

Physical cognition in parrots: a comparative approach

Dissertation

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Anastasia Krasheninnikova

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Professor Dr. C. Lohr
Vorsitzender des
Fach-Promotionsausschusses Biologie

Dennis Neal Cory

Alsterdorfer Straße 371b

22297 Hamburg

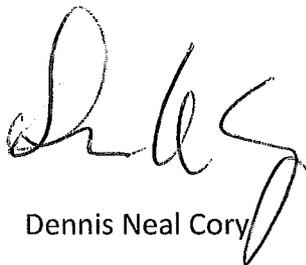
13. April 2014

Use of English in Thesis by Anastasia Krasheninnikova

To whom it may concern,

As a native English speaker I am writing in support of Anastasia Krasheninnikova's thesis entitled "Physical cognition in parrots: a comparative approach". Having read through Anastasia's thesis I can confirm that the use of English is correct.

Sincerely,

A handwritten signature in black ink, appearing to read 'DNC', with a long, sweeping underline that extends to the right and then loops back down.

Dennis Neal Cory

*The evolution of sense is,
in a sense,
the evolution of nonsense.*



from 'Pnin'
Vladimir Nabokov, 1953

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SUMMARY

Animals differ considerably in intelligence, defined as the speed and the success with which they solve problems related to surviving in their environment. There are a number of evolutionary hypotheses which attempt to explain cognitive variation across species as well as how cognitive traits may have evolved. A comparative approach allows us to test these evolutionary questions on the origins of and the ecological pressures on cognitive abilities. For example: Do phylogenetically closely related species share similar cognitive abilities? What kind of evolutionary pressures shape cognitive abilities across species? Does the social environment play a special role in shaping cognition? Comparisons across species require careful consideration of the experimental methods used and the factors that may affect an individual's performance in an experiment.

In this thesis, I studied the abilities of different parrot species to solve physical problems. I used the string-pulling paradigm to investigate this issue – a method that has been proved to be suitable for investigating cognitive evolution across species. I present the following new findings:

The considerable variation in the ability to solve patterned-string problems found among parrots was not related to their phylogenetic relationship. Rather, the variation in psittacines' cognitive abilities such as the understanding of mean-end relations, connectedness, and functionality was best explained by social components of their natural environment such as fission-fusion dynamics, breeding system and the size of the daily groups. It appears that parrots' enhanced cognition in the physical domain is of a domain-general nature, rather than an adaptive specialization to a certain ecological niche, and might have been evolutionarily favoured by the cognitive challenge of living in a complex social environment.

In my thesis, I provide the first evidence for an interrelation between visual-spatial and motor abilities in non-mammalian animals by showing that more highly developed motor abilities correlate positively with parrots' performance in patterned-string tasks.

Furthermore, parrots tested in a social context and those tested singly showed similar cognitive capacity in solving patterned-string problems. In contrast to previous studies, my findings revealed that, at least in the case of highly social species the testing in social settings does not appear to bias the results obtained in physical cognition experiment. On the contrary, testing of problem-solving in a social context better reflects natural behaviour and is thus more ecologically relevant for highly social species that often have to deal with cognitive challenges under conditions of social competition. Furthermore, I could show that the parrots' willingness to participate in the tasks was significantly higher in a social context. Thus, the social settings may provide advantages by decreasing the level of individual fearfulness and stress.

The study species consistently showed individual differences in personality, which correlated with individual cognitive differences in solving string-pulling problems, showing that more explorative individuals were less accurate in solving more complex string patterns. My findings also suggest that the effect of personality on cognitive performance might depend on the complexity of the task. Moreover, differences in personality traits may also determine whether social context facilitates or impairs an individual's response to a novel situation. Differences in personality traits as well as social context thus must be carefully considered when designing setups, interpreting findings and comparing them across species.

ZUSAMMENFASSUNG

Tiere unterscheiden sich in ihrer Intelligenz, d.h. in der Geschwindigkeit und im Erfolg, mit dem sie Probleme in ihrer Umwelt lösen. Es existiert eine Reihe von Evolutionshypothesen, die versuchen, diese Variation und die Entwicklung kognitiver Fähigkeiten bei verschiedenen Arten zu erklären. Ein vergleichender Ansatz erlaubt die Überprüfung dieser und anderer evolutionärer Fragen zu den Ursprüngen von und den Selektionsdrücken auf kognitive Mechanismen. Zum Beispiel: Haben phylogenetisch eng miteinander verwandte Arten ähnliche kognitive Mechanismen? Welche Selektionsdrücke formen kognitive Mechanismen bei verschiedenen Arten? Spielt das soziale Umfeld eine besondere Rolle bei der Entwicklung von Intelligenz? Vergleiche zwischen Arten erfordern dabei eine sorgfältige Berücksichtigung der verwendeten experimentellen Methodik sowie der Faktoren, welche die Leistung eines Individuums in einem Experiment beeinflussen.

In dieser Arbeit habe ich die Fähigkeiten verschiedener Papageienarten, physikalische Probleme zu lösen, untersucht. Ich habe dafür das sogenannte *string-pulling*-Paradigma verwendet - eine Methode, die sich bereits für die Untersuchung kognitiver Fähigkeiten verschiedener Arten als geeignet erwiesen hat. Die Arbeit brachte folgende neuen Erkenntnisse hervor:

Die erhebliche Variation in der Fähigkeit verschiedener Papageienarten, *string-pulling*-Probleme zu lösen, ist nicht durch phylogenetische Verwandtschaftsverhältnisse zu erklären. Stattdessen wird die Variation der kognitiven Fähigkeiten, wie z.B. das Verständnis des Ursache-Wirkung-Prinzips, des Prinzips der physikalischen Verbundenheit und der Funktionalität am besten durch soziale Komponente der Umwelt erklärt. Dazu zählen die sogenannte Fission-Fusion-Dynamik einer Gruppe, das Brutsystem und die Größe der Tagesgruppen. Es scheint, als ob das fortgeschrittene physikalische Verständnis aus evolutionärer Sicht durch kognitive Herausforderungen des Lebens in einem komplexen sozialen Umfeld begünstigt wurde. Das Verständnis physikalischer Zusammenhänge erscheint deshalb genereller Natur, und stellt keine adaptive Spezialisierung auf eine bestimmte ökologische Nische dar. Die vor-

liegende Arbeit liefert auch erste Hinweise auf einen Zusammenhang zwischen visuell-räumlichen und motorischen Fähigkeiten bei Nicht-Säugetieren. Sie zeigt, dass feinere motorische Fähigkeiten positiv mit der Leistung der Papageien in *string-pulling*-Aufgaben korrelieren.

Darüber hinaus zeigten einzeln getestete Papageien und solche, die in einem sozialen Kontext getestet wurden, keine signifikanten Unterschiede in ihrer Fähigkeit *string-pulling*-Probleme zu lösen. Im Gegensatz zu früheren Studien, legen die Ergebnisse meiner Untersuchung nahe, dass das Testen der Tiere in einer Gruppe, zumindest bei sozialen Arten, keine Beeinträchtigung der Leistungsfähigkeit in einem Experiment nach sich zieht. Im Gegenteil, die Problemlösung im sozialen Kontext spiegelt das natürliche Verhalten sozialer Arten besser wider, da sie mit kognitiven Herausforderungen oft unter den Bedingungen des sozialen Wettbewerbs umgehen müssen. Das Testen sozialer Arten in der Gruppe hat somit ökologische Relevanz. Darüber hinaus kann der soziale Kontext auch Vorteile durch die Verringerung der Ängstlichkeit und des Stress-Niveaus einzelner Individuen mit sich bringen. Denn, wie ich zeigen konnte, war die Bereitschaft, sich an den Aufgaben zu beteiligen, signifikant höher bei im sozialen Kontext getesteten Individuen.

Meine Untersuchungen haben gezeigt, dass alle getesteten Arten individuelle Unterschiede in der Persönlichkeit zeigten und diese mit individuellen kognitiven Unterschieden bei der Lösung von *string-pulling*-Aufgaben korrelierten. Bei allen Arten waren neugierige Individuen weniger genau bei der Lösung komplexer *string-pulling*-Muster. Meine Ergebnisse deuten auch darauf hin, dass der Effekt der Persönlichkeitsmerkmale auf die kognitive Leistung von der Komplexität der Aufgabe abhängen kann. Darüber hinaus können Unterschiede in Persönlichkeitsmerkmalen auch bestimmen, ob ein sozialer Kontext die Reaktion eines Individuums auf eine neue Situation erleichtert oder beeinträchtigt. Unterschiede in der Persönlichkeit, sowie im sozialen Kontext müssen deshalb bei dem experimentellen Design, der Interpretation der Ergebnisse sowie beim Vergleich verschiedener Arten sorgfältig berücksichtigt werden.

INTRODUCTION

Cognition is the ability to acquire, process, store and use information to respond to changes in the environment (Shettleworth 2010). Animals differ in the ways they respond to similar environmental challenges. In some species, these responses are based on enhanced cognitive processes such as learning and reasoning. Charles Darwin argued that such between-species differences in cognitive skills were differences “of degree, and not of kind” (Darwin 1871). Darwin’s argument is consistent with the general process view, according to which the same fundamental processes of cognition are used across an extensive range of problems based on different inputs (Papini 2002). An alternative view to generalized processes is that cognition is adaptive and domain-specific, i.e. animals have evolved specific cognitive skills to solve problems associated with their particular ecological niches (Pinker 2010). Associated with the latter, numerous hypotheses have been postulated to explain cognitive variation among species and to analyse how cognitive traits may have evolved. While some authors emphasize complex foraging strategies and ecological pressures as the primary forces shaping the evolution of animal cognition (Byrne 1997; Milton 1981), others suggest that increased social complexity favoured the evolution of cognitive flexibility (Dunbar & Shultz 2007; Emery et al. 2007a).

Comparative approaches make it possible to extensively study questions regarding the origins of and evolutionary pressures on cognitive mechanisms (Deaner et al. 2000; Deaner et al. 2006; Harvey & Pagel 1991; MacLean et al. 2012). However, although this field is designated, ‘comparative’ cognition, there is a lack of broad comparative studies which assess cognition through behavioural performance; instead, neuroanatomical proxies (e.g., brain size) for cognitive abilities have been used to classify differences in cognition among species (Barton 1996; Burish et al. 2004). Empirical evidence, however, suggests that there is no one-to-one relationship between cognitive abilities and brain size (Banerjee et al. 2009; Deaner et al. 2006; Emery & Clayton 2004; Hare et al. 2002; Herrmann et al. 2007; Liedtke et al. 2011; MacLean et al. 2008). Alternatively, pairs of

closely related species have been compared in terms of their behavioural performance (Bond et al. 2003; MacLean et al. 2008). However, such comparisons often use different tests for different pairs of species, making it difficult to generalize results across species. Therefore, broad comparisons using direct measures of cognition are urgently needed for testing hypotheses of cognitive evolution (Tomasello & Call 2008).

Comparisons across species require careful consideration of the experimental methods used. An adequate experimental paradigm for broad comparative studies should 1) require no training, 2) be easily applicable across species, and 3) require only few trials per subject (MacLean et al. 2012). String-pulling is a widely used and accepted paradigm in comparative cognition and fulfils these methodological requirements. The string-pulling paradigm is easy to handle and to apply across a wide range of species, and it requires little training.

The paradigm can be used to address a wide variety of aspects of animal cognition (Gagne et al. 2012). For example, it gives insight into an animal’s understanding of connections, whether it grasps the functionality of strings, generalizes across conditions, and applies knowledge flexibly (Wasserman et al. 2013). The basic task – pulling an out-of-reach reward attached to a string – is simple but can be presented in various patterns. Moreover, patterned-string tasks are ecologically relevant as they provide a reasonable analogue to a natural foraging situation, whereas other physical cognition studies are often considered not to bear such relevance (Edwards et al. 2011). There are many observations of pulling-like behaviour in the wild, e.g. various birds pull and step on twigs to obtain insects or berries (Obozova & Zorina 2013; Seibt & Wickler 2006; Thorpe 1963), elephants pull on twigs to feed on treetop (Van Lawick-Goodall 1970), and various primates pull branches of trees that hold fruits or leaves towards them (Chevalier-Skolnikoff 1983; Halsey et al. 2006). As the vegetation of trees is often dense, it is likely that they need to choose the right branch to pull.

Many different cognitive skills have been suggested to be required to pull the “right”

string, including associative learning, means-end understanding and insight. In the following I outline some of the abilities most commonly tested by different patterned-string tasks.

(a) Means-end understanding

Pulling a string does not always require means-end understanding (Thorpe 1963) as the pulling action or the string itself can be rewarding. Sometimes the subject pulls an unrewarded string at a similar rate to the rewarded one, implying that the string-pulling is rewarding in itself (Schuck-Paim et al. 2009; Whitt et al. 2009). An animal can reasonably be said to use a string as a mean to an end when the string-pulling is reward-orientated, i.e. when it can be shown that pulling a string itself is not self-rewarding. The parallel-string condition in Figure 1 tests for such reward-orientation of string-pulling behaviour, which is given when animals repeatedly choose the rewarded string (Mason & Harlow 1961).

(b) Understanding connectedness

Pulling the string next to the reward might be the most common strategy animals employ when faced with patterned-string tasks. This so-called proximity error has been observed in numerous species, including birds, dogs, and primates (Bagotskaya et al. 2012; Gagne et al. 2012; Koehler 1927; Osthaus et al. 2005; Riemer et al. 2014; Taylor et al. 2010). Relying on proximity can lead to a failure in a number of task configurations, including when two rewards are present but only one can be obtained. Whether animals understand the mechanism of connectedness can be tested by placing the reward close to, but not touching the “incorrect” string: the so-called broken string condition (Figure 1).

(c) Understanding functionality

Whether the subject relies on the relevant functional or structural aspects of the problem rather than on arbitrary cues can be tested by using strings of different colour, length or texture (Dücker & Rensch 1977). In the crossed-string condition (Figure 1) animals may either follow the strings visually – then the difference in appearance (e.g. colour) of the strings should not matter much – or they may associate the colour of the string at the reward with the colour of the string at the perch.

The behaviours necessary for successful string-pulling are unlikely to be entirely innate (Thorpe 1963). Behavioural innovations and learning, coupled with physical cognition appear to be required (Huber & Gajdon 2006). This makes the string-pulling paradigm particularly useful for investigating physical cognition. However, divergent methods and unstandardized reporting have previously limited its comparative utility. For all the vast number of publications on the string-pulling paradigm, we know surprisingly little about the cognitive mechanisms behind the solutions which animals find for the many patterns.

Another point that has attracted less attention in comparative studies of physical cognition, so far, is the fact that different species and different individuals have diverse anatomical and psychological prerequisites for successful problem-solving (Stevens 2010). Although factors such as motivation, inhibition, timidity, social competition, and motor skills are often not the immediate focus in studies of physical cognition, understanding them may be essential to designing experimental setups, interpreting findings, and comparing them across species, not least when applied to string-pulling.

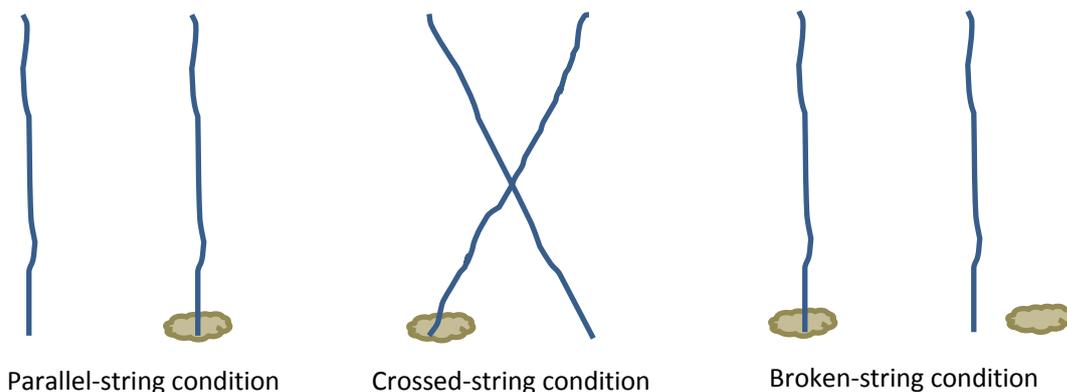


Figure 1: The most commonly used string patterns

In my thesis, I combine experimental work with comparative analyses to advance the understanding of specific cognitive skills in the domain of physical cognition. I test hypotheses of cognitive evolution by using the string-pulling paradigm as a direct measure of cognitive abilities. I investigate an interrelation between motor performance and the visual-spatial abilities needed to solve patterned-string problems. Furthermore, I compare the physical cognition of one particular species in different experimental paradigms. I also investigate factors that may affect the performance in physical cognition tests. I show the importance of personality in solving problems. I also show the influence of testing in social settings on cognitive performance.

Study organisms

Besides primates, corvids and parrots are the most often studied taxa for investigating physical cognition. These non-primate, non-mammalian animals possess enhanced cognitive abilities, such as understanding of spatial relationships between objects (Auersperg et al. 2009; Auersperg et al. 2011; Auersperg et al. 2010), cooperative problem-solving (Péron et al. 2011; Seed et al. 2008), creating tools (Auersperg et al. 2012; Weir et al. 2002) and not least, means-end understanding of string-pulling problems (Heinrich & Bugnyar 2005; Taylor et al. 2010). Studies on string-pulling were found for a variety of parrot species, including keas and members of both true parrots and cockatoos (Dücker & Rensch 1977; Krasheninnikova et al. 2013; Krasheninnikova & Wanker 2010; Magat & Brown 2009; Pepperberg 2004; Schuck-Paim et al. 2009; Werdenich & Huber 2006). However, it is not clear whether or not the cognitive skills required to solve string-pulling problems are domain-general or an adaptive specialization.

Parrots are a particularly suitable model organism for testing predictions about cognitive evolution in birds. With over 360 species worldwide, they exhibit high levels of diversity in many evolutionarily relevant characteristics such as diet, sociality and life-history traits.

In my thesis, I test string-pulling behaviour in two neotropical species, *Myiopsitta monachus* and *Amazona amazonica*, three 'Old World' species, *Agapornis roseicollis*, *Poicephalus senegalus*, and *Coracopsis vasa*, and three species from the Australian region, *Eclipticus roratus*, *Eolophus roseicapilla*, and *Nymphicus*

hollandicus. For all species, except *E. roseicapilla* and *N. hollandicus*, this constitutes the first report of string-pulling behaviour. In addition, I also use published data obtained from comparable experimental protocols for meta-analyses.

Study objectives

Cognitive phylogeny (Chapter 1)

An important initial question for comparative cognition is whether phylogeny predicts cognitive abilities across species (MacLean et al. 2012). Quantifying the degree to which closely related species share similar cognitive traits is thus a first step in testing evolutionary hypotheses. However, only few studies directly compare different species performing the same task (Auersperg et al. 2011; Krasheninnikova et al. 2013; Liedtke et al. 2011; MacLean et al. 2013; Rosati et al. 2014; Schloegl et al. 2009), and even fewer attempts have been made to compare cognitive performances phylogenetically (MacLean et al. 2012). In chapter 1, we draw data on the ability to solve patterned-string problems in 23 parrot species. To test whether the variation in this ability is explained by phylogenetic relatedness, we investigate the phylogenetic signal in the data using phylogenetic trees based on taxonomic and molecular data.

Correlated evolution (Chapter 2)

A second important question is, whether the variation in specific cognitive skills correlates with changes in ecological, social, or life-history traits (MacLean et al. 2012). One of the main goals of comparative cognition is thus to document variation in mental abilities across species to reveal the processes by which cognition evolves (Balda et al. 1996; Deaner et al. 2000; Stevens 2010; van Horik & Emery 2011; van Horik et al. 2012). In chapter 2, I investigate the variation in certain modules of cognitive skills among parrot species using performance in the patterned-string tasks as a direct measure of cognition. Furthermore, I quantitatively examine the relationship between this direct measure of cognition and several explanatory variables such as socio-ecological, life history and morphological traits.

Factors which affect the cognitive performance in experimental paradigms should also be addressed when comparing physical cognition between and within species (Halsey et al. 2006;

Ohl et al. 2002; Toxopeus et al. 2005; Ward 2012). In chapters 3 to 6, I address some of these factors.

Motor skills (Chapter 3)

For birds, the most critical part of string-pulling, in terms of motor skills, appears to be stepping on the string (Heinrich & Bugnyar 2005; Huber & Gajdon 2006; Magat & Brown 2009). Many authors have argued that such stepping only occurs in species that use their feet for feeding (Seibt & Wickler 2006; Skutch 1996). In chapter 3, I test the hypothesis that the use of feet during foraging is a prerequisite for solving the vertical string pulling problem. In addition, the mammalian and the avian cerebellum interrelate motor and cognitive functions (Petrosini et al. 1998; Spence et al. 2009) implying that there may be an interrelation between visual-spatial and motor performance. Therefore, in chapter 3, I also test whether the fine motor skills needed for advanced beak-foot coordination may be interrelated with certain visual-spatial abilities needed for solving patterned-string tasks.

Inhibition (Chapter 4)

A lack of inhibition could cause an animal to choose an option (e.g. string, cloth or drawer) in a choice paradigm at random or simply to choose the closest one (Osthaus et al. 2005; Pfuhl 2012). Inhibition of behaviour towards an incorrect option saves time and energy and indicates behavioural flexibility (Seibt & Wickler 2006; Taylor et al. 2010). In chapter 4, we investigate the physical cognition in green-winged macaws. This parrot species has one of the largest relative brains in the avian taxa but previously showed limited understanding in physical cognition (Liedtke et al. 2011). It has been suggested that this failure might have been caused by the species' lack of inhibitory control (Krasheninnikova et al. 2013; Liedtke et al. 2011). In chapter 4, we presented the macaws with the trap-table paradigm - a task with equivalent causal relationships but one which facilitates the birds' inhibitory control. We tested the macaws with two further physical tasks – support problem and tube lifting – problems with different physical causal relations requiring different levels of inhibitory control.

Testing conditions (Chapter 5)

Testing animals individually in problem-solving tasks limits distractions of the subjects

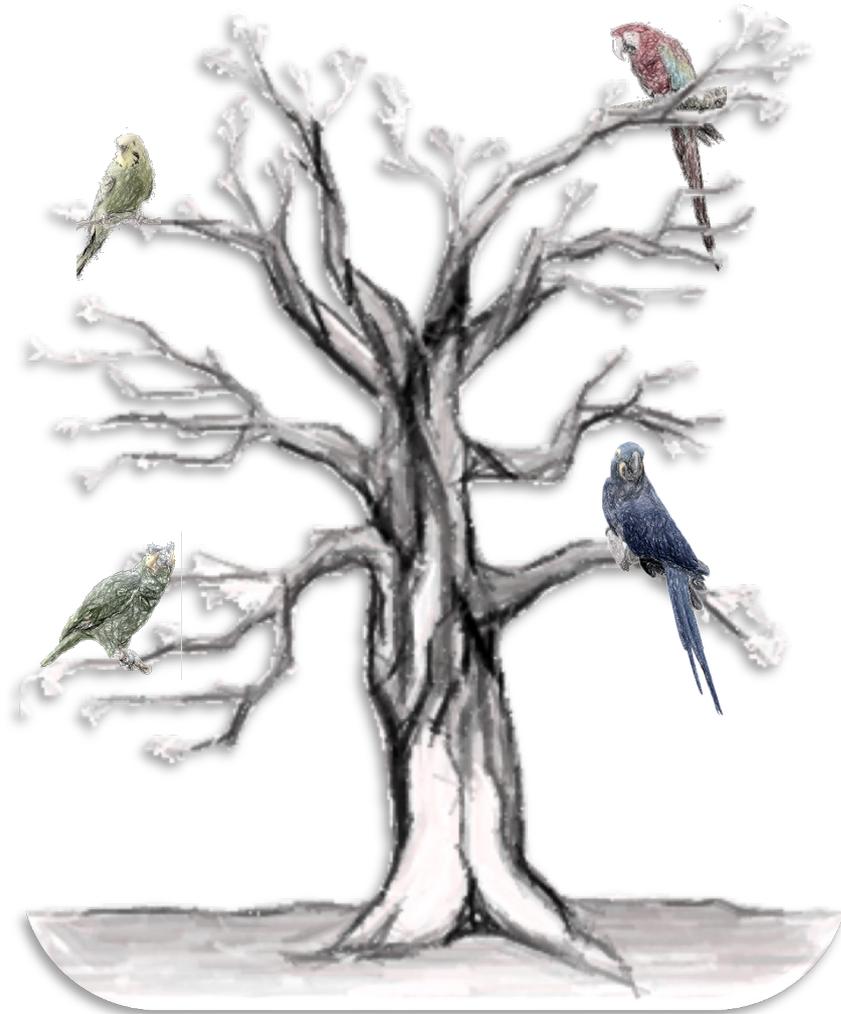
during the test, so that they can concentrate completely on the problem. However, the resulting individual performance may not resemble the problem-solving capacity that is commonly employed in the wild when individuals are faced with a novel problem in their social group (Halsey et al. 2006). Within such a social context, the presence of a conspecific influences an individual's behaviour (Stöwe & Kotrschal 2007). On the one hand, a subject's inability to solve complex patterned-string problems might be a result of difficulties in simultaneously monitoring its own actions and attending to social competitors or predators at the same time (Boere 2001; Gazes et al. 2012). In chapter 5, I thus assess the validity of data gathered on parrots when tested jointly by comparing the performance in patterned-string tasks between parrots tested singly and those tested in social context. On the other hand, social isolation in test settings may result in differences in motivation, which may possibly even cause failure in singly-tested animals (Heinrich 1995; Itoh 2001; Ohl et al. 2002; Toxopeus et al. 2005). In chapter 5, I also assess the fearfulness of the subjects and investigate how this affects their willingness to participate in experiments.

Personality (Chapter 6)

Research on animal cognition generally reveals substantial variation in the performance of individuals (Carere & Locurto 2011; Sih & Del Giudice 2012). Personality traits such as explorative tendencies and timidity have been suggested to be an important source of this variation (Vonk & Povinelli 2011). However, studies that connect personality with cognition are surprisingly rare (Coleman et al. 2005; Cussen & Mench 2014). In chapter 6, I test whether individual differences in the performance in patterned-string paradigms relate to differences in personality traits such as timidity and exploration tendency.

Note

The individual chapters of this thesis were written to stand alone, without the need for referring to other sections. A certain degree of overlap in the descriptions and explanations was therefore unavoidable.



Chapter 1

NO EVIDENCE FOR AN ASSOCIATION OF PHYLOGENY AND
COGNITIVE PERFORMANCE IN PARROTS

No evidence for an association of phylogeny and cognitive performance in parrots

Anastasia Krasheninnikova • Ulrike Busse • Jutta M Schneider

Comparative cognition needs to know how well phylogeny predicts cognitive abilities across species. Quantifying the extent to which closely related species share similar cognitive skills is thus a first step in testing evolutionary hypotheses. However, only few studies directly compare different species for the same task. Here we draw data on the ability to solve patterned-string problems in 23 parrot species and we investigate the phylogenetic signal in these data using phylogenetic trees based on taxonomic and molecular data. The mean proportion of correct choices made by each species was used as the dependent measure for a phylogenetic analysis. Our findings indicate that despite considerable variation between species, more closely related species do not exhibit more similar cognitive skills. We suggest that patterned string tasks detect interspecific variation due to different selection regimes.

