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Gaze following and play as windows to social cognition in dinosaurs

Zeiträg, Claudia

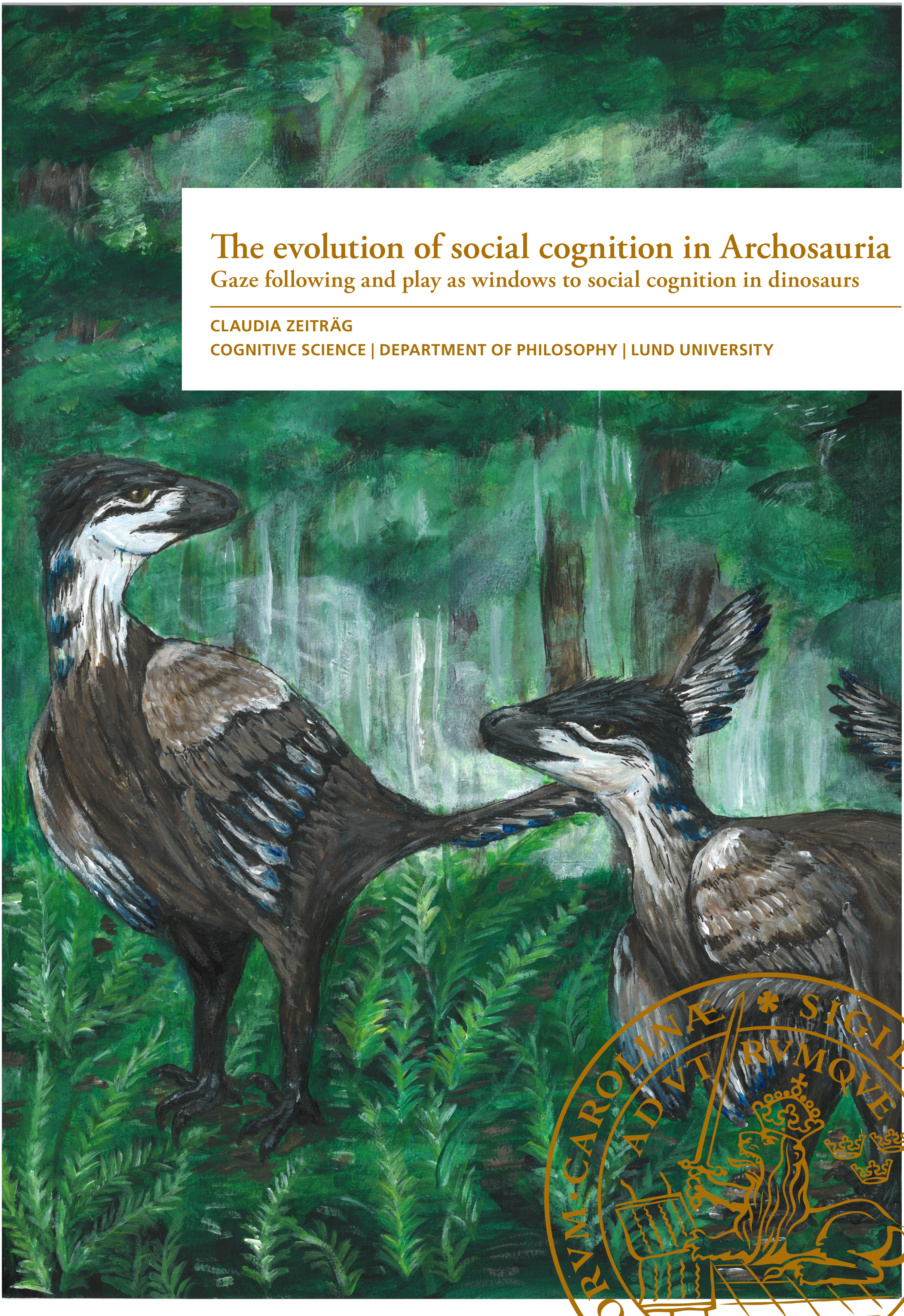
2022

Document Version:
Early version, also known as pre-print

Link to publication

Citation for published version (APA):
Zeiträg, C. (2022). *The evolution of social cognition in Archosauria: Gaze following and play as windows to social cognition in dinosaurs*. [Doctoral Thesis (compilation), Department of Philosophy]. Lund University (Media-Tryck).

