

Charles University

Faculty of Science

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Nikola Schlöglová

Performance of birds in model cognitive tasks: a cross-taxon comparison

Performance ptáků v modelových kognitivních úlohách: mezitaxonové srovnání

Bachelor's thesis

Supervisor: doc. Mgr. Alice Exnerová, Ph.D.

Consultant: MSc. Anita Szabó

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Prohlášení

Prohlašuji, že jsem závěrečnou práci zpracovala samostatně a že jsem uvedla všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

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Nikola Schlögllová

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Abstrakt

Ptačí kognice je mimořádné složité téma. Mnoho faktorů ovlivňuje způsob, jak ptáci získávají, zpracovávají a využívají získané informace. Některé ptačí taxony dosahují lepších výsledků v kognitivních úlohách než jiné a důvody těchto rozdílů jsou rozsáhle zkoumány a diskutovány. Ptáci se přirozeně setkávají s různými faktory prostředí, které mohly vést k evoluci specializovaných kognitivních adaptací ne vždy uplatnitelných v různých kontextech. Na druhé straně, někteří ptáci si vedou dobře v široké škále kognitivních úloh a mohou mít obecnou inteligenci.

Modelové kognitivní úlohy nám umožňují získat standardizovaná data o performanci ptáků. Poté můžeme porovnávat tato data napříč různými taxony a pokusit se identifikovat případné paralely. Tato práce se zabývá vybranými modelovými kognitivními úlohami: úlohy s taháním provázku, rozhodování na základě vyloučení jedné možnosti, tranzitivní inference, úlohy související s využíváním zrcadel a úlohy založené na odpovědi při změně odměňování. U těchto úloh analyzuje a porovnává performanci jak dobře zkoumaných, tak i nedostatečně zkoumaných taxonů ptáků. Práce popisuje vybrané kognitivní úlohy, shrnuje dostupná data, zdůrazňuje korelace mezi performancí ptáků a dalšími faktory a diskutuje možná vysvětlení pro jejich různorodost. Nakonec se práce věnuje otázce obecné inteligence a specializovaných kognitivních adaptací a identifikuje mezery v našich znalostech ptačí kognice.

Klíčová slova

ptačí kognice, kognitivní úlohy, řešení problémů, učení, srovnávací studie, flexibilita chování

Abstract

Bird cognition is an immensely complex topic. Many factors influence how birds acquire, process and act upon obtained information. Some bird groups outshine others regarding their cognitive skills, and the underlying reasons for these differences are extensively researched and discussed. Birds naturally face varying environmental factors that could have driven the evolution of specialised cognitive adaptations not generalisable across all contexts. In contrast, some birds perform well in a broad range of cognitive tasks and may possess general intelligence.

Model cognitive tasks help us gain standardised data on birds' cognitive performances to compare them across different taxa, which enables us to identify any parallels. This thesis covers selected model cognitive tasks: string-pulling tasks, reasoning by exclusion tasks, transitive inference tasks, tasks related to mirror use and reversal learning tasks, for which it analyses and compares the performance of both well-studied and understudied bird taxa. The thesis describes the selected cognitive tasks, summarises available data and highlights correlations between birds' performances and other factors while discussing possible explanations for their varying performances. Finally, the thesis addresses the question of general intelligence versus specialised cognitive adaptations and identifies gaps in our knowledge of bird cognition.

Keywords

bird cognition, cognitive tasks, problem-solving, learning, comparative study, behavioural flexibility

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1 Introduction

Researchers have studied bird cognition for a long time. Ways to approach this phenomenon are numerous. Model cognitive tasks bring standardised tests that apply to most bird taxa. Thanks to them, we can compare birds across orders and species. Assessing the differences in birds' performance can help us determine what factors play a role in developing individual cognitive skills. Moreover, it can give us an idea of the evolution of cognition as, in many instances, birds perform similarly to primates, their very distant relatives (Pika et al., 2020; Taylor et al., 2009; Wright et al., 2017).

If birds perform well in cognitively demanding tasks, it tells us about their possible behavioural flexibility and survival ability in challenging environments. In everyday life, they face decisions that influence their chance of survival. They must behave effectively and deal with trade-offs, as avoiding predators, finding food and finding a suitable partner are all fundamental needs that cannot be done simultaneously.

Analysing birds' performance may allow us to establish whether a general intelligence or a specific adaptation is the leading cause behind birds' differences. Also, it can point us in the right direction regarding which ecological strategies relate to which cognitive abilities. For instance, birds foraging on the ground with dense vegetation may benefit from increased physical cognition as they need to be able to access hard-to-reach food (Krasheninnikova, 2014). On the other hand, the food caching strategy requires spatial memory and object permanence (Salwiczek et al., 2009).

Additionally, we can find correlations with life-history traits. The ability to discriminate and transitively infer may be associated with sociality as birds need to recognise individual members of their flock and keep track of their position in complex hierarchies (Bond et al., 2007). Furthermore, other aspects, such as a long lifespan, delayed maturity, monogamy, large relative brain size and neuron density, are believed to predict better cognitive abilities (Emery et al., 2007; Sol et al., 2005, 2016, 2022; Zorina & Obozova, 2012).

This thesis covers the most studied bird groups, such as Columbiformes, Psittaciformes, and Passeriformes, and understudied groups, such as Galliformes, Anseriformes, Cuculiformes, Phoenicopteriformes, Sphenisciformes, Bucerotiformes, Charadriiformes, Accipitriformes, Strigiformes and Falconiformes. For the purposes of this thesis, the Passeriformes group will be divided into two groups, Corvidae and Passeriformes other than Corvidae, as they are very distinctive regarding their cognitive abilities. Moreover, the amount of available data varies significantly between them.

The studied tasks involve string-pulling, reasoning by exclusion, transitive inference, mirror use and reversal learning. They are selected based on two main criteria: there is enough comparative data, and they test different cognitive abilities.

String-pulling tasks, which have many variations, assess birds' comprehension of physical properties, such as continuity and connectivity. Reasoning by exclusion tasks focus on birds' capacity to make correct choices by logically eliminating other potential options. Transitive inference tasks evaluate whether birds can comprehend relational representation by first learning simple associations. Tasks involving mirror use may focus on birds' understanding of mirror properties or attempt to provide insight into their concept of self-awareness. Lastly, reversal learning tasks initially test birds'

ability to discriminate between stimuli and later assess their ability to adapt to changed rewarding contingencies.

Undeniably, this list of cognitive tasks only includes a limited selection of the existing cognitive tasks, as several others could not be included due to the limited scope of this thesis. Tasks omitted from the list include tool use, trap-tube tasks, innovative problem-solving, spatial cognition, object permanence, motor inhibitory control, delayed gratification and categorisation.

There are multiple reasons behind not selecting these tasks. Tool use and categorisation have been the subject of previous theses. Data on trap-tube tasks are scarce, and the task is closely related to tool use. Innovative problem-solving tasks encompass a heterogeneous category with diverse experimental designs, making comparisons difficult. Spatial cognition has mainly been investigated in corvids and other caching passerines. Object permanence can be inferred partially from performance in other tasks. Motor inhibitory control tasks mainly assess the inhibition of prepotent responses, and birds may not necessarily make intentional decisions. Finally, delayed gratification tasks have multiple experimental designs with insufficient data to compare them properly.

Each chapter describes a cognitive task and compares the performance of different bird taxa in the given task, and by the end of the thesis, there is a cross-task comparison.

The aims of this thesis are: to describe selected model cognitive tasks, review and compare the performance of various bird taxa, find any tendencies or correlations within the gathered data, discuss possible causes of any differences and gather evidence for general intelligence and adaptive specialisation in birds.

2 Model cognitive tasks

2.1 String-pulling tasks

The string-pulling task is among the most used tests in bird cognition studies for assessing birds' physical cognition. Indeed, in many test variations, birds must understand physical properties and causal relations such as continuity and connectivity to solve the tasks successfully.

One can easily set it up and present it to many birds while gaining standardised data for further comparisons (Ortiz et al., 2019). There are still some limitations as to which species can undergo this test, but they mainly concern the morphology of the tested bird; for example, hummingbirds are just too small to manipulate any sizable object. The main objective is for the subject to pull on a string connected to a reward, usually a desirable food or sometimes a favourite toy (Werdenich & Huber, 2006). This act requires sufficient motivation, and the subject has to identify the string as a means to get access to the reward. Some forms of restrictions usually limit alternative ways to obtain the reward. Multiple studies use a plastic cylinder to cover the baited string (Audet et al., 2016), while others use a wire mesh barrier to separate the subject from the apparatus (Heinrich, 1995; Manrique et al., 2017; Schuck-Paim et al., 2009).

The setup can be horizontal or vertical, with the latter being a more complicated variant as the birds must pull the string upwards, which demands specific sensorimotor abilities such as coordination between the feet and the beak (Krashennnikova, 2013). Subjects must complete numerous steps in a specific order to achieve the result (Heinrich, 1995). Furthermore, the subjects' view is constricted as they view the task from above. Another technically similar but counterintuitive variant is a pull-down

task (**Figure 1A**). The reward goes up by pulling, but the birds must pull the string down, making it more challenging to pay attention (Gaycken et al., 2019; Heinrich & Bugnyar, 2005; Ortiz et al., 2019).

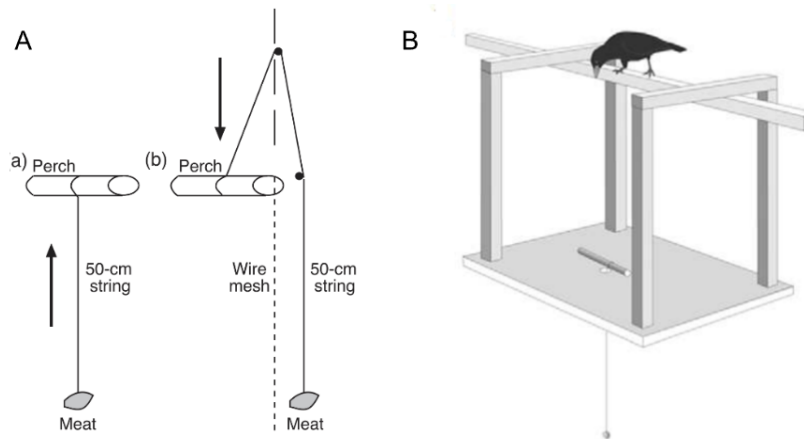


Figure 1: A - vertical single string-pulling task vs pull-down task (Heinrich & Bugnyar, 2005), B - visually restricted single string-pulling task (Taylor et al., 2010)

Researchers widely use the single string-pulling test, but it has limitations regarding the conclusions they can gather from it. It is problematic to say that birds have further developed physical cognition when they only pull on a single string, as it is possible to train them to succeed (Hofmann et al., 2016). For instance, by slowly lengthening the string, those who were unsuccessful later succeeded (Vince, 1961; Wakonig et al., 2021). Therefore, we should focus on birds solving the task spontaneously. While preprogrammed behaviour could explain birds' success, researchers have disputed this idea. Birds do not rely on any species-specific techniques, and individual birds use multiple different techniques in quick succession (Krasheninnikova & Wanker, 2010; Seibt & Wickler, 2006). Some authors argue that the insight hypothesis could be the main reason for spontaneous string-pulling (Heinrich, 1995), as some individuals can solve the problem within seconds in their first trial. That would require the birds to represent the task mentally and essentially see into the problem without needing trial-and-error learning.

However, the birds can pull the string only thanks to exploiting a random discovery: they perform behaviours already in their repertoire, and when the reward moves towards them, they create an association and repeat the previous action (Manrique et al., 2017). Taylor et al. (2010) call it a positive motor feedback hypothesis, a form of simple operant conditioning tested by presenting a visually restricted task (Manrique et al., 2017; Molina et al., 2019) (**Figure 1B**).

Nonetheless, there needs to be another explanation, as only some birds can solve the simple string-pulling task even with a full view of the reward (Vince, 1956, 1958). What comes as a more plausible explanation could be the need for efficient attention dividing: the bird needs to watch the reward moving closer and at the same time, concentrate on its body movement (Taylor et al., 2010). However, this explanation stands only partially regarding horizontal string-pulling tasks where the birds can obtain the reward more freely, yet many individuals still fail (Lamarre & Wilson, 2021).

When there is only a single string, researchers cannot indisputably tell whether the birds' behaviour is goal-directed, as manipulating the string can be rewarding (Dücker & Rensch, 1977; Schuck-Paim et al., 2009). Therefore, transforming the simple task into patterned string-pulling tasks can be beneficial. By observing how birds make decisions when using two or more strings in complex

positions and with varying lengths, materials, or colours, we can delve deeper into their cognitive processes and determine whether they pay attention to connectivity and continuity.

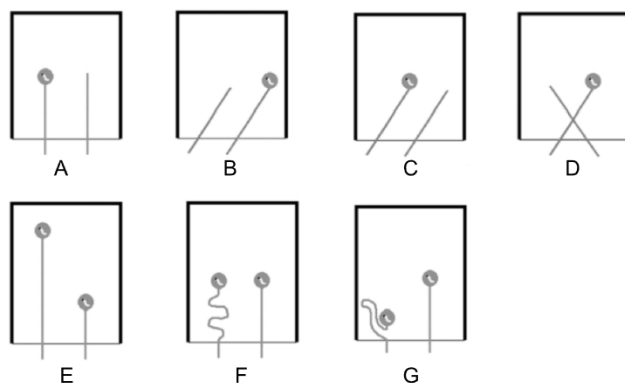


Figure 2: patterned string-pulling conditions. A - parallel, B - slanted, C - slanted with a reward appearing above the unbaited string, D - crossed, E - two straight strings with one being shorter, F - longer coiled string appearing to be the same length as the second one, G - longer coiled string appearing closer than the second string (Hofmann et al., 2016)

There are countless patterned string-pulling task configurations (**Figure 2**). The simplest scenario involves two parallel strings; in some cases, there may be more (Bagotskaya et al., 2012; Obozova et al., 2014; Ortiz et al., 2019). One of these strings connects to a reward. The two parallel strings can be slanted, which creates two situations: the reward is in front of the rewarded string or the unrewarded string, with the latter being more perplexing for the subject (Bagotskaya et al., 2012). The strings can also converge in the middle without touching each other (Danel et al., 2019). Alternatively, they can cross each other, bringing the reward in front of the end of the empty string (Bagotskaya et al., 2012; Hofmann et al., 2016; Krasheninnikova, 2013; Wang et al., 2019). The strings can be the same colour, making it harder for the birds to distinguish between them (Krasheninnikova, 2013) or they can differ in colour, which makes it easier to track them separately, as the birds can associate the coloured end of the string with the reward (Werdenich & Huber, 2006). However, the baited strings' position and colour are pseudorandomised, so it cannot be the answer throughout the experiment (Schuck-Paim et al., 2009). Furthermore, randomising the order in which we present the tasks to the birds can also prevent memorisation (Wakonig et al., 2021).