Keywords: Cognitive phylogeny, Comparative cognition, Evolution, Parrots, Patterned-string task

Introduction

An important question for comparative cognition is how well phylogeny predicts cognitive variation across species. Therefore, quantifying the extent to which closely related species share similar cognitive abilities must be done when testing an evolutionary hypothesis. One of the comparative phylogenetic approaches is based on the concept of phylogenetic signal (MacLean et al. 2012). The phylogenetic signal describes to which degree closely related species exhibit similarities in a trait (e.g. relative brain size), suggesting that it is a heritage from a common ancestor. Some behavioural phenotypes also exhibit a phylogenetic signal (Kamilar & Cooper 2013), but few attempts have been made to phylogenetically compare cognitive performances (MacLean et al. 2012).

We investigated the phylogenetic patterns of performance in patterned-string tasks and relative brain size of 23 parrot species, including measurements of 147 individuals in total. Patterned-string problems fulfil the methodological requirements for large-scaled comparative studies as proposed by MacLean et al. (2012), since this task 1) requires no training, 2) is easily to apply across species, and 3) requires only few trials per individual. To solve the task the subject has to choose between two or more strings, only one of which is connected to a reward. A patterned-string task thus requires both perceptual and cognitive abilities as the subject has to determine the difference in the strings and to understand which string leads to the reward.

Material and Methods

Cognitive data

We analysed the parrots' performance on two basic patterned-string configurations: the crossed-string task and the broken-string task. We used data set of 12 species tested by AK and UB and completed it with published data for 11 additional species [keas: Werdenich and Huber (2006); Hyacinth macaws, Lear's macaws, and blue-fronted amazons: Schuck-Paim et al. (2009); spectacled parrotlets, green-winged macaws, sulphur-crested cockatoos, and rainbow lorikeets: (Krasheninnikova et al. 2013); galahs and cockatiels: Krasheninnikova (2013)].

In the crossed-string configuration two differently coloured strings were presented to allow birds tracing the strings from one end to the other more easily. In the broken-string configuration two parallel strings of equal length were presented, one connected to a reward, the other one with a gap between string and reward. Note that in the broken-string configuration the procedures used by AK, UB and Werdenich and Huber (2006) differed from that used by Schuck-Paim et al. (2009) in terms of possibility of perceptual feedback (Taylor et al. 2009; Taylor et al. 2012). The procedure used by Schuck-Paim et al. (2009) in the broken-string task excluded the possibility of using the string's weight or reward's movement as a cue helping to determine whether a string was or was not connected to the reward. Thus species' differences in the performance showed in the broken-string configuration must be considered with caution. A correct choice was scored if the subject started with a pulling action at the rewarded string and reached

the end of the string. The mean proportion of correct choices made by each species was used as the dependent measure for the phylogenetic analysis. Data for body and brain sizes of the target species were obtained from (Iwaniuk et al. 2004; Iwaniuk & Nelson 2003; Schuck-Paim et al. 2008). The ability to pull up a rewarded string in the single string task had been tested for all subjects. Furthermore, all subjects were tested with the parallel string tasks to ascertain that their string-pulling behaviour was reward-orientated.

Phylogenetic data

We constructed a phylogenetic tree from sequences of the Cytochrome b gene (parts), and the protein coding region of mitochondrial NADH dehydrogenase 2 genes. The sequences were obtained from GenBank using the data published by various authors (for Genbank accession number see Table S1). Unfortunately, genetic data were not available for all species tested, thus the phylogenetic tree based on molecular data contained only 16 species. Sequences for each gene region were aligned separately in ClustalW (Chenna et al. 2003) using the default settings for gap opening and extension penalties followed by limited manual correction of gap placement in MEGA 5.2 (Tamura et al. 2011). The resulting alignments were combined in MEGA 5.2 to create a data set of 1.555 aligned nucleotide positions for 16 species. The phylogenetic tree based on genetic information was created in MEGA 5.2 using maximum likelihood (ML) criteria. Nodal support was assessed with 1000 bootstrap replicates. We then built a second phylogenetic tree from a set of nested taxonomic variables for all species tested ($n = 23$) in R using *as.phylo* function from the *ape* package (Paradis et al. 2013). The taxonomic variables have been passed in the correct order: the higher clade on the left of the formula (e.g. ~Order/Family/Genus/Species). The taxonomic information was obtained from Joseph et al. (2012); Schodde et al. (2013). Both trees are mostly congruent to each other (for the phylogenetic tree based on molecular data see Figure S1).

For additional details on data used such as housing facilities and sample sizes see Table S2.

Analysis

We performed a generalised linear mixed model (GLMM) using *lmer*s [package '*lme4*',

Bates et al. (2012)] in R 3.0.1 (RDTTeam 2013), with 'individual' as random factor to assess the variation in the proportion of successfully solved trials in the two patterned-string configurations. Following fixed effects were used: 'species', 'age' (juvenile/adult), 'origin' (Afrika/ Neotropics/ Australia/ Indo-Pacific) and 'housing facility'. Effect of significance was tested by dropping terms individually from the full model, and non-significant terms were removed via backwards elimination.

We estimated the phylogenetic signal in the cognitive traits using Pagel's Lambda with *phytools* package (Revell 2012) in R. To test whether the maximum likelihood estimate of λ is significantly better than a model in which λ is fixed to 0 (no phylogenetic signal) or 1 (covariance between species is directly proportional to shared evolutionary history), we used the likelihood ratio test from R package *geiger* (Harmon et al. 2008).

Results

Variation in performance on patterned-string tasks

We found a considerable variation across the parrot species tested (Figure 1). The proportion of correctly solved trials in both task configurations differed significantly across species (crossed-strings configuration: GLMM, $\text{Chi}^2 = 5.384$, $\text{df} = 22$, $p < 0.0001$; broken-string configuration: GLMM, $\text{Chi}^2 = 5.088$, $\text{df} = 20$, $p < 0.0001$).

Phylogenetic signal in cognitive trait (performance on patterned-string tasks)

We found no statistically significant phylogenetic signal in both in the crossed-strings and the broken-string configuration data. In each case, the λ was close to zero, indicating that closely related species do not have more similar trait values. Our estimate of λ was not significantly greater than 0 but significantly smaller than 1, confirming that the trait distribution showed no association with phylogeny and rather indicated that variance in the trait has accumulated over time as predicted by Brownian motion. Table 1 summarises the analysis of phylogenetic dependence of cognitive data.

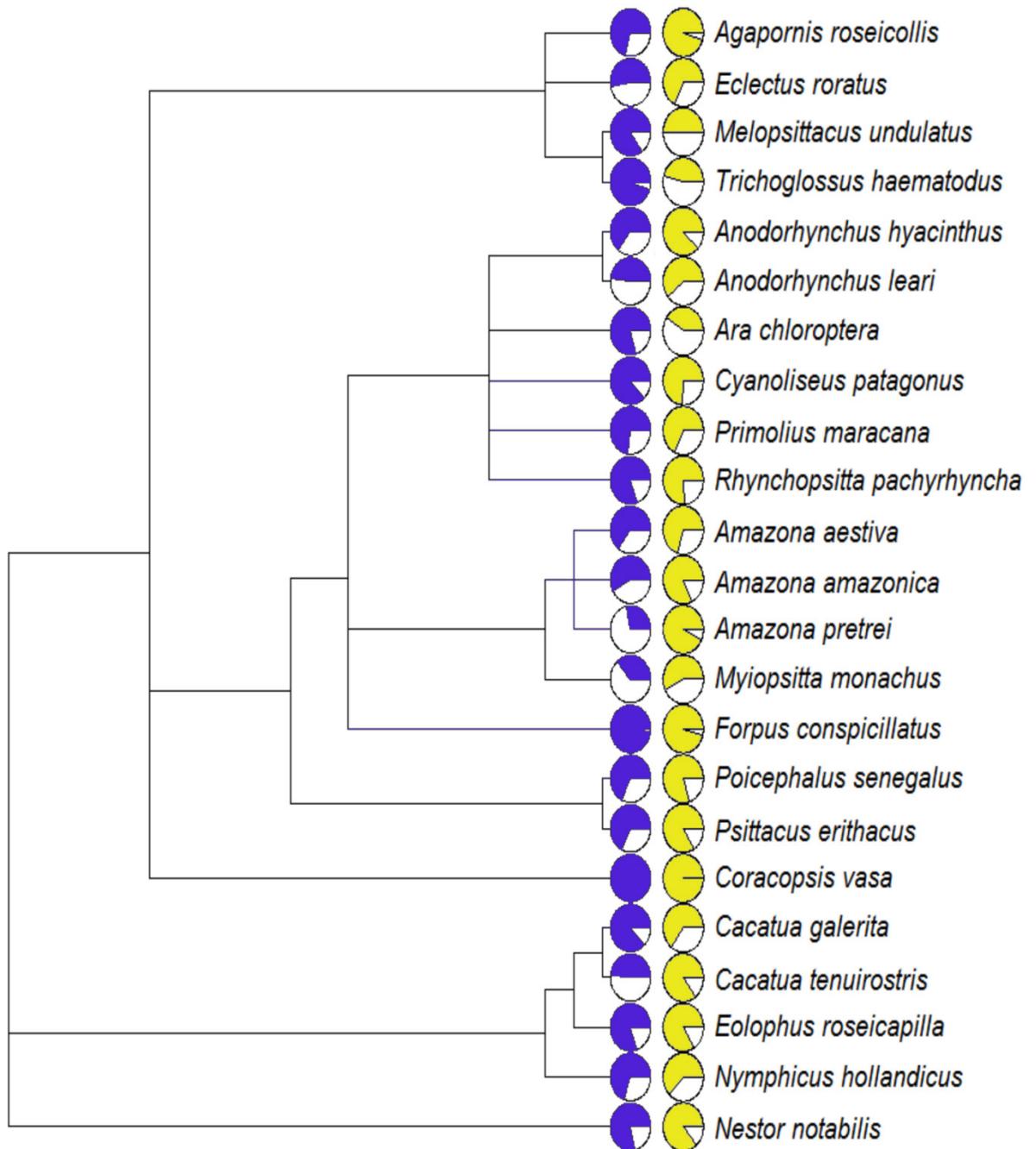


Figure 1: Phylogeny of parrot species tested on patterned-string tasks (n=23). The phylogenetic tree was generated using nested taxonomic information. The pie-diagrams represent the percentage of correctly solved trials per species. Blue: crossed-string task; Yellow: broken-string task. The percentage refers to the percentage shown by each species divided by the maximum percentage shown.

Table 1: Analysis of phylogenetic signal of “cognitive” and “morphological” data.

Tree	Trait	λ	In lik	In lik ($\lambda=0$)	In lik ($\lambda=1$)
Taxonomic (n=23)	Performance on crossed-string task	0.000068	9.247	9.247 ^a	11.501 [*]
	Performance on broken-string task	0.000069	12.656	12.657 ^a	15.746 [*]
	Brain size	0.898	- 30.318	- 28.318 ^{**}	- 28.142 [*]
	Relative brain size	0.6	- 71.345	- 72.685 [*]	- 72.863 [*]
Molecular (n=16)	Performance on crossed-string task	0.000066	7.258	7.258 ^a	8.452 [*]
	Performance on broken-string task	0.000061	8.902	8.902 ^a	11.641 [*]
	Brain size	0.63	- 42.546	- 49.182 ^{***}	- 49.037 ^{***}
	Relative brain size	0.99	- 18.516	- 21.732 [*]	- 21.558 [*]

Note: We estimated Pagel's Lambda λ , the degree of phylogenetic dependence of the data, defined as the maximum likelihood estimate. The maximum likelihood estimate of λ is given together with its associated log likelihood. Also shown are the log-likelihood values for the model, with λ set to either 0 or 1. Values significantly different from the test value (determined from a log-likelihood ratio test) are indicated in bold, together with the significance level. ^a Not significant; ^{*} $P < 0.05$; ^{**} $P < 0.01$; ^{***} $P < 0.001$.

Phylogenetic signal in morphological trait (brain size)

Brain size and relative brain size exhibited a strong phylogenetic signal (taxonomic tree: $\lambda = 0.89$ and $\lambda = 0.6$, respectively; molecular tree: $\lambda = 0.63$ and $\lambda = 0.99$, respectively), showing that more closely related species have a more similar neural basis. The likelihood ratio test indicated that the maximum likelihood estimates for λ in both cases provided a better fit to the cognitive data than a model in which λ is fixed to 0 or 1 (Table 1).

Discussion

The findings indicated 1) that the considerable variation in the ability to solve patterned-string problems across species was not related to phylogenetic relationship, and 2) that both brain size and relative brain size were predicted by species relatedness. Hence, closely related species do not show more similar cognitive performance on the tasks presented, despite the fact that the anatomical proxy for cognitive abilities showed phylogenetic dependence. Similar findings were made in a recent meta-analysis on various experimental paradigms: closely related species were not similar in their performance on object permanence, mirror self-recognition or causal reasoning (Thornton & Lukas 2012).

Cognitive traits may be functionally associated with socio-ecological (e.g. diet, group size etc.) or morphological (e.g. brain size) traits. Lack of a phylogenetic signal in the data suggests, however, that environmental factors (e.g. social and/or ecological selective forces) might have

influenced the evolution of the cognitive trait (e.g. performance in patterned string tasks) independently from phylogeny. A small phylogenetic signal is often interpreted as evolutionary liability or high rates of trait evolution leading to large differences among close relatives (Kamilar & Cooper 2013). For instance, we would expect a relatively weak phylogenetic signal in ecological traits of species during adaptive radiation because closely related species that diversified into different niches will exhibit distinct adaptive characteristics. In fact, ecological and behavioural traits generally tend to show low dependency on phylogeny compared to morphological or physiological traits (Blomberg et al. 2003) due to ecological and behavioural plasticity across species. A recent study by Kamilar and Cooper (2013) on primate behaviour investigated phylogenetic signals for 31 ecological and life-history variables including brain size, social organization, diet, climatic variation etc. Only brain size revealed a strong phylogenetic signal value, whereas low values were found for most of the analysed ecological and social variables (Kamilar & Cooper 2013).

Cognitive abilities involved in solving patterned-string tasks in parrots might be linked to certain socio-ecological variables rather than only to anatomical proxies. For example, the patterned-string task has been suggested to provide a reasonable simulation of natural foraging situations encountered by frugivorous species (Halsey et al. 2006). As the vegetation of trees is often dense, it is likely that species feeding mostly on fruits benefit from the ability to choose the 'right' branch to pull. Con-

sequently, we would expect that diet conditions that species experience drive variation in the specific cognitive skills needed to understand the relationship between objects. That would then result in low phylogenetic signal in both the ecological variable and the associated cognitive trait.

This study is the first to compare the performance of several parrot species in the same task directly. However, further studies are needed to generate larger datasets allowing comparative research to quantitatively examine the relationship between a cognitive trait (e.g. causal understanding) and explanatory variables (e.g. socio-ecological or morphological traits).

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Supplementary Material

Table S1: Gene sequences obtained from GenBank and used in this study.

Taxon name	Genbank accession number ND2	Genbank accession number Cyt b
<i>Anodorhynchus hyacinthus</i>	KF017462.1	DQ143286.1
<i>Anodorhynchus leari</i>	AY669446.1	AF370764.1
<i>Amazona aestiva</i>	AY194434.1	AY286203.1
<i>Amazona amazonica</i>	AY194466.1	JQ235571.1
<i>Cacatua galerita</i>	JF414344.1	AB177977.1
<i>Coracopsis vasa</i>	EU327612.1	AF346355.1
<i>Cyanoliseus patagonus</i>	EU327613.1	DQ143283.1
<i>Eclectus roratus</i>	EU327619.1	AB177965.1
<i>Forpus conspicillatus</i>	JX877387.1	JX877362.1
<i>Melopsittacus undulatus</i>	EU327633.1	DQ143295.1
<i>Myiopsitta monachus</i>	EU327635.1	DQ150996.1
<i>Nestor notabilis</i>	EU327641.1	AF346389.1
<i>Nymphicus hollandicus</i>	EU327643.1	AF346399.1
<i>Psittacus erithacus</i>	EU327661.1	AY082076.1
<i>Rhynchopsitta pachyrhyncha</i>	EU327665.1	DQ143297.1
<i>Trichoglossus haematodus</i>	EU327671.1	AB177942.1
<i>Falco peregrinus</i>	EU327624.1	X86746.1

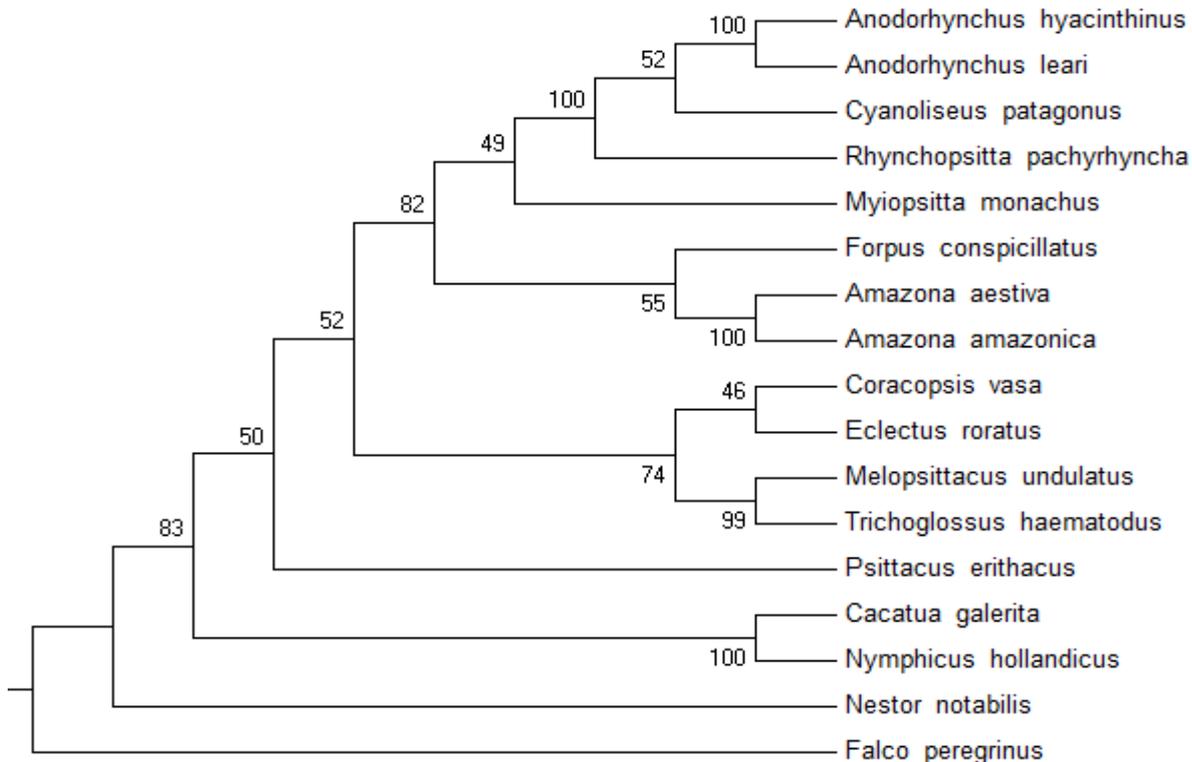
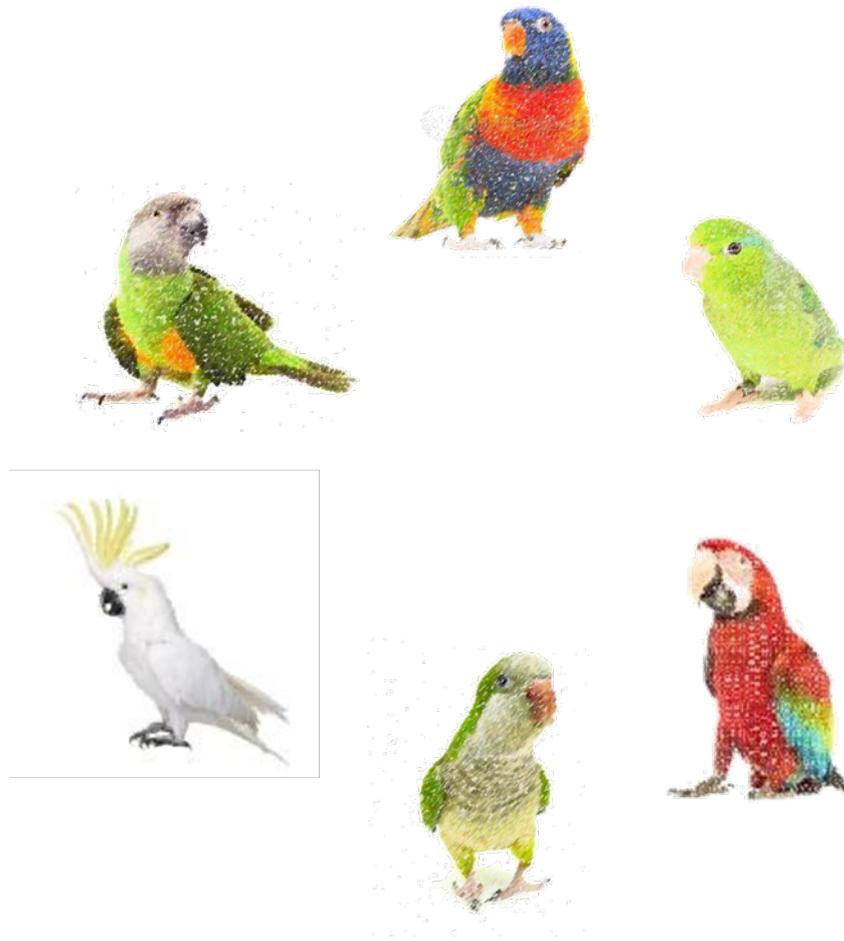


Figure S1: Phylogeny of parrot species tested on patterned-string tasks ($n=16$). The phylogenetic tree was generated in MEGA 5.2 based on genetic information from a part of Cytochrome b gene, and the protein coding region of mitochondrial NADH dehydrogenase 2 genes using maximum likelihood (ML) criteria. Nodal support was assessed with 1000 bootstrap replicates. *Falco peregrinus* was used as an out-group.

Table S2: Data sources used, housing facilities, sample size per species, and testing conditions

Species	N	Data source and housing facilities	Testing conditions
<i>Anodorhynchus hyacinthus</i>	4		
<i>Anodorhynchus leari</i>	4	Schuck-Paim et al. 2009	Pair-wise
<i>Amazona aestiva</i>	2		
<i>Amazona amazonica</i>	23	Krasheninnikova & Schneider 2014 (Chapter 5)	Group, individually
<i>Electus roratus</i>	10		
<i>Coracopsis vasa</i>	10	AK	group
<i>Myiopsitta monachus</i>	7	The Parrot Zoo, UK	
<i>Poicephalus senegalus</i>	12		
<i>Cacatua galerita</i>	3		
<i>Ara chloroptera</i>	4	Krasheninnikova et al. 2013	
<i>Eolophus roseicapilla</i>	6		group
<i>Nymphicus hollandicus</i>	10	Krasheninnikova 2013 (Chapter 3)	
<i>Agapornis roseicollis</i>	15	AK Tierpark Gettorf, Germany	group
<i>Melopsittacus undulatus</i>	5		
<i>Psittacus erithacus</i>	1	Krasheninnikova (MSc-Thesis 2010)	group
<i>Forpus conspicillatus</i>	8		
<i>Trichoglossus haematodus</i>	10	Krasheninnikova et al. 2013	group
<i>Cyanoliseus patagonus</i>	3		
<i>Rhynchopsitta pachyrhyncha</i>	3		
<i>Cacatua tenuirostris</i>	6	UB	group
<i>Amazona pretrei</i>	2	Loro Parque / Loro Parque Fundación, Spain	
<i>Primolius maracana</i>	2		
<i>Nestor notabilis</i>	7	Werdenich & Huber 2006	individually



Chapter 2

COMPARATIVE ANALYSIS OF STRING-PULLING BEHAVIOUR
IN PARROTS: REVEALING EVOLUTIONARY PRESSURES THAT
SHAPE COGNITIVE ABILITIES

Comparative analysis of string-pulling behaviour in parrots: revealing evolutionary pressures that shape cognitive abilities

Anastasia Krasheninnikova

Although it is generally acknowledged that there is a large variation in how animals cope with the cognitive challenges in their environment, the question of what actually shapes the evolution of different cognitive skills is still unresolved. Do cognitive skills evolved as responses to ecological or social factors and how important is phylogeny? One of the main goals of comparative cognition is to document variation in mental abilities across species and to identify selection pressures behind the evolution of cognition. In the present study I investigate the variation in certain modules of cognitive skills across parrot species using performance in the patterned-string tasks as a direct estimate of cognition. Furthermore, I examine the relationship between this direct measure of cognition and several explanatory variables such as socio-ecological, life history, and morphological traits. The variation in individual performance during patterned-string tasks could largely be explained by variables belonging to the category 'social organisation'. This study reveals a link between the social complexity and cognition and provides first empirical evidence for the domain-general nature of cognitive challenges imposed by living in a complex social environment.

Keywords: Comparative cognition, Evolution, Parrots, Social complexity

Introduction

Animals differ greatly in how they respond to changes in their environment. Some species cope with these challenges using enhanced cognitive processes such as memory, associative learning and reasoning (Shettleworth 2009). As such, cognition can be defined as the ability to acquire, process, and store information and to use this information for response to environmental challenges. There are several evolutionary hypotheses explaining cognitive variation across species and how cognitive traits may have evolved. Although these hypotheses are not mutually exclusive, they often have been presented as alternatives.

For example, the *social intelligence hypothesis* (Dunbar & Shultz 2007; Holekamp 2007; Humphrey 1976; Jolly 1966) proposes that increases in social complexity have driven the evolution of cognitive flexibility at least in primates. Two other hypotheses explain cognitive variation across species by ecological selection pressures; The *spatiotemporal mapping hypothesis* (Clutton-Brock & Harvey 1980; Milton 1981) emphasizes the demands of exploiting ecological resources dispersed in time and space. The *extractive foraging hypothesis* (Byrne 1997; Parker & Gibson 1977) stresses the selective impact of manually (or with the help of the beak) processing a variety of embedded foods.

The strongest test of such evolutionary hypotheses is to investigate variation of cognitive traits in a specific domain across species by using a comparative approach (Deaner et al. 2000; MacLean et al. 2012). Therefore, one of the most important questions in the field of comparative cognition appears to be, whether differences in particular cognitive abilities correlate with changes in independent variables, such as life history, ecological, or social factors. However, such studies have rarely been conducted with large taxonomic samples. Usually only pairs of closely related species were compared (Bond et al. 2003; MacLean et al. 2008), often with different tests used for different pairs of species, thus making any generalization across species very difficult.

To overcome these constraints, some large-scale comparative analyses have been undertaken relating an anatomical proxy for cognitive capacity (e.g., relative brain size) and to socio-ecological features (Barton 1996; Dunbar 1998; Isler & van Schaik 2009; Lefebvre et al. 1997; Reader & Laland 2002). Although analyses of anatomical proxies for cognition (e.g., brain size) allow researchers to compare across larger datasets, researchers rely on the assumption that brain size somehow reflects cognitive abilities (Healy & Rowe 2007). Empirical evidence suggests, however, that there is no one-to-one relationship between cognitive ability and brain size (Banerjee et al. 2009; Deaner et al. 2006;

Emery & Clayton 2004; Hare et al. 2002; Herrmann et al. 2007; Liedtke et al. 2011; MacLean et al. 2008). Therefore, broad comparisons of problem-solving abilities as direct measures of cognition are highly desired for testing hypotheses regarding cognitive evolution (Tomasello & Call 2008).

