheses that were proposed to explain my first observation, like the possibility that chimpanzees would share only as a result of harassment from the beggars or that they would share meat only to gain sexual favors. This confirms the potential in controlling for many alternative hypotheses with these new statistical tools and so uncovers unexpected cognitive skills.

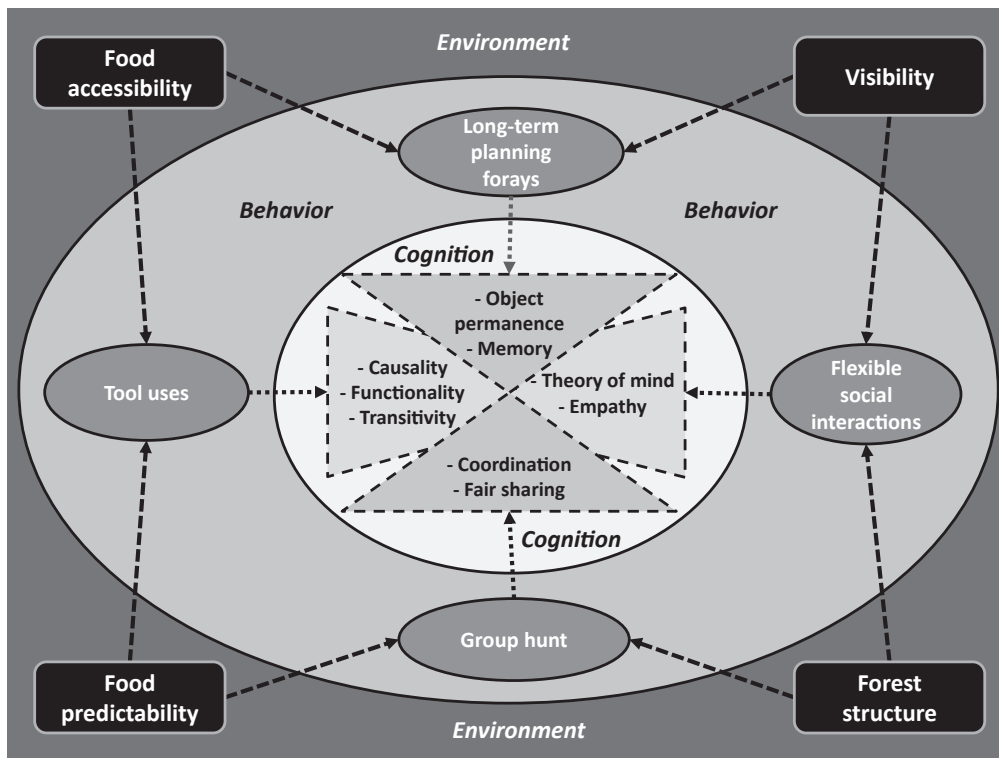
### Cognitive specialization in animals and humans

The notion of "experienced-based cognition" acquired by the individuals as they grow in a social and ecological context would capture much of what has been discovered through the study by neuroscientists about the importance of the environment reviewed above. The main conclusion from Table 1 is that cognition is a more complex notion if one considers that, in humans and animals, we see that different cognitive capacities are developing under different contexts. Like the brain structures that react to the demands the individuals are performing, cognitive capacities develop as they are required. In this sense, the "one cognition" model needs to be modified for a view of cognition as a specialization to react optimally to the challenges of daily life. This would help to reconcile the divergent results that have been accumulating between cognitive studies in captivity and the wild (e.g. Benson-Amram et al., 2013; Boesch, 2012; 2020; Calisi and Bentley, 2009; Gardner and Gardner, 1989; Lambrechts et al., 1999; Marino and Frohoff, 2011; Stevens and Carlson, 2008).

Figure 3 provides a simplified two-dimensional illustration of environmental factors known to affect the behavior of animals and requiring better performance on different cognitive abilities. For the sake of visibility, I limited the graph to the interactions of 2 of 4 factors, while obviously more factors and interactions are often present in nature that will influence the individuals, as seen with my example of hammer selection or finding ripe fruits in chimpanzees (see above). The individual being immersed in the environment will simultaneously be affected by multiple factors. For example, low visibility in natural habitats interacts with food availability so that when both are low, long-term planning when foraging will be required to find wide-spread rare resources (Figure 3), while this would not be necessary for abundant food sources (Normand et al., 2009). At the same time, low visibility in a complex forest will interact with food diversity, which would make flexible social interactions like fission-fusion society, possible when food diversity is high (Aureli et al., 2008; Cunningham and Janson, 2007; Janmaat et al., 2016).