Sometimes, an object, such as a wood block or a rock, can be at the end of the unrewarded string (Werdenich & Huber, 2006). There may be combinations of the food and the other item placement to observe if the birds exhibit economic behaviour by choosing the option requiring the least effort (Pfuhl, 2012). We can also examine economic reasoning by presenting the birds with strings of different lengths (Krasheninnikova, 2013). Slacking one of the strings to appear shorter complexifies this pattern even more and tests for self-control (Hofmann et al., 2016; Wang et al., 2019). An extreme example of a length difference between strings is offering a string so long that the subjects can access the reward from the ground (Krasheninnikova et al., 2013; Werdenich & Huber, 2006). In other studies, researchers used a heavy food item to see whether the birds would recognise they could not pull it up and would not even try (Pfuhl, 2012; Werdenich & Huber, 2006).

Another scenario involves one string connected to a reward and another disconnected from the reward (**Figure 3**) (Bagotskaya et al., 2012; Danel et al., 2019; Obozova et al., 2014). They usually are the same length or can differ, with the baited string being longer (Krasheninnikova & Schneider, 2014). There are more possible setups than the two strings being next to each other. Both strings can be coiled, making it impossible for the birds to receive weight cues and eliminating positive perceptual feedback in the first few pulls (Bastos et al., 2021). In other cases, the baited string is at an angle, making the bait appear closer to the unrewarded string, presenting the task as a classic broken string

test (Bagotskaya et al., 2012; Wang et al., 2020a). Lastly, a pull-down string-pulling task can also implement the broken string condition (Ortiz et al., 2019).

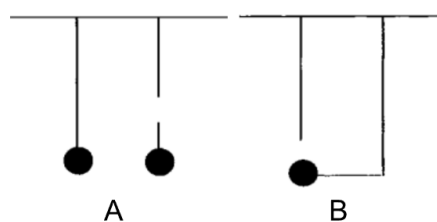


Figure 3: A - classic broken string condition, B - baited angled string with a reward appearing above the unbaited string (Bagotskaya et al., 2012)

Similarly to single string-pulling tasks, birds can alternatively succeed in patterned string-pulling tasks using trial-and-error learning and improve after adequate trials (Wasserman et al., 2013). However, that is only the case in some situations, as some birds fail by choosing randomly throughout the experiment and withhold from switching (Heinrich, 1995). The potential causes may include side or colour biases that birds can develop during the experiment (Hofmann et al., 2016; Molina et al., 2019; Wakonig et al., 2021). Others, on the contrary, seem to solve the tasks thanks to proximity bias as they prefer to choose the string closest to the reward (Hofmann et al., 2016; Wakonig et al., 2021; Wang et al., 2020a).

Apart from the experimental setup, other variables like the age and sex of the subject, previous experience with the task and rearing conditions can also influence the results (Pfuhl, 2012; Vince, 1958), while exploratory behaviour does not seem to play a role (Cole et al., 2011). In addition, whether the testing takes place individually (Danel et al., 2019), in pairs (Schuck-Paim et al., 2009), or a group (Krasheninnikova & Wanker, 2010) is also relevant. When the birds interact with apparatus alone, they can focus more on the task (Heinrich, 1995). However, some species can be more neophobic as they usually encounter problems together in the wild (Krasheninnikova & Schneider, 2014). Moreover, social learning can occur in a group setting and influence individual results (Krasheninnikova, 2013). Lastly, the subjects' motivation should also be considered, as the birds would not cooperate when not rewarded accordingly (Cole et al., 2011).

2.1.1 Columbiformes

Pigeons are rarely subjects for string-pulling experiments as they are mainly known for their discrimination and categorisation skills (Castro & Wasserman, 2014; Rayburn-Reeves et al., 2011). Schmidt & Cook (2006) tested transfer skills between two unconnected task arrangements. Their results showed that the birds could solve the tasks but relied on perceptual cues. They suggested that it may be more efficient for the pigeons to rely on trial-and-error learning rather than to understand the means-end problems as they presumably do not have to encounter them often.

Other studies (Brzykcy et al., 2014; Wasserman et al., 2013) presented the string-pulling task in a virtual environment (**Figure 4**). This model allows thousands of trials and gives the pigeons more time to solve various patterned string-pulling tasks. The birds achieved 90% of successful choices in parallel conditions at the end of the last session. In slanted conditions, this percentage dropped to 62% and 83% for collinear and noncollinear conditions, respectively. The same trend was observed for convergent and divergent conditions. Collinearity was a significant cue that misled the birds as the reward appeared above the unrewarded string in the collinear alignment. These results suggest they adopted a proximity rule. However, the birds reached 74% accuracy in crossed strings tasks which they faced intermixed with all the other tasks indicating they appreciated connectedness to some extent

(Wasserman et al., 2013). This assumption further supports their performance in a gap task where they reached 86% accuracy at the end of the last session (Brzykcy et al., 2014).

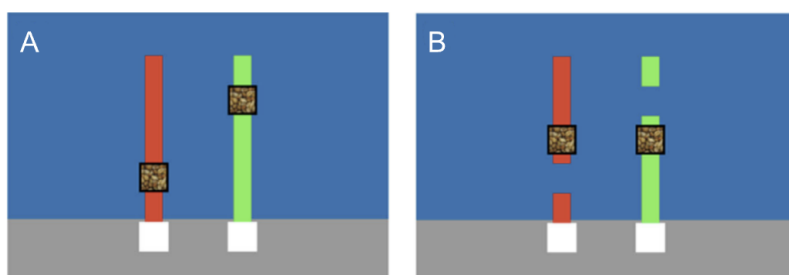


Figure 4: string-pulling tasks in a virtual environment. A - short vs long string condition, B - broken string condition (Brzykcy et al., 2014)

All of the abovementioned studies comprised only four subjects, who did not solve the tasks spontaneously and required a substantial number of sessions to reach the accuracy scores. In conclusion, although pigeons did not show a profound understanding of task properties, their success confirms that they have demonstrable skills in some variations of the string-pulling task. However, more individuals need to be tested to better understand the string-pulling abilities of this species. Additionally, a virtual testing environment proved effective in studying the string-pulling paradigm and could be presented to more bird species.

2.1.2 Charadriiformes

Lamarre & Wilson (2021) conducted the only study of string-pulling in Charadriiformes. Specifically, they tested ring-billed gulls (*Larus delawarensis*). These birds are social, monogamous, long-lived species with delayed maturity, similar to parrots and corvids. However, they are non-perching and do not use their feet to manipulate food. Therefore, this study used a horizontal setup.

One hundred four individuals were tested in the wild in their nests. The test apparatus consisted of a transparent plastic box associated with food through a series of habituation trials where researchers placed sausage pieces at the edge of the box and in the open box on a petri dish connected to a ribbon.

A quarter of the subjects succeeded at least once in the three trials, with 22 achieving the reward in their first trial and three individuals succeeding twice. Due to the uncontrollable testing conditions, some birds underwent testing all three times, and some only once. In addition, researchers could not eliminate possible social learning occurrences or control for birds' food drive.

Due to the low number of trials and previously described conditions, further research is needed to clarify the processes behind the birds' success. Whether they succeeded by accident or learned by trial and error is unclear. Nevertheless, they could be promising candidates for horizontal patterned string-pulling tasks in future studies as we need more data on this taxon.

2.1.3 Strigiformes

Despite owls having large relative and absolute brain sizes (van Overveld et al., 2022), relatively high neuron density (Kverková et al., 2022), a long lifespan and delayed maturity, they were tested only in one study (Obozova & Zorina, 2013). Twelve great grey owls (*Strix nebulosa*) participated in a single string-pulling task. Six succeeded in a group setting, and out of those, five in an individual setting afterwards. In a broken string task, only one owl performed above chance levels.

However, this task's methods were incorrect as the birds did not need to grab the string's end and could reach the reward underneath the barrier. The only successful bird did precisely that and succeeded without needing to understand the task's properties.

Undoubtedly, more research needs to be conducted testing Strigiformes to draw conclusions about their cognitive abilities regarding string-pulling.

2.1.4 Accipitriformes

Hawks and vultures belong to another understudied and overlooked taxon with many qualities indicating their potential for high cognitive abilities. They have a long lifespan, delayed maturity, hunt or scavenge for unpredictable and scarce food and have relatively big brain sizes (van Overveld et al., 2022) and high neuron density (Kverková et al., 2022).

One Harris's Hawk (*Parabuteo unicinctus*) was tested in a single vertical string-pulling task (Colbert-White et al., 2013). It successfully retrieved the reward in all eight trials using different techniques and showing an apparent learning curve with its efficiency increasing across trials.

Turkey Vultures (*Cathartes aura*) also faced a simple vertical string-pulling task (Ellison et al., 2015). Four out of six birds showed high levels of neophobia, with dominant birds not approaching the test apparatus before the less dominant ones. Two birds spontaneously solved the task on their first trial and another after watching a conspecific, demonstrating their potential social learning capacity. Interestingly, they all used a novel pulling technique: teasing the string through their beak using their tongue until they could reach the reward. Furthermore, their efficiency improved as their time to solve the task significantly decreased throughout trials.

In short, Accipitriformes show great potential as subjects for future research as they have demonstrated the ability to pull strings using various techniques, sometimes without any trial-and-error learning.

2.1.5 Bucerotiformes

Hornbills have the potential to perform well in cognitive tasks as they have relatively large brain sizes, delayed maturity, and a complex social system. Additionally, they are flexible foragers, sometimes catching the prey using pulling actions (Danel et al., 2019).

They were the subjects of one string-pulling-based study by Danel et al. (2019). She and her team tested three subjects, one northern ground hornbill (*Bucorvus abyssinicus*) and two southern ground hornbills (*Bucorvus leadbeateri*), in five horizontal patterned string-pulling tasks. Two birds solved parallel and convergent string tasks with more than 75% accuracy, and one solved the broken-string task with the same accuracy. None of the birds solved the connection problem where the disconnected strings overlapped. One individual showed a strong side bias. In the coiled condition, with both strings rewarded, all subjects completed all trials. However, the birds unnecessarily switched from their initial choice in most trials when they noticed the reward did not move. Nevertheless, they finished pulling the string despite no initial visual feedback.

To sum up, hornbills demonstrated the ability to solve a few patterned string-pulling tasks while failing others. Nevertheless, future research with more subjects is needed to determine their physical cognition level better.

2.1.6 Psittaciformes

Parrots are subjects of countless experiments, including string-pulling tasks, as they possess versatile beaks, which they use for foraging and climbing and strong zygodactyl feet with fine motor skills (O'Neill, 2020). Additionally, their brain is relatively big with high neuron density (Iwaniuk et al., 2005), and they usually live in highly complex social groups (Krasheninnikova et al., 2013). Some parrots are also known to be very playful (Gajdon et al., 2014) and neophilic (Auersperg et al., 2011), which might be the reason behind their success, as they actively participate in almost every experiment.

Overall, all tested species were highly successful in a vertical single string-pulling task. Still, interspecific differences can be found, as all galahs (*Eolophus roseicapilla*) (Krasheninnikova, 2013) and orange-winged amazons tested (*Amazona amazonica*) (Krasheninnikova & Schneider, 2014) solved the task, whereas only 80% of rainbow lorikeets (*Trichoglossus haematodus*) (Krasheninnikova et al., 2013), 66% of wild kaka (*Nestor meridionalis*) (Loepelt et al., 2016), and no budgerigars (*Melopsittacus undulatus*) or cockatiels (*Nymphicus hollandicus*) (Magat & Brown, 2009) succeeded. However, cockatiels performed well in another study by Krasheninnikova (2013), implying that they can solve the task and that we cannot always rely on a single study to conclude a species's ability in a given task.

Spectacled parrotlets (*Forpus conspicillatus*) (Krasheninnikova & Wanker, 2010), keas (*Nestor notabilis*) (Werdenich & Huber, 2006) and green-winged macaws (*Ara chloroptera*) (Gaycken et al., 2019) solved a vertical single string-pulling task spontaneously on their first trial in under 20 seconds. However, the last mentioned species did not solve a transfer pull-down task even after having experience with classic string-pulling, indicating that means-end understanding probably did not occur (Gaycken et al., 2019). Only some peach-fronted conures (*Eupsittula aurea*) could reliably solve the pull-down task (Ortiz et al., 2019).

One study proposed an unconventional way to solve a single string-pulling task using learned referential language (Pepperberg, 2004). African grey parrots (*Psittacus erithacus*) trained to ask for objects tried this strategy instead of attempting to pull the string, whereas those with limited vocabulary pulled the string immediately.

