Who's a clever bird — now? A brief history of parrot cognition

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Abstract

Parrots are renowned for their intelligence and ability to imitate human speech ever since they have been kept as pets. Despite of impressive pioneering work on the cognitive abilities of parrots, research on parrot cognition has only recently gained momentum, probably given the new wave of interest in possible convergent evolution of complex cognition within the vertebrates. Together with corvids, they often parallel primates if not great apes in cognitive performance and have become important model systems to study the evolution of cognition. We briefly review the history of parrot cognition within the field of comparative cognition and introduce some of the laboratories that have contributed to this special issue as well as the studies they present.

1. Introduction

This special issue features a selection of articles that focus on parrot cognition.

First reports of the sophisticated cognitive abilities of *Psittaciformes* have existed for over half a century, but, recently, the topic has sparked new interest and studies on parrot cognition as well as research groups dedicated to the subject have been augmenting increasingly, particularly within the past decades.

The only very recent surge of parrot cognition is surprising, considering that parrots have existed in close association with humans as pets for a very long time and in many cultures. This occasionally unpleasant fate was probably something that these birds owed, aside from their beauty, to their cognitive abilities. Our relationship with parrots date back several decades BC, when Indian parakeets (*Psittaculidae*) were brought to Europe by travelers and sailors. These brightly coloured birds were not only desired for their attractiveness but also for their ability to reproduce human language and to learn physical tricks with ease (Lach, 1977). The ability of parrots to imitate speech was recorded as early as five centuries BC when the Greek physician Ctesias, who travelled India, described a hawk-like bird with a red beak, which spoke Indian like a native and could learn Greek (Lach, 1977; Bigwood, 1993). Trade of parrots as pets for the wealthy continued throughout ancient Rome into the middle ages during which parrots were famously owned by clerics and royalty. Famous historical examples are Roman philosopher Pliny who noted in his Natural History Records that his ring-necked parakeet (*Psittacula krameri*) could say 'Hail Ceasar' and was particularly 'merry in vino' (Lach, 1977). Images of an Australasian cockatoo that was brought to Sicily as a gift to the roman emperor Frederick II by the Sultan of Babylon converted debates on trade routes during the 13th century (Dalton, 2014) and Henry VIII kept an African grey parrot (*Psittacus erithacus*) who is reported to have called the boatman over the waters to Hampton court who then had to be paid for his effort (Sparks & Soper, 1990).

The first attempts to address the cognitive abilities of parrots on a scientific level were, to our knowledge, made by Nadeszha Ladygina-Kohts in Russia. Nadia Kohts was a contemporary zoopsychologist of Robert Yerkes and Wolfgang Köhler during the beginning of the last century, yet less acknowledged on an international level because she published mostly in Russian. Her cognitive studies focused mainly on an infant chimpanzee on whom she was arguably the first to employ the Matching to Sample Paradigm. Nevertheless, she also studied several parrots, including three species of macaws, three cockatoo and three amazon species as well as African grey parrots on a series of colour discrimination tasks. She targeted their ability to discriminate seven colours of the visible light spectrum, as well as colour combinations. Additionally, she seems to have tested the African grey parrots' ability to associate visual and acoustic cues. Sadly, these data have never been published

Figure 1. Alex the African grey parrot confronted with a tray of blocks while being asked to count specific colours. Photograph by Irene Pepperberg.

apart from a short report for the Darwin museum (Ladygina-Kohts, 1921), and the original monography about her work with carnivores (wolves) and birds (including parrots) is now lost (Zorina et al., 2014).

In the 1920s and 1930s Otto Köhler and his doctoral student Werner Fischel studied numerical assessment in several birds. Using various methodologies they established the respective species' limit at differentiating quantities. The upper limit they found for pigeons was five, for jackdaws and budgerigars six, for magpies, ravens and amazon parrots seven and for an African grey parrot eight (Fischel, 1926; Köhler, 1937, 1943). Their data has in several cases been affirmed by contemporary research. Köhler's experiments were published in German but neither replicated nor pursued in the next couple of decades (note that this time was largely dominated by behaviourist approaches).

The first long-term study on parrot cognition was initiated much later by Harvard graduate Irene Pepperberg. Encouraged by previous attempts to teach chimpanzees American sign language throughout the 1960s and 1970s, she started her prominent Animal Language EXperiment on the African grey parrot 'ALEX' (Pepperberg, 2009) in 1976 (Fig. 1).

