

‘IS MY ANIMAL SMARTER THAN YOURS?’: CONCERNS IN COMPARING ANIMAL INTELLIGENCE

AUGUSTO VITALE · IGOR BRANCHI

SUMMARY: 1. *Introduction*. 2. *First Approaches to Animal Intelligence*. 3. *Can We Define Animal Intelligence?* 4. *Intelligence and Innovation*. 5. *Intelligence and Flexibility*. 6. *Animal Cognition and Intelligence*. 7. *Evolutionary Perspectives*. 8. *The Integrative Model*. 9. *Let’s Contextualise: Tinbergen’s Four Questions*. 10. *Biases in Understanding Animal Intelligence*. 11. *Conclusions*.

1. INTRODUCTION

A CHIMPANZEE is sitting together with other two group-mates on the forest floor of a national park in Gabon. Suddenly, she catches an insect in the air and applies it on her own wounds and on the wounds of her companions sitting close to her.¹ The researchers, at the moment of this writing, are still wondering whether those insects had any curative properties (chimpanzees are known to use medical herbs to get rid of intestinal parasites):² if this is so, it would open new prospects on the evolution of cognitive and prosocial behaviour in non-human primates (from now on ‘primates’). However, what is of interest here is whether we can consider this behaviour observed in chimpanzees an example of non-human animal intelligence (from now on ‘animal intelligence’).

In 1986 Emil Menzel underlined a difficulty researchers meet when dealing with the concept of animal intelligence, when he wrote: “We can never know with dead certainty whether or not any given animal is really intelligent, let alone precisely how intelligent is”.³ He was telling us that what we

augusto.vitale@iss.it, Istituto Superiore di Sanità, Center for Behavioural Sciences and Mental Health, Viale Regina Elena 299, 00161 Roma, Italia.

igor.branchi@iss.it, Istituto Superiore di Sanità, Center for Behavioural Sciences and Mental Health, Viale Regina Elena 299, 00161 Roma, Italia.

¹ A. MASCARO, L. M. SOUTHERN, T. DESCHNER, S. PIKA, *Application of Insects to Wounds of Self and Others by Chimpanzees in the Wild*, «Current Biology», 32/3 (2022), pp. R112-R113.

² M. A. HUFFMAN, *Animal Self-Medication and Ethno-Medicine: Exploration and Exploitation of the Medicinal Properties of Plants*, «Proceedings of the Nutrition Society», 62/2 (2003), pp. 371-381.

³ E. W. MENZEL, *How Can You Tell if an Animal is Intelligent?*, in R. J. SCHUSTERMAN, J.

are lacking are tools to really understand what animal intelligence is about. But perhaps we have to step back even further: can we actually talk about animal intelligence at all? Does it make any sense? Is it really interesting? In what terms?

The topic of the present collection of articles is about creativity. As a matter of fact, we will try to show that different scholars in animal behaviour have made a link between intelligence, creativity, and innovation, so we feel at home here. Later on we will actually show a cognitive and behavioural process that link creativity with innovation, with cognitive and behavioural flexibility on the background.

However, we also have to underline some conceptual issues at stake. A first thing to point out is that we feel uncomfortable, both theoretically and methodologically, when speaking of, to compare, confront (or oppose?) animal intelligence to / with / against human intelligence. In evolutionary terms, human and animal are two terms which cannot be intended as distinct entities, at least in biological terms: we are all animals, sharing common ancestors, as Darwin explained to us in a way that still remains the most convincing scientific theory on the subject. Darwin presented also very strong arguments in favour of the graduality of characters among different species, and this goes from anatomical to physiological and behavioural characters as well. So, talking about animal intelligence versus human intelligence suggests a sort of qualitative point of view, which does not seat comfortably with a Darwinian framework. It is probably more appropriate to ask what elements we attribute to being intelligent are shared or not among different species, including humans, in a more horizontal perspective, rather than a vertical one. This effort has to be made taking into account the natural history and the ecological context of different species, as we will see later on. It can also be pointed out that different species may have developed different kinds of intelligence, in relation to the particular demands of the environment they live in and their cognitive complexity.⁴ The question remains whether we can really free ourselves from identifying those elements from a human point of view. When we talk about other animals, is it possible to talk about intelligence without using inevitably human parameters, with the great risk of jumping into conclusions that would not make much sense to a bird or an elephant? As a matter of fact, the comparison between animal and human intelligence has been very perva-

A. THOMAS, F. G. WOOD (eds.), *Dolphin Cognition and Behavior: A Comparative Approach*, Psychology Press, London 1986, pp. 167-181. As a matter of fact, such argument would also hold for human intelligence, where intelligence tests are rarely considered informative and reliable.

⁴ Z. A. ZORINA, *Animal Intelligence: Laboratory Experiments and Observations in Nature*, «Entomological Review», 85/1 (2005), pp. S42-S54.

sive in the study of intelligence, and probably still is also in the present contribution (despite the good intention of who is writing here...)!

Is it really worth to engage in this discussion? Despite our doubts, we think that it is definitively worth talking about animal intelligence. In this contribution we will illustrate inspiring theories dealing with the evolution of animal intelligence, and the relationship between intelligence and cognition, flexibility, innovation and so on. And then we will point out to some theoretical and interpretative difficulties. We will refrain from engaging in a discussion on concepts like mind, sentience, consciousness. These are, obviously, tremendously interesting topics and have to do with the discussion on intelligence in animal species. Unfortunately, we do not have neither the space nor the competence to discuss such issues. Our background is on the relationship between evolution, ecology and behaviour: these are the terms of reference we have chosen to discuss the question of animal intelligence. A focus on consciousness would also lead us on the need to enrich our discussion covering some philosophical aspects, which is beyond our expertise. So, although we are aware of the conceptual necessity of linking the issue of animal intelligence with the notion of consciousness and/or sentience, we feel more comfortable remaining within our field of expertise.