Parrots underwent many patterned string-pulling tasks as well. In the parallel condition, most individuals made little to no mistakes (Krasheninnikova et al., 2013; Schuck-Paim et al., 2009; Wakonig et al., 2021; Werdenich & Huber, 2006). In a slanted condition where the reward appeared above the empty string, and the birds could not use a proximity rule, keas (Werdenich & Huber, 2006) and peach-fronted conures (Ortiz et al., 2019) performed surprisingly well.

The results differ in short versus long string conditions. Most orange-winged amazons, galahs, and cockatiels chose the shorter string (Krasheninnikova, 2013; Krasheninnikova & Schneider, 2014), while Goffin's cockatoos (*Cacatua goffiniana*) did not (Wakonig et al., 2021). These results could be due to no significant disadvantage in choosing the longer string as it may not require a disproportionate effort. In an overlength task where the incorrect solution did require substantially more energy, most individuals continued to pull the string regardless, and only a few took the reward from the ground (Krasheninnikova et al., 2013; Ortiz et al., 2019; Werdenich & Huber, 2006). Only keas were tested in an overload task, and their accuracy reached 93% in 20 trials (Werdenich & Huber, 2006).

In a broken string condition, the results varied depending on the length of the broken string. Orange-winged amazons succeeded immediately (Krasheninnikova & Schneider, 2014), while peach-fronted conures needed more trials in a task with the same length strings (Ortiz et al., 2019). When the broken string was short, only galahs solved the problem and others, such as green-winged macaws and sulphur-crested cockatoos (*Cacatua galerita*), failed (Krasheninnikova et al., 2013). One budgerigar solved an angled broken string condition with an average accuracy of 80% (Dücker & Rensch, 1977). When the strings were coiled, keas (Bastos et al., 2021) and African grey parrots (Molina et al., 2019) failed in their initial choice, while hyacinth's (*Anodorhynchus hyacinthinus*) and Lear's macaws (*Anodorhynchus leari*) succeeded (Schuck-Paim et al., 2009).

Most species struggled with crossed-string conditions regardless if they were coloured the same or different (Dücker & Rensch, 1977; Krasheninnikova & Schneider, 2014; Ortiz et al., 2019). Sometimes, birds even chose the empty string significantly above chance, indicating they tried to use a proximity rule (Schuck-Paim et al., 2009; Wakonig et al., 2021). Nevertheless, cockatiels, rainbow lorikeets, sulphur-crested cockatoos and green-winged macaws solved the task only when strings differed in colour (Krasheninnikova, 2013; Krasheninnikova et al., 2013). Three species solved this more straightforward version and also the more complicated version with uniformly coloured strings. These include galahs, spectacled parrotlets and keas (Krasheninnikova et al., 2013, 2013; Werdenich & Huber, 2006).

In conclusion, most parrot species were able to complete the single string-pulling and simpler patterned string-pulling tasks with ease. Only the peach-fronted conures solved the pull-down task, keas the overlength and overload task, one budgerigar the angled broken string condition, hyacinth's and Lear's macaws the coiled condition, and six species solved the most challenging conditions with crossed strings.

2.1.7 Passeriformes: Corvidae

Corvids are a distinct passerine group frequently studied in string-pulling tasks mainly because of their innovativeness, playfulness and well-known ability to solve problems requiring complex physical cognition (Auersperg et al., 2014; von Bayern et al., 2018). Similarly to parrots, they possess relatively large brains with high neuron density (Olkowicz et al., 2016) and are long-lived and monogamous. However, they have differing ecology and anatomy, such as less curved beaks that can be more effective in object manipulation and anisodactyl feet, which are less efficient (Auersperg et al., 2011).

The results greatly varied among species and individuals in a single string-pulling task. Three out of four New Caledonian crows (*Corvus moneduloides*) (Taylor et al., 2010), three out of 27 American crows (*Corvus brachyrhynchos*) (Pendergraft et al., 2020), four out of eight hooded crows (*Corvus cornix*) (Obozova et al., 2014) and one oriental magpie out of eight (Wang et al., 2020a) succeeded spontaneously in their first trial. Other species' success ranged from 100% in azure-winged magpies (*Cyanopica cyanus*) (Wang et al., 2019), 83% in captive common ravens (*Corvus corax*) (Heinrich & Bugnyar, 2005), 60% in green jays (*Cyanocorax yncas*) (Manrique et al., 2017), to 25% in wild-caught common ravens (Heinrich, 1995). In some cases, the unsuccessful birds succeeded after observing a conspecific or after training by gradually lengthening the string (Pendergraft et al., 2020; Wang et al., 2020a).

Experience is a highly influential factor regarding variations on single string-pulling tasks. In a pull-down task, only common ravens already proficient in pulling up a string succeeded (Heinrich & Bugnyar, 2005). As for a visually restricted task, all green jays solved it even more quickly than the previous string-pulling tasks (Manrique et al., 2017). New Caledonian crows struggled more with the task, but all of the experienced New Caledonian crows succeeded, and so did half of the naive ones when they had access to a mirror (Taylor et al., 2010). The mirror helped them track the reward's position, which they otherwise could not see. However, when they had no experience with string-pulling and no mirror providing visual feedback, only one individual out of four solved it through trial-and-error learning.

A single tested western jackdaw (*Coloeus monedula*) and two green jays performed below chance levels in the parallel condition (Dücker & Rensch, 1977; Manrique et al., 2017). Common ravens in one study chose the unrewarded string but never fully retrieved it and switched their initial choice (Heinrich, 1995), but in another, 75% succeeded immediately (Bagotskaya et al., 2012). The successful solvers comprised all New Caledonian crows (Taylor et al., 2010), 75% hooded crows (Bagotskaya et al., 2012), 60% California scrub jays (*Aphelocoma californica*) (Hofmann et al., 2016), 50% Eurasian jays (*Garrulus glandarius*) (Baciadonna et al., 2022), 33% azure-winged magpies (Wang et al., 2019) and one oriental magpie out of eight (Wang et al., 2020a).

When the task involved one baited string out of four, all common ravens and all hooded crows performed above chance levels, with some birds even reaching an accuracy of 94% (Bagotskaya et al., 2012; Obozova et al., 2014). The more straightforward version of the slanted condition did not pose a problem for most corvids, as all New Caledonian crows, common ravens, California scrub jays and 75% of hooded crows solved it (Bagotskaya et al., 2012; Hofmann et al., 2016; Taylor et al., 2010). In contrast, in the more perplexing slanted condition, birds struggled (Manrique et al., 2017; Wang et al., 2020a), with only half of the hooded crows (Bagotskaya et al., 2012) and one magpie being able to solve it accurately (Wang et al., 2019).

All New Caledonian crows and most common ravens inhibited themselves from pulling an overweight object and pulled the string with achievable reward (Heinrich, 1995; Pfuhl, 2012; Taylor et al., 2010). However, corvids did not behave economically in all the long versus short-string tasks. In the classic one, 50% of azure-winged magpies (Wang et al., 2019), 40% of common ravens (Pfuhl, 2012) and one magpie out of eight preferred the shorter string (Wang et al., 2020a). When the task increased in complexity and the long string was slacked, the birds mainly chose at random levels as the cost of error was not high enough or the proximity of the reward was irresistible (Hofmann et al., 2016). The same outcome applied to a task where a piece of meat and wood were attached to strings in different combinations (Pfuhl, 2012).

The broken string condition was solved by 75% of hooded crows (Bagotskaya et al., 2012; Obozova et al., 2014), 50% of azure-winged magpies (Wang et al., 2019) and none of the oriental magpies (Wang et al., 2020a). When the strings were coiled, New Caledonian crows failed as they did not even pull the reward in a way so it would move closer (Taylor et al., 2010). In the angled broken string condition, 66% of azure-winged magpies (Wang et al., 2019) and 50% of hooded crows solved it (Bagotskaya et al., 2012), with one oriental magpie reaching the criterion after trial-and-error learning (Wang et al., 2020a).

Apart from one, none of the birds could solve any crossed strings tasks (Manrique et al., 2017;

Taylor et al., 2010; Wang et al., 2020a). Only one common raven solved the task with 80% accuracy when the strings were coloured the same (Heinrich, 1995). Others chose randomly (Hofmann et al., 2016; Taylor et al., 2010) or relied on a proximity rule and preferred the unrewarded string significantly more often (Manrique et al., 2017; Wang et al., 2019).

Despite evident intra-specific differences, most corvid species solved the single string-pulling and simple patterned string-pulling tasks. In the pull-down task and visually restricted task, subjects needed previous string-pulling experience or visual aid in the form of a mirror. Most birds solved the overload and the broken string tasks but struggled with unevenly long, coiled and crossed strings.

2.1.8 Passeriformes

Researchers primarily tested passerines other than Corvidae on a vertical single string-pulling task. These studies showed that different passerine species could pull the string spontaneously or learn it after training (Vince, 1961). The results varied considerably among closely related species, with 43% of Barbados bullfinches (*Loxigilla barbadensis*) and only 6% of Carib grackles (*Quiscalus lugubris fortirostris*) completing the task (Audet et al., 2016). Similarly, 23% of European goldfinches (*Carduelis carduelis*) and 62% of Eurasian siskins (*Carduelis spinus*) succeeded by themselves with an additional 25% and 10%, respectively, completing the task after observing a conspecific (Seibt & Wickler, 2006). Some individuals were interested in the string and only sometimes exhibited goal-directed behaviour (Seibt & Wickler, 2006; Vince, 1961). However, in other individuals, the ability to pull the string was food directed and consistent across time, as 80% of great tits (*Parus major*) succeeded again after one year (Cole et al., 2011). Also, in a study with 570 individuals, neophobia or exploratory behaviour did not correlate with string-pulling skills, whereas natal origin and age slightly did (Cole et al., 2011). Vince (1958) revealed even more apparent differences in success between ages, as no canary (*Serinus canaria forma domestica*) or greenfinch (*Chloris chloris*) adults succeeded, while some juveniles did.

Only a few studies presented the birds with patterned string-pulling tasks. In a vertical task with one baited string out of four, blue tits (*Cyanistes caeruleus*) performed flawlessly, and red crossbills (*Loxia curvirostra*) made only a few mistakes and maintained over 80% accuracy (Obozova et al., 2014). None of the birds succeeded in vertical crossed and broken string tasks. Some Estrilid finches (*Taeniopygia guttata*, *Lonchura striata var. domestica*, *Stagonopleura guttata*) succeeded in the latter task, with 25% of them solving it in their only trial (Schmelz et al., 2015). Significant differences existed between species but not between four strains of genetically separated Zebra finches. The study methodology differed as the apparatus used plastic tubes with strings lying inside them, which could make the task more accessible.

On the other hand, a single Indian myna (*Acridotheres tristis*) displayed a different way of solving the string-pulling tasks (Dücker & Rensch, 1977). At first, it seemed to complete multiple horizontal tasks where strings were parallel, slanted and crossed with 100% accuracy. However, this perfect performance was due to attending to a visual cue on the rewarded string, a greyish spot. After replacing the string, the bird's performance dropped to a random chance level and remained like that regardless of the task throughout a thousand subsequent trials. Nevertheless, it has to be said that this study consisted of only one subject, unlike the others, and we cannot draw any general conclusions about the species.

To sum up, most passerines other than Corvidae exhibited the ability to pull a single string and solve certain patterned string-pulling tasks. Tits performed equally well as finches and their allies, whereas starlings were unsuccessful. Nonetheless, the findings suggest that the birds primarily relied on a proximity rule or visual cues rather than causal relationships. Further research is required to explore more cross-taxon similarities and differences.

2.1.9 Summary

Available data suggest that most bird species can pull a single string. However, we need more research on the remaining bird taxa. Therefore, it is problematic to generalise birds' performance. Tested birds used different techniques when solving the tasks as they pulled the string upwards, sideways or teased it through their beaks in the case of vultures (Ellison et al., 2015; Werdenich & Huber, 2006).

In patterned string-pulling tasks, parrots, specifically keas, were highly successful, as they reached over 90% accuracy in most of the tasks they faced, including crossed strings tasks (Werdenich & Huber, 2006). Similar performance was reported for corvids which did overall well, with one hooded crow (Bagotskaya et al., 2012) and one azure-winged magpie (Wang et al., 2019) completing most of the tasks. Similarly, hornbills achieved success in multiple patterned string-pulling tasks. In contrast, only blue tits, red crossbills and individual Estrilid finches solved simpler patterned string-pulling tasks, while other passerines other than Corvidae failed. Individual great grey owls also succeeded, but their success was most likely due to an incorrect methodology. Pigeons, on the other hand, succeeded in many tasks but probably thanks to trial-and-error learning. A single hawk, vultures and ring-billed gulls underwent only a simple string-pulling task, thus, more research needs to be done before drawing further conclusions.

Interestingly, sometimes birds solved the more complex tasks and had difficulties solving the more straightforward ones (Bagotskaya et al., 2012; Krasheninnikova et al., 2013), possibly due to insufficient exposure at the time. One option for future studies could be to prolong the exposure of subjects to the tasks overall. Regarding poor performances in the more complex tasks, it is plausible that birds were influenced by their previous experience in a different task and needed more time to realise that their strategy was no longer successful, an ability which could be associated with behavioural flexibility. In general, birds took different approaches to solve the tasks. They either chose randomly, followed perceptual cues, used a proximity rule even when it meant always choosing wrong, or, in the case of keas, galahs, spectacled parrotlets and a single raven, understood connectedness and continuity and followed the rewarded string's path.

2.2 Reasoning by exclusion

The reasoning by exclusion task is usually a two-item choice task in which the experimenter demonstrates one item as unrewarded, leaving the other item the only possible solution. Put simply, if it is not A, it must be B. The task can focus on visual (Mikolasch et al., 2012b; Tornick & Gibson, 2013) or acoustic modality (Danel et al., 2022a; Schloegl et al., 2012; Shaw et al., 2013). The latter is considered more demanding as birds must first infer that food produces noise and then decide based on its presence or absence (Schloegl, 2011).