Total number of authors:
1



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Gaze following and play as windows to social cognition in dinosaurs

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COGNITIVE SCIENCE | DEPARTMENT OF PHILOSOPHY | LUND UNIVERSITY

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Claudia Zeiträg

DOCTORAL DISSERTATION

Doctoral dissertation for the degree of Doctor of Philosophy (PhD) at the Joint Faculties of Humanities and Theology at Lund University to be publicly defended on 25th of November at 10.00 in the Upper Auditorium at LUX, Department of Philosophy, Helgonavägen 3, 223 62 Lund

Faculty opponent
Anna Wilkinson

Organization LUND UNIVERSITY	**Document name** Doctoral dissertation
	Date of issue 25th of November 2022
Author(s) Claudia Zeiträg	Sponsoring organization

Title and subtitle The evolution of social cognition in Archosauria – Gaze following and play as windows to social cognition in dinosaurs

Abstract

Social cognition entails all cognitive processes involved in social interactions. To study the evolution of social cognition, it is crucial to investigate several distantly related lineages. Studies in comparative cognition have traditionally been biased towards primates and a few social mammalian species, limiting evolutionary interpretations to few and closely related lineages.

To obtain a better understanding of the evolution of social cognition in the avian lineage, this thesis investigates species phylogenetically bracketing the lineage of dinosaurs from which the birds derived. Crocodylians and modern birds form the clade Archosauria that also comprises the extinct dinosaurs. Through studying socio-cognitive capacities in extant archosaurs, it is possible to draw inferences on the social cognition of non-avian dinosaurs. In this light, two topics are covered in this thesis: gaze following and play.

We found shared low-level gaze following skills in birds and alligators, while only birds demonstrated visual perspective taking. The more sophisticated gaze following repertoire of birds is likely caused by their dramatic increase of neurons in the cerebellum. This structure has been proposed to be involved in the formation of so-called internal forward models that allow for the formation of social predictions. We moreover studied the development of gaze following skills in ravens and found an extraordinarily early ontogenetic onset of such predictive capacities.

Furthermore, we regarded socio-cognitive skills and their development through the lense of play. We studied play behaviours of greater rheas and found a pronounced aspect of sociality in their play repertoire early in their ontogeny.

Finally, we used our findings to hypothesize about social cognition in extinct dinosaurs. Our findings are indicative of an earlier evolution of visual perspective taking in dinosaurs than in mammals. This is probably linked to the evolution of refined visual senses in this lineage. Non-avian paravian dinosaurs likely followed each other's gazes and might have been capable of generating social predictions based on observed gaze. Moreover, they most likely played, and their play probably contained a pronounced aspect of sociality. Taken together, the findings of this thesis suggest that non-avian paravians possessed a variety of socio-cognitive skills surpassing those of mammals living at the same time.

Key words social cognition, evolution of cognition, gaze following, play, development, dinosaurs

Classification system and/or index terms (if any)		
Supplementary bibliographical information		**Language** English
ISSN and key title 1101-8453 Lund University Cognitive Studies 184		**ISBN** 978-91-89415-45-4 (print) 978-91-89415-46-1 (digital)
Recipient's notes	**Number of pages** 82	Price
	Security classification	

Signature

Date 2022-10-28

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UNIVERSITY

Cover illustration by Sofia Haley
Back cover photos by Ivo Jacobs and Helena Osvath

Joint Faculties of Humanities and Theology
Department of Philosophy

ISBN 978-91-89415-45-4 (print)
ISBN 978-91-89415-46-1 (digital)
ISSN 1101-8453
Lund University Cognitive Studies 184

Printed in Sweden by Media-Tryck, Lund University
Lund 2022

NORDIC SWAN ECOLABEL
Printed matter
3041 0903
Media-Tryck is a Nordic Swan Ecolabel certified provider of printed material. Read more about our environmental work at www.mediatryck.lu.se
MADE IN SWEDEN

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Acknowledgements

This thesis would not have been possible without the support of a number of people. I would like to start by thanking my supervisor Mathias Osvath. First off, for giving me the opportunity to pursue my PhD and welcoming me to the Cognitive Zoology group. And moreover, for his project ideas, scientific discussions, and relentless reading of my manuscript attempts. Thank you for not losing your patience when manuscript version 500 landed in your inbox. You have truly shaped the way I think about evolution, cognition, and scientific writing.

Secondly, I want to thank Stephan Reber for teaching me (almost) everything I know about alligators and crocodiles in general. Thank you for the help with my data collection, the tips and tricks on my statistical analyses, your time as my secondary supervisor, the field work in the US, and co-teaching our course on crocodylian cognition.

Another big thank you goes to my second secondary supervisor, Steve Brusatte, for his input on my manuscripts and his corrections on palaeontological statements. I also want to thank you for always having encouraging words about my work.

Further, I would like to thank Helena Osvath for the hours she invested trying to convince baby birds to cooperate with me, for beautifying my scientific illustrations, and for the constant supply of good mood.

Next on my list is Thomas Rejsenhus Jensen who – after two years of being a single child/PhD student in the group – became my PhD cohort. Thank you for the collaboration on several projects and the exchanges about life as a PhD student.