2. FIRST APPROACHES TO ANIMAL INTELLIGENCE

As nearly always the case, the argument starts with Charles Darwin. He made reference to animal intelligence in terms of continuity between humans and the other species. In his book *The Descent of Man, and Selection in Relation to Sex*,⁵ he acknowledges that the difference between the mind of "the lowest man and that of the highest animal" is immense, however, he also emphasises that such immense difference is "one of degree and not of kind". Furthermore, Darwin himself and his supporters declared, later in the 19th century, that animals have intelligence comparable to humans. One of those supporters was George Romanes (an evolutionary biologist), who is considered one of the founders of comparative psychology, looking for similarity in the cognitive processes by humans and other animal species. Romanes attributed emotion, morality and learning in non-human animals in his book *Animal Intelligence*, an assertion that sounds very familiar to us today, but not so in Romanes' times. He specifically claimed that animals could form abstract ideas, learning from their own sensory experiences, and that they experience "all the human emotions except those which refer to religion and to the sublime". He dedicated three books to the subject of animal intelligence. The first one,

⁵ C. DARWIN, *The Descent of Man, and Selection in Relation to Sex*, Murray, London 1871.

Animal Intelligence,⁶ the most successful one, presented a large number of observations, aimed at showing indications of intelligence in different animal activities (perhaps exceeding on the anecdotal side...), inferring mental states from the behaviours observed. The other two books⁷ explored the more theoretical aspects of the author's intent. One crucial aspect of Romanes' idea was the development of mental abilities in a phylogenetic perspective, allowing then for continuous evolution of such abilities, culminating in human intelligence.

Romanes' approach was later criticised for its excessive anthropomorphism by younger colleagues. For example, Lloyd Morgan did not appreciate the behavioural descriptions contained in *Animal Intelligence*, advocating for a more rigorous and experimental approach, in particular concerning the issue of consciousness. Despite these criticisms, Romanes is nowadays considered among the most important pioneers of comparative psychology.

Another fundamental name in the history of the study of animal intelligence is Edward Thorndike. He was raised as a psychologist at the end of the 19th century, when two main positions held court in the debate on animal behaviour. The first one was Romanes', as already mentioned, documenting examples of high-reasoning in different species of animals, with a rather anecdotal flavour. At the opposite point there was Jacques Loeb, who intended animal behaviour just as examples of tropisms or involuntary movements. Thorndike's volume *Animal Intelligence: An Experimental Study of the Associative Processes in Animals*,⁸ refuses both interpretations (mainly Romanes'), in favour of a laboratory approach, in the framework of experimental psychology. As a result, he interpreted animal behaviour as a combination of instincts and associative learning, judging unnecessary the call for a sort of reasoning in animal species beyond humans: neither abstract nor conceptual thinking were to be found in non-human species. The experiments he conducted were basically problem-solving situations proposed to cats, dogs and chicks. With his experimental approach, and his insistence on objectivity, Thorndike paved the way to the following work of the behaviourists Skinner and Watson. John Watson first, and then Burrhus Skinner, expanded Thorndike's efforts and focused on the experimental analysis of behaviour, carrying out a series of experiments documenting learning process in different animal species, founding the seminal "Journal of the Experimental Analysis of Behavior".

⁶ G. ROMANES, *Animal Intelligence*, Appleton, London 1883.

⁷ G. ROMANES, *Mental Evolution in Animals*, Trubner & Co, London 1883; ID., *Mental Evolution in Man*, Paul, Trench 1888.

⁸ E. L. THORNDIKE, *Animal Intelligence: An Experimental Study of the Associative Processes in Animals*, «The Psychological Review: Monograph Supplements», 2/4 (1898), pp. 1-109.

All of these authors dedicated much effort and time in comparing non-human animal behaviour with the behaviour of humans. The experimental research on learning processes was used to delineate similarities and differences in the supposed mental abilities of different animal species, to better identify what makes us able to adopt higher reasoning process, and to escape from anecdotes and anthropomorphism, which characterised Romanes' efforts.

It is worth to point out here that, compared with the aseptic and controlled environment of the laboratory proposed by the American psychologist, in Europe ethologists advocated for the study of animal behaviour in a natural environment: animals learn in nature and usually together with conspecifics, not within the walls of a laboratory.⁹ Needless to say the fathers of modern ethology, Konrad Lorentz and Nikolas Tinbergen, called for a stronger attention to the behaviour of animals in their natural environment (the need to look at the ecological context when talking about the evolution of animal intelligence will be referred to several times in this paper).¹⁰

In summary, in the early days of the study of animal intelligence the contraposition between instincts and learned behaviour (now considered unrealistic and obsolete), and the comparison between simple associative way to learn and more sophisticatedly reasoned way to learn was used to draw a line between humans and other animals. That line is rather blurred, and those contrapositions hide a more complex and stimulating reality: any discourse on the ways in which animals acquire information and use that information to relate in an appropriate way with the environment, must imply a wide perspective, including evolutionary and ecological points of view.

Another important issue has to do with the use of the term intelligence when dealing with non-human animals. Over time, the term intelligence has become increasingly difficult for ethologists to stand on its own. In this context, it is not very fruitful to compare different species on their level of intelligence. What is more interesting is to analyse particular contexts in which natural selection could have had an influence on the evolution of particular cognitive abilities. Therefore, topics like 'cultural intelligence hypothesis',¹¹

⁹ R. W. BURKHARDT, *Patterns of Behavior: Konrad Lorenz, Niko Tinbergen, and the Founding of Ethology*, University of Chicago Press, Chicago 2005.

¹⁰ We did not include here a discussion on language studies in great apes, which were crucial to add knowledge on the cognitive abilities of these species. We prefer to focus our discussion trying to avoid areas of research which would use human intelligence as a term of reference. But to know more about these studies please see, for example, S. SAVAGE-RAMBAUGH, S. G. SHANKER, T. J. TAYLOR, *Apes, Language, and the Human Mind*, Oxford University Press, Oxford 1998.

¹¹ C. P. VAN SCHAIK, J. M. BURKART, *Social Learning and Evolution: The Cultural Intelligence Hypothesis*, «Philosophical Transactions of the Royal Society B: Biological Sciences», 366/1567 (2007), pp. 1008-1016.

or 'social intelligence hypothesis'¹² become particularly interesting and worth investigating. Then, in those theoretical frameworks, the term intelligence now becomes more meaningful from both an etho-ecological and evolutionary point of view.