Typically, the task involves two cups, with only one containing a reward (**Figure 5A**). Alternatively, both cups can be baited at first, with one of the baits thrown out during the demonstration (Mikolasch et al., 2011, 2012b). The demonstration of the cups can be in the subject's sight (visible condition) (Mikolasch et al., 2012b), or the subject can only see its results (invisible condition) (Mikolasch et al., 2011). The cups can be presented simultaneously or one by one, with the manipulation order having an impact on the subjects' decision, as birds tend to remember and focus on the last manipulated cup (Mikolasch et al., 2012a). This phenomenon may be attributed to the movement acting as a local enhancement (Mikolasch et al., 2012b), which can be reduced by touching both cups during manipulation (Danel et al., 2021). On the other hand, placing a small, opaque or transparent cup underneath the main cups eliminates the local enhancement effect completely (Mikolasch et al., 2012b).

The experiment typically contains multiple testing conditions. One condition involves both cups being lifted, which provides complete information about the reward's position. Another condition involves only the empty cup being lifted, which creates an exclusion condition. Alternatively, only the baited cup can be lifted, forming a baited condition (Tornick & Gibson, 2013). In addition, researchers usually add a control condition where none of the cups is lifted to control for olfactory cues and mix the order in which they present the conditions to the subjects (Schloegl et al., 2012). The task undoubtedly involves some level of object permanence as the cup conceals the reward, and the subject needs to realise it is still there even though it is not visible (Danel et al., 2021). This demand significantly limits the range of taxa that can undergo the task.

There are multiple strategies researchers believe the birds use to tackle this task. The most straightforward strategy requires solely learning to avoid the empty cup, thus processing information only about option B (Mikolasch et al., 2011). The other, more cognitively demanding strategy is to infer the location of the reward based on the given information (Danel et al., 2021). Although it is challenging to determine which strategy the subjects use as they are not necessarily exclusive (Jelbert et al., 2015), the latter would exhibit spontaneous success, while avoidance learning should take time (Schloegl et al., 2009).

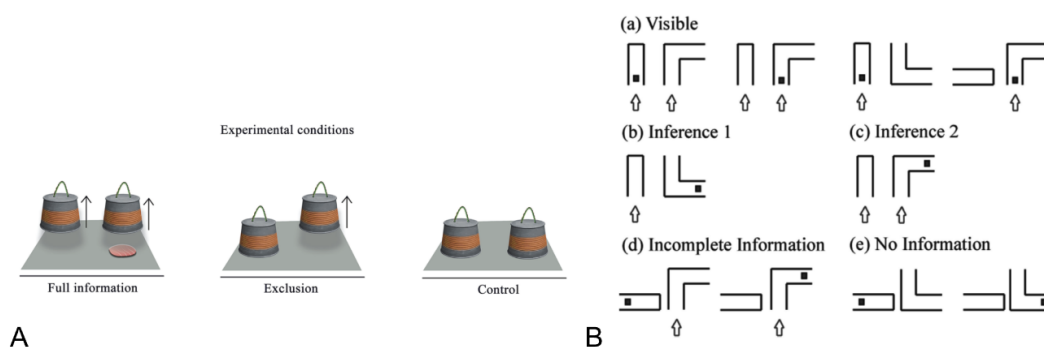


Figure 5: A - classic two-cup task (Danel et al., 2021), B - two-tubes task (Jelbert et al., 2015)

Another way to control for avoidance versus exclusion strategy is to introduce a task with straight and bent tubes (**Figure 5B**) (Jelbert et al., 2015; Schloegl et al., 2009). Here the birds can see different parts of the tubes being empty and need to realise without any further inspections that the reward can be in the other part of the bent tube, thus not avoiding an empty tube.

2.2.1 Columbiformes

Pigeons are often believed to learn only perceptual properties in discrimination tasks rather than the logic behind them (Maes et al., 2015). They underwent two slightly modified reasoning by exclusion experiments using touchscreens to investigate whether they could infer and exclude logically.

In a study by Clement & Zentall (2003), pigeons were first trained on a matching-to-sample task. Later, they received trials where the sample and one of the two comparisons were new. Birds had to exclude the one comparison they had already learned to associate with the previous sample and choose the novel stimulus, which they did in 72% of trials. Aust et al. (2008) implemented a differing methodology, where birds had to first discriminate between S+ and S- stimuli and afterwards prefer a novel stimulus S' when presented with an S- stimulus. Only one bird succeeded, but its success was later linked to neophilia as the bird chose another novel stimulus in the same comparison.

Indeed, more research is needed as testing pigeons in the classic cups task could bring new valuable information. Moreover, their success in the first task could also be due to neophilia, as the researchers did not specifically control for it.

2.2.2 Charadriiformes

Brown skuas (*Stercorarius antarcticus*) were tested in two recent studies. One focused on visual modality (Danel et al., 2021), while the other on acoustic modality (Danel et al., 2022a). Both studies were performed in the field and used wild-ranging individuals of this long-living, highly innovative species.

One-fourth of the birds solved the exclusion condition in the visual experiment. The birds exhibited side biases and learning across trials as their performance slowly improved. Nevertheless, some birds succeeded in their first trial, suggesting they used reasoning by exclusion and not an avoidance strategy.

The acoustic experiment posed a greater challenge for the birds. When both cups were shaken, they found identifying the baited cup in the full information condition difficult, and only one bird succeeded in the exclusion condition. This bird reached an accuracy of 85%, was successful in the first trial and did not show any apparent learning. Therefore it seems that brown skuas can reason by exclusion with acoustic cues, and more research needs to determine whether this ability is more prevalent in the species.

2.2.3 Bucerotiformes

Southern ground-hornbills (*Bucorvus leadbeateri*) underwent both visual and acoustic experiments (Danel et al., 2022c). They are opportunistic foragers spending most of their time scanning for food on the ground, thus, the ability to reason by exclusion could be beneficial, as it could help them exclude already scanned locations when searching for prey.

None of the birds solved the acoustic experiment. In the visual experiment, over a third of the birds solved the exclusion condition significantly above chance, most of them in their first trial. No apparent learning occurred, making it plausible that southern ground-hornbills can reason by exclusion.

2.2.4 Psittaciformes

Parrots are very exploratory and neophilic birds. Thus, the experimenter's contact should not hinder their performance, but they could still be sensitive to local enhancement. That was likely the case with keas (*Nestor notabilis*), who failed the classic two-cup task as they at least partially attended to the experimenter's movements and chose by chance (Schloegl et al., 2009). Red-tailed black cockatoos (*Calyptorhynchus banksii*) succeeded, but the reward was in the experimenter's hands instead of cups, and the birds could pick up on inadvertent cues (Subias et al., 2019).

When the two-cup task involved object manipulation, African grey parrots (*Psittacus erithacus*) failed in one study (Mikolasch et al., 2012a) and, in contrast, succeeded in another study (Mikolasch et al., 2011). In the former, their performance improved when they were given a delay of ten seconds before choosing, but local enhancement still impacted them, and they seemed to lose attention. In the study by Pepperberg et al. (2013), all birds succeeded even when sometimes only a part of the reward was removed, as they kept track of the number of treats under each cup and reasoned by exclusion whenever needed. Furthermore, one African grey parrot succeeded spontaneously in a four-cup task (Pepperberg et al., 2019). Also, this parrot species solved an acoustic experiment spontaneously with no apparent learning (Schloegl et al., 2012).

Only keas faced the two-tubes task, where they showed reasoning by exclusion in only 4% of trials (Schloegl et al., 2009). They were more inclined to investigate both tubes before choosing, presumably due to their exploratory nature and no cost of such a decision.

To control for neophilia and exploratory behaviour, researchers gave keas and Goffin's cockatoos (*Cacatua goffiniana*) a two-choice task in a virtual environment (O'Hara et al., 2015a; O'Hara et al., 2016). Most birds in both studies succeeded, though they simultaneously used other less cognitively demanding strategies, and only one kea chose solely by exclusion (O'Hara et al., 2016).

In summary, parrots seem to not rely heavily on reasoning by exclusion. Only red-tailed black cockatoos and some African grey parrots succeeded in a classic two-cup task, while other species needed the experiment to be transferred into a virtual environment.

2.2.5 Passeriformes: Corvidae

Corvids are, with some exceptions, caching birds, which requires them to ideally exclude empty sites and visit the ones that contain food (Schloegl, 2011). They must also overcome local enhancement when they see conspecifics at a site, as they will probably retrieve all the food there. Therefore, many researchers attempted to find parallels between the ability to reason by exclusion and dependency on caching in corvids (Mikolasch et al., 2012b).

In a classic version of the two-cup task, Clark's nutcrackers (*Nucifraga columbiana*), which are intensive cachers, succeeded spontaneously and averaged 88% accuracy (Tornick & Gibson, 2013), while regularly caching ravens (*Corvus corax*) solved it with 67,5% accuracy (Schloegl et al., 2009). On the other hand, non-caching jackdaws (*Coloews monedula*) (Schloegl, 2011) and caching Eurasian jays (*Garrulus glandarius*) failed, with the latter also failing in the acoustic version of the task (Shaw et al., 2013).

When the task involved a visible manipulation of the contents of the cups, the setup proved difficult for jackdaws (Mikolasch, 2012; Schloegl, 2011) and carrion crows (*Corvus corone*) (Mikolasch et al., 2012b). Researchers implemented modifications designed to decrease local

enhancement bias, but not all of them worked. Jackdaws' performance slightly improved when they had to wait ten seconds before choosing (Mikolasch et al., 2012a), but they failed when smaller cups were placed underneath the larger cups. Carrion crows, on the other hand, succeeded when the second condition was implemented (Mikolasch et al., 2012b). In an invisible condition, Clark's nutcrackers failed when the rewards were unequally favoured food rewards, as they constantly chose the side their favourite one was on, regardless of the cue they were given. However, one individual consistently succeeded when the rewards were equally favoured toys (Tornick & Gibson, 2013).

In the two-tubes task, only a few New Caledonian crows (*Corvus moneduloides*) chose entirely based on exclusion, while others also employed an avoidance strategy (Jelbert et al., 2015). Ravens and jackdaws used reasoning by exclusion only in 19% and 8% of trials, respectively (Schloegl, 2011; Schloegl et al., 2009).

To conclude, many corvid species were attentive to the local enhancement and only succeeded after researchers modified the tasks. However, Clark's nutcrackers demonstrated the capacity to perform well in a classic setup and succeed in an invisible condition. At last, only New Caledonian crows chose consistently by exclusion in the two-tubes task.

2.2.6 Cuculiformes

Riehl et al. (2015) studied reasoning by exclusion in a unique setup. They tested whether cooperatively breeding Greater ani (*Crotophaga major*) could infer that an egg could not be theirs and remove it. In a typical scenario, female A of this cuckoo species lays an egg in a shared nest, and female B removes it and lays her own. After that, both females continue laying eggs and share parental responsibilities. Researchers interfered in this process by removing eggs after each of the two females laid at least one. They hypothesised that the birds would repeat the same process but revealed that female B did not remove the relaid egg of female A even though it could not be hers. All five Greater ani failed to show reasoning by exclusion. However, this performance could be related to hormonal status rather than cognitive abilities, and more research is needed to draw any conclusions.

2.2.7 Summary

Many tested species demonstrated the ability to reason by exclusion, with the most spontaneous solvers being Clark's nutcrackers, red-tailed black cockatoos and Southern ground-hornbills. On the other hand, some species, like greater ani and Eurasian jays, failed. Conditions like the invisible two-cups and two-tubes tasks were more difficult than others as they prohibited the subjects from using a simpler avoidance strategy. Touchscreen tasks, on the other hand, helped parrots to concentrate better on the properties of the task instead of being distracted by neophilic tendencies and local enhancement. Pigeons also succeeded when tested with touchscreens, but probably only thanks to their neophilia.

Local enhancement played the most prominent role for keas, a few African greys and many corvid species. Intra-specific differences were also prevalent as, for example, African grey parrots performed dissimilarly in multiple studies.

The capacity to reason by exclusion has been demonstrated in various distantly related bird taxa, and more research needs to be done to determine the underlying factors behind it. In corvids, the hypothesis that caching may correlate with their ability to reason by exclusion was not confirmed,

primarily due to the poor performance of Eurasian jays, which cache intensively but failed in the task. However, this could be attributed to the experimental setup that did not control for local enhancement. A more suitable experimental approach is needed to confidently accept or reject the caching hypothesis.

2.3 Transitive inference

The transitive inference task involves a form of logical reasoning and an excellent memory. The experiment usually consists of five (Daisley et al., 2021) to seven (Bond et al., 2003) stimuli in the form of coloured cards or cards with distinctive symbols. Unconventionally, the stimuli can be flags of different countries (Zentall et al., 2019). The stimuli form an overlapping series of dyadic comparisons - the subject has to discriminate between them and remember their hierarchy. The series is linear and ordered: $A > B > C > D > E$. The birds need to learn that one stimulus can be rewarded in one scenario and unrewarded in another when combined with novel stimulus - partial reversal learning (Weiß et al., 2010).

Only with training the transitive inference can be a valid concept, as birds need to learn the relations between each pair before they can infer the relation between a transitive pair BD (Lazareva & Wasserman, 2006). The method of the training can significantly influence the results. When the training is successive, birds face one pair, which, once learned, is added to the subsequent pair learning and so forth (Mikolasch et al., 2013; Steirn et al., 1995). Ultimately, the reinforcement history will not be equal among the stimuli, and birds can choose the one they have seen the most (Zorina et al., 1996). Alternatively, the four training pairs can be divided into two groups (AB + CD and BC + DE) and later intermixed (Wynne, 1997). Also, indefinite correction trials can change the frequency with which the birds encounter each stimulus (Wynne, 1997).