First suggested to be important for the evolution of primate intelligence, there is equally impressive evidence that the same socio-ecological variables also influence the evolution of avian cognition (Emery 2006; Marler 1996). Furthermore, relationships between brain size and innovative behaviour (Lefebvre et al. 2004), behavioural flexibility (Lefebvre et al. 1997), and social structure (Burish et al. 2004) have been found in large-brained birds such as corvids and parrots. Recently, the first empirical evidence for a link between social complexity and non-social cognition module has been found in parrots (psittacines) (Krasheninnikova et al. 2013). Psittacines include over 360 species worldwide that exhibit high levels of diversity in many evolutionary relevant characteristics, such as diet, sociality and life-history traits. In recent years, psittacines have proven to be a particularly interesting group for testing predictions about cognitive evolution in birds.

In the present study, I investigated, the variation in certain modules of cognitive skills across parrot species using their performance in the patterned-string tasks as a direct measure of cognition. Furthermore, I quantitatively examined the relationship between cognitive performance and socio-ecological, life history, and morphological traits.

Comparisons across species require careful consideration of the experimental methods used. MacLean et al. (2012) proposed that tests for broad comparative studies should 1) require no training, 2) be easily applicable across species, and 3) require only few trials per subject. Patterned-string problems fulfil these methodological requirements. Moreover, a patterned-string task provides a reasonable analogue to a natural foraging situation for species of animals that often pull branches with fruits or leaves. As the vegetation of trees is frequently dense, it is likely that they often have to choose the right branch to pull.

Material & methods

Socio-ecological data

I used a data set of 5 captive species obtained between April 2011 and October 2012 and completed it with published data for 7 additional species [spectacled parrotlets, green-winged macaws, sulphur-crested cockatoos, and rainbow lorikeets: Krasheninnikova et al. (2013); galahs and cockatiels: Krasheninnikova (2013); orange-winged amazons: Krasheninnikova and Schneider (2014)].

Socio-ecological data were obtained from the literature. For an overview see Table 1. The data set contains 20 variables representing nine trait categories: 1) anatomical proxy, 2) life history, 3) sexual selection, 4) social organization, 5) diet, 6) habitat, 7) ranging, 8) motor skills, and 9) climatic variability.

I focus on traits that were readily available for numerous species in the literature and suggested to be related to the evolutionary hypotheses for cognitive variation across species. For example, frugivore species feeding on more patchily distributed food resource tend to have larger brains compared to granivore species corresponding with the ecological demands of spatiotemporal mapping (MacLean et al. 2009). Both, a long developmental period and extended longevity are traits which presumably correlate with the development of complex cognition (Emery 2006). Schuck-Paim et al. (2008) have shown that large-brained parrot species possess a higher tolerance to climatic uncertainty such as rainfall or temperature variability. Species inhabiting complex habitats (e.g. forest edge) are more frequently confronted with new situations than species which live in simply structured habitats (e.g. savannah) and thus possess greater behavioural flexibility (Mettke-Hofmann et al. 2002). Living in groups with high fission-fusion dynamic has been suggested to provide an enhancement of various information-processing skills due to the highly variable party composition and thus more fluid nature of information gathered by the group members of such societies (Aureli et al. 2008). The respective mating system provides another measure of social complexity emphasizing the importance of relationship quality rather than relationship quantity (Emery et al. 2007b). Finally, using one's feet to manipulate food items requires fine motor skills that may be interrelated with certain visual-

spatial abilities also needed for solving patterned-string tasks (Krasheninnikova 2013).

Table 1: Variables examined in the study

Trait category	Variable
Anatomical proxy	Body mass (g), Brain mass (g), relative brain size, telencephalon size
Life history	Fledging age (d), max. longevity, nesting (tree hole / nest)
Sexual selection	Mating system (monogamous / polygynandrous), parental food provision (biparental / male)
Social organization	Breeding system (cooperatively / non-cooperatively), fission-fusion-dynamic (high / low) ^a , roosting size, daily group size ^b
Diet	Feeding strategy ^c (granivorous / frugivorous / nectarivorous / omnivorous), foraging (ground / canopy)
Ranging	Ranging pattern ^d (migratory / nomadic / sedentary)
Habitat	Habitat ^e (rainforest / woodland / savannah / grassland), geographic region ^f (Australian / Ethiopian / Neotropical)
Motor skills	Foot-use (yes / no), foot-lateralisation (left / right / no preference)
Climatic variability	Rainfall tolerance ^g (high / medium / small), temperature tolerance ^h (high / medium / small)

^a Fission-fusion dynamic levels were defined as followed: high – groups consisting of different social subunits (e.g. crèche, daily groups), which frequently split and merge throughout the day; low – groups living in small, stable family groups centred around a single breeding pair and their offspring; medium – species living in fluid social groups of 10–40 individuals and congregating to large communal night roosts, but lacking subunits such as crèches or juvenile groups

^b Daily group size refers to the groups that move together (e.g. when looking for food) during the day

^c Feeding strategy: granivorous (diet over 90 % seeds), frugivorous (diet over 90 % fruits), nectarivorous (diet over 90 % nectar and pollen), omnivorous (all remaining species including those feeding on animal matter)

^d Ranging pattern: migratory (seasonal movements between breeding and wintering grounds), nomadic (generally wandering from place to place, usually within a well-defined range), sedentary (remaining in the same area)

^e Habitat: rainforest (dominated by trees often forming a closed canopy with little light reaching the ground), woodland (low-density forest forming open habitats with plenty of sunlight and limited shade), savannah (a grassland with scattered trees or scattered clumps of trees), grassland (vegetation is made up mostly of grasses)

^f Geographic region: Australian (living in Australia, New Zealand, Tasmania, New Guinea and associated islands), Ethiopian (living in sub-Saharan Africa (south of 30 degrees north) and Madagascar), Neotropical (living in Central and South America)

^g Rainfall tolerance was defined as followed: high (>1000 mm seasonal difference), medium (500-1000 mm seasonal difference), small (<500 mm seasonal difference)

^h Temperature tolerance was defined as followed: high (> 20°C diel or seasonal difference), medium (10-20°C diurnal or seasonal difference), small (<10°C diurnal or seasonal difference)

Cognitive data

Each subject was first tested in its string-pulling ability by using a single rewarded string (T1). All subjects that spontaneously solved this task were then tested with patterned-string problems. The performance in patterned-string tasks was used as a direct measure for specific modules of cognition. The following string problems were presented: 1) two parallel strings, with one string rewarded and the other not (T2), testing whether the string-pulling behaviour was food-directed; 2) two crossed strings, which were differently coloured to allow for easier tracing of the strings (T3) either by tracking the continuous path signalled by the string leading to the reward and choosing accordingly or by recognizing the connection of the food to a particular colour; 3) two crossed strings, which were of the same colour (T4), to test the ability to recognize physical continuity visually; 4) two rewarded strings of different length (T5), to test the preference for a shorter string; 5) two parallel, rewarded strings, with one string connected to the reward and the other not (T6), to test the ability to visually recognize physical connection between objects; and 6) two parallel, rewarded strings of different length with the shorter string disconnected from the reward (T7), to test the inhibitory control.

Each subject was presented with 10 trials per task with two sessions per day, one in the morning (after 9 a.m.) and one in the afternoon (after 3 p.m.). Tests were presented in the same order for all species.

Housing conditions

Tierpark Gettorf, Germany

The rosy-faced lovebirds were kept together with Reeves's pheasant (*Syrnaticus reevesii*) in an outdoor aviary (10 x 2.5 x 3 m) with two heated compartments (each 1.5 x 1.5 x 1 m) containing several nest boxes at Tierpark Gettorf, Germany. The group contained 22 lovebirds (15 adults, 7 juveniles). Birds were fed every day between 9 a.m. and 11 a.m. with mixture of different fruits and seeds. Water was available *ad libitum* and vitamins were given twice a week. The aviary was provided with several trees, branches and trunks. Seven rosy-faced lovebirds showed no interest and did not approach the string-pulling apparatus, thus they were excluded from the analysis.

No subject has had contact with string-like objects before or was trained on any object-

pulling task prior to present experiments. The animal care during the study was continued by the zoo keepers. The experiments reported were integrated as part of the regular animal welfare activities into the daily routine. During and after the study all tested birds were left in their flock.

The Parrot Zoo, UK

The greater vasa parrots (*Coracopsis vasa*), the eclectus parrots (*Eclectus roratus*), the Senegal parrots (*Poicephalus senegalus*), and the monk parakeets (*Myiopsitta monachus*) were housed at the Parrot Zoo in Skegness, UK.

The group of greater vasa parrots (*Coracopsis vasa*) was consisted of 10 birds (5 males, 5 females) and kept together with one smaller vasa parrot (*Coracopsis nigra*) in an outdoor aviary (4 × 4 × 4 m) with an adjacent indoor aviary (2 × 2 × 2 m). After the finishing the string-pulling experiments the birds were moved to another aviary. After an acclimatization period of one week the birds' personalities were tested.

For the experiments the eclectus parrots, the Senegal parrots, and the monk parakeets were moved consecutively from their home aviaries to a test outdoor aviary (6 × 2.5 × 2 m) with an adjacent indoor aviary (1 × 2 × 1 m). After the experiments the individuals were moved to other aviaries.

The birds at The Parrot Zoo were provided with a seed mix in the morning and with fresh fruits in the afternoon also on experimental days. Water was available *ad libitum*. The outdoor aviaries were provided with several trees, branches and trunks. No artificial toys, only green branches for playing and nibbling, were provided regularly. All subjects could be recognized individually at all times during the experimental sessions. Some subjects (e.g. some individuals of orange-winged amazons) kept at The Parrot Zoo, UK, came from private owners, so that the individual history of these subjects was unknown. After the study all tested birds of all study species were left in their flock.

Analysis

Regression tree analysis was used to analyse the relationship between cognitive abilities (measured by the proportion of correctly solved trials in patterned-string tasks, Table S1) and explanatory predictors (Table S2). Regression tree analyses (Lewis 2000) work by splitting the dataset of response variables into two groups,

and thus minimizing the variation in response variables within these groups. After the first split, the process is repeated for the two sub-groups etc. until no significant amount of additional variance can be explained by additional splits. This approach allows for more flexibility in the types of models that can be fitted. It involves the successive partitioning of a data set into increasingly more homogeneous subsets and provides a more flexible alternative to linear and additive models. Therefore, it is a particularly useful exploratory tool for the identification of relationships between variables in complex, multivariate datasets (De'ath & Fabricius 2000). Regression tree analysis was implemented using *rpart* package (Therneau et al. 2006) in R (RDTeam 2013).

Results

The proportion of correctly solved trials in all patterned-string tasks differed significantly across species (Table 2). Only the preference for a shorter string (T5) did not differ significantly ($P = 0.054$).

Table 2: GLMM* analysis of the proportion of correct choices in patterned-string task across species

Task	χ^2	df	P
T2	4.669	13	< 0.001
T3	6.195	13	< 0.001
T4	3.489	13	0.005
T5	2.208	13	0.054
T6	7.292	13	< 0.001
T7	5.811	7	0.001

*with individual as random factor

The variation in the reward-oriented behaviour (T2) was best predicted by the dietary strategy with omnivorous and nectarivorous birds choosing the rewarded string more frequently (94% correct trials) than frugivorous and granivorous species. This split accounted for 0.36% of the total variance in proportion of correct choices in parallel-strings task. The remainder could be split further into "breeding in groups" and "breeding colonially" (Table 3, Figure 1a). Birds breeding in pairs were split further by the ranging pattern showing that sedentary birds performed better in the task (being correct in 81% of the trails) than migratory and nomadic species (62% correct choices).

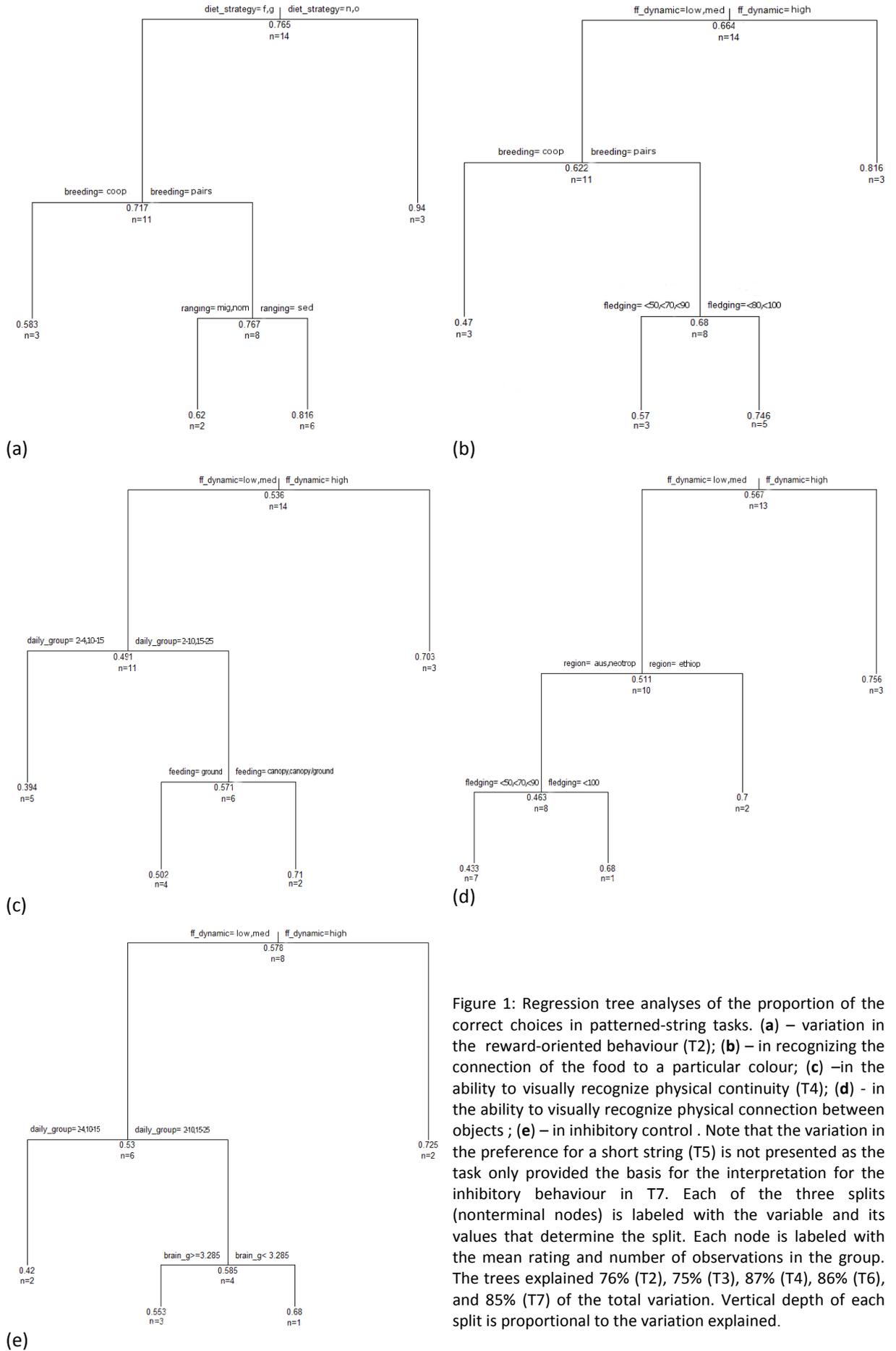


Figure 1: Regression tree analyses of the proportion of the correct choices in patterned-string tasks. (a) – variation in the reward-oriented behaviour (T2); (b) – in recognizing the connection of the food to a particular colour; (c) – in the ability to visually recognize physical continuity (T4); (d) – in the ability to visually recognize physical connection between objects; (e) – in inhibitory control. Note that the variation in the preference for a short string (T5) is not presented as the task only provided the basis for the interpretation for the inhibitory behaviour in T7. Each of the three splits (nonterminal nodes) is labeled with the variable and its values that determine the split. Each node is labeled with the mean rating and number of observations in the group. The trees explained 76% (T2), 75% (T3), 87% (T4), 86% (T6), and 85% (T7) of the total variation. Vertical depth of each split is proportional to the variation explained.

Table 3: Mean values and mean standard error (MSE) values that determine the split and the variation explained by each of the main predictors.

Main predictors	mean	MSE	Explained variance %
T2			
Diet strategy	0.765	0.023	36
Breeding	0.717	0.018	22
Ranging	0.767	0.011	18
T3			
Fission-fusion dynamic	0.684	0.023	37
Breeding	0.622	0.019	20
Fledging	0.680	0.009	18
T4			
Fission-fusion dynamic	0.536	0.020	37
Daily group size	0.491	0.015	30
Feeding	0.571	0.011	20
T5			
Fission-fusion dynamic	0.567	0.025	43
Region	0.511	0.018	27
Fledging	0.463	0.011	16
T6			
Fission-fusion dynamic	0.576	0.015	46
Daily group size	0.530	0.009	29
Brain mass	0.565	0.003	10

The performance in the crossed-string task (T3) was best predicted by fission-fusion dynamic (ff-dynamic) (Figure 1b). The proportion of correctly solved trials in the group with high ff-dynamic was higher (82 %) than in the group with low or medium ff-dynamic. Smaller amounts of variation could be accounted for by splitting the low to medium ff-dynamic group by breeding strategy (Table 3). Furthermore, the variance in the ability to distinguish between crossed strings, facilitated by differently coloured strings, could be explained by splitting low/medium ff-dynamic and pairwise-breeding birds by the length of the fledging period.

The fission-fusion dynamic was also the best predictor for the variance in the ability to visually recognize physical continuity (T4, Figure 1c). Group-living birds with high ff-dynamic performed better (70 % correct trials) than those with low or medium ff-dynamic. A smaller part of the variation was explained by the daily group size. Birds living in larger daily groups (15-25 individuals) chose the correct string more frequently (57% correctly solved trials) than species with small daily groups (39 %). However, the former could be split further by their feeding mode. Birds feeding in the canopy or searching food both, on the ground and in the trees were more successful in the task (71% correct choices) than those feeding on the ground only (50%).

The largest explanatory contribution to the variation in the ability to visually recognize physical connection between objects (T6) came from fission-fusion dynamic as well (Figure 1d). A smaller part of the variation was explained by splitting the low/medium ff-dynamic group by biogeographic origin. Birds inhabiting sub-Saharan Afrika and Madagascar (Ethiopian region; 70% correctly solved trials) performed better than Australian and neotropical birds (43%). The latter were split further by the length of their fledging period, showing that birds with a longer association with the parents performed slightly better than those fledging earlier.

Finally, the variation in the inhibitory control (T7) was again best predicted by the ff-dynamic (Figure 1e). The high ff-dynamic group could inhibit their preference for a shorter string when it was not rewarded and chose the longer one more frequently (72%) than the low/medium dynamic group (53%). Smaller parts of the variation could be accounted for by splitting the low/medium ff-dynamic group by the daily group size (Figure 1d) and the latter again by the brain mass.

Discussion

The results showed that the variation in the performance in patterned-string tasks was largely

predicted by social traits. The largest contribution to the variation in the ability to discriminate between two differently coloured strings (T3) (either by tracking the continuous path signalled by the string leading to the reward and by choosing accordingly or by recognizing the connection of the food to a particular colour), the ability to recognize visually a physical continuity (T4), the ability to recognize visually the physical connection between objects (T5), and the inhibitory control (T6) all correlate with (and maybe even be derived from) fission-fusion dynamic, breeding system, or daily group size – all variables belonging to trait category “social organisation” (Table 1). Only the variation in the reward-oriented behaviour (T2) was best predicted by the diet strategy.

Obtaining food that appears at certain times of the year (e.g. flowers, nectar), that has a clumped distribution or has to be extracted from casings (e.g. fruits, nuts), requires more cognitive skills (e.g. spatial memory, problem-solving) than obtaining food that is available all year, located in the same place and requires little processing, such as leaves. For example, in primates, frugivorous species have both comparatively larger brains (Barton 2006) and – as a more direct measure of cognition – a more reliable spatial memory (Rosati et al. 2014) compared to folivorous species. Consistent with these findings, omnivorous parrot species feeding on a variety of fruits, nuts, and even animal matter – all food sources that require extractive foraging and vary in their temporal availability – were found to possess an enhanced ability to discriminate between rewarded and unrewarded strings. This task (T2) may best simulate natural situations where the birds just have to decide which branch or flower that holds fruit or pollen to pull without the need to recognize relationships such as the physical connection between objects.

The idea that a broad diet might be one of the drivers of cognitive evolution is supported in primates (Reader & MacDonald 2003), bats (Ratcliffe et al. 2006), and birds (Overington et al. 2008). However, besides omnivorous species the nectarivorous parrots also performed extremely well in parallel strings tasks. This suggests that temporal and spatial patchiness might be cognitively more demanding than extractive foraging of fruits or seeds (Healy & Hurly 2013).

Altogether, it is remarkable that in all tasks that tested for abilities to understand visual-spatial and causal relationships between objects

(T3-T7), the social environment explained most of the variation across species. Groups with a high fission-fusion dynamic, breeding in pairs, and moving in groups comprising several families rather than only the breeding pair with offspring, consistently appear to have enhanced visual-spatial and cognitive skills tested in patterned-string tasks. These findings support the hypothesis that social complexity may have an important role in the evolutionary history of certain cognitive skills in parrots.

The rationale behind the *social complexity hypothesis* is that selection favours those animals that proficiently keep track of the identities and interactions of numerous individuals within a large social group. Two views of the influence of group living on cognitive skills exist. The domain-specific view proposes that larger social group sizes should select for cognitive skills that are specific to social living (Gigerenzer 1997). In contrast, the domain-general view asserts that cognitive traits for reasoning about social and non-social environments are not independent of one another (Reader et al. 2011). Accordingly, this view argues that any cognitive changes favoured by group living should be similar for both social and non-social cognition (MacLean et al. 2013).

In primates, group size likely played an important role in the evolution of brain size and social cognition (Dunbar & Shultz 2007; MacLean et al. 2013). In birds, however, the potential relationship between sociality and cognition is more complex (Emery et al. 2007b). The key issue is actually how to measure social complexity in birds. For example, estimating social group size is not trivial as flock size of most birds tends to be very flexible, both temporally and spatially (Emery et al. 2007b). Indeed, no clear relationship between brain size and group size (Beauchamp & Fernández-Juricic 2004) or social structure (Emery 2004) has been found. However, by using a broader social category ‘transactional’ that included species living in fission-fusion societies, a strong relationship between social complexity and size of avian telencephalon emerged (Burish et al. 2004).

Fission-fusion dynamic as an alternative measure of social complexity has been suggested by Aureli et al. (2008). The authors proposed that frequent splitting and merging in subgroups of variable composition is the main aspect of social complexity, as such dynamics may create unique challenges for social interaction (Aureli et al.

2008). Species that live in fission-fusion groups are confronted with the additional cognitive challenge of adjusting to frequent social changes resulting from movement of individuals into and out of groups at various times.

Thus the fluid nature of information gathered by members of higher fission-fusion societies may enhance various information-processing skills as well as analogical reasoning (Aureli et al. 2008). For species living in groups with higher fission-fusion dynamic, these abilities seem to be more important as their party composition is highly variable. In contrast, in groups with lower fission-fusion dynamic, the majority of social interactions are exchanged within parties with mostly fixed composition. Therefore, the need to store information about various group members may be reduced. The finding that species that move in larger daily groups performed better than those in small groups of 2-4 birds appears to be consistent with this hypothesis. Furthermore, my finding that non-cooperatively breeding parrots consistently performed better than cooperatively breeding species corresponds well with Iwaniuk and Arnold (2004) who showed that cooperative breeding does not correlate with relative brain size in birds. Moreover, this finding supports the *relationship intelligence hypothesis* which proposes that type and quality of the bonded relationship may also be crucial for cognition (Emery et al 2007b).

The variables that explained smaller parts of variation in the skills under investigation were fledging age, ranging pattern, and feeding mode. The contribution of fledging age to the cognitive variation across species is not surprising as it has been found to correlate with relative brain size in psittacines (Iwaniuk & Nelson 2003). A prolonged post-hatching period has been suggested to enable the development of a relatively large brain because there is more time for neuron growth and neurogenesis. This allows for more neural connections being formed before fledging facilitating responsiveness to the environment (Iwaniuk & Nelson 2003). Moreover, extended periods of juvenile development may serve to accommodate the acquisition of knowledge either by social learning from adults (e.g., through tradition) or of individual learning by trial-and-error (van Horik & Emery 2011). However, more neural connections during a prolonged post-hatching period may not necessarily be detected by proxy variables such as increased brain size, for example. (MacLean et al. 2013).

The natural ranging pattern of the species also predicted the performance in patterned-string tasks across species. Sedentary species chose the correct string more frequently than migrating or nomadic species corroborating findings that sedentary birds have the largest relative telen-cephalon (Burish et al. 2004). A possible explanation might be that sedentary birds have to endure and to adapt to environmental changes without the option of leaving their habitats, thus requiring more behavioural flexibility (Schuck-Paim et al. 2008). Alternatively, migration could also favour enlarged brains given the cognitive demands of processing information about the distribution of resources in new areas (Healy & Rowe 2007).

Finally, species searching for food in the canopy (or both on the ground and in the canopy) were better able to recognize visually a physical continuity (T4) compared to species feeding on the ground only. This finding appears reasonable as feeding in the canopy often requires detecting which branch to pull for certain fruits (Halsey et al. 2006). Thus the ability to track physical continuity between objects may be favoured in species feeding in dense vegetation compared to those pecking seeds or bulbs from the ground.

This study reveals a link between the social complexity and a direct measure of cognitive abilities and provides first evidence for the domain-general nature of the cognitive challenges of living in complex social environments. Additional comparative research using a variety of standardized paradigms is needed to understand what exactly are the cognitive demands of living in groups with a high fission-fusion dynamic. This would improve our understanding of how cognitive challenges in social environments may affect the cognitive performance even in non-social contexts.