3. CAN WE DEFINE ANIMAL INTELLIGENCE?

We have avoided it so far, but it is time for us to propose some tentative and operational definition of animal intelligence. One interesting definition comes from Alan Kamil, where he defines intelligence as those processes by which animals obtain and retain information about their environments and use that information to make behavioural decisions.¹³ Another definition we want to propose comes from the primatologist Richard Byrne in his book *The Thinking Ape: Evolutionary Origins of Intelligence*,¹⁴ where he claims that intelligence is the ability to respond in a flexible way to novel situations, being able to deal with complexity (both in the physical and social domain, as we will see later) and to innovate (see the chimpanzees in the introduction of this contribution). Further on, this author also offers the stimulating interpretation of intelligence in terms of grasping the essentials of a situation and responding appropriately. These definitions embrace any kind of animal, human and non-human, and also diminish the relevance of comparing different species in search of the most or the less intelligent ones. This is so because each species has its own way to respond to environmental challenges, and this argument makes it also problematic to identify less intelligent species: as a matter of fact, it all depends on the ecological context, and on what the latter requires from that particular species (see below). In this perspective, the notion of 'less intelligent' species in a comparative perspective loses its relevance. In the 1980s Euan Macphail argued that no real differences, both in qualitative and quantitative terms, exist among different species.¹⁵ Though this statement cannot be applied in absolute terms as brain complexity does vary across species, the correlation of brain features with degrees of intelligence yields large inconsistencies especially when broad phylogenetic comparisons are considered.¹⁶

¹² R. M. SEYFARTH, D. L. CHENEY, *Social Cognition*, «Animal Behaviour», 103 (2015), pp. 191-202.

¹³ A. C. KAMIL, *A Synthetic Approach to the Study of Animal Intelligence*, «Papers in Behavior and Biological Sciences», 14 (1987), pp. 1-53.

¹⁴ R. BYRNE, *The Thinking Ape: Evolutionary Origins of Intelligence*, Oxford University Press, Oxford 1995.

¹⁵ E. M. MACPHAIL, *The Comparative Psychology of Intelligence*, «Behavioral and Brain Sciences», 10/4 (1987), pp. 645-656.

¹⁶ J. B. SMAERS, R. S. ROTHMAN, D. R. HUDSON, A. M. BALANOFF, B. BEATTY, D. K. DECHMANN, K. SAFI, *The Evolution of Mammalian Brain Size*, «Science Advances», 7/18 (2021), eabe2101. U. DICKE, G. ROTH, *Neuronal Factors Determining High Intelligence*, «Philo-

All kind of behaviours that could be labelled as intelligent, were in reality variations of associative learning processes, depending of purely contextual factors, rather than real differences in cognition (he was referring to vertebrate animals' intelligence). This point of view belongs to the tradition of comparative psychology, characterised by precise laboratory experiments, aimed at detailing learning processes in different species, such as associative learning or operant conditioning. These are ways of knowing about the world which are very general, very successful in evolutionary terms, and common to many different animal species. This is a common background. It is a sort of 'minimal standard' for different species, selected by natural selection, to get along with the requests of the environment. On this common background, due to the natural history of different species and the way this influences the response to environmental challenges, the result is different cognitive strategies to deal in an 'intelligent way' with the physical and social world.

Macphail was also arguing for a difference between humans and the other animals, ascribing just to our species something that could be labelled as intelligence. As it should be clear now, we are not particularly interested in a contraposition between humans and non-humans in this sense (although we refer to it in methodological sense...).

If we were suggesting here a link between intelligence and adaptation, talking about a species more adapted than another to the environment because it uses its intelligence to respond appropriately to environmental challenges, we will fall in the same conceptual trap. Then, it would be more appropriate to use the term adaptation at the level of the individual, rather than the group or species.

Therefore if we encounter difficulties in comparing different species, can we compare intelligence among different individuals in a population of a particular species? Some authors suggest that intelligence would vary in its behavioural manifestations from individual to individual, but within species-specific features. Such specific features would be more hard-wired than individual differences, then with a stronger genetical connotation, heavily linked with the evolutionary history of that particular species. A classical case in this respect would be potato-washing, observed in the late 1950s by Japanese primatologists in a troop of Japanese macaques (*Macaca fuscata*) in the island of Koshima.¹⁷ These animals were provisioned with sweet potatoes on the beach near the sea, so that the researchers could habituate the animals to their presence, and observe at a close range the social dynamics among the members of the group. One day, a young female called Imo collected few sweet

sophical Transactions of the Royal Society of London Series B: Biological Sciences», 371 (2016), p. 20150180.

¹⁷ M. KAWAI, *Newly-Acquired Pre-Cultural Behavior of the Natural Troop of Japanese Monkeys on Koshima Islet*, «Primates», 6/1 (1965), pp. 1-30.

potatoes and ran toward the sea. The potatoes were most probably covered in sand. Is it possible that some potatoes accidentally were dropped in the sea, but when Imo picked them up to eat them, she surely appreciated the clean potatoes as well as, perhaps, the new salty taste? From that day on, Imo purposely washed the sweet potatoes in the sea water before eating them, brushing away the sand with one hand, while dipping the potato in the water with the other. This new behaviour was soon acquired by other 11 members of Imo's group. This is a novel behaviour, shown in the contest of the feeding repertoire, leading probably to a better exploitation of a food resource. Can we consider this behaviour a particularly intelligent one? Was Imo more intelligent than the other macaques in her group? To add to this, subsequently the same monkey Imo found a way better to consume the rice throw in the sand by the researchers: she would just pick up sands and rice together, throw it into a puddle of water, so that the rice would remain on the surface, whereas to sand would drop to the bottom of the puddle. Imo was a very innovative individual, more than the other group-mates. Does more innovative means more intelligent? Does innovative behaviour really require sophisticated cognitive processes, like the high-reasoning abilities advocated by Romanes? By the way, Imo has been defined 'The Monkey Genius'.

4. INTELLIGENCE AND INNOVATION

Innovation is a behavioural characteristic present in all of the human populations, and it has been proved again and again to lead to successful answers to environmental challenges. Innovation is linked with behavioural flexibility, in the sense that an individual cannot innovate without making a choice among different possible solutions to an environmental challenge. The behavioural response has then to be 'flexible' to adapt to possible variations of such challenge. Otherwise, flexibility of the behavioural response can also help an individual to find new solutions to old problems.¹⁸ But innovation is also significantly present in animals with important consequences for the ecology and evolution of those animals especially, for example, when related to the evolution of animal culture. In this latter case, the study of innovation, and how it spreads within a population, is closely linked with the study of social learning in its different aspects. Innovation can be considered a behavioural result of a creative process. This process can start with the recognition of potential novelty (a potential tool, a social ally...), through seeking behaviour, then possibly individual or social learning (observational learning) and, in the end, finalising in an innovative solution to an ecological or social problem.