Thank you also to Ivo Jacobs for his help with my data collection, his endless knowledge of useful references, his contribution of cute animal photos, and the constant supply of dad jokes.

With that, I would like to thank the rest of the Cognitive Zoology group: Can Kabadayi and Thibault Bohely, both of whom I didn't get the opportunity to directly work with, but that have contributed to a pleasant atmosphere in the group.

My data collection would not have been possible without the hard work and dedication of a number of people that I will, for the sake of simplicity, list alphabetically: Nina Thierij, Mark Kernkamp, Mathias Andersson, Morgan Luce, and Simon Grendeus. You are the real heroes here. I could not have done it without you. Thank you for sweating in the alligator house, freezing in the icy winds of Ystad, endless car rides to remote animal facilities, discussing experimental ideas, and for repeating trials over and over with me.

Further, I would like to thank Sofia Haley for providing the beautiful artwork on the cover of this thesis. Moreover, thank you for the practical help on several of my research projects and for being a good friend over the years. It's been a wild couple of years for both of us. Thank you for sticking it out with me.

Another warm thank you goes to everyone at the Department of Philosophy and Cognitive Science. Thank you for welcoming me into the group, for interesting discussions and seminars, fun retreats, and administrative help.

None of my studies would have been possible without our animal research subjects. Thank you for the (more or less) cooperation, for not eating me (though some might have tried), and for providing me with the most fun part of this research – the hands-on work with animals. Involved in this thesis were six American alligators (Bestla, Ivar, Kåra, Toke, Siggi, and Gudrun), six emus (Snow, Tufty, Harry, Alberta, Crowned, and Uncrowned), six greater rheas (Nox, Hamilton, Yvette, Arroz, Lucia, and Salsa), six red junglefowl (Rooster, Red, Pink, Yellow, Green, and White), six elegant-crested tinamous (Pretty Boy, Jon Snow, Sandy, New Tinamou, Alicia, and Sleepy Genius), and four raven chicks (Baby Red, Blue, Conrad, and Indie). Thank you all, it was my pleasure to work together.

Last but not least, I would like to thank my family and friends. My mother, who always believed in me and my stubbornness to pursue this career. My brother who taught me to stand my ground from an early age. My friends that always had an open ear for my complaints and were ready to celebrate my successes. And finally, Ray; the love of my life. I could not have done this without you. I can't wait for our future together.

List of original papers

PAPER I:

Zeiträg, C, Reber, S.A., Osvath, M. (submitted): Gaze-following in Archosauria – alligators and palaeognath birds suggest dinosaur origin of visual perspective taking.

PAPER II:

Zeiträg, C., Jensen, T.R., Osvath, M. (in review): Gaze following: A socio-cognitive skill rooted in deep time.

PAPER III:

Zeiträg, C., Osvath, M. (submitted): Differential responses to con- and allospecific visual cues in juvenile ravens (*Corvus corax*): The ontogeny of gaze following and social predictions.

PAPER IV:

Zeiträg, C., Jensen, T.R., Osvath, M. (accepted): Play in juvenile greater rheas – Different modes and their evolutionary and socio-cognitive implications.

1 Introduction

Just imagine standing in a crowd at St Mark's square in Venice. You are queuing together with hundreds of other tourists to be let into the famous Basilica. Suddenly, the person in front of you lifts their head and starts to scan the sky. What will you do? Most likely, and without thinking about it, you will copy the movement and start looking up yourself.

This phenomenon is called *gaze following* – a socio-cognitive skill central to this thesis. The focus, however, will not lie on human gaze following, even though we are skilled gaze followers. This thesis concerns gaze following in non-human animals (hereafter "animals").

In the last decades, many animal species have proven their skills in gaze following experiments, ranging from chimpanzees to lizards (e.g. Povinelli & Eddy, 1996; Simpson & O'Hara, 2019). However, these studies have primarily described gaze following skills of one or few closely related species. Moreover, like most studies in animal cognition, gaze following experiments have traditionally focused on our own closest relatives, the non-human primates, and few other social mammalian species. This led to a sound understanding of the distribution of gaze following in some lineages, while others have been left unexplored for the most part. By largely disregarding some taxa, we are left with a patchy understanding of the evolution of this fundamental socio-cognitive skill. To better grasp the evolutionary roots of gaze following, and the evolution of social cognition in general, it is crucial to study it in distantly related lineages.

When thinking about animals exhibiting complex cognition, primates come to mind naturally. However, the field of comparative psychology by now commonly acknowledges that at least some bird species, such as corvids and parrots, exhibit striking cognitive capacities, paralleling great apes in several domains (e.g. Emery & Clayton, 2004; Seed et al., 2009; Kabadayi & Osvath, 2017; Pika et al., 2020).