Complex cognition, in which an individual needs to balance multiple factors at a time to make an optimal decision, is required in natural habitats in many situations, as the natural world is a complex one. The





**Figure 3. Schematic representation of some ecological factors selecting for some cognitive abilities**

Taking four factors of the environment as an example (black rectangle in the dark gray environment area), the graphic shows how each one may interact with two other factors to elicit specific behavior patterns (gray circle in the middle behavior gray area) that select for improved specific cognitive abilities (triangles in the white cognition area). Any of these four factors could represent an increasing cognitive challenge, where less visibility, or low food predictability or accessibility is present in the environment, the more cognitive skills will be required as long as the behavior is present in the population.

accuracy of this cognitive specialization has nicely been demonstrated in the human case, the animal species most studied on the planet. For example, within families, the competition between siblings tends to favor the first born who are likely to be stronger than the younger ones. Consequently, a linear increase in the understanding of false belief was observed with the number of older siblings and not with the younger ones (Ruffman et al., 1998). Similarly, many studies showed that young children from low socioeconomic families fare less well in different cognitive skills, like reduced language skills, show less memory, less attention, and mathematical skills than children from richer families (Hackmann and Farah, 2009; Schoentgen et al., 2020). Concurrently, Asian kids follow more contextual arguments when judging about conflict situations while US kids will include more individualistic arguments (Nisbett et al., 2001). Mounting evidence in other animal species is supporting the notion of cognitive difference within a same species among populations facing different ecological challenges (see Table 1).

Following the cognitive specialization model (Figure 3), if we want to understand the more complex cognitive capacities of a species, we need to study individuals from populations that have faced some of the challenging factors that select for them. Therefore, if, for example, we want to understand the natural cognition of memory and action planning in a species, we should study individuals living in an environment where visibility is low, fruit production is seasonal, and fruiting trees are dispersed, large, and rare (see Figure 3 and Normand and Boesch, 2009; Janmaat et al., 2013a, 2013b). Equally revealing would be to study individuals from populations with good visibility but where access to food is challenged like not directly visible food, such as underground resources. Alternatively, if we are interested in complex social cognition, we should study individuals living in large social groups with access to resources constrained by within-group competition (Ruffman et al., 1998). Such biased samples of subjects would allow us to identify the upper limit of the cognitive capacities of a species.

On the other side, if we want to study the cognitive capacities in a species with “minimal ecological challenges”, then we need to continue to study individuals from captive populations living in small social groups with food being daily provided in ample quantities. This biased sample of subjects allows us to understand the cognition capacities developing in individuals subject to limited ecological challenges. If, lastly, we want to study the cognitive capacities developing in subjects that have been subject to “early life traumatic experiences”, as this has been done with humans in orphanages, we should study, for example, captive chimpanzees from wildlife sanctuaries that are victims of the illegal pet and bushmeat trade and had their mothers killed to capture them (Herrmann et al., 2007). In the end, it is the comparison between those different samples that will allow us to obtain an exhaustive knowledge of the cognition achievement and flexibility within a species. This is certainly more demanding than studying a species under only one type of ecology, but hold the promise of providing, for the first time, a complete understanding of cognition of a species. This would be the first step toward a deeper knowledge into the evolution of cognition.

To conclude, an awareness that cognition develops in contact with the outside world would be the first steps toward a more complete understanding of the evolution of cognition, and by comparing the performance of individuals experiencing different ecologies would help us to obtain a more complete knowledge of the cognitive abilities and variation within a species. Only once we have gained such a knowledge within species would comparisons of the cognitive achievement between species be able to help us understand how unique each one is.

### Limitations of the study

This article concentrates on the advantage of natural observations to understand the complex cognitive performance of chimpanzees, without entering in details in the different advantages of captive animal studies. Furthermore, the amplitude of the effects of different aspects of the environment and of experience in life on the development of cognition are still not well understood and a more complete understanding of these effects could affect some of the conclusions of this review. Especially, detailed studies on the connectivity within the brain as a function of different lifestyles and ontogenies within a same species could have profound effects on the understanding of development of cognition.

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The author declares no competing interests.

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