¹⁸ A. S. GRIFFIN, D. GUEZ, *Innovation and Problem Solving: A Review of Common Mechanisms*, «Behavioural Processes», 109 (2014), pp. 121-134.

Different authors have linked the concept of intelligence to novelty, to be creative and innovative. For example, again Richard Byrne characterises intelligence with a series of abilities, which show the procedural link from creativity to innovation, through novelty seeking and observational learning: i) to gain knowledge while interacting with the physical and social environment; ii) to organise such knowledge, resulting in behaviours which are effective in that particular physical and social environment; iii) to be able to deal with challenges proposed by such environments and, in doing so, create novel behaviours, after re-organising the knowledge acquired. This is exactly what Imo did, and so she would be characterised as an intelligent individual. However, when we look at the performance of different individuals in a population, we must also consider that differences in performance do not necessarily mirror differences in innovative abilities. There are many factors, social and generally environmental, that can influence the manifestation of innovative behaviour by a particular individual. For example, in primate societies the simple access to a location or features of the environment promoting innovation could be influenced by social rank.¹⁹ Therefore, innovation shown by an individual should not be seen automatically as proof of particular cognitive abilities, as well as its absence as a sign of less prompt 'smartness'.

It has been noticed that, generally speaking, episodes of innovative behaviours appear to be more frequent in large-brained animals, favouring these animals to exploit environmental challenges better,²⁰ and several authors have reported that species differences in innovative ways to cope with environmental changes are strongly correlated with relative size of brain structures generally associated with intelligence.²¹ There are series of issues with this line of argument. We have already mentioned our difficulty in comparing different species when it comes to measure intelligence. Furthermore, an operational and shared definition of intelligence is still lacking, and the tests to measure cognitive abilities (as a proxy of intelligence) in this and other theoretical contexts are carried out on captive individuals in laboratories. These tests can still lack ecological validity, and then can be not really significant in relation to the natural history of a particular species. Therefore, also when it comes to innovation and intelligence, we must seek a collaboration between laboratory

¹⁹ S. COUSSI-KORBEL, D. M. FRAGASZY, *On the Relation between Social Dynamics and Social Learning*, «Animal Behaviour», 50/6 (1995), pp. 1441-1453.

²⁰ A. C. WILSON, *The Molecular Basis of Evolution*, «Scientific American», 253/4 (1985), pp. 164-175.

²¹ D. SOL, L. LEFEBVRE, J. DOMINGO RODRÍGUEZ-TEIJEIRO, *Brain Size, Innovative Propensity and Migratory Behaviour in Temperate Palaearctic Birds*, «Proceedings of the Royal Society B: Biological Sciences», 272/1571 (2005), pp. 1433-1441. S. BENSON-AMRAM, B. DANTZER, G. STRICKER, K. E. HOLEKAMP, *Brain Size Predicts Problem-Solving Ability in Mammalian Carnivores*, «Proceedings of the National Academy of Sciences», 113/9 (2016), pp. 2532-2537.

and field data. Cognitive abilities related to innovation and, possibly, as an indication of relative individual intelligence, must consider all different factors, internal and external, which accompany the manifestation of that particular innovative behaviour.

5. INTELLIGENCE AND FLEXIBILITY

Another interesting link is the one which connects the concept of intelligence with flexibility, where cognition is not typically defined in terms of behaviour, but it is often equated with the proximate mechanisms that produce flexible behaviour. To have flexibility means to choose the most appropriate behaviour for a particular circumstance. Then, a particular solution could represent an innovation to incorporate in the ethogram of that individual. There is consensus among scholars in comparative cognition that flexible behaviour is underlined by cognitive processes, and the more flexible the behaviour is, the more complex are the underlying cognitive processes. It also means, as we will see, that the behaviour is relatively hard-wired, from a genotype point of view (see next paragraph for a discussion on animal cognition). Some authors would even affirm that behavioural flexibility is the only significant parameter to measure higher cognitive abilities.²²

But what is flexibility? A behaviour can be considered flexible when it is modifiable by experience, during the life of an individual. Some authors consider behavioural flexibility as type of behavioural plasticity which, in turn, is a form of phenotypic plasticity.²³ If we are talking about behavioural flexibility, every behaviour has a certain degree of plasticity. We now know that even behaviours traditionally considered as 'fixed', can vary in relation to environmental change (like, e.g., the foraging behaviour of some species of ants).²⁴ In general, behavioural flexibility can arise when an individual is in the position to detect and process a series of environmental signals, and these signals vary in time and space. Lea and colleagues identify behavioural flexibility as a quality that frees the individual from hard-wired responses to environmental changes. This would allow for a more efficient adaptation to the environment for that particular individual.²⁵

²² I. MIKHALEVICH, R. POWELL, C. LOGAN, *Is Behavioural Flexibility Evidence of Cognitive Complexity? How Evolution Can Inform Comparative Cognition*, «Interface focus», 7/3 (2017), ID 20160121.

²³ P. GODFREY-SMITH, *Complexity and the Function of Mind in Nature*, Cambridge University Press, Cambridge 1996.

²⁴ X. ARNAN, A. LÁZARO-GONZÁLEZ, N. BELTRAN, R. ANSELM, P. RODRIGO, *Short-Term Ecological and Behavioural Responses of Mediterranean Ant Species *Aphaenogaster Gibbosa* (Latr. 1798) to Wildfire*, «Insect Conservation and Diversity», 6/5 (2013), pp. 627-638.

²⁵ S. E. G. LEA, P. CHOW, L. A. LEAVER, I. P. L. McLAREN, *Behavioral Flexibility: A Review, a Model, and Some Exploratory Tests*, «Learning & Behavior», 48/1 (2020), pp. 173-187.

Flexibility can be related to solving problems, and/or finding general rules which help to solve new problems. If this is the case behavioural flexibility becomes an essential part of the creative process, in which the individual is able to choose a novel action to solve a problem, in relation to the characteristics of the problem itself. In this sense, the novel behavioural answer observed does not rely on instinctual or rather phylogenetically restrained behavioural patterns, but more on the cognitive plasticity of the behavioural trait.