Birds can employ multiple alternative strategies. They can avoid the new stimulus when coming across a new dyad. However, such a strategy must be revised after the initial discrimination learning when presented with combinations of already-known stimuli (Weiß et al., 2010). Another tactic is to recall the relevant pairs. Engaging in this tactic would result in a first-item accuracy phenomenon - lower performance or increased latency if the objects were further in the sequence (von Fersen et al., 1991). However, that is only sometimes the case, as in many studies, birds reached higher accuracies the further the items were apart (Steirn et al., 1995). This phenomenon may be explained by value transfer theory (von Fersen et al., 1991). The value of stimulus A never diminishes, but the items lower in the series decrease in associative strength due to multiple partial reversals with all the previous comparisons.

2.3.1 Galliformes

Domestic chickens (*Gallus gallus domesticus*) are precocial birds with relatively small brains and a dominance hierarchy known as the pecking order (van Overveld et al., 2022). They were test subjects in two studies with artificial stimuli (Daisley et al., 2010, 2021) and one where conspecifics were the tested stimuli (Hogue et al., 1996). The latter study indicated that hens could infer their dominance status by observing agonistic interactions between their former dominant and a stranger.

In the other two studies, all the birds learned to discriminate between training pairs equally well. The differences emerged when birds faced non-adjacent pairs. In the transitive BD pair, the

strongly right-hemisphere lateralised birds performed better than the less lateralised birds (Daisley et al., 2010). Furthermore, Daisley et al. (2021) found a correlation in performances with sex and rank. Females outperformed males, with the lowest-ranking females performing the best. On the other hand, the highest-ranking males performed at chance levels, indicating that the ability to infer transitively is not necessary for them as they only have to focus on keeping their position.

2.3.2 Anseriformes

Weiß et al. (2010) tested five free-living greylag geese (*Anser anser*) in the transitive inference task. These birds are precocial like chickens and have relatively small brains (Iwaniuk & Nelson, 2003) with low neuron density (Kverková et al., 2022). They, too, live in large and stable flocks with dominance hierarchies, requiring them to track and infer relationships to know where they stand, thus making them promising candidates for the task.

All birds learned to discriminate between five colour stimuli in four training pairs but struggled across successive training as more stimuli were introduced. Also, some geese developed side and colour biases which were corrected during training. Interestingly, they kept their accuracy levels when retested after two and six months (Weiß & Scheiber, 2013). This remarkable long-term memory occurred even when twelve other individuals discriminated between seven stimuli and faced the task again in a year (Weiß & Scheiber, 2013).

Most subjects succeeded when presented with non-adjacent pairs (Weiß et al., 2010). They reached 87,5% accuracy in transitive pair BD. The further in sequence the items were, the higher the accuracy for non-adjacent pairs was. In some cases, that accuracy was higher than for the training pairs and even reached 100%.

2.3.3 Columbiformes

Pigeons (*Columba livia*) were part of most transitive inference-based studies. Despite their small brains (van Overveld et al., 2022) and moderate neuron density (Kverková et al., 2022), they are highly social and known for their high cooperation during operant conditioning and excellent long-lasting object recognition skills (Delius, 1992; Vaughan & Greene, 1984). Moreover, they are willing to complete thousands of trials without a decrease in motivation (Wynne, 1997).

Most birds successfully learned to discriminate between training stimuli (Lazareva & Wasserman, 2006; Steirn et al., 1995). When the training was successive, it prolonged the training process, and some birds did not reach the criterion to move to the testing phase (Wynne, 1997). However, those who did succeed in training performed significantly above chance levels in the non-adjacent pairs, including transitive pair BD (Steirn et al., 1995; von Fersen et al., 1991). This performance did not change even when researchers added a bias reversal phase and presented subjects with more DE trials attempting to manipulate the birds to choose D later in the transitive inference task (Lazareva & Wasserman, 2006). Furthermore, pigeons did not need ordered feedback stimuli after each trial and reached the same accuracy levels without it (Lazareva & Wasserman, 2006).

2.3.4 Passeriformes: Corvidae

Corvids differ in ecology and sociality among species. For example, pinyon jays (*Gymnorhinus cyanocephalus*) depend more on caching and form enormous stable flocks with a

dominance hierarchy. On the contrary, California scrub jays (*Aphelocoma californica*) rely less on caching and live in pairs with their offspring. A unique case is Clark's nutcrackers (*Nucifraga columbiana*), who cache intensively but live solitarily. Researchers believe that analysing these factors could explain differences in transitive inference performance (Bond et al., 2010).

All species succeeded in stimuli training, even with seven stimuli instead of five (Bond et al., 2003, 2010). Hooded crows (*Corvus cornix*) needed a feedback stimulus (circles with diameters transitively corresponding to the order of the primary stimuli) presented after each training trial to succeed later in testing (Lazareva et al., 2004). Pinyon jays and Clark's nutcrackers experienced higher accuracy with the end-anchor training pairs (containing A or G) than the middle pairs (Bond et al., 2010). On the other hand, California scrub jays showed a significant first-item effect as their accuracy dropped from 92% in BC to 37% in EF (Bond et al., 2003).

In test pairs, the results differed among species, but most birds reached an accuracy of over 80% in the transitive pair BD (Bond et al., 2010; Mikolasch et al., 2013). With non-adjacent pairs, azure-winged magpies (*Cyanopica cyanus*) and Clark's nutcrackers were more accurate the bigger the symbolic distance between non-adjacent pairs was (Bond et al., 2010).

Overall, pinyon jays and Clark's nutcrackers reached the highest accuracy levels and seemed to rely on relational learning rather than associative (Bond et al., 2003, 2010). The success of pinyon jays could relate to their complex sociality. Paz-y-Miño C et al. (2004) revealed that birds could infer their dominance status relative to strangers they have seen interact with known individuals, thus utilising the transitive inference in ecologically relevant settings.

2.3.5 Summary

Although the criteria to succeed in training differed across studies, all birds generally learned to discriminate between presented stimuli. The fastest learners were hooded crows (Lazareva et al., 2004), followed by domestic chickens (Daisley et al., 2021), while slower learners were greylag geese (Weiß et al., 2010) and pigeons (Lazareva & Wasserman, 2006). Other corvid species faced a higher number of stimuli (seven), so their training took naturally longer (Bond et al., 2003, 2010). In addition, a study with geese showed that the ability to memorise the training pairs could be decently long-term (Weiß & Scheiber, 2013).

While some individuals had difficulty inferring the relationship between the pair BD during testing, representatives from all tested bird groups completed the task, and most reached a high accuracy. The birds performed even better when presented with other non-adjacent pairs, further proving their ability to use relational learning. They were able to remember abstract relationships between stimuli rather than only memorise individual pairs.

2.4 Mirror use

Researchers mainly use mirrors to investigate mirror self-recognition (MSR) using the mark test, the most known paradigm.

Typically, the subjects first experience a period of mirror image stimulation where the researchers observe their reactions to the mirror and look for changes in exhibited behaviours. These include social displays, exploratory behaviours, including looking behind the mirror, and self-directed and contingency behaviours - repetitive movements to test correspondence between their movements

and the mirror image (Vanhooland et al., 2020). The initial mirror exposure is crucial as some individuals may need more time to overcome social behaviours and exhibit self-directed behaviours (Clary et al., 2020; Vanhooland et al., 2020). Furthermore, initial neophobia can influence the subjects' willingness to approach the mirror (Baciadonna et al., 2023).

In the mark test, the subjects are marked on an out-of-view body part that can only be seen by looking into the mirror, and researchers analyse their mark-directed behaviour in front of a mirror compared to a control non-reflective surface. The mark used and its placement is essential as the birds can sense it tactilely (Soler et al., 2014) or see it without needing a mirror (van Buuren et al., 2019). The mark can be either a painted spot (Vanhooland et al., 2022), a coloured sticker (Prior et al., 2008), a coloured powder (Wang et al., 2020b) or even food - a honey-coated wafer (van Buuren et al., 2019). Its position is usually on the forehead (Smirnova et al., 2020) or the throat (Kraft et al., 2017), with the latter potentially less appropriate as researchers argued that the birds can be more sensitive there (Lin et al., 2021; Parishar et al., 2021) or they can peripherally see the place (Smirnova et al., 2020). The subjects typically undergo sham trials where the mark is a sticker in the colour of their body (Clary et al., 2020), water (Brecht et al., 2020) or, for example, transparent odourless glycerin (Vanhooland et al., 2020) to ensure they do not associate the handling and marking process with the mark and only act upon it. Moreover, the application of the mark can be hinted at more locations to give subjects more stimuli to focus on (Buniyaadi et al., 2020; van Buuren et al., 2019).

Interpreting mark test results is challenging as the birds may not be motivated to remove the mark (van Buuren et al., 2019) or remove it by accident during regular or stress-induced preening (Lin et al., 2021). The former may be controlled by placing the mark on a visible body part to test the birds' motivation (Vanhooland, 2020; Wang, 2020). Since this procedure does not eliminate the possibility of birds habituating to the mark, researchers try to reduce this by conducting a limited number of trials (Prior et al., 2008; Soler et al., 2014).

Furthermore, the mark test results in an all-or-nothing outcome which is unsuitable if we assume a gradualist concept of self-recognition exists (Wittek et al., 2021). Moreover, the experimental design needs to control for many potential methodologic issues (Vanhooland et al., 2022), and cautiously analysing the test results is crucial to interpreting them correctly.

A necessary precondition for passing the mark test is for the birds to understand the principle of the mirror. Without making claims about self-recognition, we can obtain a more comprehensive outlook on that by exploring birds' reactions to mirrors and conducting additional tasks. These include mirror preference (Gallup & Capper, 1970), mirror-mediated object recognition (Pepperberg et al., 1995), string-pulling (Baciadonna et al., 2022; Taylor et al., 2010) and food-locating tasks (Medina et al., 2011; Wang et al., 2020b). Alongside these tasks, some researchers compared the subjects' reactions to a mirror versus a conspecific in feeding (van Buuren et al., 2019) or caching conditions (Dally et al., 2010) to determine whether the birds perceive the mirror image as a conspecific, as themselves, or something in between (Wittek et al., 2021). Furthermore, researchers manipulated the transparency of the mirror, making it graded and the reflection blurred, which could resemble the water reflections seen in natural environments (Clary & Kelly, 2016).

2.4.1 Galliformes

Amongst Galliformes, only domestic chickens (*Gallus gallus domesticus*) were tested with mirrors. When the birds faced the mirror, they were attracted to it and perceived their image as a conspecific (Montevecchi & Noel, 1978). Kaufman & Hinde (1961) recognised that the birds' approach to the mirror differed based on rearing conditions. While socialised birds habituated to the mirror and made fewer distress calls, unsocialised birds did not get accustomed to the image, making more distress calls when facing a mirror than alone. In addition, some birds possibly considered the mirror image a supernormal social stimulus as they were significantly more aggressive in its presence than with a conspecific (Gallup et al., 1972).

Unfortunately, there are no recent studies presenting Galliformes with mirror-related tasks. Thus, we cannot determine whether these birds understand mirror properties at least partially in other ways than self-recognition, as that would require a different experimental design with prolonged mirror exposure and more detailed behavioural analysis.

2.4.2 Columbiformes

Pigeons (*Columba livia*) were part of various studies. Initially, they failed the mark test (Epstein et al., 1981). However, when researchers trained them to peck at visible dots on the walls of the experimental compartment and dots on their bodies, they later succeeded in the mirror condition even when having a bib that obstructed the direct view of the mark (Epstein et al., 1981; Uchino & Watanabe, 2014). However, despite using the same experimental protocols, Thompson & Contie (1994) could not replicate the results, as their pigeons had difficulty learning mark-directed behaviours and only searched for dots around them. The researchers attributed the results to the pigeons' inability to connect their bodies with their mirror image or to the imperfect replication of the study.

In two studies, pigeons aggressively attacked their reflection as if they recognised it as a conspecific (Cohen & Looney, 1973; Ünver et al., 2017). Having said that, when the birds experienced both a mirror and a conspecific, they showed higher competitiveness and lower latency when feeding in the presence of a conspecific (Wittek et al., 2021). Presumably, they could not fully identify the mirror reflection and perceived it as something strange in between - not themselves but not a conspecific.

Toda & Watanabe (2008) trained their subjects to discriminate between trial-unique live videos of themselves or pre-recorded ones. Researchers demonstrated that the birds could succeed even if the live videos were delayed by 1 to 7 seconds. However, the birds did not need to perceive the video recording as themselves, as they could rely on temporal contiguity and visual feedback.

When presented with a mirror-mediated food-locating task, pigeons succeeded without trouble. However, by covering one of their eyes, researchers revealed that they used peripheral vision, not mirror reflection (Ünver et al., 2017).

To conclude, pigeons can be trained to succeed in some mirror-related cognitive tasks and understand movement synchronicity even though they failed to pass the mark test spontaneously.

2.4.3 Phoenicopteriformes

Lesser flamingos (*Phoeniconaias minor*) were tested in a single study by Pickering & Duverge (1992). They typically perform mass group courting displays with ritualised behaviours. Researchers

exposed a group of thirty individuals to mirrors for multiple days and observed the emergent effects. The birds perceived their mirror image as conspecifics, performed displays four times more often and continued to exhibit these behaviours longer as the mirror reflection maintained their excitement. No other studies investigated flamingos' abilities to use mirrors.

2.4.4 Sphenisciformes

Adélie penguins (*Pygoscelis adeliae*) were test subjects in a recent preliminary study in Antarctica (Dastidar et al., 2022). The cognitive abilities of these social birds have not been studied before, adding to the significance of this study.

Researchers exposed the free-ranging penguins to a mirror, which sparked their interest, making them stare at it but not touch it. Moreover, the unique movement of their heads and wings has not been accounted for in any other context.

When a circular sticker hiding the subjects' upper body reflection was placed on the mirror, their behaviour changed, and they started pecking at the mirror while moving frantically. Researchers hypothesise that they either wanted to see what they had just seen or were nervous due to not seeing the eyes of the reflection. In the last task, penguins received a colourful bib on their neck but did not direct any behaviour towards it when they could see themselves with it in a mirror.