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Supplementary Material

Table S1: Overview of string-pulling performance and the proportion of correct choices in patterned-string tasks across species

species	String-pulling T1	Directedness T2	Colour T3	Continuity T4	Connectivity T6	Inhibition T7
<i>Agapornis roseicollis</i>	yes	0.86	0.67	0.72	0.75	0.68
<i>Amazona amazonica</i> ⁱ	yes	0.68	0.51	0.49	0.68	0.59
<i>Coracopsis vasa</i>	yes	0.92	0.88	0.69	0.81	0.80
<i>Eclectus roratus</i>	yes	0.60	0.48	0.52	0.41	0.52
<i>Eolophus roseicapilla</i> ⁱⁱ	yes	0.77	0.71	0.65	0.68	0.65
<i>Myiopsitta monachus</i>	yes	0.44	0.32	0.29	0.47	0.47
<i>Nymphicus hollandicus</i> ⁱⁱ	yes	0.71	0.61	0.49	0.51	0.37
<i>Poicephalus senegalus</i>	yes	0.68	0.60	0.70	0.65	0.55
<i>Ara chloroptera</i> ⁱⁱⁱ	yes	0.86	0.70	0.44	0.33	NA
<i>Cacatua galerita</i> ⁱⁱⁱ	yes	0.88	0.77	0.56	0.53	NA
<i>Forpus conspicillatus</i> ⁱⁱⁱ	yes	0.85	0.86	0.77	0.78	NA
<i>Melopsittacus undulatus</i> ^{iv}	yes	0.56	0.76	0.42	0.41	NA
<i>Psittacus erithacus</i> ^{iv}	yes	1.00	0.60	0.40	NA	NA
<i>Trichoglossus haematodus</i> ⁱⁱⁱ	yes	0.90	0.83	0.37	0.37	NA

ⁱ Data from Krasheninnikova and Schneider (2014)

ⁱⁱ Data from Krasheninnikova (2013)

ⁱⁱⁱ Data from Krasheninnikova et al. (2013)

^{iv} Unpublished data from Krasheninnikova (2010)

Table S2: Overview of the variables under investigation across species.

species	brain g ¹	body g ¹	rel brain [*]	telen- cephalon ²	fledging ³	longevity ³	nesting ⁴	mating system ⁴	parental care ⁴	breeding ⁴
<i>Agapornis roseicollis</i>	1.86	45.80	4.207	1454.88	<50	15	nest	monogam	male	pairs
<i>Amazona amazonica</i>	8.29	338.0	2.541	NA	<90	50	tree hollow	monogam	male	pairs
<i>Coracopsis vasa</i>	NA	480.0	NA	NA	<50	50	tree hollow	polygyn- androus	male	co- operative
<i>Eclectus roratus</i>	7.36	428.0	1.782	4583.16	<80	30	tree hollow	polygyn- androus	male	co- operative
<i>Eolophus roseicapilla</i>	6.43	351.0	1.898	4908.67	<70	30	tree hollow	monogam	bi- parental	pairs
<i>Myiopsitta monachus</i>	4.08	120.0	3.891	2733.19	<50	20	nest	monogam	male	co- operative
<i>Nymphicus hollandicus</i>	2.39	83.00	2.983	1676.78	<50	15	tree hollow	monogam	bi-parental	co- operative
<i>Poicephalus senegalus</i>	4.71	155.0	3.148	NA	<70	25	tree hollow	monogam	male	pairs
<i>Ara chloroptera</i>	20.88	1185.0	2.277	NA	<100	50	tree hollow	monogam	male	pairs
<i>Cacatua galerita</i> ³	14.24	765.0	1.928	NA	<80	50	tree hollow	monogam	biparental	pairs
<i>Forpus conspicillatus</i>	1.20	26.4	5.284	NA	<50	15	tree hollow	monogam	male	pairs
<i>Melopsittacus undulatus</i>	1.50	35.0	4.440	825.12	<50	15	tree hollow	monogam	male	pairs
<i>Psittacus erithacus</i>	9.18	405.5	2.345	4726.89	<90	25	tree hollow	monogam	male	pairs
<i>Trichoglossus haematodus</i>	3.66	116.0	3.269	2726.62	<50	20	tree hollow	monogam	male	pairs

Sources:

¹ Data for brain and body size from Iwaniuk et al. (2005)² Data for telencephalon volume from Burish et al. (2004)³ Data for fledging age, and longevity from Avian Diversity Web <http://animaldiversity.ummz.umich.edu/accounts/Aves/>⁴ Data for mating system, nesting, breeding, and parental care from Burger and Gochfeld (2005); Burish et al. (2004); Ekstrom et al. (2007); Heinsohn (2008); Heinsohn et al. (2007); Heinsohn and Legge (2003); Heinsohn et al. (2003); Millam et al. (1995); Ndithia et al. (2007); Rowley (1990); Spoon (2006); Spoon et al. (2007); Symes and Marsden (2007)⁵ Data for ff-dynamics, roosting group size, and daily group size from Burger and Gochfeld (2003); Eberhard (2002); Gilardi and Munn (1998); Heinsohn and Legge (2003); Rowley (1990); South and Pruett-Jones (2000); Spoon (2006); Symes and Marsden (2007); Wanker et al. (1998)⁶ Data for diet strategy and feeding mode from Bollen and van Elsacker (2004); Koutsos et al. (2001); McDonald (2003); Ndithia and Perrin (2006); Rozek and Millam (2011); South and Pruett-Jones (2000); Symes and Marsden (2007)^{*} rel. brain = relative brain size^{**} ff-dynamic = fission-fusion-dynamic

ff dynamic** ⁵	roosting ⁵	daily group ⁵	diet strategy ⁶	feeding ⁶	habitat ³	region	ranging ³	foot use ⁷	rainfall variation ⁸	temp variation ⁸
medium	100-200	15-25	granivorous	ground	grassland	ethiopian	sedentary	no	large	large
low	50-100	2-4	frugivorous	canopy	rainforest	neotropical	sedentary	yes	large	large
high	100-200	10-15	omnivorous	canopy	rainforest	ethiopian	sedentary	yes	medium	small
medium	50-100	2-4	frugivorous	canopy	rainforest	australian	sedentary	yes	medium	small
high	200-500	2-10	granivorous	ground	woodland	australian	sedentary	yes	large	large
medium	50-100	2-10	granivorous	canopy/ ground	woodland	neotropical	sedentary	no	large	large
low	100-200	10-15	granivorous	ground	grassland	australian	nomadic	yes	medium	medium
low	50-100	2-4	granivorous	ground	woodland	ethiopian	migratory	yes	large	large
low	50-100	2-4	frugivorous	canopy	rainforest	neotropical	sedentary	yes	large	large
low	100-200	2-4	granivorous	canopy/ ground	grassland	australian	sedentary	yes	medium	small
high	50-100	15-25	granivorous	canopy/ ground	woodland	neotropical	sedentary	no	small	medium
medium	100-200	10-15	granivorous	ground	grassland	australian	nomadic	no	medium	small
medium	200-500	2-10	omnivorous	canopy	grassland	ethiopian	migratory	yes	small	small
medium	100-200	2-10	nectarivorous	canopy	rainforest	australian	nomadic	yes	small	medium



Chapter 3

PATTERNED-STRING TASKS: RELATION BETWEEN FINE MOTOR SKILLS AND VISUAL-SPATIAL ABILITIES IN PARROTS

Patterned-string tasks: relation between fine motor skills and visual-spatial abilities in parrots

Anastasia Krasheninnikova

String-pulling and patterned-string tasks are often used to analyse perceptual and cognitive abilities in animals. In addition, the paradigm can be used to test the interrelation between visual-spatial and motor performance. Two Australian parrot species, the galah (*Eolophus roseicapilla*) and the cockatiel (*Nymphicus hollandicus*), forage on the ground, but only the galah uses its feet to manipulate food. I used a set of string pulling and patterned-string tasks to test whether usage of the feet during foraging is a prerequisite for solving the vertical string pulling problem. Indeed, the two species used techniques that clearly differed in the extent of beak-foot coordination but did not differ in terms of their success in solving the string pulling task. However, when the visual-spatial skills of the subjects were tested, the galahs outperformed the cockatiels. This supports the hypothesis that the fine motor skills needed for advanced beak-foot coordination may be interrelated with certain visual-spatial abilities needed for solving patterned-string tasks. This pattern was also found within each of the two species on the individual level: higher motor abilities positively correlated with performance in patterned-string tasks. This is the first evidence of an interrelation between visual-spatial and motor abilities in non-mammalian animals.

Keywords: *Eolophus roseicapilla*, Motor skills, *Nymphicus hollandicus*, Patterned-string problem, Problem solving, Visual-spatial skills

Introduction

The perceptual and cognitive abilities necessary for everyday problem-solving such as foraging vary depending on the ecological niche of a species. For example, estimating distances and spatial relationships between oneself and objects, or between several objects in the environment, requires visual-spatial abilities and is a prerequisite for tracing causal relations among objects. Comparing perceptual and cognitive abilities among species requires a paradigm that allows a broad comparison across species and is easy for a subject to understand and handle (MacLean et al. 2012). The string-pulling task and its extended versions such as patterned-string tasks fulfil the requirements of being simple and feasible while testing certain abilities such as perceptual capacity (Balasch et al. 1974), means-end knowledge (Pepperberg 2004), and understanding of spatial relationships (Bagozkaya et al. 2010; Tomasello & Call 1997).

A patterned-string task in which the subject must choose between two or more strings, only one of which is connected to a reward, requires both perceptual and cognitive abilities as the subject has to determine the difference in the strings and understand which would lead to the reward. The ability to solve patterned string tasks has been tested in numerous mammals (Finch

1941; Osthaus et al. 2005; Whitt et al. 2009) and birds (Schuck-Paim et al. 2009; Seibt & Wickler 2006; Vince 1961) (in both horizontal and vertical apparatus settings).

Several authors have suggested that fine motor skills play an important role in the ability of a species to solve a string-pulling task (Heinrich & Bugnyar 2005; Huber & Gajdon 2006; Magat & Brown 2009). According to this sensorimotor argument, usage of feet to manipulate food items and finely tuned beak-foot coordination may both be crucial manipulative skills needed for vertical string-pulling in birds (Skutch 1996). A large number of different motions performed in a very precise order and involving accurate beak-foot coordination are necessary to pull up and retrieve food attached to the end of a string. Therefore, species that occupy niches which do not require particular sensorimotor skills (for example, a feeding technique which requires fine beak-foot coordination) may be less well equipped for manipulating such objects successfully. The first empirical evidence that finely tuned beak-foot coordination influences success in a vertical string-pulling task came from Magat and Brown (2009) who analysed the influence of lateralization on problem-solving. In their study on Australian parrots, all six species that successfully mastered the task use their feet to manipulate food items. The remaining two

species, the cockatiels and the budgerigars, which do not use their feet when feeding and do not have pronounced body part coordination, failed entirely in the vertical string-pulling task. It appears that the usage of the feet to manipulate food items is species-specific and could be related to the specific ecological demands faced by a species (Magat & Brown 2009). Altevogt (1954) suggested that fixing an item under the foot or holding it in the foot could be innate.

A neural basis for an interrelation between visual-spatial and motor skills may be manifested in brain structures. For example, the cerebellum is not, as traditionally assumed, only responsible for motor coordination and motor control, but is also involved in a wide range of processes (Paulin 1993; van Mier & Petersen 2002). In humans, both clinical observations (Hokkanen et al. 2006; Kalashnikova et al. 2005; Molinari et al. 2004) and functional neuroimaging data (Fink et al. 2000) showed cerebellar involvement in a variety of visual-spatial tasks. Data from behavioural studies on children underpin the hypothesis of an interrelation between visual processing and fine motor control (Davis et al. 2011). In rats, cerebellar lesions provoked impairment in visual-spatial problem-solving and in right /left discrimination (Petrosini et al. 1998), and behavioural observations in Kunming mice showed a correlation between non-spatial cognitive and sensorimotor performances (Chen et al. 2004). The avian cerebellum shares much histological and physiological similarity with that of mammals (Paula-Barbosa & Sobrinho-Simões 1976), including an involvement in visual processing (Clarke 1974). In large-brained birds, i.e. corvids and parrots, Sultan and Glickstein (2007) found enlarged visual and beak-related cerebellar parts, which might be associated with elaborated beak control. Finally, findings from cerebellar lesion study in a songbird suggest that also the avian cerebellum also interrelates motor and cognitive functions (Spence et al. 2009).

Patterned-string tasks have been used to assess a variety of capabilities in animals, but a link to motor-skills has not been tested. The single string task is an appropriate method to test the motor-skills of birds in particular, as the set-up requires complex string manipulations and, presumably, fine beak-foot coordination. Thus, enhanced manipulative skills may facilitate the handling of a vertical string. Patterned-string problems are commonly used to examine the visual-spatial aspects of string pulling (Gagne et

al. 2012; Pfuhl 2012). If motor and perceptual-cognitive development relies on common mechanisms, a species without pronounced motor skills will probably also lack a predisposition to perform certain aspects of patterned-string problems.

Here, I examine the string-pulling performance of two Australian parrot species which show differences in feeding technique and hence in fine beak-foot coordination, the galah (*Eolophus roseicapilla*) and the cockatiel (*Nymphicus hollandicus*). Both species are widely distributed on the Australian continent. They share a preference for open, semi-arid habitats close to water (Collar 1997; Forshaw 2010), and thus occur partially sympatrically. Both species subsist primarily on small seeds from native or cultivated plants and grasses (Jones 1987; Magat & Brown 2009; Rowley 1990), and both forage on the ground, but only one of them, the galah, uses its feet to manipulate food items. Hence, as they share various ecological parameters, such as diet and feeding mode but differ in their manipulative capabilities, these two species present an interesting opportunity to test the hypothesis that certain motor skills need to be present to perform well in patterned-string tasks requiring specific visual-spatial skills (e.g. distance perception, and visual-spatial processing). By using string-pulling and patterned-string tasks with different degrees of difficulty, I test (1) motor skills, and (2) visual-spatial abilities in both species. I hypothesized that the galahs would outperform the cockatiels in the motor task due to their pronounced beak-foot-coordination. Assuming an interrelation between visual-spatial skills (e.g. estimating distances and spatial relationships between objects) and motor performance I also hypothesized that the galahs would solve the patterned-string tasks more successfully than the cockatiels.

Materials & Methods

Study Subjects

Six galahs and ten cockatiels were tested. All parrots were hatched in a zoo and were raised by their parents. No artificial toys were available, but green branches were provided regularly for playing and nibbling.

The galahs were kept in a walk-through outdoor aviary (12 x 7 x 5 m) with an adjacent indoor aviary (6 x 1.6 x 2.5 m) at Tierpark Gettorf, Germany. The group contained five adults and

one subadult (3 males, 3 females), which were not related to each other. All individuals participated in the study. Birds were fed every day between 9 a.m. and 11 a.m. with parrot pellets and fruits. The indoor aviary was lit by several windows and provided with several perches and a nestbox. The outdoor aviary contained several trees and a trunk. Water was available *ad libitum* and vitamins were given twice a week. The galahs were housed together with a group of golden pheasants (*Chrysolophus pictus*). The zoo visitors were able to enter the outdoor aviary and to feed the animals with zwieback.

The cockatiels were kept together with budgerigars (*Melopsittacus undulatus*) in a walk-through outdoor aviary (18 x 5 x 7 m) with an adjacent indoor aviary (11 x 1.6 x 2.5 m) at Tierpark Gettorf, Germany. The group contained 20 cockatiels (15 adults, 5 juveniles), and over 60 budgerigars. Birds were fed every day between 9 a.m. and 11 a.m. with a mixture of different fruits and seeds. Water was available *ad libitum* and vitamins were given twice a week. The indoor aviary was lit by several windows and provided with several perches and nestboxes. The outdoor aviary contained several trees, branches and trunks. The zoo visitors were able to enter the outdoor aviary and to feed the animals with proso millet (*Panicum miliaceum*). Ten cockatiels showed no interest and did not approach the string-pulling apparatus: thus, they were excluded from the analyses. The size (thickness) of the string allowed the budgerigars to land on the string; they did not show any pulling attempts. Therefore, the budgerigars' performance was not included in the analyses.

The galah and cockatiel aviaries were close to each other, so that the birds were not acoustically isolated, but a barrier prevented any visual cues from one group to the other during the experiment in the outdoor aviary. All subjects of each species could be individually recognized at all times during the experimental sessions.

No subject had contact with string-like objects or had been trained in any object-pulling task prior to the present experiments. The animal care during the study was performed by the regular zoo keepers. The daily feeding conditions were adapted to the testing situation. The experiments reported were integrated into the daily routine as part of the regular animal welfare activities. After the study, all tested birds remained in their respective flocks.

Experimental set-up

The birds were given their regular variety of seeds on test days, but they were deprived of their preferred fruits and vegetables on those days. Water was available *ad libitum*. To keep birds motivated, highly favoured food rewards were used which were not available outside the experimental context: peanut halves for the galahs and pieces of foxtail millet (*Setaria italica*) for the cockatiels. To reduce any potential neophobic reaction towards the strings, two days prior to the beginning of the experiments small pieces of string (<5 cm) were left hanging on the lateral wire walls of the aviaries. The birds had access to the string, but could not pull it or remove it from the wire. Each subject was presented with 10 trials per task. I conducted two sessions per day, one in the morning (from 9 a.m.) and one in the afternoon (from 3 p.m.). Tests were presented in the same order for both species. To ensure that the bird's performance in patterned-string tasks was not based on local enhancement, that is, choosing the string that had been manipulated last or that had moved last, I always manipulated both strings. To minimize the possibility of monopolization of the set-up, several apparatuses were presented. Trials ended when a subject reached the free end of the string (regardless of whether it had the reward attached to it or not), or after a pre-determined maximum of 5 min, whichever came first. In all choice tasks, the colours and sides associated with the reward attached to the string were alternated randomly across trials. The weight of both the string and the reward was appropriately adjusted for each species. The distance between the strings was twice the body length of the target species. To cross the strings in the crossed string configuration of patterned-string tasks, I used thin wire attached to lateral walls or poles and visible for the birds. The string that every bird first interacted with was scored as its choice in every trial. The choice was scored as 'correct' if the subject started with a pulling action on the rewarded string and reached the end of the string. All tests were video recorded. The solution time, i.e. time needed to reach the food, the number of efficient ("pulls") and inefficient ("drops") actions, and the techniques used to pull the string were noted for subsequent analysis of the birds' behaviour.

The subjects were tested jointly in their respective groups to simulate conditions in which subjects deal with a novel problem (e.g. new food

sources) in the natural environment, where usually a set of individuals is faced with a new situation at the same time.

String-pulling task to assess body part coordination as a measure of motor ability

- Motor task (T1): This task tested the parrots' ability to pull up a reward suspended from a horizontal perch by a single string and examined the techniques used to obtain this reward.

Patterned-string tasks to assess visual-spatial skills as a measure of perceptual ability

- Parallel strings (T2): To test if string-pulling behaviour is food-directed, two strings, one with the reward attached as before and one without, were simultaneously presented to the birds. Pulling up the string with the reward more frequently than expected by chance would indicate that the subject could recognize the string as a means to obtain the reward even if string-pulling behaviour in T1 had been self-rewarding.
- Crossed strings – a (T3): To assess whether the parrots' choice was based on the spatial or the functional relationship between string and reward, I crossed the strings. If their choice was based on the functional connection between food and string, they would pull the baited string. If the choice was based on the spatial relationship only, they would pull the string directly above the bait, as in the earlier trials. In T3, two differently coloured strings (green/white or green/yellow or white/red) were used to allow the birds to trace the strings from one end to the other more easily, assuming that both species have similar colour sensitivity (Aidala et al. 2012). Thus, the birds could either visually trace the paths signalled by the strings (which is easier to discern when the strings are differently coloured) or choose the string with the same colour as that connected to the reward (which means that they were at least able to recognize the connection principle). The rewarded strings, and therefore the rewarded colours, were varied randomly across trials, so that any association rule of a particular colour with the food was excluded (e.g. choosing the colour that has been last rewarded would lead to a failure at the task).
- Crossed strings – b (T4): This was in principle the same test as in T3, but with two crossed strings of the same colour (white/white or

red/red or green/green), and thus expected to be more difficult for the birds to discern.

- Preference task (T5): To test if the subjects show a preference for the shorter string (with a reward which could be obtained more easily), two rewarded strings of different lengths were presented.
- Broken strings – equal (T6): To test the ability to visually determine whether or not objects are physically connected, two strings of equal length were presented to the subjects. While one string was connected to a reward, the other one had a gap between string and reward. Both rewards were placed on a small platform on a wire (attached to the lateral walls or poles). The distance between the string and the unconnected reward was 5 cm.
- Broken strings – different (T7): To test if the birds realize that the string must be connected to the reward in order to work properly, I presented two strings of different length as in T5, but the shorter string was disconnected from the reward. To succeed the birds would abandon any preference for the short string, and chose the longer, rewarded string instead.

The position of the rewarded string in choice tasks was determined randomly across the sessions by tossing a coin.

Analysis

For each species, I calculated the proportion of birds that met the criterion of choosing correctly in the first trial and in at least 8 out of 10 trials in total. For the analysis of quantitative differences between species, I performed a generalised linear mixed model (GLMM) analysis using lmers (package 'lme4', (Bates et al. 2012)) in R 2.15.2 (RDTTeam 2013), with 'individual' as random factor to assess the difference in the proportion of successfully solved patterned-string tasks, and with 'task' as random factor for differences in the proportion of the birds that met the success criterion. The distribution was set as binomial for event data (success or no success) with logit link function and Gaussian (identity link function) for continuous variables (e.g. time, relative efficiency).

Each individual received a score for its relative efficiency in solving the task by comparing frequencies of effective reactions, namely "pulls", and ineffective reactions, namely "drops". The score was calculated using the formula: (frequency of effective actions –

frequency of ineffective actions) / total number of actions [see also (Schuck-Paim et al. 2009)].

Table 1: Definition of the techniques used by the subjects to obtain the reward.

Technique	Definition	BFC score
Sliding	pulling up the string through the bill without fixing or holding it with the foot	0
Flip	reaching down and flipping the string to the other side of the perch	0
Looping	reaching down, pulling up string with the beak, placing the foot on the string, letting go of the string with the beak, remaining in place, reaching down again	0.5
Side walking	reaching down, pulling up the string with the beak, walking to the side of the perch, placing the foot on the string, and reaching down again	0.5
Turn	turning the whole body 180° while holding the string and stepping on the additional string with the feet	0.5
Upright pull	pulling up the string till the body is in a completely upright position, holding with the beak, and gaining more string by grabbing it with the foot	1

BFC score is the beak-foot coordination coefficient

To quantify the extent of beak-foot-coordination (BFC), a score was calculated quantifying the extent of foot usage in the technique preferred when solving the novel motor task (T1). A score of 0.5 was assigned to pulling the string with the beak and using the foot just to fix the string on the perch: this was considered moderate coordination. Conversely, pulling the string first with the bill and then using the foot to pull the rest of the string while holding it in the bill and repeating the foot movements (i.e. to the bill to hold the string in the foot and away from the bill with the string in the foot to gain more string, repeating this action up to seven times) was considered highly coordinated and scored as 1.0 (being in general the same movement as the touching of the nose used as a part of the LOS test measuring fine motor skills in children (Davis et al. 2011); techniques where the foot was not used at all scored 0 (Table 1). The primary technique used was defined as the one used for more than 75 % of the total number of trials. For

example, when the subject used the foot just to fix the string to the perch in over 75 % of its trials, its overall beak-foot-coordination was scored as 0.5.

To quantify the performance in patterned-string tasks, a score for visual-spatial abilities (VSA) was calculated using the number of patterned-string tasks (T2, T3, T4, T5, T6, and T7) in which the subject met the success criterion – i.e. reaching the reward in at least 8 out of 10 trials.

Finally, Spearman rank correlations were computed between motor and visual-spatial skills using both scores, to assess the interaction between motor and visual-spatial skills within both species.

Ethical Notes

All data collection was carried out in accordance with the guidelines of the University of Hamburg and with permission of the Tierpark Gettorf, Germany. The present study was strictly non-invasive and based on behavioural observations; all reported experiments were classified as non-animal experiments and required no approval from the relevant body in accordance with the German Animal Welfare Act (Federal Law Gazette I, p. 1094, Section V, Article 7).

Results

Comparison between Species

In the motor task (T1), individuals of both species performed very well and pulled the rewarded string spontaneously. All but one galah and one cockatiel pulled the string on their first attempt. Although the relative length of the string was the same for each species (twice as long as the body size), the galahs needed significantly longer to pull it (GLMM, factor “species”: $Chi^2 = 14.189$, $df = 1$, $P < 0.0001$), but showed a greater relative efficiency in their string-pulling behaviour than the cockatiels (GLMM, factor “species”: $Chi^2 = 4.9698$, $df = 1$, $P = 0.026$). The number of pulls needed to reach the reward differed across individuals, varying in both species between 3 and 7 pulls. However, in patterned-strings tasks (T2-T7) the relative efficiency did not differ significantly (with the exception of the crossed strings-b task, T4), despite significant differences in time (Figure 1ab).

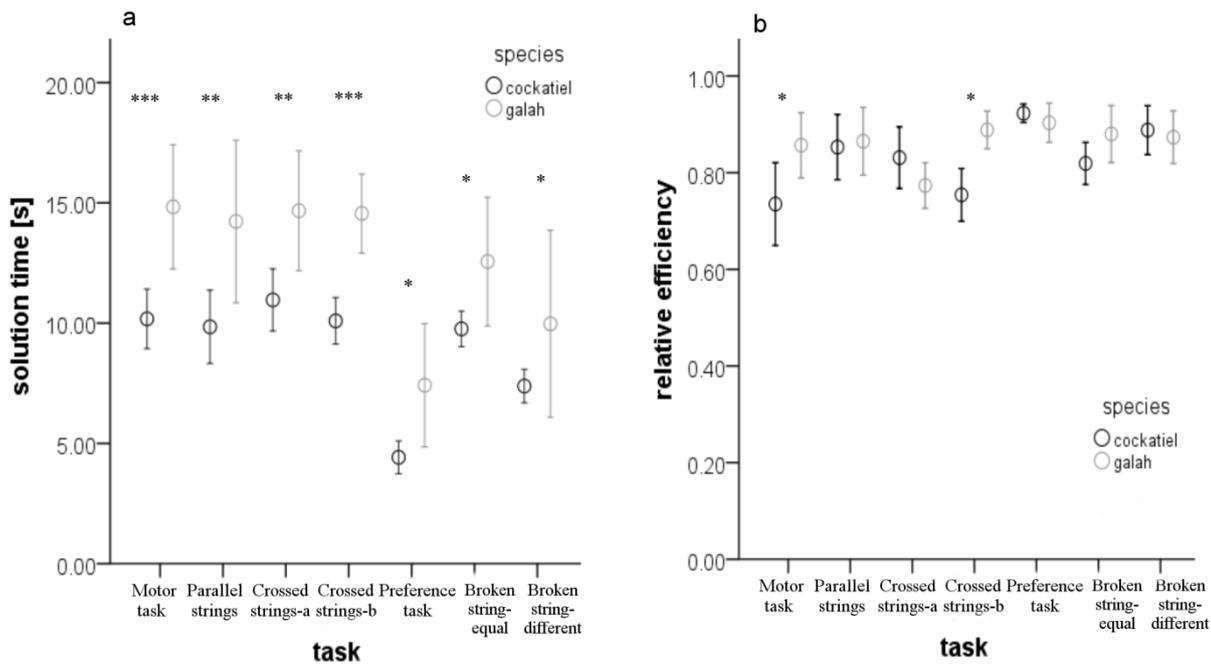


Figure 1: **Performance across tasks.** The time (a) needed to pull the rewarded string and the relative efficiency (b) of string-pulling shown in the motor task and in the patterned-string tasks. The circles represent the mean values and the whiskers represent the standard errors. The stars indicate the tasks where the differences between the species were significant; * P<0.05, ** P<0.01, *** P<0.001. Relative efficiency was calculated by the formula: (frequency of effective actions – frequency of ineffective actions)/total number of actions

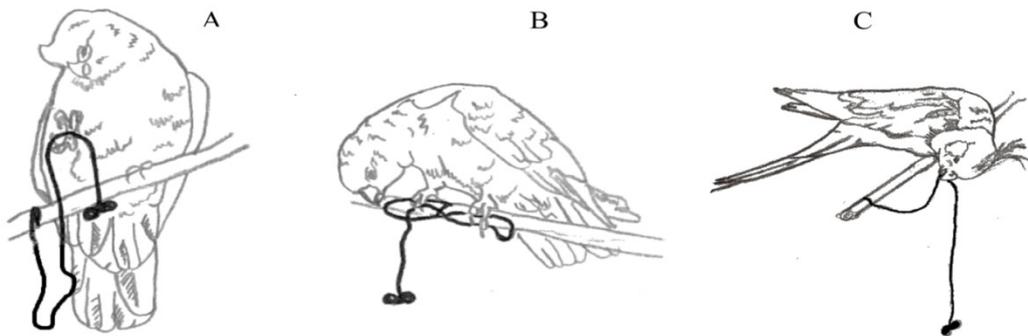


Figure 2: **Different techniques used.** Three samples for strategies used by birds to obtain the reward (A – upright pulling, occurred only in galahs; B – looping, occurred in galahs and cockatiels, C – sliding, occurred only in cockatiels)

Techniques used

Although the task appears to lend itself to straightforward solutions, considerable variation in techniques and in the frequency with which they were used were displayed and appeared both across and within species. Generally, the galahs manipulated the string with the foot rather than only stepping on it to fix it to the perch, whereas the cockatiels used the foot only to step onto the looped string (Figure 2). Overall, the group of galahs employed five and the group of cockatiels four different techniques when confronted with the various tests. Some subjects used elements of two different techniques to pull the string. Upright pulling occurred in galahs only, whereas sliding was shown only by cockatiels. Two methods, looping and side walking were shown by all subjects. In both species, there was considerable intraspecific variation in the preference for the techniques used (one-way ANOVA, $F = 6.58$, $df = 5$, $P = 0.009$, $F = 3.04$, $df = 9$, $P = 0.03$, respectively). There was also a significant difference in the mean BFC score (one-way ANOVA, $F = 10.95$, $df = 1$, $P = 0.01$) reflecting the fact that on average galahs used techniques with a higher BFC score. Patterned string tasks

The galahs scored significantly higher than the cockatiels in patterned string tasks (T2-T7): they had a higher number of successfully solved patterned-string tasks (GLMM with individual as random factor, $\chi^2 = 5.341$, $df = 1$, $P = 0.019$), i.e. in the number of tasks where they made the right choice the first time and rarely made any errors thereafter. The proportion of birds that met the success criterion also differed between species (Figure 3), being on average significantly higher for galahs than for cockatiels (GLMM with task as random factor, $\chi^2 = 7.756$, $df = 1$, $P = 0.005$). In task 4 and task 7, only some galahs (50 % and 75 %, respectively) met the criterion. Success varied between species depending on the task (GLMM, species*task, $\chi^2 = 3.712$, $df = 1$, $P = 0.034$). The individual performance in the patterned-string tasks is summarised in Table 2.