6. ANIMAL COGNITION AND INTELLIGENCE

Animal cognition, in a very simplified definition, studies the mental capacities of animals. For example, animal cognition questions would ask how animals perceive the world around them, how do they learn about it, how they categorise it. For Sarah Shettleworth cognition implies all ways animals collect information through the senses, process it and act on it.²⁶ There could be some overlapping between the two terms cognition and intelligence. If we adopt Shettleworth's idea, intelligence could be involved in the actions taken on the world, after having perceived what is about. So, one could say, a behaviour dedicated to gaining information could belong to the realm of animal cognition, whereas a behaviour which reflects a reaction or a way to intervene on that information about the world could be closer to the concept of animal intelligence.

In this respect we could perhaps talk, more meaningfully, about cognitive adaptations that could be more or less complex, depending on the quantity of information an individual has to deal with. Rosati²⁷ has recently offered a convincing interpretation of the link between cognition and intelligence. She identifies cognition as a collection of mental processes which helps to collect and store information. On the basis of this, where intelligence stands? In cognition there can be both domain-specific systems (operating in an independent fashion) as well as domain-general processes (which, for example, update responses in novel situations).²⁸ Rosati argues that animals show intelligent behaviour, both in the domain-specific system (robust space cognition, for example) and in the general domain (for example, showing behavioural

²⁶ S. J. SHETTLEWORTH, *Animal Cognition and Animal Behaviour*, «Animal Behaviour», 61/2 (2001), pp. 277-286.

²⁷ A. G. ROSATI, *Foraging Cognition: Reviving the Ecological Intelligence Hypothesis*, «Trends in Cognitive Sciences», 21/9 (2017), pp. 691-702.

²⁸ S. J. SHETTLEWORTH, *Modularity, Comparative Cognition and Human Uniqueness*, «Philosophical Transactions of the Royal Society B: Biological Sciences», 367/1603 (2012), pp. 2794-2802. D. C. PENN, K. J. HOLYOAK, D. J. POVINELLI, *Darwin's Mistake: Explaining the Discontinuity between Human and Nonhuman Minds*, «Behavioral and Brain Sciences», 31/2 (2008), pp. 109-130.

flexibility). Therefore, the evolution of cognitive abilities could be interpreted as the background to understand how animals have arrived at finding flexible and innovative solutions to environmental challenges, and this has a link to one of the definitions of intelligence mentioned above.²⁹

The study of primates has been and still can be particularly informative, as a general model, although we run the risk of falling into the trap of searching a model of intelligence to be more easily compared with humans. We are aware of this, but it is also true that the literature in this sense is particularly stimulating.³⁰

We also like to point out that interesting new findings about animal intelligence have been produced when the phylogenetic perspective was abandoned in favour of a more ecologically contextual point of view. To focus on primates to find examples of intelligent behaviour that would resemble human intelligence generally misled this kind of research. When the attention shifted to what could be expected by a particular species in relation to its ecology, rather than just phylogenetic closeness then, for example, the impressive caching behaviour of scrub jays (*Aphelocoma californica*) was described.³¹ And this would also help to avoid a pyramidal view on the evolution of cognitive abilities in animals.

7. EVOLUTIONARY PERSPECTIVES

When it comes to an evolutive perspective, two major theories have been proposed. The ecological intelligence hypothesis suggests that ecological features drove the development of cognitive capacities, such as looking for food in a complex environment. The social intelligence hypothesis proposes that the complexity of social life, and the need to solve social challenges, has heavily influenced the evolution of cognition. As we will see, these two factors are not necessarily mutually exclusive, although authors have been focusing on one or the other.

7. 1. *The Ecological Drive*

The knowledge of the world around, the connection between objects, space, direction, is essential for any animal, in order to function appropriately. However, a major specific problem all animals share is to find food. If we again

²⁹ I. MIKHALEVICH, R. POWELL, C. LOGAN, *Is Behavioural Flexibility Evidence of Cognitive Complexity?*, cit.

³⁰ See, for example, A. SEED, M. TOMASELLO, *Primate Cognition*, «Topics in Cognitive Science», 2/3 (2010), pp. 407-419.

³¹ N. S. CLAYTON, J. M. DALLY, N. J. EMERY, *Social Cognition by Food-Caching Corvids. The Western Scrub-Jay as a Natural Psychologist*, «Philosophical Transactions of the Royal Society B: Biological Sciences», 362/1480 (2007), pp. 507-522.

consider primates, most of them forage in a complex world, and also spend a big portion of their time looking for, processing and consuming food. In this scenario is easy to hypothesise that cognitive abilities have evolved especially in the context of foraging behaviour.

For example, if we consider the development of spatial memory as a parameter related to cognition, we can observe species differences related to the diet, and to how the food resources are distributed in the natural habitat of those species. Observations in captivity have revealed differences in the response to tests aimed at measuring spatial memory (tests such as radial arm maze and delayed matching-to-sample) between two species of New World primates: golden lion tamarins (*Leontopithecus rosalia*) showed better spatial memory than the Wied's marmosets (*Callithrix kuhli*). Researchers believe that the difference is due to differences in diet, and related style of foraging: marmosets rely mainly on feeding gum, a resource which is very locally distributed in defined small areas, whereas tamarins feed mainly on insects and patchily distributed fruits over larger areas.³² Another interesting example in this sense comes from a comparison between different species of corvids, where different corvids perform equally well in colour-based tasks, but caching species are much better at spatial tasks than non-caching ones.³³ Caching corvids have been attributed with episodic-like memory, future planning and mental attribution on conspecifics.³⁴

Ecology seems then to play an important role in shaping cognitive abilities, and there is the possibility than even more example will be available when other species will be investigated in this perspective.

7. 2. The Social Drive

The second important hypothesis deals with the complexity of social life. The prediction here is that socially complex environments require a very good memory and sophisticated general cognitive abilities, therefore social complexity drives the evolution of cognitive skills and intelligence. The majority of data in this case comes again from the primatological literature. In these animals the web of social interactions, the presence of dominance hierarchies,

³² M. L. PLATT, E. M. BRANNON, T. L. BRIESTE, J. A FRENCH, *Differences in Feeding Ecology Predict Differences in Performance between Golden Lion Tamarins (Leontopithecus Rosalia) and Wied's Marmosets (Callithrix Kuhli) on Spatial and Visual Memory Tasks*, «Animal Learning & Behavior», 24/4 (1996), pp. 384-393.