Adélie penguins proved to be adequate candidates for further research as they showed high interest in mirrors and behaviours requiring more investigation.

2.4.5 Bucerotiformes

Hornbills are known to be territorial, and there are sightings where they have attacked their reflections (Chiweshe, 1994). Brereton et al. (2021) presented mirrors to a pair of Southern ground hornbills (*Bucorvus leadbeateri*). The birds demonstrated heightened alertness in the presence of the mirror and actively engaged with it by poking it with their beaks and feet. However, there was no noticeable increase in self-directed behaviour. As no further analysis was done, the reasoning behind this behaviour is unclear. The birds could be curious to interact with another conspecific or be alert due to identifying the mirror image as a rival.

2.4.6 Psittaciformes

Several parrot species underwent multiple mirror-related tasks. Overall, they expressed a high interest in mirrors, which lasted over a year in the case of keas (*Nestor notabilis*) (Diamond & Bond, 1989). Budgerigars (*Melopsittacus undulatus*) preferred their image over a conspecific (Gallup & Capper, 1970), and some sought social stimulation from it (Buckley et al., 2017).

Only African grey parrots (*Psittacus erithacus*) faced a mirror-mediated object recognition and food-locating task (Pepperberg et al., 1995). Birds succeeded in both by avoiding aversive stimuli and correctly locating the food using a mirror reflection, demonstrating their understanding of basic mirror properties.

Birds generally exhibited social behaviours towards mirrors and were more aggressive toward vertical rather than horizontal mirrors (Pepperberg et al., 1995). Few individuals of all tested parrots performed contingency testing such as swaying to sides, pirouetting and peekabooing, and they also

looked behind the mirror (Lin et al., 2021; van Buuren et al., 2019). However, the interpretation of these actions is ambiguous as some could fall under play behaviour.

No parrot species passed the mark test regardless of the mark used (Lin et al., 2021; van Buuren et al., 2019). This failure was probably not due to low motivation to remove the marks, as Goffin's cockatoos (*Cacatua goffiniana*) readily removed them when they could see them directly and marks used for keas were a highly desirable treat (van Buuren et al., 2019). African grey parrots were sensitive to throat sticker marks and bristled their feathers to prevent them from attaching, so researchers used coloured lipstick marks on their heads for the mark test (Lin et al., 2021). Keas were marked both on the throat and the head, but they removed the throat marks in all conditions and did not direct any behaviour toward the head marks (van Buuren et al., 2019).

In short, parrots are highly interested in mirrors and can use them to locate objects. The absence of MSR in parrots underlines the need for additional research to determine whether these results are due to inadequate methodology or if parrots truly cannot pass the mark test.

2.4.7 Passeriformes: Corvidae

Most mirror-related studies focused on corvids, mainly due to the reported success of a few species in the mark test (Buniyaadi et al., 2020; Prior et al., 2008). Corvids tend to be neophobic, as shown by the reluctance of New Caledonian crows (*Corvus moneduloides*) (Medina et al., 2011) and azure-winged magpies (*Cyanopica cyanus*) (Wang et al., 2020b) to approach the mirror. Their first reactions to the mirror are often agonistic, as in the case of ravens (*Corvus corax*) (Vanhooland et al., 2022), New Caledonian crows (Medina et al., 2011) and jungle crows (*Corvus macrorhynchos*) (Kusayama et al., 2000). Conversely, no social behaviours occurred in Eurasian jays (*Garrulus glandarius*) (Baciadonna et al., 2023) and most of the hooded crows (*Corvus cornix*) (Smirnova et al., 2020). Other species, such as jackdaws (*Corvus monedula*) (Soler et al., 2014), Indian house crows (*Corvus splendens*) (Parishar et al., 2021) and Eurasian magpies (*Pica pica*) (Prior et al., 2008; Soler et al., 2020) expressed self-directed and contingency behaviours and looked behind the mirror.

In the mark test, results greatly varied. Most species, like azure-winged magpies (Vanhooland et al., 2022; Wang et al., 2020b), jackdaws (Soler et al., 2014), ravens (Vanhooland et al., 2022) and hooded crows (Smirnova et al., 2020), did not pass. In some cases, the negative result could be due to improper methodology, such as using unfitting marks and not controlling for motivation to remove them (Smirnova et al., 2020; Soler et al., 2014). On the other hand, Wang et al. (2020b) tested birds with a red powder mark that they removed when visible but did not tactilely notice as it did not clump their feathers, indicating the methodology was correct.

The only successful individuals, two out of five Eurasian magpies (Prior et al., 2008) and four out of six Indian house crows (Buniyaadi et al., 2020), were all marked with a sticker. They intentionally performed mark-directed behaviours until they removed the mark only in front of the mirror, not in front of the control surface and did so spontaneously. Clark's nutcrackers succeeded only in a graded mirror condition which the researchers explained by the blurry image allowing them to follow contingency movements easier (Clary & Kelly, 2016). However, some subjects also detected the mark in the control condition, thus potentially invalidating the results, a view also supported by Soler et al. (2020).

Several corvid species were tested with tasks requiring the use of a mirror. New Caledonian crows succeeded (Medina et al., 2011) in the mirror-mediated food-locating task, while azure-winged magpies searched for the food but not at the correct location (Wang et al., 2020b). When the task revolved around string-pulling, New Caledonian crows, naive to the setup, used the mirror information to solve it (Taylor et al., 2010), but Eurasian jays did not succeed (Baciadonna et al., 2022).

California scrub jays (*Aphelocoma californica*) (Clary et al., 2020; Dally et al., 2010) and Clark's nutcrackers (*Nucifraga columbiana*) (Clary & Kelly, 2016) faced mirror-related caching tasks. When caching while observed by a conspecific which could be even behind a graded glass (Clary et al., 2020), they later re-cached more to misinform potential thieves. However, this behaviour did not occur as much when they were alone or when they faced a mirror. The researchers proposed two hypotheses: either the birds did not perceive their mirror image as a conspecific or they evaluated the conspecific as odd or non-attentive and therefore, non-threatening.

In conclusion, most corvids did not pass the mark test. While the positive results of the two species can be challenged by alternative explanations such as regular grooming, heightened activity or an accidental discovery while preening and using peripheral vision, they nevertheless provide promising evidence of the birds' capacity to succeed in MSR. Moreover, New Caledonian crows demonstrated an ability to use a mirror to locate objects and solve problems related to physical cognition. Lastly, California scrub jays and Clark's nutcrackers showed no difference in behaviour when observed by a conspecific versus facing a mirror while caching, which calls for further research.

2.4.8 Passeriformes

Passerines other than Corvidae are less studied with mirrors, as only a few comparative studies exist. Regarding a mirror versus conspecific preference task, zebra finches (*Taenopygia guttata*) and house sparrows (*Passer domesticus domesticus*) initially preferred their conspecific (Gallup & Capper, 1970; Ryan, 1978). However, their interest in the mirror increased later in trials, exhibiting social behaviours towards it. Java sparrows (*Padda oryzivora*) displayed similar behaviour, but their preference diminished when viewing a conspecific through frosted glass, despite hearing the other bird vocalising (Watanabe, 2002). European starling (*Sturnus vulgaris*) females and pair-raised males calmed in the presence of a mirror, but the exposure was too brief to make further conclusions (Henry et al., 2008).

None of the tested birds passed the mark test. Great tits (*Parus major*) were marked on the throat with stickers and paint, with the varying marks not having an effect, as the only self-directed behaviours were a regular part of preening (Kraft et al., 2017). One subject removed its sticker mark at the end of a mirror trial, but the action was not repeated, which makes it difficult to interpret. Zebra finches and common hill mynas (*Gracula religiosa*) had to be marked on the forehead as they removed throat marks after application (Lin et al., 2021; Parishar et al., 2021). Both species exhibited more self-directed behaviours in the mirror condition, with no evident MSR. Instead, researchers explained the behaviour by the mirror being a social buffer to the subjects (Lin et al., 2021).

While the great tits could not look behind the mirror due to experimental setup, zebra finches could and did so (Parishar et al., 2021). Additionally, they demonstrated contingency testing by quick head-turning.

In conclusion, passerines other than Corvidae perceived their mirror image as a conspecific, with no decrease in social behaviours during mirror exposure (Parishar et al., 2021) and no success in the mark test. However, they did not undergo any other mirror-related tasks. Therefore we cannot claim they have no understanding of mirrors, as more research needs to be conducted.

2.4.9 Summary

Although most birds regarded their mirror image as a conspecific, some demonstrated at least a partial understanding of mirror properties. African grey parrots and New Caledonian crows succeeded in mirror-mediated food-locating tasks. Penguins exhibited unique behaviours and pigeons understood movement synchronicity even with a delay. Additionally, pigeons and some caching corvids behaved differently towards their mirror image compared to a conspecific as they conceivably noticed synchronicity disparities.

Individuals from two corvid species passed the mark test, even though the experimental setup was originally designed for apes (Gallup, 1970). Unlike apes, many birds have tetrachromatic vision and commonly used mirrors absorb UVA wavelengths. Considering the birds' vision, visual field and tactile sensitivity, the optimal marks should be placed on the forehead and made of powder. Sham marks should only be hinted at multiple locations to prevent the birds from seeing or feeling them during the test.

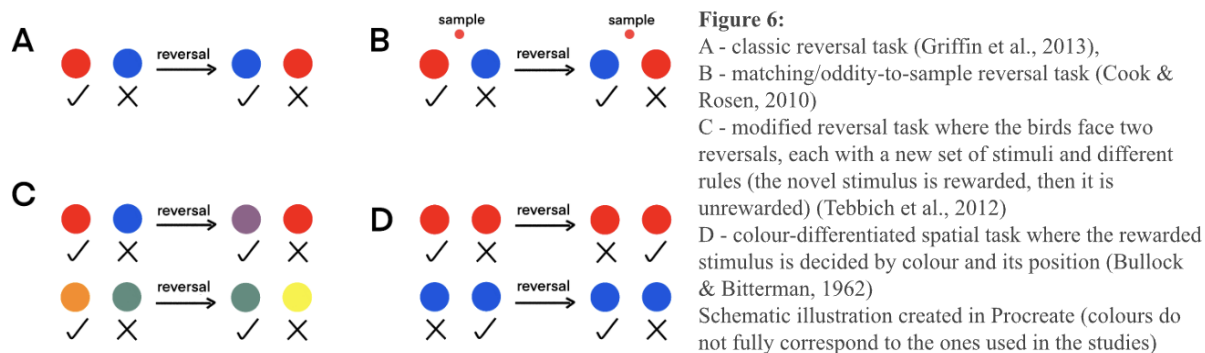
More research needs to be done with new experimental designs as getting more profound insights into the birds' understanding of mirrors and even potential self-awareness with the currently available literature is challenging.

2.5 Reversal learning

Reversal learning paradigms primarily test behavioural flexibility using associative learning. Birds need to be receptive to changes in food availability and avoid repeatedly visiting locations that are no longer rewarding, and being able to switch quickly may give them an advantage.

Typically, researchers assign subjects a two-choice task, reinforcing only one stimulus and later reversing the contingencies. The point of the reversal varies depending on the experiment. In a mid-session reversal task, the contingencies switch in the middle of each session, always at the same point (Stagner et al., 2013), with a possible modification involving placing the reversal point semi-randomly somewhere in the session (McMillan et al., 2014). In another frequently used design, subjects have to pass a criterion, and only after that, the reversal occurs. The reversal can either happen only once during an experiment (Isden et al., 2013) or successively, creating a serial reversal task (Gossette et al., 1966). The learning criterion varies across studies, ranging from a very stringent - 85/90 correct choices (Staddon & Frank, 1974) to a relatively lenient - 15/20 correct choices (van Horik & Emery, 2018). Generally, a more lenient criterion forms a weaker association, making it easier for the birds to reverse as they will have more experience with the unrewarded stimuli (van Horik & Emery, 2018).

The stimuli used and the design of the experiment can influence the difficulty of initial acquisition and affect reversal learning (Laude et al., 2014). The stimuli can differ in the cues they provide and in their modality. The rewarded stimuli can be identified by spatial cues (left or right side; Rayburn-Reeves et al., 2013), visual cues (a colour regardless of its position; Tebbich & Teschke,



2014) or both (a colour always on the same side; McMillan & Roberts, 2012). Alternatively, the two choices can be differentiated based on matching-to-sample/odddity rules (Cook & Rosen, 2010), colour-differentiated spatial discrimination (Bullock & Bitterman, 1962), and discrimination associated with novel stimuli (Tebbich et al., 2012) (**Figure 6**). Additionally, the cues can be acoustic in the form of successively presented notes (Guillette et al., 2011). Lastly, some experimenters complicated the task by adding a requirement for object permanence as they used wells with coloured lids as stimuli. The birds had to remove the lids from all the rewarded wells before they could examine the others to pass a criterion (Brust et al., 2013). However, this lowered the cost of error as the difference between obtaining all the rewards or one less was insignificant (Boogert et al., 2011).

The length of the intertrial interval (ITI), usually around 5 seconds, is another factor that can be very influential, as longer ITIs can increase the memory load for subjects (Laude et al., 2014). Similarly, a longer reinforcement delay can also negatively impact the subjects' performance by weakening the association (Halloran & Zentall, 2020). Conversely, a pre-reversal time gap can be added to signal to the birds that a reversal will occur, potentially leading to better performance (Cook & Rosen, 2010). Additionally, we must be careful about potential colour (Zidar et al., 2018) and side biases subjects might develop (Diekamp et al., 1999).