Table 2: Individual performance showing how many trials the subject solved successfully and the VSA scores of the subjects tested.

Subject	Task						VSA score	
	T2	T3	T4	T5	T6	T7		
Galah	G1m	8	9	9	8	8	10	5
	G2f	5	8	5	10	8	8	4
	G3f	8	7	8	8	8	8	4
	G4m	8	6	6	9	5	4	2
	G5f	8	8	6	8	6	4	2
	G6m	9	8	8	5	9	9	5
Cockatiel	C1m	9	6	6	10	8	5	2
	C2m	10	9	8	6	8	6	2
	C3m	4	6	5	9	5	4	1
	C4m	5	8	3	6	4	3	1
	C5m	6	6	8	8	5	5	1
	C6f	8	5	3	8	4	2	2
	C7f	6	4	4	5	4	1	0
	C8f	6	6	5	8	5	2	0
	C9m	8	5	4	10	8	6	2
	C10m	9	8	5	10	3	3	3

Numbers represent the number of correctly solved trials (out of 10 in total) per task; the numbers in bold show that the criterion (at least 8 correct choices out of 10 trials) was met; VSA score refers to the number of patterned-string tasks (T2-T7) in which the subject met the criterion; m=male, f=female

Interaction between Motor Skills and Perceptual Skills at the Individual Level

At the individual level, preferences for different solving techniques were found. Several individuals switched techniques between trials, but no consistent pattern was detectable. In both species, a correlation between motor skills in terms of the extent of beak-foot coordination and the overall performance in patterned-string tasks (number of meeting the criterion) was found (Spearman rank correlation; $r_s = 0.94$, $P = 0.005$ for galahs, and $r_s = 0.79$, $P = 0.005$ for cockatiels). The higher the score for beak-foot coordination measured in T1, the higher was the number of successfully solved patterned-string tasks (Figure 4). No correlation was found between BFC and time or between BFC and relative efficiency (see data in Table S1).

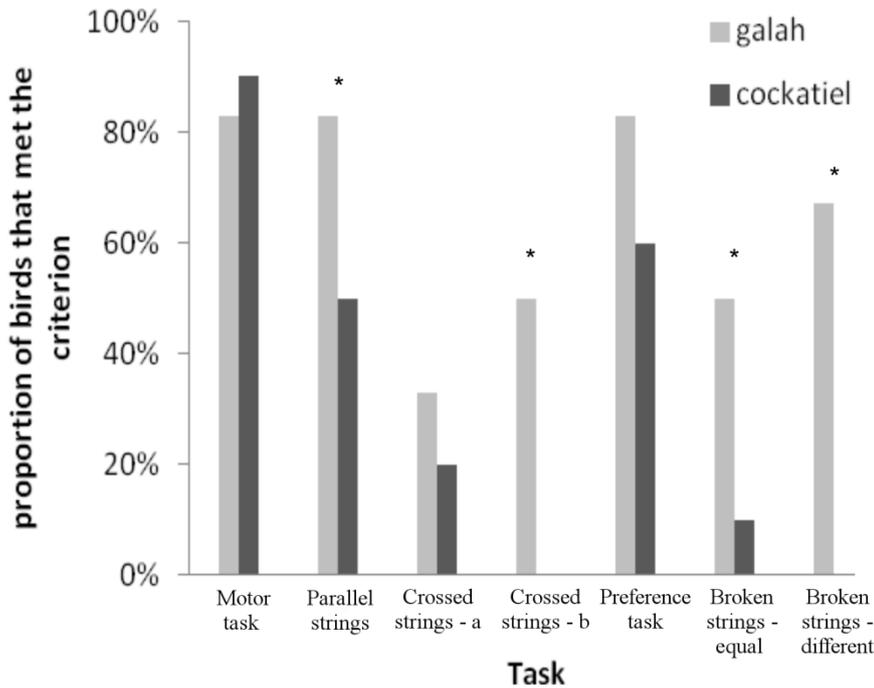


Figure 3: **Proportion of birds that met the success criterion.** The success criterion means choosing the correct string in the first trial and in at least 8 out of 10 trials in total. The values for the preference task (T5) show the preference for a shorter string when presented with two rewarded strings of different length. The stars indicate the tasks where the differences between the species were significant; * $P < 0.05$.

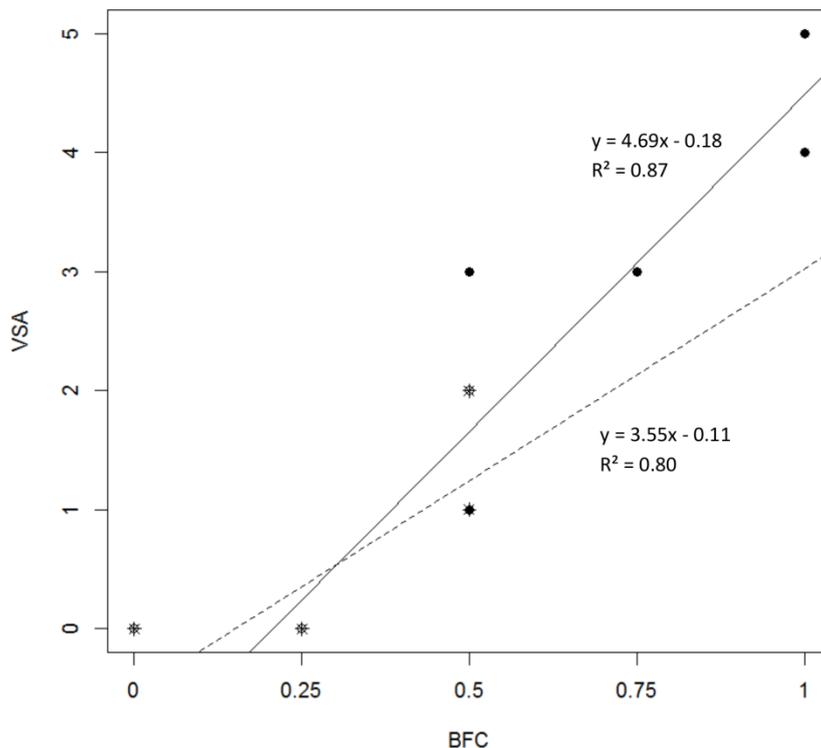


Figure 4: **Correlation between the visual-spatial skills and the motor skills.** Spearman rank correlation using the score for beak-foot-coordination (BFC score), measured in terms of the extent of foot usage in the technique preferred when solving the novel motor task (T1), and the score for visual-spatial abilities (VSA score) which reflects the number of correctly solved patterned-string tasks (T2, T3, T4, T5, T6, and T7). Filled circles represent the data for the galahs and the stars represent the cockatiel data; the dashed line represent regression line ($F = 36.14, P = 0.003$) for the galah data and the solid line ($F = 9.46, P = 0.008$) the cockatiel data. The score for the preferred technique refers to the technique used in over 70 % of all trials in T1. If no technique was clearly preferred (i.e. above 70 % threshold), the mean score for the two most frequently used techniques was calculated.

Discussion

Contrary to expectation, the cockatiels managed the vertical string-pulling problem despite the fact that they do not naturally perform pronounced beak-foot coordination activities. Most individuals of both species pulled the single baited string spontaneously. Hence, I found no support for the hypothesis that the use of feet and beak in the feeding context indicates the presence of the manipulative skills needed for successful string-pulling. However, members of the two species used different sets of techniques to pull the string and the techniques clearly differed in terms of the extent of beak-foot coordination shown. Whereas the galahs manipulated the string with their feet (grabbed it to pull it through the beak in alternate sequences), the cockatiels either just lifted the string by drawing it up through their beak without using their feet at all or they used a foot but only to step on the looped string and to fix it to the perch. Therefore, the performance of the cockatiels showed that using the feet while feeding is not necessary to solve the vertical string-pulling problem, but that it may well determine how the task is solved.

A larger difference between the species was found in the tasks that tested visual-spatial skills (T2, T3, T4, T6, and T7). Measured in terms of how many trials were solved correctly and of how many individuals were successful at a specific task, the galahs outperformed the cockatiels. Three galahs and one cockatiel were able to visually determine a physical connection between objects (T6), whereas only three galahs (and no cockatiel) were able to distinguish between two crossed strings of the same colour (T4). Most of the subjects in both species preferred the shorter rewarded string (T5), thus choosing the most efficient solution. However, only galahs were able to suppress this preference when the shorter string was not connected to a reward (T7), thus showing some kind of understanding that the string must be connected to the reward to work properly. Note that both species pulled the string in patterned string tasks, each using techniques reflecting the extent of their motor skills – in this way both species had the skills to solve the patterned testing problem – but the capacity to recognize the spatial relation between string and reward appeared to differ between them. Of course, birds can fail for other reasons, such as motivation (Pepperberg 2004).

However, as the birds participated in the test, but did not meet the criterion, motivation was probably not a key factor.

Clearly, two species are not sufficient to draw conclusions about an interrelation between motor and specific visual-spatial skills needed to recognize spatial relations between objects in parrots. However, as this is the first attempt to investigate the possibility of such an interrelation, the patterns are encouraging and call for more research. Support can be found in a within-species comparison, as fine beak-foot coordination and performance in patterned-string tasks were positively correlated. The higher the score for motor abilities (defined as a preference for techniques that require finer beak-foot coordination) was, the more successful were the performances achieved by the subject. Furthermore, the published literature on vertical patterned string problems in parrots shows that all species tested so far (keas; (Werdenich & Huber 2006), hyacinth macaws, Lear's macaws, and blue-fronted amazons; (Schuck-Paim et al. 2009)) used techniques with pronounced beak-foot-coordination, performing similarly at the patterned string tasks to the galahs in the present study. Furthermore, spectacled parrotlets (*Forpus conspicillatus*) that do not use their feet to manipulate food items were found to use techniques with a medium beak-foot coordination score when pulling a single rewarded string (Krasheninnikova & Wanker 2010). However, when presented with a set of patterned-string tasks spectacled parrotlets performed unexpectedly well (Krasheninnikova et al. 2013). These findings suggest that there might be a constellation of reasons for success or failure in these types of tests, i.e. there could be further mechanisms responsible for differences in ability to solve patterned-string tasks. However, further studies are needed to determine these possible reasons.

Contrary to the findings of Magat and Brown (2009), who suggested that species that failed to pull the string probably never encountered problems requiring advanced manipulative skills, the present study provides evidence that prior fine motor skills such as pronounced beak-foot coordination are not necessary for the ability to perform string-pulling in general. Interestingly, while findings in the present study suggest that fine motor coordination may be interrelated with visual-spatial skills, it appears that success in other tasks such as object permanence may not

be. In the study comparing object permanence in four parrot species (Pepperberg & Funk 1990), a cockatiel and a budgerigar, species which do not hold their food with the foot, exhibited object permanence just as well as a grey parrot and an Illiger's macaw – both “feet users” – did.

The patterned string task has been suggested to provide a reasonable simulation of natural foraging situations encountered by frugivore species (Halsey et al. 2006). For example, common marmosets have been observed to pull branches of trees towards them that hold fruit but that are too small to walk across (Bonvicino 1989; Peres 2000). As the vegetation of trees is often dense, it is likely that the marmosets have to choose the right branch to pull. The same foraging pattern is true for parrot species feeding on fruits and plants (Cannon 1983; Randler et al. 2011; Warburton & Perrin 2005). However, most of the diet of both galahs and cockatiels consists of seeds gathered mainly on the ground (Jones 1987; Rowley 1990). The differences found between the two species are thus particularly remarkable, as it is unlikely that the tasks used in this study favour the ecological niche of one species more than that of the other. Furthermore, parrots' exploratory play and their climbing mode of locomotion require strong visually guided beak usage to manipulate and explore external objects. Indeed, parrots show an enlargement of specific visual and beak-related cerebellar parts, suggesting that this may be related to their repertoire of visually guided goal-directed beak behaviour (Sultan 2005).

A potential limitation of the present study may be that when testing subjects jointly, different social learning speeds may have influenced the group performance as a whole as well as individual performance. If the birds had used social learning, a sequential pattern of similarity in the techniques applied could be expected. Yet, I found no such pattern: the birds

that followed after the first one used different techniques, suggesting that imitation did not play a role. However, types of social learning such as local enhancement, object enhancement or social facilitation – that only guide the attention of the observer to a location or item but still require individual learning by trial and error – likely played a motivational role in galahs. All six birds in the group showed an interest in the tasks, while only 10 of 22 cockatiels participated in the tests even though all subjects were able to observe the successful individuals, and even though monopolization of the set-up was prevented by the presence of several apparatuses. Finally, birds that initially failed a task did not improve their performance in the following trials even though they clearly observed successful companions. Therefore, social learning did not appear to influence the birds' success rate.

Further studies using standardized paradigms to test visual-spatial and motor skills across a wide range of parrot species are necessary to show whether the patterns found at the individual level are consistent across a wider range of species and to support the possibility that specific abilities such as visual-spatial skills may interrelate with motor skills not only in mammals but also in birds.

Acknowledgements

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Supplementary Material

Table S1: **Individual data for solution time, relative efficiency, and BFC.** Spearman's rank correlation coefficients and significance level are given for intraspecific correlations between BFC and solution time and between BFC and relative efficiency in each of the task.

Species	ID	Solution time $\bar{x} \pm$ SD	Relative Efficiency	BFC	Correlation BFC- solution time		Correlation BFC- relative efficiency	
					r_s	p	r_s	p
Task 1								
galah	G1m	14.62 ± 5.1	0.73	1.00	0.43	0.397	-0.51	0.295
	G2f	14.17 ± 4.39	0.89	0.50				
	G3f	18.17 ± 4.01	0.88	0.75				
	G4m	10.70 ± 5.13	0.90	0.50				
	G5f	15.37 ± 4.19	0.85	0.50				
	G6m	16.00 ± 4.84	0.89	1.00				
cockatiel	C1m	10.47 ± 3.19	0.87	0.50	0.24	0.505	0.62	0.054
	C2m	7.94 ± 2.32	0.77	0.50				
	C3m	11.48 ± 3.39	0.47	0.25				
	C4m	8.12 ± 1.42	0.76	0.50				
	C5m	7.63 ± 1.34	0.71	0.00				
	C6f	11.37 ± 2.69	0.81	0.50				
	C7f	11.87 ± 2.17	0.63	0.25				
	C8f	9.64 ± 2.41	0.68	0.25				
	C9m	12.20 ± 1.96	0.86	0.50				
	C10m	11.05 ± 2.17	0.79	0.50				
Task 2								
galah	G1m	9.83 ± 3.09	0.86	1.00	-0.31	0.542	0.29	0.566
	G2f	12.84 ± 3.12	0.92	1.00				
	G3f	18.37 ± 6.06	0.96	0.75				
	G4m	14.77 ± 3.96	0.84	0.75				
	G5f	12.27 ± 2.67	0.84	0.50				
	G6m	17.29 ± 11.30	0.77	0.75				
cockatiel	C1m	7.70 ± 1.91	0.87	0.50	0.25	0.484	0.44	0.198
	C2m	7.60 ± 3.00	0.95	0.50				
	C3m	7.44 ± 5.25	0.75	0.00				
	C4m	8.96 ± 1.21	0.96	0.50				
	C5m	8.25 ± 1.40	0.91	0.00				
	C6f	9.92 ± 3.09	0.89	0.50				
	C7f	12.23 ± 3.12	0.77	0.25				
	C8f	12.21 ± 2.46	0.95	0.50				
	C9m	12.75 ± 2.61	0.77	0.50				
	C10m	11.41 ± 2.11	0.71	0.25				
Task 3								
galah	G1m	12.27 ± 7.08	0.73	0.75	0.52	0.287	0.63	0.178
	G2f	13.57 ± 3.69	0.77	0.75				
	G3f	16.75 ± 2.83	0.82	0.75				
	G4m	12.79 ± 3.80	0.81	0.75				
	G5f	14.36 ± 3.04	0.71	0.50				
	G6m	18.31 ± 7.03	0.80	1.00				
cockatiel	C1m	10.29 ± 2.25	0.90	0.50	-0.04	0.907	0.55	0.100
	C2m	9.84 ± 1.99	0.89	0.50				
	C3m	13.96 ± 10.46	0.90	0.50				
	C4m	9.37 ± 1.58	0.89	0.50				
	C5m	8.20 ± 1.99	0.89	0.50				
	C6f	11.31 ± 2.02	0.82	0.25				
	C7f	12.52 ± 2.04	0.75	0.50				
	C8f	9.45 ± 1.57	0.84	0.25				
	C9m	12.46 ± 1.70	0.62	0.25				
	C10m	12.22 ± 1.58	0.81	0.50				

Table S1: Continued.

Species	ID	Solution time $\bar{x} \pm$ SD	Relative Efficiency	BFC	Correlation BFC- solution time		Correlation BFC- relative efficiency	
					r_s	p	r_s	p
Task 4								
galah	G1m	14.20 ± 5.71	0.86	1.00	0.39	0.441	-0.67	0.148
	G2f	13.84 ± 3.20	0.88	0.50				
	G3f	17.29 ± 3.65	0.84	1.00				
	G4m	13.84 ± 3.89	0.94	0.50				
	G5f	12.83 ± 2.60	0.92	0.75				
	G6m	15.35 ± 2.91	0.89	0.50				
cockatiel	C1m	11.47 ± 4.63	0.69	0.50	0.09	0.802	-0.42	0.221
	C2m	8.04 ± 1.29	0.74	0.50				
	C3m	11.68 ± 1.55	0.72	0.00				
	C4m	10.36 ± 1.89	0.81	0.50				
	C5m	9.15 ± 1.43	0.90	0.00				
	C6f	9.61 ± 1.46	0.66	0.50				
	C7f	11.09 ± 3.15	0.72	0.25				
	C8f	9.18 ± 1.61	0.83	0.00				
	C9m	11.74 ± 1.15	0.79	0.50				
	C10m	8.64 ± 1.67	0.68	0.25				
Task 5								
galah	G1m	5.15 ± 2.25	0.94	0.50	0.61	0.195	0.44	0.387
	G2f	11.28 ± 5.48	0.88	0.75				
	G3f	8.93 ± 5.22	0.96	1.00				
	G4m	4.76 ± 1.68	0.86	0.50				
	G5f	7.63 ± 3.47	0.90	1.00				
	G6m	6.76 ± 4.20	0.88	0.50				
cockatiel	C1m	3.95 ± 1.36	0.85	0.00	0.11	0.750	0.33	0.343
	C2m	6.75 ± 2.24	0.93	0.50				
	C3m	4.68 ± 0.90	0.93	0.25				
	C4m	3.95 ± 1.30	0.92	0.50				
	C5m	4.67 ± 1.26	0.93	0.00				
	C6f	3.21 ± 0.94	0.92	0.50				
	C7f	4.15 ± 1.04	0.94	0.25				
	C8f	4.21 ± 0.87	0.94	0.00				
	C9m	3.81 ± 0.91	0.93	0.50				
	C10m	4.87 ± 1.10	0.94	0.50				
Task 6								
galah	G1m	8.61 ± 3.75	0.96	1.00	-0.55	0.255	0.55	0.255
	G2f	13.97 ± 3.35	0.84	0.50				
	G3f	15.15 ± 2.22	0.92	0.50				
	G4m	12.58 ± 3.59	0.81	0.50				
	G5f	10.50 ± 2.84	0.90	0.50				
	G6m	14.56 ± 4.10	0.85	0.75				
cockatiel	C1m	8.83 ± 3.01	0.79	0.50	-0.61	0.058	0.44	0.201
	C2m	9.32 ± 3.67	0.86	0.50				
	C3m	9.91 ± 1.80	0.85	0.50				
	C4m	10.97 ± 1.57	0.74	0.25				
	C5m	9.67 ± 2.08	0.85	0.00				
	C6f	10.18 ± 2.85	0.90	0.50				
	C7f	9.65 ± 1.43	0.79	0.25				
	C8f	11.71 ± 2.65	0.74	0.00				
	C9m	8.09 ± 1.52	0.77	0.50				
	C10m	9.28 ± 2.09	0.90	0.50				

Table S1: Continued.

Species	ID	Solution time $\bar{x} \pm$ SD	Relative Efficiency	BFC	Correlation BFC- solution time		Correlation BFC- relative efficiency	
					r_s	p	r_s	p
Task 7								
galah	G1m	6.98 ± 1.92	0.96	1.00	-0.06	0.911	0.69	0.130
	G2f	6.98 ± 1.75	0.86	0.50				
	G3f	15.03 ± 2.46	0.85	0.75				
	G4m	6.22 ± 2.01	0.82	0.50				
	G5f	12.16 ± 2.42	0.91	0.50				
	G6m	12.45 ± 5.92	0.84	0.50				
	C1m	7.50 ± 2.88	0.89	0.50				
cockatiel	C2m	9.48 ± 2.54	0.90	0.50	0.08	0.832	0.31	0.382
	C3m	6.75 ± 2.95	0.87	0.25				
	C4m	6.97 ± 2.25	1.00	0.25				
	C5m	8.13 ± 3.13	0.75	0.00				
	C6f	6.29 ± 2.20	0.93	0.50				
	C7f	6.47 ± 2.57	0.93	0.25				
	C8f	6.71 ± 2.72	0.93	0.50				
	C9m	8.05 ± 2.52	0.80	0.50				
	C10m	7.50 ± 2.89	0.88	0.50				



Chapter 4

PHYSICAL COGNITION IN PARROTS: PERFORMANCES OF GREEN-WINGED MACAWS IN THREE MEANS-END PARADIGMS

Physical cognition in parrots: Performances of green-winged macaws in three means-end paradigms

Anastasia Krasheninnikova • Sina Bohneck • Jana Verena Dave • Bianca Wist • Jannis Liedtke

Both primates and birds, such as corvids and parrots, possess enhanced cognitive abilities despite their relatively large phylogenetic distance. Both taxa have a relatively large brain in common, which is frequently used as an indication for higher cognitive abilities. In this study we investigated physical understanding in green-winged macaws. This parrot species has one of the largest relative brains among avian taxa, but previously only showed limited understanding in trap-tube paradigm experiments. It has been suggested that this failure was caused by a lack of inhibitory control. Therefore, we presented the macaws with an adapted trap-table paradigm - a task with equivalent causal relationships but facilitating the birds' inhibitory control. We tested the macaws with two additional physical tasks – support problem and tube lifting – problems with different physical causal relations. Results showed that the parrots indeed inhibit their responses more often during the trap-table task compared to the trap-tube task. However, this did not improve their performance and only one bird reached the significance criterion. Similarly, in the tube-lifting only two out of six birds solved the task and none was able to solve the support problem. However, we also found that the presence of conspecifics often led to a distraction significantly affecting the parrots' performance. Therefore, the poor overall performance may be explained by green-winged macaws' inability to cope with social competition while being tested within their social group – a problem which group-living animals are likely to have to face in the wild.

Keywords: *Ara chloroptera*, Inhibitory control, Means-end, Physical cognition

Introduction

Understanding causal relationships between objects is considered an important factor driving the evolution of intelligence (Byrne 1997). Cognitive abilities in the physical domain have been traditionally investigated in primates. Recent studies, however, provide evidence that some avian species have evolved enhanced cognitive abilities convergent to those of primates (Emery & Clayton 2004). In particular corvids and parrots, big-brained representatives of different avian taxa, have been shown to possess enhanced cognitive capabilities such as understanding causal relationships, tool use and manufacture (Hunt & Gray 2003; Pepperberg 2004). Observations in the laboratory have also shown remarkable learning abilities about the physical environment in some parrots, i.e. keas (Auersperg et al. 2009; Auersperg et al. 2010; Werdenich & Huber 2006), kakarikis (Funk 2002), amazons (de Mendonça-Furtado & Ottoni 2008), and cockatoos (Auersperg et al. 2013).

A classical means-end paradigm used to test the understanding of spatial relationships between objects is the 'Support Problem', first formulated by Piaget (1963), in which the subject has to pull a piece of cloth as a 'means' to reach a reward. Two basic configurations have been used

most frequently: In the 'On Problem', subjects have to choose between a cloth with a food reward on it and another cloth with the same reward placed next to it. In the 'Connected Problem', subjects have to choose between a reward resting on an intact piece of cloth and another one resting on a cloth that was cut in two pieces, and separated by a gap. Several parrot species have been shown to solve the 'Support Problem'- tasks. For example, young kakarikis succeeded in pulling the "right" cloth in order to obtain the seeds resting upon it (Funk 2002). A single blue-fronted amazon was able to generalize the solution of the "On" problem, but took several sessions to learn the task (de Mendonça-Furtado & Ottoni 2008). The results from Auersperg et al. (2009) indicated that keas are capable of assessing the spatial means-end relationships of support problems even spontaneously.

In the tube-lifting paradigm (Auersperg et al. 2010), captive keas rapidly developed a sensitivity for stoppers in a set-up testing for zero-order relationships between objects. Here the reward was lying freely on the tube floor and the tube was fitted with wooden stoppers at one end. The reward was available by lifting the tube at the end sealed with a stopper so that it would roll out at the open end.