Notably, this happened a time when birds were still largely considered as inflexible, stereotyped automata governed by genetically determined be-

havioural routines and when it was assumed that complex cognitive abilities required a large, primate-like brain as well as a mammalian neocortex. Note also that full scientific acknowledgement of a cortex-like region in birds was only achieved in the early 2000s (e.g., Reiner et al., 2004; Jarvis et al., 2005). By now we know that birds not only possess a cortex-like region, but the number of pallial neurons in it is also almost twice as densely packed per square inch as that of mammals with similar brain sizes and that in parrots and corvids, the neuron numbers essentially resemble those of higher primates (Olkowicz et al., 2016). Not long before this finding was published it had been pointed out that not only corvids but also parrots stand out for their relative brain size among all vertebrates alongside the dolphin and the primate lineage and that complex cognition might have evolved multiple times within the vertebrates independently (Emery & Clayton, 2004; Osvath et al., 2014).

Pepperberg and her students proceeded training Alex in the 1970s using a model-rival technique developed by Dietmar Todt (1975). The procedure involved an interaction with the experimenter and an assistant that the bird was able to interrupt. Their studies on Alex spanned over three decades until his death in 2007 and produced some of the best results of human language experiments on animals: Alex learned over 100 words, could label and categorize unknown objects (see Figure 1), developed concepts such as ‘same’ versus ‘different’, ‘bigger’ versus ‘smaller’, could count up to eight, add and subtract numbers and was learning Arabic numbers as well the alphabet (see Pepperberg, 2009 for a summary).

The Pepperberg Lab, which had operated in the University of Arizona, MIT Media Lab and Brandeis University, still exists to this date and is now back in Harvard. Currently data are being collected on two grey parrots: 24 year old Griffin and 6 year old Athena. Their research focus continues to be on human language abilities as well as on using the latter to test specific aspects of reasoning. This is exemplified by their contribution of a new study on inferential reasoning to this issue (Pepperberg et al., 2019).

While the Alex studies proceeded, interest in avian intelligence started to focused more closely on another group of large-brained birds: corvids. Corvids were already being heavily studied by behavioural ecologists throughout the 1980s for basic cognitive abilities associated to their food storing capacities such as spatial learning and memory (e.g., Vander-Wall, 1982; Kamil et al., 1985; Balda et al., 1987; Wall et al., 1998, and many

more). Their food caching behaviour and the fact that they pilfer food caches of conspecifics were later discovered as an invaluable paradigm for investigating more sophisticated cognitive skills such as the ability to follow invisible displacement, planning, episodic-like memory and theory of mind-related cognitive abilities such as perspective taking and knowledge attribution throughout the 1990s and 2000s (e.g., Clayton & Dickinson, 1998; Heinrich & Pepper, 1998; Emery & Clayton, 2001; Bugnyar & Heinrich, 2005; Zucca et al., 2007; Dally et al., 2010 and many more). The success of these studies resulted in the formation of several new laboratories and earned corvids the nickname ‘feathered apes’ (Emery, 2004). Interest in corvid cognition increased even further when Gavin Hunt discovered in 1996 that New Caledonian crows (*Corvus moneduloides*) could use and make a variety of tools in the wild (Hunt, 1996) and thereby set off an effort to also study the physical problem-solving abilities of corvids. Soon impressive flexible cognitive skills were discovered in those tool-using crows and other corvids (e.g., see Taylor, 2014 for a review).

Lagging behind the rise of cognitive studies on corvids, interest in parrot cognition, outside the Pepperberg Lab, remained at a moderate level throughout the 1980s and early 1990s despite some individual studies on perception and vocal memory in budgerigars (*Melopsittacus undulatus*) as well as studies on motor imitation learning (e.g., Dawson & Foss, 1965; Galef et al., 1986) with conflicting results, which were later confirmed and challenged respectively (Heyes & Saggerson, 2002; Mottley & Heyes, 2003). Nevertheless, in the late 1990s and early 2000s one particular and rather unusual parrot started to attract some attention, namely the New Zealand kea (*Nestor notabilis*). The results of the first extensive field study and the corresponding book by Judy Diamond & Alan Bond on the world’s only mountain parrot’s peculiar ecology and behaviour in the wild, including its playful drive to explore their physical environment and its apparent lack of neophobia, appeared just after researchers around Hans Winkler and Michael Taborsky had started to study a small group of about ten kea at the Konrad Lorenz Institute for Comparative Ethology in Vienna. After a study on coordinated behavior in these birds was published (Tebbich et al., 1996), a team around Ludwig Huber decided to take on the kea group as a systematic model for testing the technical intelligence theory (Huber & Gajdon, 2006) and supplemented them with new subjects from breeders from all over Europe. In 2009 the animals were moved to the Haidlhof Research Station in lower Austria