The optimal strategy for most reversal tasks is win-stay/lose-shift, where the subjects instantly switch their responses once they encounter a change in reinforcement (Rayburn-Reeves et al., 2013). For the mid-session task, the perfect strategy is to understand the reversal rules, precisely estimate the reversal point, and not make a single error (Laschober et al., 2021). However, most subjects make anticipatory mistakes before the reversal point and perseverative mistakes after (Laude et al., 2016). With more reversal sessions, the subjects are expected to improve within and across sessions, indicating an understanding of the rules.

In essence, the paradigm contains two parts - an acquisition of initial discrimination and the reversal(s) where the subject has to acquire new reward-stimulus associations while inhibiting responding to the previous stimulus, with the latter being more challenging than the former (O'Hara et al., 2015b). Some authors believe the acquisition and the reversal utilise unrelated mechanisms (Guillette et al., 2015), while others found a negative (Bebus et al., 2016) or positive correlation between them (Anderson et al., 2017). Some researchers explained the birds' performance by social structure (Bond et al., 2007), while others by the predictability of the environment (Hermer et al., 2018) or by slow/fast-exploratory personality paired with neophobia/neophilia levels (Brust et al., 2013).

2.5.1 Galliformes

Several Galliformes species were tested in single or serial reversal tasks, where the contingencies were reversed after passing a criterion. Although none of them reached the optimal win-stay/lose-shift strategy, they acquired the initial discrimination and improved during the reversal(s) (Gossette et al., 1966).

Common pheasants (*Phasianus colchicus*) and red junglefowl (*Gallus gallus*) underwent tasks with colour stimuli and only a single reversal. Pheasants did not reach above-chance level accuracy, possibly due to a limited number of trials (van Horik et al., 2019). Some researchers found a personality-dependent negative association between their reversal performance and survivability (Madden et al., 2018), whereas others observed a surprising negative link between reversal performance and inhibitory control (van Horik et al., 2018b). Unfortunately, the researchers did not discuss the possible explanations and only mentioned the possibility of birds self-selecting by deciding to participate in testing. Some red junglefowl reached a criterion during the reversal relatively quickly, as they only needed ten trials to make five consecutive correct choices (Zidar et al., 2018). Furthermore, their performance varied based on sex and exploratory personality. Additionally, Sorato et al. (2018) found in red junglefowl a moderate heritability across six generations for reversal performance but not for the acquisition of initial discrimination.

Domestic chickens (*Gallus gallus domesticus*) exhibited right hemisphere lateralisation while completing a single reversal (Loconsole et al., 2021). This lateralisation was not observed during multiple reversals in other studies, as chickens were able to significantly improve with only three errors before reaching the criterion during reversals while discriminating between differently coloured and shaped stimuli (Bacon et al., 1962). However, when the stimuli only differed in colour (Gossette, 1967) or position (Gossette et al., 1966), they did not reach such accuracy. Northern bobwhites (*Colinus virginianus*) also showed different reversal performances depending on the type of stimuli used. With coloured and patterned stimuli, they reached an asymptote quickly (Stettner et al., 1967), while with spatial stimuli, they gradually improved and reached higher accuracies (Gossette et al., 1966).

2.5.2 Columbiformes

Pigeons (*Columba livia*) are one of the most extensively studied bird species regarding their performance in reversal tasks, as they work well in operant chambers and maintain high motivation.

Most studies focused on a mid-session reversal task, with many making modifications to understand the mechanisms behind birds' decisions. Generally, pigeons tended to make anticipatory and perseverative errors around the reversal point, indicating that they rely on cues such as the number of trials or time into sessions to estimate the reversal rather than on the feedback from previous trials (Laude et al., 2016; Rayburn-Reeves et al., 2011; Stagner et al., 2013). However, studies have shown that their performance improves when they face shorter intertrial intervals (Ploog & Williams, 2010), have reminder cues during ITIs (Smith et al., 2017), and experience longer time gaps before each reversal (Cook & Rosen, 2010). Furthermore, Santos et al. (2019) found that pigeons performed better when reinforcement rates were High-Low, which involved leaving a 100% chance of reinforcement for the S1 stimulus before the reversal and reducing the chance of reinforcement for the S2 stimulus to 20% after the reversal. This created unreliable feedback from S2, causing the birds to focus solely on

S1 and quickly notice the reversal point. Additionally, the dimensions of the stimuli also affect the pigeons' reversal performance, with better performance observed when more cues are available (McMillan & Roberts, 2012) or when the pigeons have to choose between a left and right side (Laude et al., 2014).

Remarkably, one pigeon achieved a win-stay/lose-shift strategy from the 50th session onward, irrespective of when the reversal occurred (McMillan et al., 2014). However, researchers suggested that this optimal performance could be due to a short ITI and spatial stimuli that trigger a motor repetition pattern in which the pigeons peck one key until disrupted (Rayburn-Reeves et al., 2013).

None of the birds could reach near-perfect performance in serial reversal tasks, but they quickly reached an asymptote of 90% accuracy, regardless of criterion stringency (Staddon & Frank, 1974). In another study, Diekamp et al. (1999) conducted monocular tests and found a lateralisation-based performance favouring the left hemisphere.

Researchers conducted a field experiment on another Columbiformes species, Zenaida doves (*Zenaida aurita*), but the design differed, and the birds received only ten reversal trials (Boogert et al., 2010). Nonetheless, they revealed no correlation between individuals' performance in the acquisition and reversal and no trade-off between territorial aggression and learning ability.

2.5.3 Falconiformes

Only females of the generalist Falconiformes species, Chimango caracara (*Milvago chimango*), were tested in a reversal paradigm (Guido et al., 2017). They underwent a single reversal with colours as stimuli and relatively long ITIs (40 to 240 seconds), requiring them to remember the stimuli for a longer time. Although the learning criterion was weak (5/5 correct trials), the subjects required twice as many trials to reach the criterion and made thrice as many errors during reversal compared to acquisition. Furthermore, researchers found no correlation between individuals' performance during acquisition and reversal. However, they reported a negative correlation between neophobia and reversal performance but not acquisition, suggesting that individual differences in neophobia of Chimango caracaras may lie behind the birds' successful adaptation to changing environmental conditions.

2.5.4 Psittaciformes

Only a few studies examined parrots' reversal abilities which is surprising as parrots are often highly neophilic and live in unpredictable environments while also maintaining complex social relationships. All these characteristics are hypothesised to correlate with reversal performance in some way, and any research is beneficial.

When keas (*Nestor notabilis*) were given only a limited number of trials with a physical problem that reversed in functionality, they failed the task (Gajdon et al., 2011). However, when researchers waited longer for the birds to reach the learning criterion, keas eventually succeeded in the single reversal (O'Hara et al., 2015b). They performed better if the stimuli were solid objects rather than stimuli on a touchscreen, raising questions about the appropriateness of the latter.

In the mid-session reversal task, keas demonstrated impressive performance despite discriminating between visual stimuli on a touchscreen (Laschober et al., 2021). Keas performed the best when the stimuli did not change position across trials, as they made fewer anticipatory errors.

Some individuals accurately estimated the reversal and avoided making a single mistake during a few 40-trial sessions. Most keas adopted a win-stay/lose-shift strategy which was the optimal strategy even when the reversal point changed across sessions.

Red-shouldered macaws (*Diopsittaca nobilis*) and black-headed caiques (*Pionites melanocephalus*) performed similarly in a serial reversal task (van Horik & Emery, 2018). None of them achieved a win-stay/lose-shift strategy, and they only displayed improvement across reversals when the learning criterion was high. Contrary to researchers' predictions, the higher criterion did not impair reversal learning as the birds used it to understand the conditional rules of the experiment. Yellow-crowned amazons (*Amazona ochrocephala*) faced thrice as many reversals and significantly improved across them but still made many mistakes (Gossette, 1967; Gossette et al., 1966). They first experienced only spatial stimuli and later visual stimuli with colours changing positions, which proved more challenging for them.

In conclusion, parrots proved to be suitable subjects for reversal learning studies and future research is encouraged. Some keas displayed perfect performance in a mid-session reversal task, while other species improved in a serial reversal task with a higher learning criterion but did not achieve a win-stay/lose-shift strategy.

2.5.5 Passeriformes: Corvidae

Most studies that tested corvids studied their performance in a single reversal. Range et al. (2006, 2008) found that experimental properties could influence common ravens' (*Corvus corax*) performance, with an improvement in accuracy when birds faced spatial rather than visual stimuli (Range et al., 2006) and a decrease when stimuli differed only in their shapes (Range et al., 2008). Bebus et al. (2016) discovered that the more neophobic Florida scrub jays (*Aphelocoma coerulescens*) performed better in reversal than acquisition. These two processes were inversely related, which researchers explained by a trade-off between birds' sensitivity to environmental cues reflected by their differences in coping styles - proactive versus reactive. On the contrary, Wascher et al. (2021) found a positive correlation between the two processes in carrion crows (*Corvus corone*), but they did not discuss it further.

Furthermore, Bond et al. (2007) discovered that in a serial reversal task, the most social pinyon jays (*Gymnorhinus cyanocephalus*) outperformed the asocial Clark's nutcrackers (*Nucifraga columbiana*) and moderately social California scrub jays (*Aphelocoma californica*), which they explained by more social birds having to deal with fluctuations in relationships and hierarchies at a greater frequency. Nevertheless, all species showed improvement across reversals and eventually needed only a few unrewarded trials before correctly reversing. Red-billed blue magpies (*Urocissa oecipitalis*) exhibited similar results, making less than three errors on average in later sessions (Gossette et al., 1966).

Although corvids did not achieve an optimal win-stay/lose-shift strategy, they were relatively close to it. Furthermore, researchers found that neophobia and sociality are positively correlated with reversal learning, suggesting that these traits contribute to the cognitive flexibility of corvids. However, the data regarding reversal learning in corvids are relatively scarce, highlighting the need for further research.

2.5.6 Passeriformes

In the conducted studies, passerines other than Corvidae were subjected to one or more reversals. Song sparrows (*Melospiza melodia*) did not exhibit long-term individual repeatability of their reversal performance (Soha et al., 2019), but their individual performances in acquisition and reversal were positively correlated (Anderson et al., 2017; Boogert et al., 2011). In contrast, zebra finches (*Taeniopygia guttata castanotis*) (Brust et al., 2013), black-capped chickadees (*Poecile atricapillus*) (Guillette et al., 2015), great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) (Reichert et al., 2020) did not exhibit a correlation between their performance in initial acquisition and reversal.

Moreover, Shaw et al. (2015) examined the performance of North Island robins (*Petroica longipes*) in a cognitive battery including associative and reversal learning, spatial memory, motor task and motor inhibitory control and found weak positive correlations across the tasks. Isden et al. (2013) detected similar trends in spotted bowerbirds (*Ptilonorhynchus maculatus*), but their results did not reach significance. Interestingly, Anderson et al. (2017) reported a negative correlation between reversal performance and motor inhibitory control. However, the researchers did not provide further explanation, leaving the reasons for this negative correlation unclear.

On the other hand, results regarding the correlation between reversal performance and predictability of the environment are mostly in agreement. Great tits (Hermer et al., 2018) and mountain chickadees (*Poecile gambeli*) (Croston et al., 2017) from lower elevations, thus less harsh environments, performed better in reversal than those from high elevations. The researchers attribute these observed differences to the high-elevation birds' dependence on spatial memory and the low-elevation birds' exposure to higher population densities, faster depletion of resources, and a larger range of food choices.

However, woodpecker finches (*Camarhynchus pallidus*) from harsher variable environments performed unexpectedly better in reversal than those from stable environments and were also more neophilic (Tebich & Teschke, 2014), contradicting conclusions from even more studies. Opposite of a reasonable prediction that more neophilic birds would be less afraid to try new food resources and thus not have problems with reversals, the more neophobic zebra finches (Brust et al., 2013), small tree finches (*Camarhynchus parvulus*) (Tebich et al., 2012) and black-capped chickadees (Guillette et al., 2011) all outperformed the less neophobic individuals. This surprising effect researchers attributed to their higher sensitivity to changes.

Furthermore, Ashton et al. (2022) demonstrated long-term repeatability for both initial acquisition and reversal in Australian magpies (*Gymnorhina tibicen dorsalis*) over a three-year period. Moreover, at least one individual adopted a win-stay/lost-shift strategy in the reversal, even when encountering the task for the first time. In addition, Australian magpies living in larger groups outperformed the ones living in smaller groups (Ashton et al., 2018), which researchers attributed to the greater amount of information processing required in a more complex social environment.

Most individuals acquired the initial discrimination and reached a criterion in the reversal(s), but only one achieved a win-stay/lose-shift strategy. Common hill mynas (*Gracula religiosa*) came close to the optimal strategy by making only 1,3 incorrect responses on average before attaining the criterion following the 16th reversal with spatial stimuli (Gossette et al., 1966).&

2.5.7 Summary

As predicted, birds found reversal more challenging than the initial discrimination stage. Furthermore, researchers discovered either no correlation, a positive correlation, or a negative correlation between their performances in the two parts of the paradigm, thus, no general trend. In addition, researchers discovered surprising contrasting results regarding the correlation between reversal performance and motor inhibitory control. Hence, we need more research, ideally with a larger sample size, to disentangle this disparity, as some researchers even proposed that not all motor inhibitory tasks measure cognitive abilities accurately and performance in these tasks can differ based on experience and motivation (van Horik et al., 2018a).

Moreover, the link between neophobia/neophilia and reversal performance also differed across species. While more neophilic Chimango caracaras and woodpecker finches outperformed their neophobic conspecifics, the opposite was true for Florida scrub jays, zebra finches, small tree finches and black-capped chickadees. Regarding predictability of the environment, great tits and mountain chickadees from less harsh conditions performed well, whereas woodpecker finches from comparable conditions performed poorly.

In the mid-session task, pigeons were inclined to estimate time or trials within the session when unable to rely on other cues, mainly due to attention or memory problems. However, one individual used the win-stay/lose-shift strategy. Furthermore, keas excelled and predicted reversals accurately.