However, despite the growing evidence that parrots have some understanding of relations between objects, there appear to be certain limitations in parrots' capabilities of physical cognition. Recent studies (Liedtke et al. 2011; Schloegl et al. 2009) revealed that some types of tasks testing physical cognition appear to be more difficult for parrots compared to other big-brained birds such as corvids. For example, the trap-tube paradigm, first applied by (Visalberghi & Limongelli 1994) in capuchin monkeys, is a task often used to test the understanding of causal relationships. In this test, subjects are offered a horizontal Perspex tube with a trap attached to its ventral side. In order to obtain a reward, which is put into the tube next to the trap, the subject has to pull or push the reward with a stick. The task was subsequently adopted and used to test causal reasoning in different animal groups including corvids (Seed et al. 2006) and woodpecker finches (Tebbich & Bshary 2004). Liedtke et al. (2011) tested six keas, three green-winged macaws, and one yellow-crested cockatoo with a modified version of trap-tube task previously used by (Tebbich et al. 2007). The set-up included a rake that was pre-inserted into the tube and had to be used to pull or push the reward out. No tested parrot solved the task reliably. In contrast, in corvids (including even non-tool-using rooks), several individuals learned to solve this initial task within a few trials (Seed et al. 2006). Liedtke et al. (2011) suggested that the poor performance of parrots may be caused by their limited inhibitory control. In the trap-tube task, there is a distance of at least 32 cm between either end of the tube which must be overcome when inhibiting the initial incorrect choice and switching the sides to obtain the reward. This distance may increase the birds' reluctance to switching from the unrewarded side to the rewarded one. Indeed, Taylor et al. (2009) mentioned that in their study three successful crows could repeatedly inhibit their initial behaviour and switch sides of the tube within a given trial to obtain the reward. Thus, it was assumed that they understood the spatial configuration of the task. Unsuccessful subjects never inhibited their initial behaviour. Similarly, Liedtke et al. (2011) observed only very few trials in which parrots switched sides within a trial. This suggests that corvids may have fewer difficulties inhibiting behaviour within a larger area around a reward when it is out of reach.

The aim of this study was to test the understanding of causal relationships between objects in green-winged macaws. To allow a better comparability to previous studies of parrots' and other vertebrates' physical cognition, we used three widely distributed paradigms for means-end studies: the Support-Problem, the Tube-Lifting and the Trap-Table. To test the hypothesis that inhibitory control might have an influence on the performance in trap-tube tasks in parrots, we used the trap-table paradigm, a visually distinct but causally equivalent task to the trap-tube problem (Taylor et al. 2009), in which the distance between the two choice opportunities is reduced to 10 centimetres.

We hypothesized that in this configuration the parrots can control their pulling behaviour and switch from the incorrect side to the correct one more easily. We thus expected that the birds would perform better in the trap-table task than in the trap-tube task.

Material and Methods

Housing conditions

The study group of 21 green-winged macaws contained 12 adults (6 pairs) and nine juveniles. All parrots were hatched in the zoo Hagenbeck in Hamburg, Germany and were raised by their parents. The housing of the green-winged macaws consisted of an outdoor aviary (22 x 28 x 8 m) where they were kept together with Black-bellied whistling duck (*Dendrocygna autumnalis*) and an adjacent indoor aviary (8 x 6 x 4 m) where they were kept together with Brazilian guinea pig (*Cavia aperea*) and degu (*Octodon degus*). Both outdoor and indoor aviaries were connected by several windows. Birds were fed every day at 11 am (during breeding season from May to June, the birds were fed additionally at 7 am) with corn kernels, sunflower seeds, pumpkin seeds, and fruits. For the daily show-feeding at 11 am only nuts (walnuts, Brazil nuts etc.) were used. The indoor aviary was lit by several windows and provided several large trunks, three warm lamps, and a small lake. The outdoor aviary contained several trees and trunks, several cliff-like rocks, six nest boxes, a clay lick, and a lake with a small waterfall. Water was available *ad libitum* and vitamins were given twice a week. No artificial toys were available, but green branches were provided regularly for playing and nibbling.

Prior to the experimental phase a photo-identification database of the study subjects was

created using lateral face images of the birds' heads. All subjects could be recognized individually at all times during the experimental sessions by their beak characteristics and their facial feather markings.

General Testing Procedure

Prior to the beginning of the experiments, the subjects were presented with simplified versions of each apparatus. In this training phase the birds learned the necessary motion sequences for handling the apparatus (the tube, the drawer, and the rake, respectively). No success criteria had to be met. Testing phase lasted three weeks. Thereafter, the birds were presented with the experimental set-ups.

The experiments were carried out between 9.00 and 11.00 am. The testing apparatuses were placed in the outdoor aviary on the lawn and were freely accessible to all subjects. The green-winged macaws were tested jointly to simulate conditions in which subjects deal with a novel problem (e.g. new food sources) in the natural environment, where several individuals usually face a new situation at the same time. Once the task was set up, the animals were free to approach the apparatus, so that only motivated subjects participated in the task. All three experiment types were presented simultaneously with the exception that the second version of the Trap-Table experiment was presented only after the Support-Problem and the Tube-Lifting experiments were already finished.

The trials started when the bird touched the apparatus (the tube, the drawer, or the rake) with the beak. However, no starting point in the space could be set up as the subjects were free to approach the apparatus whenever they want. Timing was stopped when the subject interrupted the interaction with the apparatus or when it was disturbed by other individuals and continued as soon as the subject touched the apparatus again. A trial ended when the subject succeeded (by obtaining the reward) or failed (by choosing the incorrect end of the tube in test 1, or the unrewarded drawer in test 2, or allowed the reward to fall into the trap in test 3, respectively), whatever came first. Switching the side also scored failure. All trials were videotaped.

Test 1 - Tube Lifting

Training

A transparent Perspex tube (length: 32 cm, inside diameter: 3.4 cm, outside diameter: 4 cm) without stopper (Figure 1a) was presented with a reward (a Brazil nut) placed in the middle of the tube. To obtain the nut, the bird had to lift the tube until the reward drop out. The bird could either lift the tube laterally or grasp it in the middle with the beak and tip the head to the side with both ways leading to success.

Experiment

A transparent Perspex tube (length: 35 cm, inside diameter: 3.4 cm, outside diameter: 4 cm) with a stopper placed at the $\frac{3}{4}$ of the tube (ca. 12 cm) was presented. The stopper prevented the reward from sliding out at one of the two sides. Therefore, only the lifting of one of the two sides would lead to obtaining the reward. Two versions of this task were presented. In the task version 1 ("Central") the reward had been placed always in the middle of the tube, so that only lifting the side with the stopper would lead to success (Figure 1b). In the task version 2 ("Short") the reward was placed in the shorter section of the tube just behind the stopper (Figure 1c). In this case, only lifting the longer side would lead to success, regardless of whether the tube was lifted laterally or in the middle.

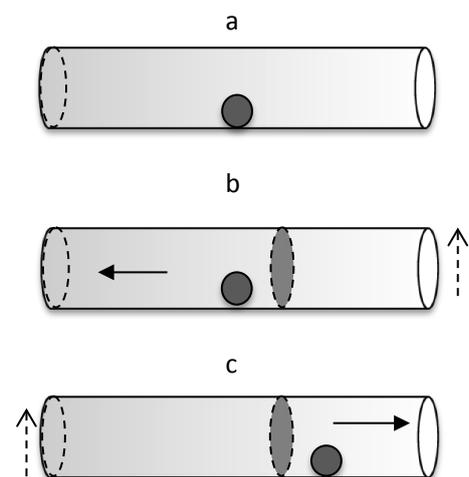


Figure 1: Testing apparatuses – Tube Lifting. **a** – Training tube lifting: a transparent Perspex tube without a stopper, the reward is placed in the middle of the tube; **b** – Tube Lifting task (version 1 - "Central"): a transparent Perspex-Tube with a stopper placed at the $\frac{3}{4}$ of the tube. The reward placed in the middle of the tube; **c** – Tube Lifting task (version 2 - "Short"): the reward placed in the shorter section of the tube, just after the stopper. The dashed arrows indicate the side lifting which would lead to success

Test 2 - Support Problem

Training

The simplified apparatus for training consisted of a wooden box (35 x 30.5 x 17.5 cm) with a transparent Perspex front and a transparent Perspex cover. A drawer with a metal handle protruded ca. 7 cm from a slot in the Perspex front. The reward was placed inside a cavity at the other end of the drawer. The whole apparatus was placed on a wooden board (35 x 40 x 2 cm; Figure 2a).

Experiment

The birds had to choose between the two drawers to obtain the reward. Again, two versions of this task were presented. In version 1 (“On Problem”), the reward was put on one and next to the other drawer (Figure 2b). The subject had to pull the drawer on which the reward was placed. The drawers were identical. In version 2 (“Connected Problem”) both drawers were rewarded. However, one of drawers had a gap (1.5 cm) between both ends (Figure 2c), so that pulling the drawer with the gap would not lead to success.

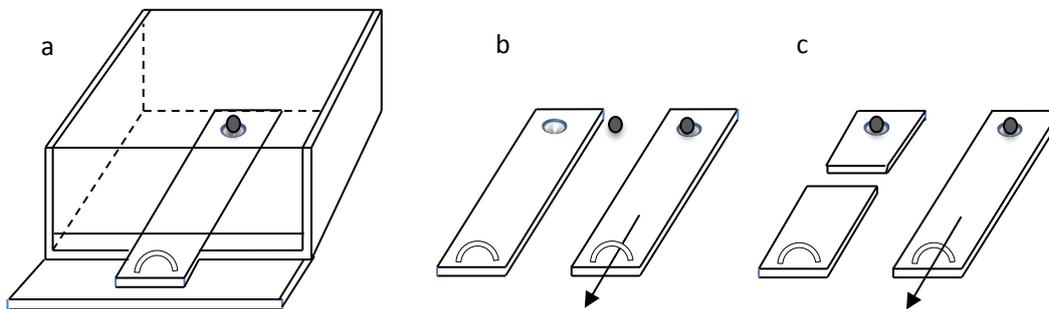


Figure 2: Testing apparatuses – Support-Problem. **a** – Training apparatus consisted of a wooden box, a transparent Perspex front, a transparent Perspex cover, and a drawer. The reward was placed in a cavity on the other end of the drawer. The training apparatus have been extended and had in the experiment two drawers. The birds had to choose between these two drawers to obtain the reward; **b** – “On Problem”: a reward was put on one and next to the other drawer. The subject had to pull the drawer on which the reward was placed; **c** – “Connected Problem”: both drawers were rewarded. However, one of drawers had a gap (1.5 cm) between both ends. The arrows indicate the correct drawer to pull.

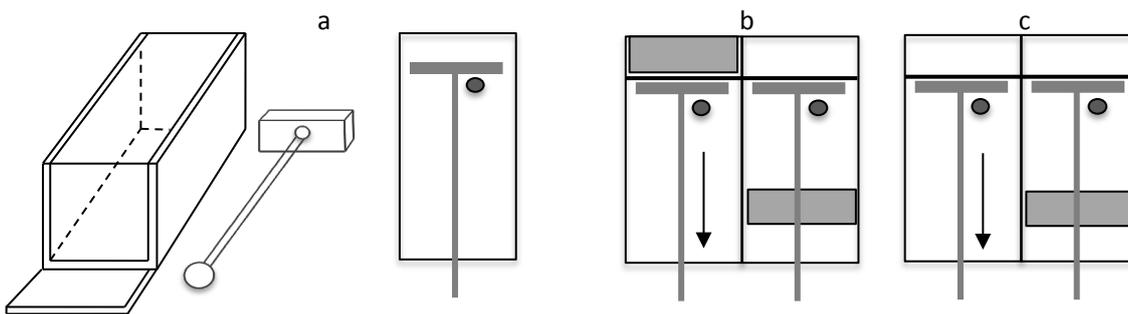


Figure 3: Testing apparatuses – Trap Table. **a** – Training apparatus consisted of a wooden box, a transparent Perspex cover, and a rake with a piece of wood on the one end and a metal sheet on the other one. The reward was placed in front of the rake. The pre-training apparatus have been extended and had in the experiment two sections, separated by a Perspex divider, two rakes, a functional and a non-functional trap. On each side a trap could be placed both in front and behind; **b** – “Two Traps”: one trap was placed in front of the rake on the one side, so that the reward would fall in this (functional) trap when pulling the rake on this side. On the other side a second trap was placed behind the rake (non-functional), so that pulling out the rake on this side would lead to obtaining the reward. Hence, the traps were placed on both sides of the apparatus; **c** – “One Trap”: here only one trap was used. Black lines represent a stopper in the front of the rear trap preventing the rake from falling into or getting stuck in the trap behind, grey squares the trap and the arrows the correct rake to pull.

Test 3 - Trap Table

Training

The simplified configuration of the apparatus consisted of a wooden box with a transparent Perspex cover. A rake with a piece of wood on one end and a metal sheet on the other was placed into the box. To obtain the reward placed in front of the piece of wood the bird had to pull the rake. The whole apparatus was placed on a wooden board (35 x 40 x 2 cm; Figure 3a).

Experiment

The apparatuses consisted of two sections, separated by a Perspex divider, two rakes, and a functional and a “non-functional” trap. Two versions of this task were presented. Version 1 (“Two Traps”) was similar to one version used by Fujita (2003) testing Tufted Capuchin Monkeys. A trap was placed in front of the rake on the one side, so that the reward would fall in this (functional) trap when pulling the rake to this side. On the other side, a second trap was placed behind the rake (non-functional), so that pulling out the rake to this side leads to obtaining the reward. Hence, contrary to the studies by Povinelli et al. (2000); Taylor et al. (2009), the traps were placed on both sides of the apparatus (Figure 3b). Thus subjects could not choose just by following the rule of avoiding the side with the trap. The birds have to attend to the position of the trap, and thus to its functionality, instead. In version 2 (“One Trap”) the task was simplified, because only one individual succeeded in the previous version. In the simplified version, only one trap was used (Figure 3c; see also (Taylor et al. 2009). In both versions of the task, we used a stopper in the front of the rear trap to prevent the rake from falling into or getting stuck in the trap behind.

Data analysis

For the analysis of the data, all trials with a given individual were divided into blocks of 10 trials. If a subject did not complete a block of trials in one day, the block was completed with data from the following day. Within a block the rewarded side was pseudo-randomised, i.e. in total, the reward was 5 times on the right and 5 times on the left side. The criterion for an entire task being solved successfully (by obtaining the reward) was set to at least 15 correct trials in each of two consecutive test blocks (i.e. 15 correct out of 20 trials; binomial test, $P = 0.021$). Subjects that participated in the tests but did not

produce a sufficient amount of data, i.e. did not complete at least 20 trials, were excluded from the analyses at the individual level (in terms of meeting the success criterion), but were included in the group-level analyses (using GLMMs).

To investigate the effect of trial number, trial duration, start position, trap side, reward side, rake switching, side switching, and audience on the successful completion of the tasks, we performed generalized linear mixed model (GLMM) analyses in R 3.0.0 (RDTTeam 2013). The distribution was set as binomial (success or no success) with logit link function. For a summary of test statistics from GLMMs see Table 1.

Table 1: Summary of test statistics from GLMMs assessing the effect of explanatory variables on the success in the tasks

Task	Variant	Explanatory variable	df	p
Tube-Lifting	“Central”	Trial number	1	0.101
		Reward side	1	0.020
		ID	8	<0.001
		Audience	1	0.111
	“Short”	Audience*ID	8	0.133
		Trial number	1	0.002
		Reward side	1	<0.001
		ID	8	<0.001
Support-Problem	“On-Problem”	Audience*ID	8	0.541
		Trial number	1	0.186
		Reward side	1	<0.001
	“Connected-Problem”	Audience*ID	6	0.029
		Trial number	1	0.037
		Reward side	1	0.264
Trap-Table	“Two-Traps”	Audience*ID	3	0.019
		Trial number	1	0.718
		Reward side	1	<0.001
		ID	4	0.953
		Side switching	1	0.486
	“One-Trap”	Audience	1	0.580
		Audience*ID	4	0.828
		Audience*Side switching	4	0.910
		Trial number	1	0.368
		Reward side	1	0.002
		ID*Side switching	1	0.024

Models were reduced starting with the least significant interaction until only significant interactions were left in the model. Then, main effect reduction started with the least significant. Models were compared using ANOVA and treated as significantly different with p-values smaller than 0.05. All p-values presented here are

derived from ANOVA (χ^2) model comparisons between one model containing the focus variable and one model having the variable removed.

Results

Test 1 - Tube Lifting

Generally, very few birds produced a sufficient amount of data of at least 20 trials. The overall performance of these individuals was poor across the tasks (Table 2, Table S1).

In task version 1 (“Central”), one individual showed a clear preference for the wrong side of the tube (see Table S1), always choosing the end of the tube, where the reward was placed. In task version 2 (“Short”), two birds met the success criterion. Notably, one individual exhibited the same preference as in the task version 1 for the wrong side during the first ten trials, changing then to chance level within the next 80 trials, and meeting the success criterion within its last 20 trials. In contrast, another individual performed at chance level during the first 30 trials, then meeting the success criterion within the next 20 trials for the first time, and subsequently in consecutive 4, 6, and 5 blocks, respectively, during the next 200 trials.

In the “Central” task, birds were more successful when the reward was placed on the right ($df = 1$, $p < 0.02$). There was also a variation in performance among the individuals ($df = 8$, $p < 0.001$). In the “Short” task, birds succeeded more frequently when the rewarded side of the tube was orientated to the left ($df = 1$, $p < 0.001$), the number of correct choices increased over time ($df = 1$, $p = 0.002$), and in case of social competition ($df = 1$, $p = 0.02$). When a conspecific was present, the individuals succeeded more frequently in the task. There was also a variation in performance among the individuals ($df = 8$, $p < 0.001$).

Test 2 - Support Problem

No bird met the success criterion either in “On Problem” or “Connected Problem” task. However, in the “On Problem” task, birds succeeded more frequently when the reward was placed on the left side ($df = 1$, $p < 0.001$). There was also an effect of interaction between individual and presence of an audience on the success ($df = 6$, $p < 0.029$), i.e., some individuals succeeded more frequently when conspecifics attended their trial, whereas other individuals were not or sometimes even negatively influenced by the presence of an audience.

Success in the “Connected Problem” task depended on the trial number ($df = 1$, $p = 0.038$) with the number of correct trials declining over time. Furthermore, the interaction between individual and audience ($df = 3$, $p = 0.02$) influenced the success also in this task with the performance of some birds being negatively influenced by the presence of conspecifics.

Test 3 - Trap Table

One bird met the success criterion in the “Two-Trap” task within 110 trials (by choosing 7 trials from one block and 8 trials from the consecutive block, respectively). The birds were most successful when the reward was placed on the left side ($df = 1$, $p < 0.001$).

The success criterion was not met in the “One-Trap”. However, the birds were more successful when the reward was placed on the left side ($df = 1$, $p = 0.002$). Furthermore, the success depended on the interaction between ID and side switching ($df = 4$, $p = 0.023$), i.e., some birds switched more frequently to the incorrect drawer/side, whereas others switched from “wrong” option to the successful one.

Table 2: Performance of the green-winged macaws across tasks

Task	Variant	Group size	Number of birds participated in the test	Number of birds produced data (at least 20 trials)	Number of birds that met the success criterion
Tube Lifting	„Central“	21	11	7	0
	„Short“	21	11	6	2
Support Problem	„On Problem“	21	10	4	0
	„Connected Problem“	21	9	2	0
Trap Table	„Two-Trap“	21	5	5	1
	„One-Trap“	21	7	7	0

Discussion

To test the understanding of spatial relationships between objects, we exposed a captive green-winged macaw group living in semi-natural conditions to three means-end paradigms: the Tube-Lifting, the Support-Problem, and the Trap-Table. We found only little evidence for understanding of such relationships between objects. This was unexpected because other parrot species tested with these or comparable tasks showed advanced performances (Auersperg et al. 2009; Funk 2002) and, in addition, green-winged macaws have one of the largest telencephalic volumes of all avian species (Burish et al. 2004). Albeit, we have to point out that the macaws disturbed each other during testing often and thereby crucially impaired their problem solving abilities, which indeed might be a common problem in group living animals. Therefore, we cannot determine conclusively their abilities regarding these cognitive tasks. However, a few individuals were able to solve some tasks after considerable time and thereby reveal their learning abilities.

Tube Lifting Task

In the first version of the task the reward was placed in the centre of the tube and only lifting the side with the stopper would have led to success. However, none of the seven birds that participated in this version reached the success criterion (yet one individual was getting close to it several times). A likely explanation is that the macaws chose to lift the side where the view on the reward was not blocked by the stopper. But that action inevitably resulted in an incorrect response.

In the second version the reward was placed near to the end of the tube on one side. Two of the six participating birds met the success criterion. The observed behaviour of the subjects suggests that if the reward was near one of the tube's ends, it was easier for the macaws to learn that the correct response was to lift the opposite end. This rule was not available in the first version with a centrally placed reward. Although there were possible rules to solve both versions of the task, i.e. "lift the side where you can see the stopper" or alternatively "where you do not see the reward", the parrots obviously did not use these, because they may have been unintuitive for the birds. It appears that the

macaws mostly paid attention towards the reward and less to the barrier (stopper).

Support Problem

The green-winged macaws did not solve the Support Problem at all. None of the birds met the success criterion either in the "On-Problem" or in the "Connected-Problem" condition. Furthermore, there was no evidence for trial-and-error learning as the performance of the birds deteriorated over time, i.e., with increasing trial number, rather than becoming more successful. One possible reason for this decline may have been the increased distraction by conspecific during the later phase of the experiment, which probably was caused by familiarisation of the birds with the experimental set-up. Indeed, the presence of an audience had a significant effect on the birds' performance. Some individuals succeeded more frequently when conspecifics attended the trial, whereas others were either not or - in some cases - even negatively influenced by the group members (see below). Another explanation for the unexpectedly poor performance may be that green-winged macaws simply need more trials to learn about a relationship between the objects in the Support-Problem paradigm. For example, keas needed only few trials to solve the "On-Problem" task (Auersperg et al. 2009), whereas blue-fronted amazon needed over 600 trials to learn the solution (de Mendonça-Furtado & Ottoni 2008).

Trap-Table

In a previous study, (Liedtke et al. 2011) suggested that the poor performance of parrots tested with a Trap-Tube might have been caused by the lack of inhibitory control as it has been suggested for other bird species, too (Taylor et al. 2009). The Trap-Table task was conducted to test whether the macaws could increase their performance, if their side-switching behaviour would be facilitated. Indeed the shorter distance between the two choice-opportunities appeared to facilitate side-switching (211 out of 1176 trials, 18%) with the Trap-Table in comparison to 6 out of 3300 trials (0.2%) with the Trap-Tube. However, this relaxation of inhibitory control did not lead to an improvement in the performance of the macaws. Some birds even switched from the correct option to the wrong one more frequently than vice versa.

Nevertheless, in the "Two-Trap" condition, one bird met the success criterion, but in the

presumably easier “One-Trap” condition, no bird succeeded at all. This is remarkable, because the birds were not able to solve the Two-Trap version by simply avoiding the side with the trap or by associating the continuous surface of the table with the reward as it had been suggested in other studies (Cunningham et al. 2006; Girndt et al. 2008; Taylor et al. 2009). However, the birds could still solve the problem by associating the continuous surface of the table with the side where the trap is further away. It is difficult to discern, why the one subject that had solved the first version did not solve the second. Possibly the bird was not able to transfer the knowledge it gained or it may have forgotten it. Otherwise, it could have reached the significant criterion in the Two-trap version simply by change. Alternatively, the decrease in performance in One-Trap version might have been caused by higher disturbance by conspecifics in the later phases of the experiment

Effects of social competition

It has been pointed out that social interactions may affect problem-solving performances. On the one hand, skilled but low-ranked individuals might be prevented from performing particular tasks by dominant individuals (Anderson et al. 1992; Drea & Wallen 1999; Pongrácz et al. 2008). On the other hand, the monopolization of accessible resources by higher ranking individuals might drive lower ranking individuals to search for alternative resources, which may require problem-solving and innovation abilities (Reader 2004). Similarly, scrounging behaviour of high-ranking individuals may reduce their need for problem-solving behaviour to access “difficult achievable food resources” (Chalmeau & Gallo 1993; Giraldeau et al. 1994). Finally, competition for access might distract individuals and thereby reduce their problem-solving abilities irrespectively of their rank.

In this study, high-ranking individuals tended to monopolize access to test devices and thus prevented lower-ranking individual from solving the tasks. Indeed, some lower-ranking individuals showed relatively good performance when they had access to the devices. Scrounging was exhibited by most birds and not by dominant individuals alone. While agonistic behaviours occurred frequently, harsh fighting over food was not observed. Even high-ranking individuals tolerated theft, perhaps because it may not have

been worth fighting over food that was abundant in the aviary (Blurton Jones 1984; Jones 1987).

Significant effects of the presence of conspecifics occurred during the Support-Problem-task only. It might have been that the effect of disturbance increases with the complexity of the task and its specific configuration. Animals might be able to solve simple cognitive tasks even when distracted by conspecifics. Moreover, when test devices are easy to monopolize, effects of high-ranking individuals might diminish, because subordinate scroungers will find no chance to steal the reward. Both situations may have been the case in the Tube-lifting task. However, in complicated tasks we expect an individual to perform at chance level while any interaction with another individual will neither increase nor decrease the performance. The largest effects may be expected when the problem to solve is complex yet within the individual’s cognitive capacities. When attempting to solve such complex cognitive tasks, a stronger division of attention between social competition and obtaining the reward may be needed.

However, testing problem-solving in a social group setting appears to be ecologically relevant, because in the wild, animals often face cognitive challenges under conditions of social competition (e.g. when parrots congregate in groups to search for food). Particularly, in highly social groups, where distractions by conspecifics are frequent, it may be more difficult for an individual to focus its full attention on a given problem. Evidence from New Caledonian crow (Holzhaider et al. 2011) supports the hypothesis that a modest degree of sociality might allow greater inhibitory competence and facilitate the ability to focus on cognitive aspects of a physical problem.

Although there are some limitations of testing problem-solving abilities in social context, such settings might give us a better understanding of how problem-solving may occur and evolve in nature. There is ample evidence that living in social groups might facilitate or necessitate higher cognitive abilities (Reader & Laland 2002). Considering findings of this and other studies (Drea 1998; Munkenbeck Fragaszy & Visalberghi 1990), hierarchical structures of social groups appear to affect, i.e. facilitate or hinder, the development of problem-solving abilities. For example, in a group with strong hierarchical structure low-ranking individuals might be forced to search for alternative food sources and thus develop alternative problem-solving strategies

(Reader 2004). Alternatively, skilled but low-ranking individuals might be prevented from access to food source by their dominant group members (Cronin et al 2014, Drea and Wallen 1999)

In summary, the overall poor performance of our captive group of green-winged macaws in the three means-end tasks appears to have been a consequence of social interactions which appeared to have distracted the birds when attempting to solve complex means-end tasks. These findings suggest that green-winged macaws may not lack the cognitive capacity to solve means-end problems, but rather the ability

to focus on cognitive tasks when coping with its natural social environment. Further studies need to investigate, possible differences between a laboratory environment and the natural environment.