and the Vienna kea are now part of the Messerli Research Institute at the Vetmeduni Vienna. The 520 m² aviary presently holds 28 animals making it the world's largest group of kea in captivity to date which are notably kept and administered there for the purpose of studying their cognitive abilities. The Vienna kea lab, currently lead by Raoul Schwing, correspondingly contributed greatly to parrot cognition research over the past two decades. Amongst many other things, it was shown that kea have some appreciation for connectivity (Werdenich & Huber, 2006), attend to social information during problem solving (e.g., Gajdon et al., 2011), can cooperate (Schwing et al., 2016) and even used objects as tools to gain access to an out-of-reach food reward (Auersperg et al., 2010, 2011; Gajdon et al., 2014). The Vienna kea lab additionally placed efforts in studying cognition in the field, conducting several experiments on the spread of innovation in wild kea at Mount Cook National Park in New Zealand (Gajdon et al., 2003, 2004, 2006). They further showed that wild birds used specific vocalizations as an emotional contagion eliciting play behaviour (Schwing et al., 2017). We should also point out that only recently a second kea lab was established at a Sanctuary in Auckland, New Zealand by researchers around Alex Taylor (see e.g., Heaney et al., 2017a,b). The Vienna kea lab contributed a new study based on the Aesop's fable paradigm to this issue (Schwing et al., 2019). The task requires the animals to drop stones into a vertical tube in order to raise the water level inside. The study implemented novel controls and investigated the mechanisms underlying the task acquisition. Since 2013, Vienna additionally incorporates a lab around Marisa Hoeschele studying vocal learning, synchronization and rhythm in the budgerigar within a group working on bioacoustics at the Department of Cognitive Biology at the University of Vienna. The Vienna Budgie lab contributes a new study on octave equivalence perception, which budgerigars do not appear to exhibit despite of their vocal learning ability (Wagner et al., 2019).

In the 2010s interest in parrot cognition started to increase considerably and it became clear that if corvids presented a case of possible convergent evolution as pointed out by Clayton and Emery in 2004, the same should apply to psittaciforms equally. This accruing notion was finally put out in 2014 when Osvath et al. elaborated that parrots, alongside with corvids, dolphins and primates, stand out among all vertebrates in terms of their relative brain size and cognitive abilities. Lambert et al. (2019) in this issue discuss this topic at length reassessing whether the state-of-the-art science is

still in alignment with the notion that parrots should equally be referred to as “feathered apes” symbolically as corvids.

By the end of the 2000s a second group interested in African grey parrot cognition and, more recently, also in cockatiels (*Nymphicus hollandicus*) was created and still exists around Dalila Bovet at the University of Paris Nanterre. They investigate several topics such as referential communication, self-control and cooperation on their subjects (e.g., Vick et al., 2010; Peron et al., 2011; Giret et al., 2012). Their most recent study featured in this issue examines how cockatiels combine objects to deliberately produce sound effects during unrewarded object play (Le Covec et al., 2019).

Around 2010, the Wildlife Park in Lincolnshire, which incorporates the largest parrot sanctuary in the UK, (housing over 1000 rehomed parrots from 100 species) started to work collaboratively with the University of Lincoln granting scientists around Anna Wilkinson access to their animals. The collaboration produced a number of studies (e.g., O’Hara et al., 2017; Picard et al., 2017), notably identifying a new mode of tool use in the Vasa parrot (*Coracopsis vasa*) (Lambert et al., 2017). This issue will include new findings on the mechanism underlying vertical string pulling from green-winged macaws (*Ara chloropterus*) at Lincolnshire (Gaycken et al., 2019).