Birds generally improved during serial reversals. Domestic chickens, Northern bobwhites, all tested corvids and common hill mynas approached the optimal strategy. An Australian magpie achieved it in a single reversal.

3 Cross-task comparison

This thesis describes five selected tasks in detail. However, not all bird groups were tested in all of them. If available, results of other studies focusing on the tasks not selected here will also be briefly discussed to offer a more comprehensive perspective.

3.1.1 Anseriformes

Besides succeeding in a transitive inference task, greylag geese (*Anser anser*) demonstrated a remarkable ability to memorise up to seven colour discrimination pairs for a year. In addition to this selected task, researchers examined other members of Anseriformes' object permanence and relational concept skills. Muscovy ducks (*Cairina moschata*) were able to locate an object they had watched disappear, but they tended to search for it where they had first seen it (Woodhouse, 2018). Mallard ducklings (*Anas platyrhynchos domesticus*) attended to the same/different concepts when presented with stimuli soon after hatching (Martinho & Kacelnik, 2016).

While we have no data on other cognitive tasks involving Anseriformes, their limited object permanence skills and morphological constraints would likely impair their performance in most physical cognition tasks. Nevertheless, this bird taxon is capable of relational learning, which may be attributed to its high sociality. Further research is necessary.

3.1.2 Cuculiformes

Cuculiformes are primarily tested in tasks related to their breeding strategies. In a unique experiment, researchers tested Greater anis' (*Crotophaga major*) ability to reason by exclusion. The birds did not pass the test and since we have no more data on the cognitive abilities of this bird taxon, it is impossible to make further conclusions.

3.1.3 Phoenicopteriformes

Most research on flamingos aims to describe their feeding ecology and social behaviours. Lesser flamingos (*Phoeniconaias minor*) were tested with mirrors and they recognised their mirror image as a conspecific. However, the experimental procedure was not comparable to similar experiments, and it would be interesting to test flamingos in further studies to truly assess their cognitive abilities.

3.1.4 Sphenisciformes

Researchers mainly study penguins' ecology and breeding behaviour. The only cognitively-focused study tested Adélie penguins' (*Pygoscelis adeliae*) reactions to a mirror and obtained intriguing results - behaviours not seen in any other contexts - which could be connected to their high sociality. There is definitely a potential for future cognitive research.

3.1.5 Accipitriformes

A Harris's hawk (*Parabuteo unicinctus*) and turkey vultures (*Cathartes aura*) faced a single vertical string-pulling task. Both species demonstrated the ability to pull a string successfully, while turkey vultures succeeded spontaneously using a novel technique. However, we cannot conclude they understand physical properties as we need more research also involving patterned string-pulling tasks. In addition, we have no data on Accipitriformes regarding other cognitive tasks beyond a few studies involving tool use (i.e., using stones to break eggs) in Egyptian vultures (*Neophron percnopterus*) (Carrete et al., 2017; Thouless et al., 1989). Further research is needed.

3.1.6 Strigiformes

While researchers commonly study owls' behaviour and ecology to develop effective conservation measures, only one study aimed to explore their cognitive abilities. Great grey owls (*Strix nebulosa*) failed in string-pulling tasks as they did not comprehend the physical causality of a string being connected to a reward. We need further research to confirm these results and to explore other aspects of Strigiformes' cognition for which we have no data.

3.1.7 Falconiformes

Falconiformes, specifically Chimango caracaras (*Milvago chimango*), have been the test subjects of more cognitive studies that could not fit into the thesis. In short, these studies have demonstrated the species' capacity to learn through social learning and high innovativeness in problem-solving tasks, with their performance being better in more urbanised populations (Biondi et al., 2008, 2010a, 2010b, 2022; Solaro & Sarasola, 2019).

When combining these findings with their reversal performance, we can conclude that Chimango caracaras are behaviourally flexible due to adapting to environmental pressures. However, more research is necessary to determine whether other Falconiformes share these cognitive traits and how they perform in other cognitive tasks.

3.1.8 Galliformes

Galliformes were tested in three of the selected tasks. Domestic chickens (*Gallus gallus domesticus*) performed well in transitive inference tasks, with a low ranking in a social hierarchy being a predictor for better performance. In reversal learning, all Galliformes generally improved across multiple reversals. When exposed to a mirror, domestic chickens deemed their mirror image a conspecific, and their reactions differed based on their level of socialisation.

Other studies revealed that wild turkeys (*Meleagris gallopavo*) could not locate a fully hidden object (Woodhouse, 2018), chickens waited longer only if the awaited reward was proportionally larger in a delayed gratification task (Abeyesinghe et al., 2005), and quails (*Coturnix coturnix*) succeeded only in some conditions of a motor inhibitory task (Zucca et al., 2005).

To conclude, the cognitive abilities of Galliformes could have evolved as an adaptation to their high sociality. However, this could be due to the prevalence of highly social domestic chickens in the studies, and we need data on the less social species. Furthermore, while there are no studies focusing on the physical cognition in Galliformes, they are not expected to perform well due to their low level of object permanence and no available records of innovativeness.

3.1.9 Columbiformes

Pigeons (*Columba livia*) were tested in all selected tasks. Their predominant success in transitive inference and reversal learning tasks suggests their associative, relational and reversal learning proficiency. On the other hand, their mixed results in string-pulling tasks point to poor physical cognition as they most likely relied on perceptual cues and not causal relations. Moreover, their success in modified reasoning by exclusion tasks could be attributed to neophilia rather than the ability to infer logically. Lastly, their ability to learn to perform mark-directed behaviours and understanding of movement synchronicity does not necessarily demonstrate a mirror self-recognition.

In addition, researchers tested Columbiformes with other tasks, where one Zenaida dove (*Zenaida aurita*) succeeded in a multi-access problem-solving task (Webster & Lefebvre, 2001), ring doves (*Streptopelia capicola*) could find a hidden object only if they started searching before it disappeared (Dumas & Wilkie, 1995), and pigeons successfully attended to abstract concepts (Bodily et al., 2008) and categorised numerous objects (Castro & Wasserman, 2014).

In conclusion, Columbiformes excel in some areas of cognition and lack in others, indicating the existence of adaptive cognitive specialisation.

3.1.10 Charadriiformes

Ring-billed gulls (*Larus delawarensis*) could solve the single string-pulling task, and brown skuas (*Stercorarius antarcticus*) demonstrated the capacity to succeed in both visual and acoustic versions of a reasoning by exclusion task, indicating an ability to infer logically and some level of

object permanence. Although these are two distinct species, they share certain characteristics, such as being opportunistic foragers with diverse feeding methods and long lifespans.

Other studies on Charadriiformes yielded mixed results. Horned puffins (*Fratercula corniculata*) were unable to locate fully hidden objects (Huffeldt, 2020), Olrog's gulls (*Larus atlanticus*) solved a multi-access problem-solving task only in controlled laboratory conditions (Castano et al., 2020, 2022), and herring gulls (*Larus cachinnans*) succeeded in a motor inhibitory task only with a non-transparent barrier (Zucca et al., 2005).

With a limited number of studies that tested different species, it is challenging to draw general conclusions. Nevertheless, existing research suggests that Charadriiformes can perform well in some cognitive tasks, and their cognitive abilities could be associated with their feeding ecology. Further research is essential to fully evaluate their cognitive abilities.

3.1.11 Bucerotiformes

Hornbills exhibited the capacity to solve convergent and broken string conditions but needlessly switched in a coiled condition in a patterned string-pulling task, indicating their understanding of connectivity and reliance on positive motor feedback. Moreover, they succeeded in a visual variation of the reasoning by exclusion task, demonstrating the ability to infer logically. Lastly, they likely perceived their mirror image as a conspecific, but the methodology was not comparable to similar experiments, and further research is needed.

Another study by Danel et al. (2022b) demonstrated hornbills' successful solution of a multi-access problem-solving task using social enhancement. The findings from this study, combined with those from the reasoning by exclusion task, suggest that hornbills can use social learning when needed but do not rely on it as they were not influenced by local enhancement in the latter task.

To conclude, hornbills display proficiency in some cognitive areas and, together with other Bucerotiformes, deserve further investigation.

3.1.12 Psittaciformes

With the exception of transitive inference, parrots were tested in all the selected tasks. Most parrot species excelled in the majority of string-pulling tasks, with some displaying an understanding of continuity and connectivity. In reasoning by exclusion tasks, they succeeded although they were prone to local enhancement. While they did not pass the mark test, some understood the mirror's properties. In reversal learning, parrots exhibited a high sensitivity to changes in contingencies and some perfectly estimated the reversal point in a mid-session task.

Other studies have also reported parrot's proficiency in physical cognition, as keas (*Nestor notabilis*) demonstrated innovative problem-solving skills (Auersperg et al., 2011) and Goffin's cockatoos (*Cacatua goffiniana*) the ability to use and even manufacture tools in the wild (O'Hara et al., 2021). Further studies reported parrots' ability to learn spatial patterns in foraging tasks (Chow et al., 2021), a high level of object permanence (Pepperberg & Funk, 1990), an understanding of abstract concepts (Pepperberg, 1987), the capacity to tolerate a delay before obtaining higher quality food (Schwing et al., 2017), but poor performance in a motor inhibitory task (Kabadayi et al., 2017).

All these results combined, parrots perform well in various tasks covering a wide range of cognitive aspects. It is perhaps possible to talk about some level of general intelligence in

Psittaciformes, which could have evolved together with their high neuron density brains, complex social structures and inhabitation of unpredictable environments.

3.1.13 Passeriformes: Corvidae

Corvids were tested in all selected tasks and many others. In the string-pulling task, they exhibited an understanding of connectivity, however they struggled to comprehend continuity in more complex conditions. While often relying on a local enhancement, corvids demonstrated the ability to infer logically. Moreover, they exhibited proficiency in a transitive inference task. In the mirror tasks, some species understood the mirror properties, with two passing the mark test as the only bird species so far. Lastly, they did not achieve the optimal strategy in reversal tasks, but they were not far from it.

Numerous other studies reported complex physical cognition in corvids. For example, tool-using New Caledonian crows (*Corvus moneduloides*) can manufacture tools (Hunt, 1996) or construct them out of compounds (von Bayern et al., 2018), plan for their specific use (Boeckle et al., 2020), and use them in various situations. Surprisingly, even naturally non-tool-using rooks (*Corvus frugilegus*) can use and modify tools (Bird & Emery, 2009).

Additionally, corvids can perform well in other problem-solving tasks, such as water displacement (Jelbert et al., 2014) and multi-access box tasks (Auersperg et al., 2011). Furthermore, they demonstrate strong spatial cognition with the ability to use many cache-protection strategies (Shaw & Clayton, 2013), exhibit a high level of object permanence (Zucca et al., 2007), and understand abstract concepts and relations (Smirnova et al., 2015; Wright et al., 2017). Finally, they can perform well in motor inhibitory tasks (Kabadayi et al., 2016) but preferably wait for a better reward than for more of the same reward (Hillemann et al., 2014).

To sum up, the remarkable cognitive abilities observed in corvids could have co-evolved with their highly neuron-dense brains in response to their high sociality and environmental factors. However, we need further research as not all corvids are highly social, and these factors cannot be the only ones to play a role. Nevertheless, some corvids may possess a certain degree of general intelligence.

3.1.14 Passeriformes

Passerines other than Corvidae were tested in three of the selected tasks. Most could pull a single string, but the majority of them struggled to understand connectivity and continuity concepts. While there is no available data on their understanding of mirror properties, they all seemed to recognise their mirror image as a conspecific and failed the mark test. Their reversal performance correlated with many factors, but overall they performed well, and some reached the optimal win-stay/lose-shift strategy.

Other studies on passerines other than Corvidae, have reported tool use in woodpecker finches (*Camarhynchus pallidus*) in the wild (Tebich et al., 2002), wide-spread innovativeness in problem-solving tasks (Griffin & Diquelou, 2015; Overington et al., 2011), good spatial cognition in caching (Heinen et al., 2021) or brood-parasitic species (Guigueno et al., 2014), moderate level of object permanence in common hill mynahs (*Gracula religiosa*) (Plowright et al., 1998), variable success in motor inhibitory tasks (Isaksson et al., 2018; Zucca et al., 2005), and an ability to categorise colour stimuli (Caves et al., 2018).

In summary, Passeriformes other than Corvidae appear to encounter numerous trade-offs regarding their cognitive capacities, and the support for general intelligence is not compelling enough with the available data. However, considering this is the largest avian group, and only a fraction of species have been tested, we need more research to make confident conclusions.

4 General conclusion

Comparing cognitive abilities across different bird taxa is challenging as not all cognitive tasks are suitable for a broadscale cross-taxon comparison, and careful evaluation is critical. Some, for example, reasoning by exclusion tasks, presuppose the presence of other cognitive abilities, like object permanence, while others, for example, string-pulling tasks, need to respect birds' distinct morphology. In addition, similar studies may use inconsistent experimental procedures that could affect the results and lead to misleading positive or negative outcomes.

Nevertheless, the data we obtain through the studies are valuable, as we can learn from them and determine the direction of further research. Transitive inference and reversal learning capacities seem almost universal, as many bird groups perform well in the related tasks. On the other hand, increased physical cognition required to solve more complex patterned string-pulling tasks is less frequent across bird groups. Similarly, mirror self-recognition appears rare in birds, but the current methodology is not ideal, and with an improved one, the results may change. Furthermore, many birds can reason by exclusion but often attend more to external cues, emphasising the need for further research with a modified methodology.

Based on currently available studies, we cannot say that all birds possess general intelligence. In most bird groups, birds' cognitive abilities seem to result from a specific adaptation. Nevertheless, evidence suggests that general intelligence may exist in specific bird taxa, such as Psittaciformes and Passeriformes: Corvidae. Further research is crucial to expand on the current findings since cognitive research has focused predominantly on a few bird groups, neglecting the potential contributions of many other deserving taxa.

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