Acknowledgments

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Supplementary Material

Table S1: Number of correctly solved trials per individual in blocks of 10 trials

Tube Lifting – “Central”																										
Block																										
ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
Bert	3	10	6	6	9	5	6	6	5	8	6	3	6	2 [#]	3 [#]	10	5	7	7							
Fritz-Erich	5	2																								
Kerbe	5	6	3																							
Kiddel	0																									
Kralle	5																									
Micha	0 [#]	0 [#]	2 [#]	1 [#]	1 [#]	2 [#]	2 [#]																			
Olli	4	7	6	5																						
Paul	1	4	2	7																						
Schwarz-schnabel	5	5	3	6																						

Tube Lifting – “Short”																										
Block																										
ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
Bert	6	8	5	6	5																					
Kerbe	2																									
Micha	3	6	6	5	6	6	7	3	6	9*	7*															
Olli	6	3	4	10*	9*	5	8	5	8*	8*	8*	9*	6	9*	8*	10*	8*	10*	8*	5	9*	9*	10*	9*	8*	
Paul	3	4	1																							
Schwarz-schnabel	5	9																								
Anni	2																									
Kim	3 [#]	2 [#]	1 [#]																							
Leon	1																									

Support Problem – “On-Problem”																										
Block																										
ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
Bert	7																									
Fritz-Erich	2																									
Kiddel	5	5																								
Kralle	5	6	6	3	7	4	2	7	2																	
Olli	3	4	6	3	4	4	3	6	3	4	4	4	3	5	4	2	5	4	5	3						
Anni	7	5	4	6	5	5	6	5	7	2	4	6	4	5												

Support Problem – “Connected-Problem”																										
Block																										
ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
Kerbe	5																									
Olli	5	5	6	6	5																					
Anni	5	4	2 [#]	0 [#]																						

Tab.S1: continued

Trap Table – “Two-Traps”																										
Block																										
ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
Bert	7	6	3	5	5	6	8	4	5	7	5	3	4	4	6	5	4									
Kiddel	6	7	6	6	4	4	4	4	3	7*	8*															
Kralle	3	4	4	7	6	6	5	6	5																	
Olli	5	7	5	4	2	5	2	5	4	7	7	7	7	5	7	6	6	6	5	5	5					
Anni	6	5	4	7	5	4	8	6	6	4	5	6	5	6												

Trap Table – “One-Trap”																										
Block																										
ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
Bert	9	4	4	7	7	6																				
Fritz-Erich	2 [#]	2 [#]	4	7	6	3	4	4	2																	
Kiddel	7	6	5	5																						
Kralle	2	5	6	5	6	4	6	5	5																	
Olli	5	4	8																							
Anni	4	3	3	8																						
Vera	5	6	7	5	5																					



Chapter 5

TESTING PROBLEM-SOLVING CAPACITIES: DIFFERENCES
BETWEEN INDIVIDUAL TESTING AND SOCIAL GROUP
SETTING

Testing problem-solving capacities: differences between individual testing and social group setting

Anastasia Krasheninnikova • Jutta M. Schneider

Testing animals individually in problem-solving tasks limits distractions of the subjects during the test, so that they can fully concentrate on the problem. However, such individual performance may not indicate the problem-solving capacity that is commonly employed in the wild when individuals are faced with a novel problem in their social groups, where the presence of a conspecific influences an individual's behaviour. To assess the validity of data gathered from parrots when tested individually, we compared the performance on patterned-string tasks among parrots tested singly and parrots tested in social context. We tested two captive groups of orange-winged amazons (*Amazona amazonica*) with several patterned-string tasks. Despite the differences in the testing environment (singly vs. social context), parrots from both groups performed similarly. However, we found that the willingness to participate in the tasks was significantly higher for the individuals tested in social context. The study provides further evidence for the crucial influence of social context on individual's response to a challenging situation such as a problem-solving test.

Keywords: *Amazona amazonica*, Parrots, Patterned-string task, Problem-solving, Testing conditions

Introduction

Research on non-social cognition has favoured the test of isolated animals. Even if they are housed socially, the subjects have traditionally been caught for their daily testing in an experimental area spatially separated from their group members (Fagot & Paleressompoulle 2009). Controlled laboratory conditions facilitate studies of learning processes and by limiting distractions during the experiment allow the subjects to pay full attention to the task (Halsey et al. 2006). Furthermore, individual tests guarantee the experimenter regular access to the same study subject. However, under natural settings group-living individuals are faced with novel problems within their social groups, where they are subject to distractions such as displacement by other members of the group. The resulting shorter decision-making time might have a negative effect on the success of problem-solving (Boere 2001). Hence, while individual conditions are ideal for investigating cognitive capacities, the results may not reflect the problem-solving performance that would be shown under natural conditions. Thus, if we want to draw conclusions about whether cognitive capacities expressed under individual conditions represent cognitive capacities prevalent in the wild, it is important to carefully consider the differences between the individual and social group settings (Halsey et al. 2006).

Testing animals in an isolated or social environment may affect problem-solving performance due to differences in the frequency of distractions, willingness to participate in testing, availability of alternative activities, and individual differences in anxiety. For example, some individually tested subjects react with increased fearfulness to challenging situations such as novel objects and/or environments compared with when tested within the context of their social groups (Toxopeus et al. 2005; Zajonc 1965). Thus, individual testing may cause failures reflecting increased fearfulness rather than missing capacity.

Studies on group operant behaviour (Graft et al. 1977; Morgan et al. 1976) and social facilitation (Grott & Neuringer 1974; Ward 2012; Zajonc 1965) have shown that when two or more animals are given access to food, each animal often eats more, responds faster, or explores a larger section of the arena than when alone. However, very few studies have compared the problem-solving performance of animals between naturalistic social and individual-based environments and the results of these studies are inconsistent. For example, Gazes et al. (2012) found that cognitive testing of monkeys in their home group yielded results comparable with those obtained in individual settings. In contrast, common marmosets tested in the wild by Halsey et al. (2006) successfully completed a patterned-string task consisting of two parallel strings with a reward attached to the end of one of them.

However, due to distractions by conspecifics, they consistently made more errors than subjects in previous individual-based tests (Halsey et al. 2006). Hence, individual tests may or may not reflect performances under natural conditions. Thus, comparisons of behaviour under different social contexts are necessary, in particular in highly social animals, if conclusions about ecological relevance are desired (Gazes et al. 2012).

Parrots are highly social species often used for problem-solving studies, including patterned-string problems, and their performances can be affected by the testing environment. The patterned-string task is a broadly accepted test of perceptual capacity and the understanding of means-end connections. It generally consists of two strings with a reward attached to the end of one of them. The subject can obtain the reward by pulling the correct string. The patterned-string task provides a reasonable analogue of a natural foraging situation at least for frugivorous parrots where the birds have to pull branches of trees towards them that hold fruits. As the vegetation of trees is often dense, it is likely that they often have to choose the right branch to pull. Hence, the task seems ideal to compare individual and group performances to elucidate the perceptual and specialised cognitive performance expressed by a species under natural conditions. However, with very few exceptions (Krasheninnikova et al. 2013; Schuck-Paim et al. 2009), all studies of patterned-string problems in parrots have been carried out in individual settings (Dücker & Rensch 1977; Pepperberg 2004; Werdenich & Huber 2006).

Here, we compared the performance on patterned-string problems of orange-winged amazons (*Amazona amazonica*) either tested individually or jointly in a social group. Based on reports in the recent literature (Halsey et al. 2006; Toxopeus et al. 2005), we hypothesised that (1) the subjects' fearfulness level is higher for birds tested singly, (2) the performance of birds tested in social context is affected by distractions from conspecifics, and (3) the birds tested singly perform better in patterned-string task due to enhanced attention and accuracy.

Materials and methods

All study subjects were housed at the Parrot Zoo in Skegness, UK. The first group ($N = 23$, 11 pairs, 1 unpaired individual) – single condition – was housed together in an outdoor aviary ($4 \times 2 \times 3$ m). The birds from this group had been subjects

of another study for which they were trained to enter a test compartment ($1.5 \times 2 \times 1$ m) singly. In the test compartment, subjects were presented with a horizontal version of a string-pulling test that in its structure was similar to task six in the present study: a choice between two strings, one was connected to a rewarded cup and the other not connected to it. However, in the present study, we used a vertical version of string-pulling tasks. The second group ($N = 35$) – social condition – was housed together in an aviary ($2.5 \times 4 \times 2$ m) with an adjacent indoor aviary ($2 \times 2 \times 1$ m), where feeding troughs were placed. The subjects from the second group had not been involved in any previous experiments. To correct for the differences in the prior experience of the groups, i.e., dealing with horizontal strings in subjects tested singly, the inexperienced birds of the second group (social condition) were given the opportunity to explore and perform the same horizontal string-pulling task that the birds in the first group were tested with. To achieve this, we presented two strings (one was connected to a cup with reward, one was not) on a board to every single individual in the second group and let them choose between the cups up to five times. If a bird refused to pull any string, it was presented with the same apparatus 1 h later one more time. Due to time constraints, no bird saw the apparatus more than five times even if it never pulled a string (ten birds never pulled). Animals in both groups participated in all tests voluntarily, so both groups were comprised of subjects with different experience.

No artificial toys, only green branches for playing and nibbling, as well as trunks, and perches were provided regularly in both aviaries. Both groups were provided with a seed mix in the morning and with fresh fruits in the afternoon, including on experimental days. Water was available *ad libitum*. All subjects of every group could be individually recognised at all times during the experimental sessions.

Experimental set-up

The subjects first faced a single rewarded string suspended from a horizontal perch (T1). Then six patterned-string tasks were presented (T2-T7, see also Figure 1). Here, we used strings that differed in colour, length, and spatial relationship: T2 - two strings, one with the reward and one without; T3 - two differently coloured strings that crossed; T4 - two crossed strings of the same colour; T5 - two parallel

rewarded strings differing in length; T6 - two parallel strings of equal length, one string to a reward, the other with a gap between string and reward; and T7 - two parallel strings, where the shorter string was disconnected from the reward while the longer one was directly connected to the reward. All tasks measure the birds' capacity to understand causal relationships between objects but they differ in their complexity. The parallel string task is the simplest form while the spatial string configuration in the crossed strings task is assumed to be more complex. The broken string configuration requires the capacity to visually determine whether or not objects are physically connected. To keep birds motivated, we used as reward highly preferred half peanuts and grapes, which were not available outside the experimental context.

Tests were conducted in the same order for all subjects, i.e., all individuals were tested in the first task, then in the second, etc. In the social condition, all individuals were present during the tests. The birds could use the testing apparatus freely. Several identical sets of testing apparatus were presented at the same time, which allowed us to test several birds simultaneously. In all experimental tests, subjects were presented with ten trials per task. Trials ended when a subject reached the free end of a string (regardless of whether it had the reward attached to it or not) or after a predetermined maximum of 15 min, whichever came first. In all choice tasks, the colours and sides associated with the reward attached to the string were alternated randomly across trials. The distance between the strings was approximately twice the body length of the orange-winged amazons. The string that every bird first interacted with was scored as its choice in every trial. The choice was scored as 'correct' if the subject started with a pulling action at the rewarded string and reached the end of the string. All tests were video recorded for subsequent analysis of the birds' behaviour. The presence or absence of conspecifics – defined as sitting near the subject bird within a distance of the twice of the body length – while the subject in the social condition attempted the task was recorded. In addition, we noted attempts to displace a bird from the apparatus.

After all subjects had completed all patterned-string tasks, we presented the birds with a novel feeder (an opaque cup filled with grapes and peanuts). Each bird was faced with a novel feeder five times on five consecutive days. We used the

latency until feeding from a novel feeder as well as the latency until the first contact with the string in the first task (T1) as measures of the fearfulness of subjects.

Analysis

To assess the difference in the number of successfully solved patterned-string tasks between the two groups, we carried out a generalised linear mixed model (GLMM) using the package '*lme4*' (Bates et al. 2012) in R 2.15.2 (RDTTeam 2013) with 'individual' as random factor. The error structure was set as binomial for event data (success or no success) with logit link function and Gaussian (identity link function) for continuous variables (latency). To test whether the members of a group tended to choose the correct string more often than by chance, 1-sample *t* tests were used. The sample size was always specified as the number of individuals that participated in the tests.

In the social condition, the proportion of trials where conspecifics were present as the subject attempted the task and also where those conspecifics were competitive, i.e., displaced the focal bird, was compared between successful and unsuccessful attempts at the task using paired *t* test.

Results

A total of 1190 trials across the seven tasks performed by 17 birds were analysed. In the individual condition group, ten of the 23 birds entered the test room. Seven participated in the test, but only five completed all tasks. In the social condition, 15 of the 35 birds participated and twelve of them completed all tasks. All subjects that participated were able to successfully pull the rewarded single string (T1).

Figure 1 shows the number of correct choices in patterned-string tasks (T2-T7). There was no significant difference between the birds tested singly and those tested in a social context (Figure 1). There were also no significant differences between birds with and without experience in horizontal string task, either for each task tested individually or for the tasks 2-7 combined (one way ANOVA, in each case $P > 0.05$). Most subjects in both groups solved the parallel string task (T2). Interestingly, when comparing the correct choices at the group level, birds tested in the social context chose the correct string more often than singly tested birds. Both groups had difficulties selecting the correct string when the

strings were crossed (T3, T4; Figure 1). When faced with two parallel rewarded strings differing in their length (T5), the birds in both settings chose the shorter string significantly more often than by chance (1-sample t test; singly tested birds, $t = 5.11$, $df = 4$, $P = 0.008$, social group, $t = 3.09$, $df = 11$, $P = 0.002$). In the broken string configuration, the subjects chose correctly when the strings were of the same length (T6), but failed when the disconnected string was shorter (T7).

Successful and unsuccessful trials at each task were compared in terms of the proportion of attempts during which a conspecific sat near the subject animal and the proportion of attempts during which the subject animal was distracted by conspecifics. The presence of a conspecific sitting near the subject during a task did not influence the proportion of correct and incorrect trials (40 and 43 %, respectively; paired t test, $t = -1.567$, $df = 5$, $P = 0.18$). There was also no significant effect of displacement attempts by a con-

specific on correct versus incorrect trials (14 and 16 %, respectively; paired t test, $t = -2.381$, $df = 5$, $P = 0.07$).

Singly tested birds needed at least two 15-min sessions, while birds in social context required 3 min on average until they made first contact with the string in the first task (T1). This difference was significant (GLMM with individual as random factor, $\chi^2 = 6.62$, $df = 1$, $P < 0.001$)

Latency until feeding from unknown feeder

Figure 2 shows that the birds tested singly needed significantly longer to take the food from the novel object than those tested in social context (GLMM with individual as random factor, $\chi^2 = 15.04$, $df = 1$, $P < 0.001$). The birds tested singly showed a significant decrease in latencies between the first and the last trials (paired t test, $t = 2.633$, $df = 1$, $P = 0.033$, Figure 2), whereas the birds tested in the social context showed constantly short latencies.

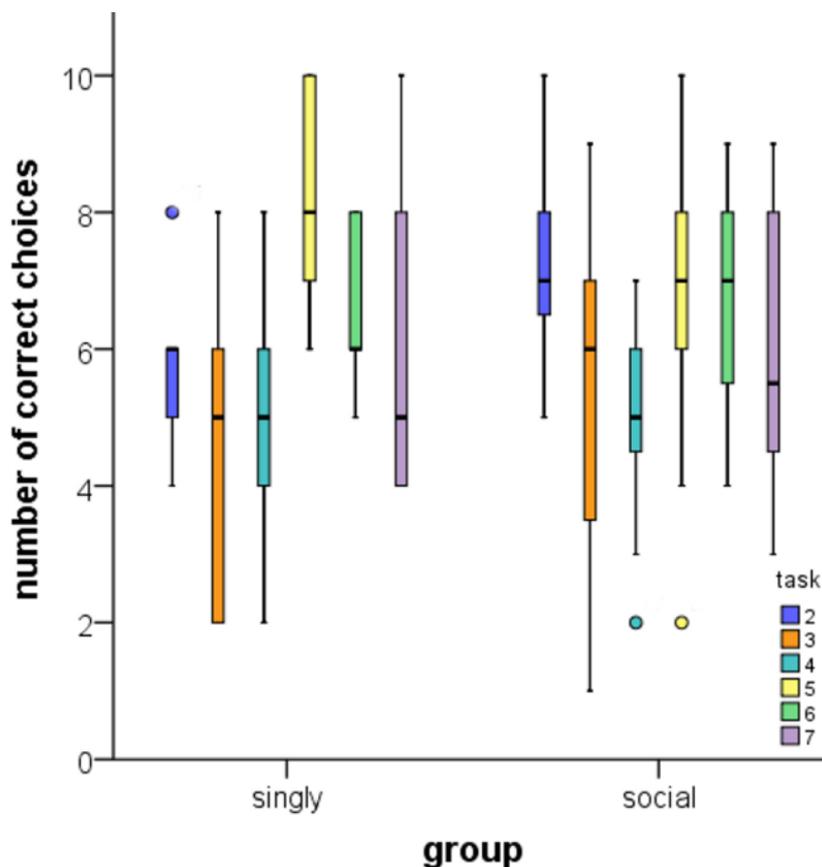


Figure 1: The number of correct choices in patterned-string tasks T2-T7 shown by individuals in both testing settings. The filled circles represent the outliers. T2: two parallel strings, T3: two crossed string of different colour, T4: two crossed strings of the same colour, T5: two parallel rewarded strings of different length, T6: two parallel string of the same length, one connected to reward and the other with a gap, and T7: the same as T6, but the disconnected string was shorter.

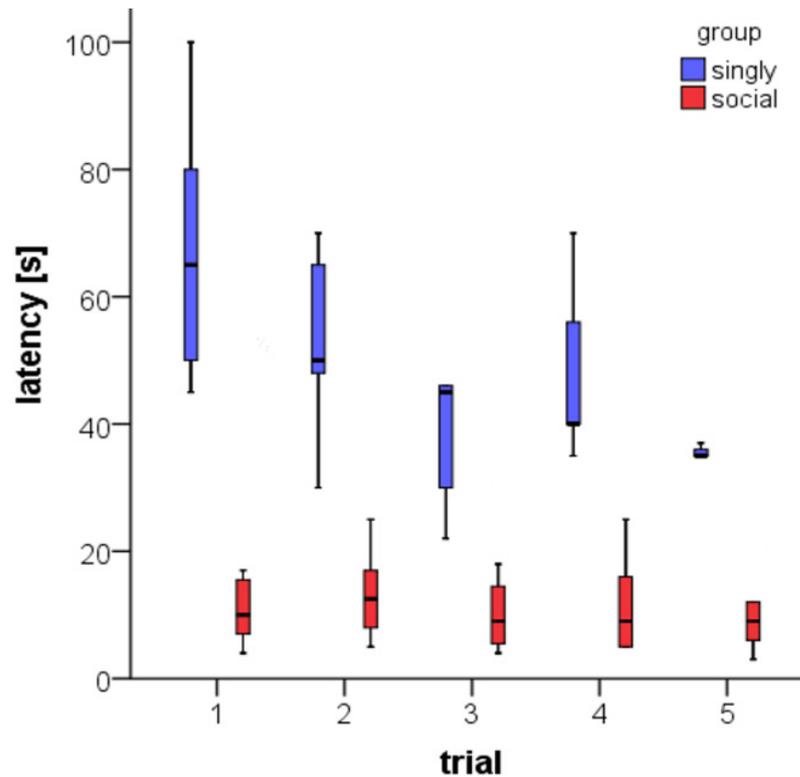


Figure 2: The latency until first feeding from a novel feeder shown by individuals in both testing settings across five trials.

Discussion

The testing environment (social versus non-social situation) had only minor influences on the overall performance of the parrots in patterned-string tasks. Birds in both testing conditions showed similar capacities in understanding causal relationships between objects although the birds in the group setting were slightly more successful in the parallel string task (T2). In the broken string configuration (T6), both groups could visually determine whether or not objects were physically connected. Birds of both groups failed to choose the longer, rewarded string instead of the short one (T7). Both groups also had great difficulties to recognise the spatial relationship between string and reward in the crossed-string configuration (T3, T4).

In summary, we found no evidence for the hypothesis that distraction by conspecifics may affect the performance accuracy. The slightly better performance in the group setting was restricted to the simplest patterned-string task, T2, and could not be explained by distraction. In all other tasks, no significant differences were found. Our results support evidence from primate studies that testing animals in problem-solving tasks in their social group produces similar results as obtained from singly tested animals [e.g. Gazes et al. (2012)].

However, we found striking differences in the willingness to participate in the tests between the two test situations. No subject tested singly approached the string within the first 15-min session, whereas the birds tested in a social context needed on average only a few minutes. These findings were confirmed by the novel feeder test, where the birds in the group were also quicker to approach an unknown opaque cup with food. Overall, singly tested individuals were much less willing to take food from the novel feeder, but their latency until feeding decreased over the trials.

Our data match findings from primate studies (Higley & Suomi 1989; Itoh 2001; Schneider et al. 2005) corroborating the notion that individually tested subjects showed a reduced willingness to participate in a test and that subjects' fearfulness level may be an important factor influencing their reaction to, and their accuracy in problem-solving tests (Toxopeus et al. 2005). Differences in subjects' fearfulness have also been shown to influence problem-solving performance in rodents (Ohl et al. 2003; Ohl et al. 2002) and humans (Eysenck 1985; Li et al. 2004).

A lower level of fearfulness in birds tested in a social context may be explained by social facilitation. The presence of group members may increase the frequencies of certain behaviours or

may even provoke behaviours that an individual would not perform at all if it was alone (Sherry & Galef 1990; Zajonc 1965). In zebra finches, the presence of conspecifics has been shown to facilitate exploration (Schuett & Dall 2009). The acceptance of novel food was assisted by the presence or action (handling or food intake) of a conspecific in both birds and mammals [for review see Stöwe and Kotrschal (2007)]. The crucial influence of the social context on the expression of key behaviour patterns has often been underestimated or even ignored in studies of animal behaviour (Galhardo et al. 2012; Ward 2012; Webster & Ward 2011).

While our data support the notion that animals tested within their social context can be feasible research subjects for problem-solving tasks, there are also some limitations of a social setting. In primate studies, the percentage of participating animals was much reduced in jointly tested subjects (Gazes et al. 2012) perhaps because low-ranked subjects are excluded from the experimental apparatus (Drea & Wallen 1999). Thus, a relatively slow rate of data acquisition combined with a relatively low percentage of animals participated may limit the efficiency of testing animals in social group settings (Gazes et al. 2012). However, no such effects have been observed in the present study.

Our study species showed an only slightly enhanced performance in cognitive tasks when tested in a group and revealed that socially housed parrots may show performance in problem-solving tests similar to that obtained in an individual setting. Our results also indicate

that careful consideration must be given to the differences in individual reaction to isolation and resulting differences in motivation, which may possibly even cause failures of singly tested animals, particularly when testing spontaneous problem-solving abilities. Moreover, particularly in highly neophobic species, the social group setting may provide advantages by decreasing the level of individual fearfulness and stress, resulting in higher willingness to participate in a test. Furthermore, testing problem-solving in highly social species in a social group setting is ecologically relevant. In the wild, such subjects must often deal with cognitive challenges under conditions of social competition. Thus, a social setting may produce results that better reflect natural behaviour of highly social species such as parrots. More such tests on other parrot species are desirable to see how general our findings are.

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Chapter 6

INDIVIDUAL DIFFERENCES IN COGNITIVE PARADIGMS
RELATE TO DIFFERENCES IN PERSONALITY

Individual differences in cognitive paradigms relate to differences in personality

Anastasia Krasheninnikova

Research in animal cognition generally reveals substantial variation in the performance of individuals and personality traits such as exploration tendency and timidness may be an important source of this variation. However, studies that connect personality with cognition are surprisingly rare. I used eight parrot species and tested, whether individual differences in the performance in three cognitive paradigms related to differences in personality. Consistent individual differences in exploration and timidness were found in a novel-object test and a novel-feeder test, respectively and correlated with individual cognitive differences in three string-pulling tasks with increasing complexity. While the proportion of correct choices in the simple parallel-string task did not relate to any measure of personality, explorative individuals were less accurate in the more complex tasks. This pattern consistently emerged across the eight species tested. My findings support the hypothesis that individual differences in cognition are related to differences in personality and further suggest that the effect of personality on cognitive performance might depend on the complexity of the task.

Keywords: Exploration, Cognition, Timidness, Parrots, Personality traits

Introduction

Recent work has revealed within-species variation in levels of aggressiveness, boldness, or exploration that are consistent across time and contexts (Sih et al. 2004). Such intra-specific differences in behaviours are referred to as animal personality (Gosling 2001), and are generally assumed to reflect differences in how individuals cope with changes in their socio-ecological environment (van Overveld & Matthysen 2010). In support of this hypothesis, associations between personality traits and fitness parameters such as behavioural flexibility (Dingemanse & Wolf 2013) and exploration of new environments (Groothuis & Carere 2005) have been found.

Research of animal cognition also revealed substantial differences in individual learning abilities that have been considered traditionally as non-meaningful noise (Wolf & Weissing 2012). Recent studies, however, highlighted the importance of taking into account personality traits in relation to cognitive performance (Dingemanse & Wolf 2010). Personality traits are an important source of variation that may affect cognitive performance. For example, individual differences in personality traits and the speed-accuracy trade-off might be linked to a variety of cognition states (Sih & Del Giudice 2012), i.e. individuals might be quick but inaccurate in their discrimination among options. Furthermore, an understanding of the effects of personality on cognition could be crucial as some individuals

might fail in a cognitive task simply because of their reluctance or inhibition to perform, not because of their actual inability (Carere & Locurto 2011). Finally, models about the evolution of cognition and of personalities may benefit from including variation in the respective traits (Houston & McNamara 1999; Wolf & Weissing 2010).

Not all personality traits may be connected to how animals solve cognitive tasks. However, one of the traits that may contribute to cognitive differences is exploration tendency. Exploration is the gathering of information about environment that does not satisfy immediate needs and is closely related to latent learning, i.e. information gathered once (e.g. profitable feeding sites) may be used much later. Indeed, differences found in exploration tendency are related to differences in learning or problem-solving (Coleman et al. 2005). Another trait that may affect cognitive performance is timidness as risk-averse individuals might have difficulties due to reduced cue utilization or attention span (Easterbrook 1959).

Parrots are extensively used in tasks testing problem-solving, including patterned string-tasks (Krasheninnikova et al. 2013; Schuck-Paim et al. 2009; Werdenich & Huber 2006). The patterned string task is a widely accepted test for problem-solving abilities and an ideal tool for comparative studies. It generally consists of two or more strings with a reward attached to the end of one of them that can only be obtained by pulling the correct string. The patterned string task provides

a reasonable analogue to a natural foraging situation in dense vegetation where the birds have not only to choose the right branch to pull but also attend to competitors and predators. Parrots not only show inter-individual variation in neophobia (Mettke-Hofmann et al. 2002), but it has been also found that in orange-winged amazons timidity predict attention bias (Cussen & Mench 2014). Being ecologically relevant the string-pulling task is thus a logical candidate for testing cognitive abilities which could be affected by personality differences. Here I tested eight parrot species using assessments of two personality traits, exploration tendency and timidity, in a novel-object test and a novel feeder test, respectively, in parallel with three string-pulling tasks.

Material & Methods

Subjects

I tested 88 individuals belonging to eight parrot species. The galahs (*Eolophus roseicapillus*), the cockatiels (*Nymphicus hollandicus*), and the rosy-faced lovebirds (*Agapornis roseicollis*) were kept at the Tierpark Gettorf, Germany. The greater vasa parrots (*Coracopsis vasa*), the eclectus parrots (*Eclectus roratus*), the monk parakeets (*Myiopsitta monachus*), the Senegal parrots (*Poicephalus senegalus*), and the orange-winged amazons (*Amazona amazonica*) were kept at the Parrot Zoo, UK (see Table S1 for a detailed description of the housing conditions).

Experimental set-up

Novel-object test

Exploration tendency as a predictor of the curiosity of the subjects was measured as latency to first contact with a novel object (a Rubik's cube and a small wooden ball) at a neutral location (distant from food, water, or the breeding box) in the familiar environment. The objects were presented on two consecutive days. The parrots could freely approach the novel object. Access to food was unlimited. The latencies towards both novel objects were measured for each individual once and the mean latency from both trials was used for the analysis.