³³ D. J. OLSON, A. C. X. KAMIL, R. P. BALDA, P. J. NIMS, *Performance of Four-Seed Caching Corvid Species in Operant Tests of Nonspatial and Spatial Memory*, «Journal of Comparative Psychology», 109/2 (1995), pp. 173-181.

³⁴ U. GRODZINSKI, N. S. CLAYTON, *Problems Faced by Food-Caching Corvids and the Evolution of Cognitive Solutions*, «Philosophical Transactions of the Royal Society B: Biological Sciences», 365/1542 (2010), pp. 977-987.

the need to solve social challenges related to the acquisition of important resources (such as the availability of females willing to breed) is thought to have led to the evolution of sophisticated cognitive abilities. For example, what is needed here is the recognition of group members' identity and their social position, as well as a memory of past interactions and the ability to forecast the outcome of potential further interactions.

Already in the 1970s, authors such as Nicholas Humphrey postulated that particularly intelligent individuals would find a way to maximise their personal fitness, while taking advantage of the benefits of group living.³⁵ This kind of intelligence must be social and in nature, argues Humphrey, the real challenges come from social life for a primate, rather than from other environmental features. Laboratory tests, he continues, cannot explore such cognitive dimension (remind that those were the 1970s...), because they inquire in some spatial and memory abilities which mainly refer to feeding behaviour.

In line with Humphrey's argument, a particularly interesting theory is the evolution of Machiavellian intelligence in primates.³⁶ Machiavellian intelligence can be described as a series of behaviours shown within a context of political engagement among the members of a social group. The first example of this kind was described by Frans de Waal in his book *Chimpanzee Politics*, where he referred to the work of Machiavelli when described social tactics observed in a group of captive chimpanzees at the Arnhem Zoo in The Netherlands.³⁷ The underlying assumption of this hypothesis is that social competition drove the evolution of sophisticated cognitive abilities in primates (including *Homo sapiens*), to take a better advantage of group-mate behaviours. Later in 1990s, Richard Byrne and Andrew Whiten published an impressive collection of social interactions among non-human primates, including misleading, breaking rules, making and breaking social alliances, cheating, (based also on anecdotal evidence...) in which they expanded the role of Machiavellian intelligence in the social organisation of these animals.³⁸ In the following years attention has been focused on the concept of tactical deception, where an individual uses a signal in a misleading fashion, in order to take advantage of a potential competitor. Although in captivity examples of tactical deception across taxa can be found, in the wild anecdotal reports are still the major sources of examples. In the first case, an example comes

³⁵ N. K. HUMPHREY, *The Social Function of Intellect*, in P. G. BATESON, R. A. HINDE (eds.), *Growing Points in Ethology*, Cambridge University Press, Cambridge 1976, pp. 303-317.

³⁶ A. WHITEN, R. W. BYRNE, *Machiavellian Intelligence II: Extensions and Evaluations*, Cambridge University Press, Cambridge 1997. R. W. BYRNE, *Machiavellian Intelligence Retrospective*, «Journal of Comparative Psychology», 132/4 (2018), pp. 432-436.

³⁷ F. DE WAAL, *Chimpanzee Politics: Power and Sex Among Apes*, JHU Press, Baltimore 2007.

³⁸ A. WHITEN, R. W. BYRNE, *Machiavellian Intelligence II*, cit.

from ravens (*Corvus corax*), where catchers would hide food behind barriers to prevent potential observers to raid for food. Furthermore, in presence of others, catchers would interrupt catching and/or change location where to deposit food.³⁹ On the other hand, in the wild, tactical deception has been described in troops of gelada baboons (*Theropithecus gelada*), where subordinate males and females would suppress copulatory vocalisations, while checking the position of the dominant male.⁴⁰ Whatever we think of the Machiavelian intelligence hypothesis, a significant amount of data has been gathered, which speaks clearly about the ability of monkeys to know each other's social lives. Robert Seyfarth and Dorothy Cheney collected a series of evidence on the ability by baboons in discriminating who's who, and what social group different individuals belong to, just by observing the reaction of focal individuals to the recording of vocalisations by other group-mates engaged in social interactions.⁴¹

There is no doubt that social complexity has been a major evolutionary pressure in developing particular cognitive abilities and intelligence. As a matter of fact, and not only: relative neocortex size is positively correlated with group size in a series of different species, such as primates, bats, carnivores and cetaceans.⁴² A bigger group size suggests the need to negotiate complex social interactions.

8. THE INTEGRATIVE MODEL

Are these two hypotheses, the foraging one and the social one, to be considered separately, if not even one opposed to the other? Several authors now suggest that this can really be not the case.

Different authors, as we have seen, regard social complexity as major force to drive the evolution of intelligence in primates. But we have also indicated that the evolution of intelligence has been linked with the extractive foraging behaviours and space mapping in a complex environment, identifying ecological factors as significant drives in its evolution.⁴³ It has happened that

³⁹ T. BUGNYAR, K. KOTRSCHAL, *Observational Learning and the Raiding of Food Caches in Ravens, Corvus Corax: Is It 'Tactical' Deception?*, «Animal Behaviour», 64/2 (2002), pp. 185-195.

⁴⁰ A. LE ROUX, N. SNYDER-MACKLER, E. K. ROBERTS, J. C. BEEHNER, T. J. BERGMAN, *Evidence for Tactical Concealment in a Wild Primate*, «Nature communications», 4/1 (2013), pp. 1-6.

⁴¹ R. M. SEYFARTH, D. L. CHENEY, P. MARLER, *Monkey Responses to Three Different Alarm Calls: Evidence of Predator Classification and Semantic Communication*, «Science», 210/4471 (1980), pp. 801-803.

⁴² R. I. M. DUNBAR, *Neocortex Size as a Constraint on Group Size in Primates*, «Journal of Human Evolution», 22/6 (1992), pp. 469-493.

⁴³ B. J. KING, *Extractive Foraging and the Evolution of Primate Intelligence*, «Human Evolution», 1/4 (1986), pp. 361-372.

this second hypothesis has been dismissed in favour of the more popular social one.⁴⁴

Are these two families of hypotheses mutually exclusive? For example, some authors have proposed an integrative model for the interpretation of the evolution of cognition, which takes into account both the ecological and the social drives.⁴⁵ They propose that, in relation to innovation, individuals able to find new solution to ecological challenges could be also able to socially exploit the discoveries of others. These individuals could have been selected over other group-mates, generating then a selective advantage to those brain regions able to support more complex cognitive abilities, both in the technological and social domain. It is then proposed a link between behavioural innovation, social learning skills and brain size in mammals and, in particular, it is pointed out that large-brained primate species innovate, use tools and learn from others more frequently than small-brained primate species.