In 2011 Alice Auersperg started the Vienna Goffin Lab, initially looking predominately at object manipulation in a notoriously investigative Indonesian Island parrot, the Goffin’s cockatoo (*Cacatua goffiniana*). After they found that these cockatoos could spontaneously innovate both, the use and manufacture of tools and that they could socially transmit the trait to conspecifics (summarized in Auersperg et al., 2017a) the team focused their research over the past seven years mainly on the Goffin cockatoo’s tool-using abilities. Despite the birds not being specialized tool users in the wild, their tool-related capacities seem to match those of tool making experts, thus suggesting sophisticated, yet domain general problem-solving abilities (e.g., Auersperg et al., 2017b, 2018; Laumer et al., 2017). However, the research group has also increased their efforts studying executive functions, as well as various aspects of the Goffin’s social cognition and general physical problem-solving abilities (see summary in Auersperg et al., 2017a). They are also teaming up with roboticists from the TU Berlin to understand algorithms involved in exploration and problem solving in their subjects. The Goffin Lab is located in Goldegg, Lower Austria and presently holds 16 subjects. It is, like the Vienna Kea Lab, associated to the Messerli Research Institute of the

University of Veterinary Medicine in Vienna. In this issue, the lab presents a new tool using study featuring a setup including two different tools and one of two different tasks. The task is either presented before or after the tools but never at the same time before the animals are asked to select a tool. The study shows that the birds can select the appropriate tool for a task prospectively while they fail in a retrospective condition (Beinauer et al., 2019).

In 2016 they additionally started studying the Goffin's cockatoos in their natural habitat, the Tanimbar archipelago in Indonesia. Their field work was initiated by Mark O'Hara and Berenika Mioduszevska in collaboration with Ludwig Huber, Alice Auersperg and the Indonesian Institute of Sciences in an effort to understand the ecology driving the Goffin's cockatoos' sophisticated problem-solving abilities. One of the first reports on the ecology of this species is also presented in this issue (O'Hara et al., 2019).

Parrot cognition in the wild is presently also being studied in the greater Sulphur-crested cockatoo (*Cacatua galerita*), a species that is also found in cities and that has a large native population in Sydney. This research by a group around Lucy Aplin at the Max-Planck-Institute for ornithology in Radolfzell has only started very recently and we are looking forward to learn about their findings in the near future.

Last but not least, in 2015, the Max-Planck-Institute of Ornithology Seewiesen started a formal collaboration with the Loro Parque Fundación in Tenerife, which owns the largest and most species-rich collection of parrots in the world (ca. 4500 birds; 350 subspecies) and which offers an unparalleled opportunity for systematic phylogenetic comparisons within the order Psittaciformes. As part of this collaboration, the research group headed by Auguste von Bayern carries out their research at the Max-Planck Comparative Cognition Research Station that was set up in the Loro Parque zoo, where the ca. 1.6 million zoo visitors per year can watch the research "live" through a one-way mirror system. This follows up the tradition of the renowned Wolfgang-Köhler-Primate research centre that has run in collaboration between the Max-Planck-Institute for evolutionary anthropology and the zoo Leipzig, Germany for many years, where zoo visitors could similarly witness cognitive research on great apes. The research group has a broad focus on the evolution of complex cognition and on vocal learning. Currently, the lab holds 44 parrots of four species, i.e., great green macaws (*Ara ambiguus*), blue-throated macaws (*Ara glaucogularis*), red-fronted macaws (*Ara rubrogenys*), blue-headed macaws (*Primolius couloni*) and African grey

parrots that can be tested routinely in the research station. Besides, there is the opportunity to conduct large-scale phylogenetic comparisons working with the 350 subspecies kept by the foundation and the possibility to run comparative developmental studies in the hand-rearing station of the Loro Parque Fundación. The young lab has published a number of comparative studies e.g., on economic decision-making or on motor regulation (Kabadayi et al., 2017; Krasheninnikova et al., 2018) and currently works on a range of topics in both social (prosociality and cooperation) and physical cognition (flexible problem solving, causal reasoning). In addition, they are developing and piloting cognitive test batteries for broad comparisons. To this issue, the Comparative Cognition group contributes a paper on physical cognition, specifically featuring a parrot compatible version of the trap tube task. The latter is a task that has been used as a benchmark paradigm to investigate causal reasoning in animals in the past (O'Neill et al., 2019). They further contribute the first direct comparison of 4 parrot species with 4 primate species in an extensive battery of cognitive tests in both the physical and social domain, referred to as Primate Cognition Test Battery (Hermann et al., 2007; Krasheninnikova et al., 2019).

Finally, they contribute a carefully controlled study on mirror self recognition in kea and Goffin's cockatoos carried out in collaboration with both the kea and Goffin lab, which could not find support for mirror self recognition in parrots (van Buuren et al., 2019).