Novel feeder test

Timidity as a predictor for risk-averse behaviour of the subjects was measured as the individual's latency to feed from a novel food

source (an opaque food container). Each bird was faced with a novel feeder five times on five consecutive days. The mean latency from the five repeated measurements was used for the analysis.

Cognitive performance

Cognitive performance was measured on the patterned-string tasks. Three string problems were presented: 1) single rewarded string (T1), 2) two parallel strings, with one string rewarded and the other not (T2), 3) two crossed strings, which were differently coloured to allow easier tracing of the strings (T3). Each subject was presented with 10 trials per task with two sessions per day, one in the morning (from 9 a.m.) and one in the afternoon (from 3 p.m.). Tests were presented in the same order for both species. The parallel string task was the simplest form while the spatial string configuration in the crossed strings task was assumed to be the most complex one.

Analysis

The sample size was 88 parrots for personality assessment and for cognitive tests. I used R 3.0.1 (RDTTeam 2013) for all data analyses. I tested whether performance in patterned-string tasks was influenced by exploration behaviour and fearfulness using an LMM (package lme4) with following fixed effects: "age" (adult/juvenile), "exploration tendency", and "timidity". Effect of significance was tested by dropping terms individually from the full model, and non-significant terms were removed via backwards elimination. The random term "species" was included in all mixed models. The relationship between personality and cognitive performance for each species was estimated using Pearson's correlations.

Results

Each subject successfully pulled the single rewarded string. However, the subjects of each species differed in the latencies until first contact with the string (Figure 1). Explorative individuals showed a shorter latency until the first contact with the string in the single rewarded task (LMM, $t = 20.439$, $df = 72$, $P < 0.0001$). More or less timid animals did not behave differently in the string pulling task (LMM, $t = 0.409$, $df = 72$, $P = 0.68$). Exploration tendency and timidity were not correlated with each other. For individual differences in exploration tendency and timidity see Figure S1ab.

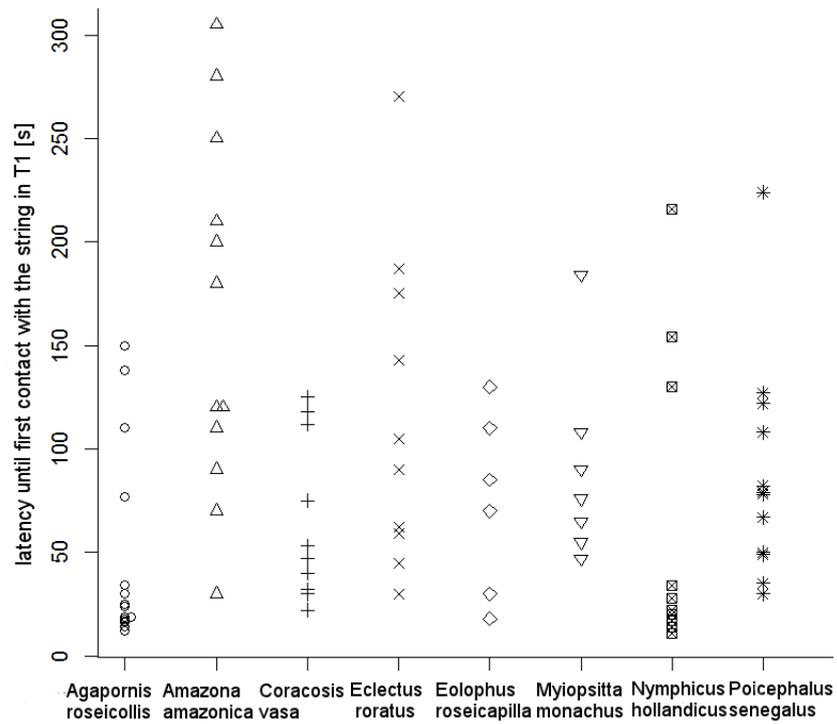


Figure 1: Variation in latency to first contact with the experimental device in T1 among individuals of different species

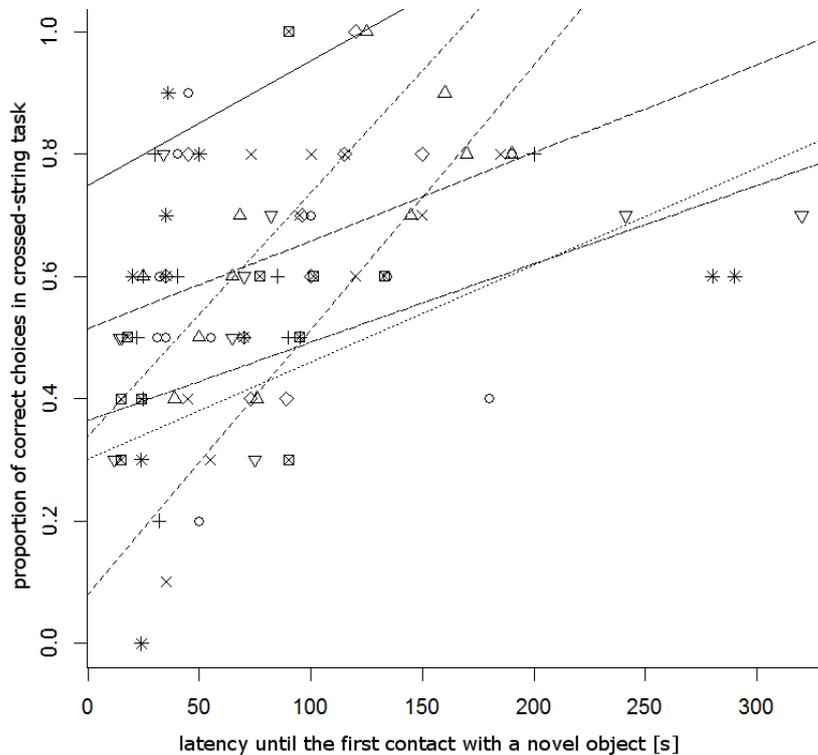


Figure 2: Correlation between exploration tendency and the proportion of correct choices in the crossed-string task (T3). *Agapornis roseicollis* – circle, dashed line; *Amazona amazonica* - triangle point up, solid line; *Coracopsis vasa* - plus, twodashed line; *Electus roratus* - cross, dotted line; *Eolophus roseicapillus* - diamond, dotdashed line; *Myiopsitta monachus* – triangle point down, longdashed line; *Nymphicus hollandicus* - square cross, gray dashed line; *Poicephalus senegalus* – star, grey solid line

I found individual differences in the proportion of correct choices in both patterned-string tasks across all species (Figure S2ab). While the proportion of correct choices in the parallel-string task (T2) was neither correlated with exploration tendency nor with timidity, performance in the crossed string task (T3) correlated positively with the exploration tendency (LMM, $t = 8.075$, $df = 72$, $P < 0.0001$, Figure 2), but not correlated with the timidity of the subjects (LMM, $t = -0.293$, $df = 72$, $P = 0.77$). Remarkably, this pattern consistently emerged across the eight species tested (Table 1).

Tab.1: Pearson correlation between the exploration tendency (measured as the mean latency to first approach of a novel object) and the proportion of correct trials in the crossed-string task (T3) for each species tested

Species	df	r	P-value
<i>Agapornis roseicollis</i>	13	0.756	<0.001
<i>Amazona amazonica</i>	10	0.555	0.061
<i>Coracopsis vasa</i>	8	0.797	0.006
<i>Eclactus roratus</i>	8	0.855	0.001
<i>Eolophus roseicapilla</i>	4	0.906	0.013
<i>Myiopsitta monachus</i>	5	0.901	0.006
<i>Nymphicus hollandicus</i>	8	0.899	<0.001
<i>Poicephalus senegalus</i>	10	0.904	<0.001

Discussion

The findings of the present study provide experimental support for a proposed relationship (Carere & Locurto 2011; Sih & Del Giudice 2012) between individual differences in cognitive performance and differences in personality within eight parrot species. The results further suggest that the effect of personality on the success in a cognitive task might depend on the complexity of the task. I found that less exploratory parrots chose the correct string more frequently in a more complex cognitive task. However, in the simple parallel-string task there was no effect of exploration tendency on the proportion of correct choices. Fast-exploring individuals were also quicker to try a new experiment device as measured by the latency until first approach the string in the single-string task showing consistency in exploratory behaviour across different contexts.

Such an effect of personality on the success in a cognitive task depending on the complexity of the task is consistent with the idea of a speed-accuracy trade-off in cognitive processes (Chittka et al. 2009). For example, some individuals might be consistently slower or more careful about how they collect and assess information than others (Sih & Del Giudice 2012). In contrast, faster explorers encounter new stimuli more quickly, compared to individuals that are less exploratory, but might be inaccurate in their discrimination among options (Verbeek et al. 1994).

Exploratory as a personality trait is related to learning speed in specific tasks (Dingemanse & Réale 2005). This relationship is supported by evidence from several studies with diverse species and learning tasks (Coleman et al. 2005; Sneddon 2003). In problem-solving tasks, however, which require understanding of relationships between objects rather than simply associative learning, more accurate information acquisition may be beneficial. Thus individuals that are more careful in the assessment of information are likely to perform in discrimination tasks more accurately than fast explorers (Carere & Locurto 2011). In the present study, crossed-strings require a higher degree of attention and accuracy than parallel strings, where it is easier to detect which string is the rewarded one. Thus, it is not surprising that fast-exploring birds being less accurate, failed to discriminate the correct option in the crossed-string paradigm.

There was no relation between the cognitive performance and the timidity of subjects. This finding is consistent with that of a previous study on differences between individual testing and social group setting showing that singly-tested orange-winged amazons were more timid when compared to birds tested in a group, but did not differ in their cognitive performance (Krasheninnikova & Schneider 2014). However, individual differences in timidity must be considered carefully as they may affect how individuals respond to novel situations such as an experimental device (Fox & Millam 2007).

In summary, this study supports the hypothesized relationship between individual differences in cognitive performance and personality, and presents the first evidence for the consistency of such a relation across different species.

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Supplementary Material

Table S1: Housing conditions

Tierpark Gettorf, Germany
For housing conditions of the galahs and cockatiels see Krashennikova (2013).
The rosy-faced lovebirds were kept together with Reeves's pheasant (<i>Syrnaticus reevesii</i>) in an outdoor aviary (10 x 2.5 x 3 m) with an (11 x 1.6 x 2.5 m) at Tierpark Gettorf, Germany. The group contained 22 lovebirds (15 adults, 7 juveniles). Birds were fed every day between 9 a.m. and 11 a.m. with mixture of different fruits and seeds. Water was available <i>ad libitum</i> and vitamins were given twice a week. The aviary was provided with several trees, branches and trunks. Seven rosy-faced lovebirds showed no interest and did not approach the string-pulling apparatus, thus they were excluded from the analysis. No subject has had contact with string-like objects or was trained on any object-pulling task prior to present experiments. The animal care during the study was continued by the zoo keepers. The daily feeding conditions were equated. The experiments reported were integrated as part of the regular animal welfare activities into the daily routine. After the study all tested birds were left in their flock.
The Parrot Zoo
For housing conditions of the orange-winged amazons (<i>Amazona amazonica</i>) see Krashennikova and Schneider 2014.
The group of great vasa parrots (<i>Coracopsis vasa</i>) consisted of 10 birds (5 males, 5 females) and was kept together with one smaller vasa parrot (<i>Coracopsis nigra</i>) in an outdoor aviary (4 x 4 x 4m) with an adjacent indoor aviary (2 x 2 x 2m). After the finish of the string-pulling experiments the birds were moved to other aviary. After an acclimatization period of one week the birds were tested in personality tests. The outdoor aviaries were provided with several trees, branches and trunks.
For the experiments the eclectus parrots, the Senegal parrots, and the monk parakeets were moved consecutively from their home aviaries to a test outdoor aviary (6 x 2.5 x 2m) with an adjacent indoor aviary (1 x 2 x 1m). After the experiments the individuals were moved to other aviaries.
The birds at The Parrot Zoo were provided with a seed mix in the morning and with fresh fruits in the afternoon also on experimental days. Water was available <i>ad libitum</i> . The outdoor aviaries were provided with several trees, branches and trunks. No artificial toys, only green branches for playing and nibbling, were provided regularly. All subjects could be recognized individually at all times during the experimental sessions. Some subjects (e.g. some individuals of orange-winged amazons) kept at The Parrot Zoo, UK, came from private owners, so that the individual history of these subjects was unknown. After the study all tested birds of all study species were left in their flock.

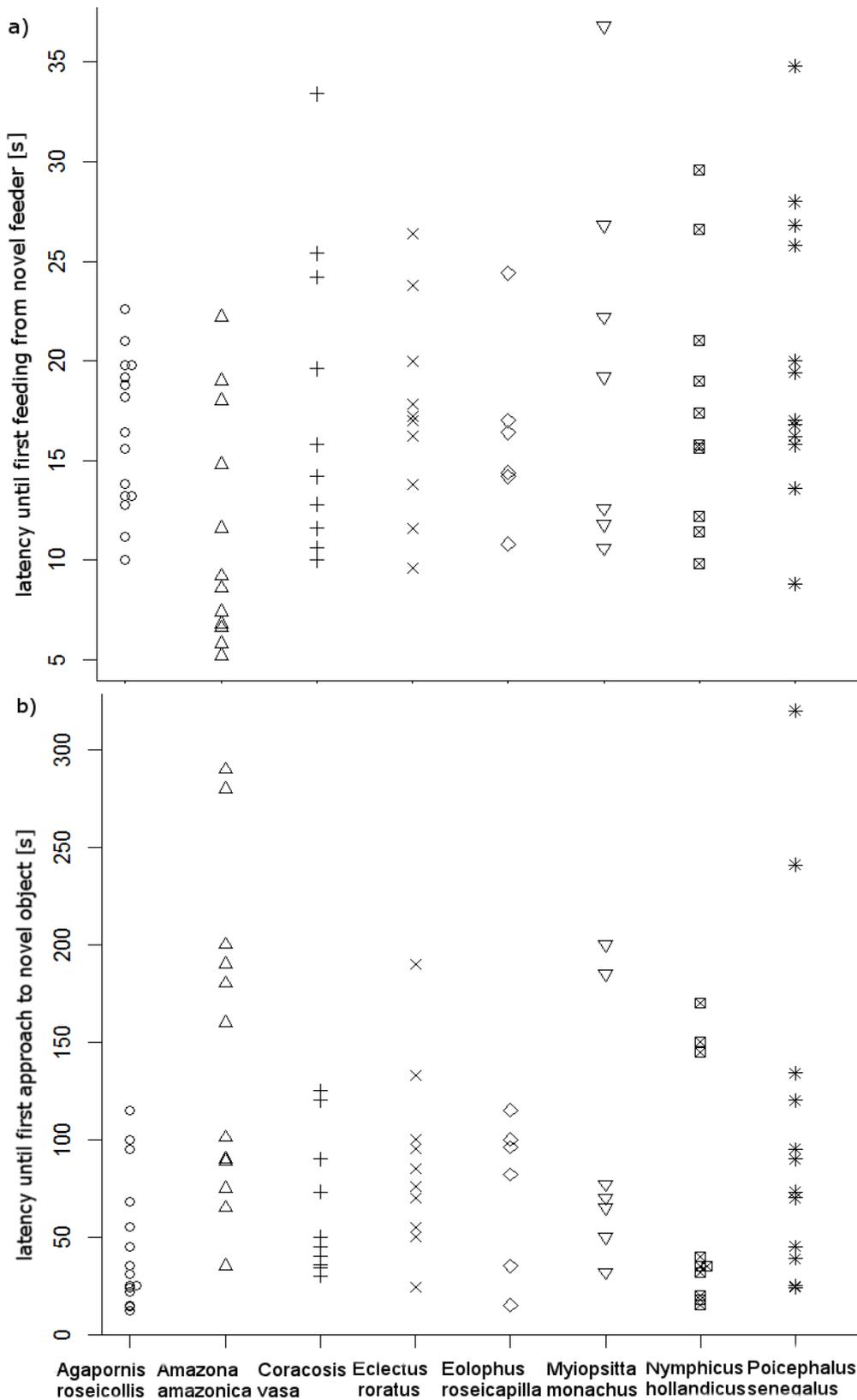


Figure S1: Individual differences in **a)** – timidity (novel-feeder test), and **b)** – exploration tendency (novel-object test) for each species

GENERAL DISCUSSION

The aim of this thesis was to test hypotheses on the evolution of specific cognitive abilities in the domain of physical cognition using the string-pulling paradigm in the parrot as model organism. Despite considerable variation between species, more closely related species do not exhibit more similar cognitive skills. Instead, the variation in performance during patterned-string tasks is largely explained by social components of the species' living conditions, thus providing the first empirical evidence for the domain-general nature of the cognitive challenges of living in a complex social environment. Furthermore, I demonstrate the influence of personality as well as of the social context on an individual's response when solving problems.

Cognitive phylogeny

Phylogeny is an important explanatory principle for understanding shared characteristics among taxa (Di Fiore & Rendall 1994). The first step when testing an evolutionary hypothesis is, thus, to test how strongly phylogenetic relatedness predicts the distribution of a trait across species (Harvey & Pagel 1991). In chapter 1, I show that the phylogenetic relatedness did not predict the performance either in the crossed-string or in the broken-string configuration, despite the fact that the anatomical proxy for cognitive abilities showed phylogenetic dependence. The findings are in agreement with a previous study of string-pulling in parrots showing no evidence for phylogenetic patterns (Krasheninnikova et al. 2013).

Moreover, a recent meta-analysis on various experimental paradigms showed that closely related species were not similar in their performance on object permanence, mirror self-recognition or causal reasoning (Thornton & Lukas 2012). MacLean et al. (2012) also found no evidence for an association between inhibitory control and phylogeny in primates. In contrast, (Brown & Magat 2011) showed that in Australian parrots, physiological traits such as the pattern and the strength of laterality were strongly associated with phylogeny. This is in accordance with findings demonstrating that ecological and behavioural traits generally tend to show a low dependency on phylogeny compared to morpho-

logical or physiological traits [(Blomberg et al. 2003; Kamilar & Cooper 2013), but see also Thierry et al. (2008); Thierry et al. (2000)].

Correlated evolution

The lack of phylogenetic patterns suggests that environmental factors, such as social or ecological selective forces (Byrne 1997; Dunbar & Shultz 2007; Milton 1981), might have influenced the evolution of cognitive traits independently from phylogeny [Chapter 1, MacLean et al. (2012)]. In chapter 2, I showed that variation in the performance in patterned-string tasks can be explained better by differences in a species' social environment than by ecological or morphological traits. This finding is in agreement with a previous study comparing the performance in patterned-string tasks across four parrot species (Krasheninnikova et al. 2013). The influence of group living on cognitive skills can be domain-specific (Gigerenzer 1997), i.e., a complex social environment is suggested to lead to selection for cognitive skills that are specific to social living. Studies of lemurs (MacLean et al. 2008; MacLean et al. 2013) which show a link between group size and social cognition support this domain-specific view. In contrast, the domain-general view asserts that any cognitive changes favoured by group-living should be similar for both social and non-social cognition (Reader et al. 2011). Tentative support for this view is given by a study of corvids which showed that highly social species possessed enhanced transitive reasoning in non-social domains compared to their less social relatives (Bond et al. 2003).

However, all previous studies have focussed on the pair-wise comparison of closely related species living in social groups of differing size to test the prediction of one of the evolutionary hypotheses (Krasheninnikova et al. 2013; MacLean et al. 2013; Rosati et al. 2014). A quantitative examination of the relationship between a direct measure of physical cognition and several explanatory variables is lacking. Chapter 2 of this thesis reveals a link between social complexity and cognition. It also provides first empirical evidence for the domain-general

nature of cognitive challenges imposed by living in a complex social environment.

Motor skills

Although less investigated in comparative studies of physical cognition so far, different species and different individuals have different anatomical and psychological prerequisites for successful problem-solving (Stevens 2010). In chapter 3, I showed both inter- and intraspecific differences in techniques used to solve the string-pulling problem that clearly differed in the extent of manipulative skills required. In contrast to previous findings for parrots (Magat & Brown 2009), I found no evidence that differences in manipulative skills result in differences in the ability to pull a string (chapter 3). This result is in agreement with other studies on string-pulling in birds which show that some individuals that use their feet when feeding may fail to pull a string successfully (Seibt & Wickler 2006, Vince 1956), whereas others were able to pull the string without using their feet when feeding (Thorpe, 1963). Although the use of feet during feeding appears to be a useful trait for predicting string-pulling performance in birds, it clearly is neither sufficient nor essential.

A possibility widely discussed in the literature is that of an interrelation between cognitive and motor skills is manifested in brain structures (Paulin 1993, Petrosini et al 1998, Spence et al 2009). Indeed, when tested for their visual-spatial skills in patterned-string problems, the species that rely on fine beak-foot-coordination during feeding outperformed those that do not use their feet to manipulate food items (chapter 3). This pattern was also found on the individual level in both species: birds with higher motor abilities performed better in patterned-string tasks. In chapter 3, I found support for the hypothesis that the fine motor skills needed for advanced beak-foot coordination may be inter-related with certain visual-spatial abilities needed for solving patterned-string tasks. This study provides the first evidence for an interrelation between visual-spatial and motor abilities in a non-mammalian animal.

Inhibition

A failure in a task requiring a choice between two or more options might be caused by the lack of inhibitory control (Liedtke et al. 2011). Indeed, in chapter 4, I showed that in a means-end task configuration facilitating inhibition, green-winged

macaws controlled their pulling behaviour and switched from the incorrect option to the correct one more easily. However, I found no support for the hypothesis that increased inhibitory control would improve performance in a physical cognition task.

The overall poor performance in means-end paradigms shown by green-winged macaws is in accordance with previous findings for this species that appears to have a poor understanding of relationships between objects (Krasheninnikova et al 2013). The findings imply that a large brain, as possessed by this species, is not necessarily connected to an enhanced understanding in the domain of physical cognition. This interpretation is supported by comparative analyses in primates which show that small-brained species often outperform their larger-brained relatives (Johnson et al. 2002; Reader et al. 2011). Another possible reason for the poor performance observed in different experimental paradigms might be the inability of green-winged macaws to focus on cognitive tasks while coping with their natural social environment (Cronin et al. 2014; Drea & Wallen 1999). However, this inability might be species-specific, as shown in chapter 5.

Testing conditions

Ecological relevance of experimental designs has often been thought to be lacking in physical cognition studies (Cook 1993). Testing in a social context is ecologically relevant for social animals such as primates and parrots - which often serve as model organisms for comparative cognition - because in the wild, individuals face cognitive challenges under conditions of social competition. The need to deal with social competition might affect individuals' performance in an experimental paradigm (chapter 4, Galhardo et al. 2012). In chapter 5, however, I found no evidence for the hypothesis that distraction by conspecifics affects performance accuracy. Singly-tested parrots and those tested in social context showed similar abilities in patterned-string task. This finding is in agreement with Gazes et al (2012) who showed that primates tested in social groups produced similar results in problem-solving tasks to singly-tested animals. Other studies on primates, however, showed that distractions by conspecifics negatively affected the subjects' performance (Halsey et al 2006, Cronin et al 2014). A possible explanation for inconsistent findings across species might be the different experimental paradigms used in the different

studies. This interpretation is supported by the fact that tasks of different complexity require different levels of attention division between social competition and obtaining the reward (Halsey et al 2006).

However, social context affects the subject's willingness to participate in the test by reducing its habituation time to a novel situation (chapter 5). The individuals tested in a social context approached the experimental device significantly faster than singly-tested birds. The data match findings from other studies on social facilitation. The presence of group members may increase the frequencies of certain behaviours, or may even provoke behaviours that an individual would not perform at all if it was alone (Schuett & Dall 2009, Sherry & Galef 1990, Toxopeus et al 2005, Zajonc 1965). Altogether, my findings imply that, particularly in highly neophobic species, the social group setting may provide advantages by decreasing the level of individual fearfulness and stress, resulting in a higher willingness to participate in a test.

Personality

Striking individual variability always occurs on experiments of animal cognition. However, the causes of this variation have rarely been considered and its potential consequences largely ignored (Thornton & Lukas 2012). Several authors recently proposed a hypothesized link between individual variation in cognitive performance and personality traits (Carere & Locurto 2011, Sih & Del Giudice 2012). Very recent studies have already shown that personality predicts an attention bias in psittacines (Cussen & Mench 2014). However, the study presented in chapter 6 is the first, to my knowledge, to provide empirical evidence that personality traits such as explorative tendencies are linked to individual differences in problem-solving ability.

I also found that the effect of personality on the success in a cognitive task might depend on the complexity of the task. While success in the simple parallel-string configuration did not relate to any measure of personality, explorative individuals were less accurate in a more complex string pattern - a pattern that consistently emerged across the eight species tested (chapter 6). This finding is congruent with the idea that some individuals might be slower or more careful about how they collect and assess information

than others. In contrast, faster explorers encounter new stimuli more quickly than less exploratory individuals, but might be inaccurate in their discrimination among options (Chittka et al 2009, Verbeek et al 1994). In accordance with this idea, more accurate information acquisition in less exploratory individuals may be beneficial in more complex physical problems. The lack of a relation between the cognitive performance and the timidity of subjects is in agreement with the fact that singly-tested individuals were more timid than birds tested in a group, but did not differ in their cognitive performance (chapter 5). However, individual differences in personality traits may also determine whether social a context facilitates or hinders an individual's performance in an experimental setting (chapter 4, chapter 5).

Conclusions

In my thesis, I focused on physical cognition, its evolutionary mechanisms, and factors which influence physical cognition in parrots. There may be good evidence, however, that some of the findings may be applied to other taxa such as corvids, primates and cetaceans. Therefore, my findings provide further support for the convergent evolution of cognition in these distantly related animal groups. An intriguing question arising from these findings is: What exactly are the cognitive demands of living in groups with a high fission-fusion dynamics and how might these cognitive challenges affect cognitive performance even in non-social contexts?

Furthermore, the results obtained in this thesis revealed that animals tested within their social context can be useful research subjects for problem-solving tasks. Social context does not affect cognitive performance, but rather reflects the natural behaviour of highly social species such as parrots, primates, corvids, dolphins and elephants. I also showed that careful consideration must be given to the differences in individual reactions to isolation and the resulting differences in motivation, which may contribute to explaining the failures of singly-tested animals in previous studies. Moreover, differences in personality may also determine whether social context facilitates or delays exploratory behaviour. Therefore, the effects of animal personality must be carefully considered in future studies.

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AUTHOR CONTRIBUTIONS

Chapter 1

Conceived and designed the experiments: AK, JS

Performed the experiments: AK, UB

Analysed the data: AK, UB

Wrote the manuscript: AK

Chapter 2

Conceived and designed the experiments: AK

Performed the experiments: AK

Analysed the data: AK

Wrote the manuscript: AK

Chapter 3

Conceived and designed the experiments: AK

Performed the experiments: AK

Analysed the data: AK

Wrote the manuscript: AK

Chapter 4

Conceived and designed the experiments: JL

Performed the experiments: SB, JVD, BW

Analysed the data: SB, JVD, BW, AK, JL

Wrote the manuscript: AK, JL

Chapter 5

Conceived and designed the experiments: AK, JS

Performed the experiments: AK

Analysed the data: AK

Wrote the manuscript: AK

Chapter 6

Conceived and designed the experiments: AK

Performed the experiments: AK

Analysed the data: AK

Wrote the manuscript: AK