To further complicate the picture, Holekamp and Benson-Amran propose another alternative hypothesis concerning the evolution of intelligence in carnivore mammals. These authors dismiss both the social and foraging theories on the evolution of intelligence as being too restrictive, and invoke instead the simple need to cope with a changing environment. Their data come both from behavioural observations in natural settings, as well as experimental tests aimed at problem solving, and their species of choice is the spotted hyena (*Crocuta crocuta*).⁴⁶ They argue that research should concentrate in answering questions related to general intelligence, rather than continue to focus on domain-specific types of intelligence. Perhaps the problem remains in the balance between finding general laws on the development of intelligence, and how it came about, together with specific circumstances related to the life-history of the species and individuals considered.

9. LET'S CONTEXTUALISE: TINBERGEN'S FOUR QUESTIONS

We have already mentioned the difficulty in comparing intelligence in different species. In the next sections we will further explore the relative critical issues, in ethological and ecological terms.

⁴⁴ A. WHITEN, C. P. VAN SCHAIK, *The Evolution of Animal 'Cultures' and Social Intelligence*, «Philosophical Transactions of the Royal Society B: Biological Sciences», 362/1480 (2007), pp. 603-620.

⁴⁵ S. E. STREET, A. F. NAVARRETE, S. M. READER, K. N. LALAND, *Coevolution of Cultural Intelligence, Extended Life History, Sociality, and Brain Size in Primates*, «Proceedings of the National Academy of Sciences», 114/30 (2017), pp. 7908-7914.

⁴⁶ K. E. HOLEKAMP, S. BENSON-AMRAM, *The Evolution of Intelligence in Mammalian Carnivores*, «Interface Focus», 7/3 (2017), p. 20160108.

In 1963, Nikolaas Tinbergen, considered one of the founders of ethology together with Konrad Lorenz and Karl Von Frish, proposed that animal behaviour should be studied asking specific questions, known as Tinbergen's Four Questions. These concern causation, ontogeny, evolution, adaptation.⁴⁷ All the four questions have to be answered for an exhaustive explanation of a behavioural response. It is worth noting that Tinbergen's questions include not only 'how' but also 'why' questions. In particular, 'why it is adaptive?', 'why it has evolved?' and 'why it manifests at different developmental phases?'. Though Tinbergen's questions were framed for behaviour, their relevance and impact in any life science discipline make them equally useful for other traits.⁴⁸ One of the most important advantages provided by this approach is the interpretation of behaviour according to its functional and species-specific eco-ethological context,⁴⁹ that is particularly relevant when investigating intelligence in a comparative perspective. We are fascinated and amazed by the sophisticated cognitive abilities of many species, but we may be even disappointed by the abilities of other species. For instance, the Caledonian crows (*Corvus moneduloides*) are often viewed as surprisingly 'intelligent' because of their ability to create and use tools to capture preys. By contrast, other species such as woodpeckers might appear less interesting because they 'simply' drill holes in the bark to prey insects. Tinbergen's approach allows to contextualise such comparison between species in a functional perspective stressing out that it is not needed to be intelligent when intelligence is not needed. So, we should appreciate both sophisticated behavioural patterns and simple responses that are highly effective in achieving their goal. The comparison of intelligence among different species must be investigated and understood considering the species-specific ethological, ecological perspective.

The evolutionary and environmental context is key in understanding the meaning of biological phenomena. Thus, broadening the study of intelligence beyond the individual is always crucial, without the need to focus on species differences (as pointed out earlier...). For instance, let us focus for a moment on collective behaviour. Individuals in many species may appear displaying a deficient behavioural repertoire when studied at individual level because these species have evolved to face environmental challenges in groups of coordinated individuals. Collective intelligence concerns a form of distributed intelligence

⁴⁷ N. TINBERGEN, *On Aims and Methods of Ethology*, «Zeitschrift für tierpsychologie», 20/4 (1963), pp. 410-433.

⁴⁸ R. M. NESSE, *Tinbergen's Four Questions, Organized: A Response to Bateson and Laland*, «Trends in Ecology & Evolution», 28/12 (2013), pp. 681-682. J. W. KRAKAUER, A. A. GHAZANFAR, A. GOMEZ-MARIN, M. A. MACIVER, D. POEPPPEL, *Neuroscience Needs Behavior: Correcting a Reductionist Bias*, «Neuron», 9/3 (2017), pp. 480-490.

⁴⁹ P. BATESON, K. N. LALAND, *Tinbergen's Four Questions: An Appreciation and an Update*, «Trends in Ecology & Evolution», 28/12 (2013), pp. 712-718.

emerging from the collaboration and competition among many individuals. Species forming groups of animals, such as schools of fishes, colonies of ants, and flocks of birds, reach high performance only when exploiting the power of social relationships and correlated behavioural responses. In these groups, individuals maximize collective intelligence exploiting individual learning and behavioural feedbacks among them that ultimately lead to consensus decisions. Therefore, even if each individual has limited knowledge of its environment and the behaviour of all the other group members, it can readily and robustly learn behaviour that maximizes performance in a collective context.

10. BIASES IN UNDERSTANDING ANIMAL INTELLIGENCE

When studying features such as intelligence from a comparative perspective, we might be biased in interpreting and understanding the differences across species. These biases include anthropocentrism and anthropomorphism. The first refers to a human-centred point of view in which our species achieved the highest levels of capabilities in all domains, including intelligence and, thus, human performance is considered the reference point for comparing cognitive abilities. The second, anthropomorphism, refers to the attribution of human characteristics or behavioural needs to another species. These biases arise from the lack of functional and evolutionary contextualization (as indicated by Tinbergen's four questions, see above) and can profoundly impair our ability to appreciate and understand animal intelligence. It is worth noting however that similarities across species do exist and, though conclusions can be drawn only after an analysis without biases, the anthropomorphic approach might provide some first important hints to interpret the behaviour of other species.⁵⁰

In the 1930, Nikolaas Tinbergen studied the aggressive behaviour in the three-spined stickleback fish.⁵¹ During the breeding season, the stickleback male develops a red belly and attack any other conspecific male with a red belly who come near his nesting territory. Tinbergen found that stickleback males attack not only other breeding males but almost any object with the underside painted in red. Interestingly, when a realistic model of a competitor male but with no red belly is introduced in the nesting territory, the male does not attack it, indicating that the red belly is a key stimulus triggering aggressive behaviour. The incapability in distinguishing a red-painted object from a breeding male apparently suggests that stickleback fishes have limited cognitive capabilities and low intelligence. However, this conclusion rises from an anthropocentric- and anthropomorphic-biased interpretation. For our species, it is so

⁵⁰ J. PANKSEPP, *Can Anthropomorphic Analyses of Separation Cries in Other Animals Inform Us about the Emotional Nature of Social Loss in Humans? Comment on Blumberg and Sokoloff (2001)*, «Psychological review», 110 (2003), pp. 376-388.