We should mention at this point that this overview is far from exhaustive. The 2000s gave rise to several other labs that also contributed to the literature on parrot cognition over but are — to our knowledge-currently not active any longer. For example Mildred Funk studied cognitive development and problem-solving abilities of yellow-crowned parakeets (kakarikis; *Cyanoramphus auriceps*) kept in a lab at Northwestern University, Illinois in the USA (e.g., Funk, 1996, 2002). In the UK, Celia Heyes studied imitation in budgerigars at the University College London (e.g., Heyes & Saggerson, 2002; Mottley & Heyes, 2002), Jackie Chappell and Zoe Demery studied object manipulation in both kakarikis and Senegal parrots (*Poicephalus senegalus*) at the University of Birmingham (Demery et al., 2010, 2011) and Jayden van Horik and Nathan Emery ran a series studies of studies on black-headed caiques (*Pionites melanocephalus*) and Hahn's macaws (*Diopsittaca nobilis*) at St Mary's University in London (Van Horik & Emery, 2016, 2018). Also in Germany, Claudia Mettke-Hoffmann at the

Max-Planck-Institute for Ornithology worked on object exploration in several parrot species (Mettke-Hofmann, 2000; Mettke-Hofmann et al., 2002) and in the late 2000s Ralf Wanker's and Jutta Schneider's group in Hamburg, Germany studied physical cognition in several species of parrots kept in zoos (e.g., Krashennikova & Wanker, 2010; Liedke et al., 2011; Krashennikova et al., 2013; Krashennikova & Schneider, 2014). In the 2010s Zoya Zorina and Tanya Obozova kept 2 orange-winged amazons (*Amazona amazonica*) at the Biology department of the Lomonosov State University Moscow, Russia, and produced an interesting study on analogical reasoning (Obozova et al., 2015).

Additionally, there are more research groups that are currently working on parrot cognition, but as a side focus, such as several scientists from Denmark, who keep peach-fronted conures (*Eupsittula aurea*) in their labs at the University of Southern Denmark (around Magnus Wahlberg and Ole Naesbye Larsen) and at the University of Copenhagen (around Torben Dabelsteen) and collaborate with Thorsten Balsby from the University of Aarhus, who has studied orange-fronted conures (*Aratinga canicularis*) and other conures for many years in the wild (e.g., Balsby & Bradbury, 2009; Balsby et al., 2012). Both labs have contributed papers to this issue (Thomsen et al., 2019; Torres Ortiz et al., 2019). A research team from the University of Barcelona tested African grey parrots for the first time at a Spanish breeding facility and contributed a paper on string pulling (Chaves Molina et al., 2019).

In the UK, there are scientists that also have an interest in parrot cognition, such as that of Amanda Seed (University of St Andrews), who works with parrots kept at Edinburgh zoo, and Katie Slocombe (University of York) who are both actively collaborating with the parrot labs mentioned above.

To conclude, the recent rise of studies on parrot cognition is symptomatic for the importance of this research in our quest to understand the evolution of intelligence from an evolutionary perspective. Last July (2018) the two parrot labs in Vienna hosted the first parrot cognition symposium at the Messerli Research Institute which was attended by nearly 60 participants and gave us great inspirations and ideas about possible future directions and collaborations between the presently existing laboratories (see Figure 2).

It is also important to mention that past research in parrot cognition from a behavioural perspective is continuously supplemented by new finding in

Figure 2. The parrot cognition symposium 2018 at the Messerli Research Institute in Vienna.

both, genetics and neurology. For example, last year researchers in Oregon found changes in the DNA repair genes of long-lived birds such as parrots and even parrot-specific changes in gene-regulating regions of the genome near genes linked to neural development and brain function. Interestingly, the same changes are associated with genes linked to cognitive abilities in humans, suggesting convergent evolution of the latter (Wirthlin et al., 2018). In primates, a brain region called the pontine nuclei plays an important role in the processing and execution of sophisticated behaviours as it transmits information between the cortex and the cerebellum. In birds another brain region, the medial spiriform nuclei (SpM), are enlarged and seem to serve a similar function. It was also found last year that parrots have much larger SpMs relative to their brain size than any other avian group tested, including corvids (Gutiérrez-Ibáñez et al., 2018). The enlarged SpM in parrots versus the enlarged pontine nuclei in primates could represent another example of convergence. These findings further highlight the importance of studying the cognitive abilities of parrots in a comparative manner not only within the order itself but also to other large brained birds and human as well as non-human primates. We hope that the first special issue dedicated exclusively to this topic will spark new ideas and discussions.

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