⁵¹ N. TINBERGEN, *The Study of Instinct*, Oxford University Press, Oxford 1951.

immediate and easy to distinguish between a real fish and a red-painted object that we expect the same should apply to all other species. However, when analysing stickleback aggressive behaviour in the light of evolution and the eco-ethological context, it appears clear that this species did not evolve such ability because, during their evolutionary history, stickleback fishes did not encounter objects and conditions that might be misinterpreted has opponents. In our species, similar limitations might occur, but the anthropocentric approach makes us blind to them. For instance, humans exploit sophisticated behavioural strategies based on fine cognitive skills to avoid starving. However, our species is less capable to implement equally sophisticated strategies to avoid eating too much leading to obesity and diabetes, which are associated to high mortality and morbidity.⁵² Among different explanations, this is likely because, as for the red objects triggering inappropriate responses in the stickleback, we rarely faced conditions of excessive food availability during our evolutionary history and consequently we did not evolve strategies to easily avoid obesity.

A further example of how biases might affect our capability to interpret intelligence in species different from ours is provided by the story of a horse named Clever Hans. This horse lived in Berlin in the late 19th and early 20th century and was celebrated for showing an apparently remarkable intelligence. During its exhibitions, Hans demonstrated its skills by providing, for instance, the solution to mathematical questions by knocking the hoof on the ground a number of times equal to the numeric solution. However, the horse had no mathematical skills. The feats it achieved were finally explained as simple behavioural responses to subtle and involuntary signals provided by his trainer. Thus, the horse stopped to hit the ground when the trainer expected it to occur. ‘Clever Hans effect’ is nowadays used to denote the unintentional cueing of the desired behavioural response by the questioner when experiments are not carefully designed.⁵³ After this, the zoologist C. Lloyd Morgan, celebrated for promoting a cautious approach to reasoning powers of animals, pointed out a strategy to avoid further biases in interpreting animal behaviour.⁵⁴ He proposed that higher mental processes should only be considered as explanations if simpler processes could not explain the behavioural response. This is known as Morgan’s Canon, and it is a fundamental precept when comparing cognitive abilities across animal species.

⁵² F. S. ZUCOLOTO, *Evolution of the Human Feeding Behavior*, «Psychology & Neuroscience», 4/1 (2011), pp. 131-141. S. GAHAGAN, *The Development of Eating Behavior-Biology and Context*, «Journal of Developmental and Behavioral Pediatrics», 33/3 (2012), pp. 261-271.

⁵³ S. LAPUSCHKIN, S. WALDCHEN, A. BINDER, G. MONTANON, W. SAMEK, K. R. MULLER, *Unmasking Clever Hans Predictors and Assessing What Machines Really Learn*, «Nature Communications», 10/1 (2019), pp. 1-8.

⁵⁴ A. COSTALL, *How Lloyd Morgan’s Canon Backfired*, «Journal of the History of the Behavioral Sciences», 29/2 (1993), pp. 113-122.

11. CONCLUSIONS

In this contribution we offered an historical overview of the study of animal intelligence, and some inspiring related theories, framed in evolutionary, ecological and ethological context. Finally, we emphasised some theoretical traps we can encounter comparing the intelligence of different species.

The literature on cognitive abilities and intelligence on a variety of different species has been steadily growing in the last years. It is a welcome scenario, which distance us from a rather anthropomorphic view of intelligence. The focus therefore is not anymore just on primates, but on other species too, which are not necessarily similar to humans. Intelligence, as we cared to point out, whatever definition we want to use, is approached more in a contextual fashion, where ecology plays a crucial role.⁵⁵ The trick however, is not to use the same cognitive tests on different species, but to use appropriate tests which are predicted to operate on abilities derived from the behavioural ecology of that particular species. Like in other fields of behavioural research, laboratory and field workers should work together: field studies could enucleate possible research ideas to be then tested in the laboratory, if some control of variables is necessary. It would also help to formulate more ecologically-sounded laboratory tests.

The study of animal intelligence remains a fascinating topic of research, but full of theoretical and experimental traps and headaches. So, referring to the title of our contribution and our question: 'Is my animal smarter than yours?', citing Douglas Adams' *The Hitchhiker's Guide to the Galaxy*,⁵⁶ an appropriate answer would probably be: '42'.

ABSTRACT · Animal intelligence emerges from the combination of skills and abilities that allow the individual to face and adapt to the challenges of their specific environments. This implies that the investigation and understanding of intelligence across animal species is a complex and environment-dependent process. Any judgement regarding the relative intelligence of a given species or direct comparisons are extremely difficult and need contextualisation. Here we present an historical overview of the field, from Charles Darwin to contemporary views, and provide examples of the link between animal intelligence, innovation and cognition. The most popular hypotheses on the evolution of animal intelligence are briefly presented and discussed. In addition, we propose to appreciate animal intelligence in the framework of an evolutionary, ecological and ethological perspective. Most common biases in measuring intelligence are also presented.

KEYWORDS · Animal Cognition, Animal Intelligence, Ecological Context, Evolution, Behavioural Innovation.

⁵⁵ J. BRÄUER, D. HANUS, S. PIKA, R. GRAY, N. UOMINI, *Old and New Approaches to Animal Cognition: There Is Not 'One Cognition'*, «Journal of Intelligence», 8/3 (2020), p. 28.

⁵⁶ D. ADAMS, *The Hitchhiker's Guide to the Galaxy*, Pan, London 1979.