What is remarkable about these cognitive parallels is the fact that the lineages leading to modern mammals (Synapsida) and birds (Sauropsida) split around 325 million years ago (Ford & Benson, 2020) and have during that period evolved vastly differing neuroanatomies. Nevertheless, both ended up with comparable cognitive skillsets. It is through studying representatives of distantly related lineages, such as mammals and birds, that we can gain an understanding of the evolutionary pressures and patterns shaping complex cognition.

Birds are, however, also interesting for a different reason. They are living dinosaurs. Accordingly, through studying social cognition in birds, we can peer through a window to the cognition of non-avian dinosaurs (hereafter "dinosaurs"). This allows for even deeper insights into the cognitive evolution of birds.

Palaeontologists have been fascinated with the social lives of dinosaurs ever since the first discovery of an accumulation of 31 *Iguanodon* skeletons in 1878. This was the first indication of herding behaviour in these creatures and sparked interest in the topic of sociality in dinosaurs. By now, evidence of gregariousness in dinosaurs has been well established through communal bonebeds (e.g. Funston et al., 2016), trackways (e.g. Lockley & Matsukawa, 1999) and nesting sites (e.g. Horner & Makela, 1979). However, this evidence is exclusively based on trace records that fail to provide insights into dinosaurs' cognitive abilities to navigate their social lives.

By studying fundamental socio-cognitive skills, such as gaze following, in extant representatives of Archosauria, the clade containing crocodylians, birds, and dinosaurs, this thesis will begin to explore social cognition in extinct dinosaurs with the objective of uncovering the evolutionary roots of such skills.

The second behaviour that will be covered in this light is *play*. Play represents a behavioural state that appears to be – just like gaze following - phylogenetically widespread. Despite this, its functions and evolutionary roots remain elusive. Play is moreover an interesting topic when studying the sociality of dinosaurs. The frequency, contagion, and categories of play are informative about a species' social repertoire. Thus, through studying play in extant descendants of dinosaurs we will obtain an understanding of the level of sociality and the associated socio-cognition of their extinct ancestors.

1.1 Structure of the thesis

This thesis revolves around two topics with implication for the social cognition of dinosaurs: gaze following and play. These subjects are covered over the course of four scientific papers – three empirical studies (PAPER I, III and IV) and one review paper (PAPER II). These papers will be introduced, explained, and discussed throughout five chapters.

Chapter 2 introduces dinosaurs, why they are interesting for studying the evolution of cognition, what is known about their brains, and how it is possible to study cognition in extinct species.

Chapter 3 describes how and why animals transfer and use social information. It moreover discusses different hypotheses about the role of social group living in the evolution of complex cognition and large brains.

Chapter 4 focusses on the central topic of this thesis: gaze following. This chapter presents the background of this research field in human developmental psychology. It moreover explains neurocognitive mechanisms involved in the processing of social gaze. PAPER I is an empirical study investigating gaze following skills in five archosaur species. Additionally, it proposes internal forward models as a possible mechanism for refined visual socio-cognitive skills of birds and possibly dinosaurs. PAPER II reviews the current state of knowledge of gaze following in animals and introduces general ideas and methods of this field. In the same chapter, the development of gaze following in humans and animals is explained. PAPER III investigates the development of gaze following in juvenile ravens with human and conspecific demonstrators.

Play is a behavioural state closely linked to ontogeny and cognitive development. *Chapter 5* introduces the study of animal play and its definitions. PAPER IV is the first systematic description of play and its ontogeny in a palaeognath bird. A novel theoretical framework for the functions of play – predictive processing – is introduced and connected to the findings of PAPER IV.

Finally, *Chapter 6* discusses the implications of the results of this thesis for dinosaur cognition. It hypothesizes about the socio-cognitive skills of non-avian paravian dinosaurs and their differences to mammals living at the same time. Finally, it discusses the impact of these findings on our knowledge about the evolution of social cognition and predictive brains.

1.2 Phylogeny

To be able to study evolutionary processes, an understanding of the phylogeny of the animals in question is required. The phylogeny underlying this work is depicted in Figure 1.

Amniota are tetrapod vertebrates that evolved a specific extraembryonic membrane – the amnion. This membrane is considered a key adaptation to terrestrial life, as it allows for egg-laying on land and thereby led to reproductive independence from water. This clade emerged around 325 million years ago (from here on MYA) and includes mammals, non-avian reptiles, and birds (e.g. Shedlock & Edwards, 2009).

Amniota further split into Synapsida, that today only contains mammals, and Sauropsida, including all non-avian reptiles and archosaurs. Archosauria comprises crocodylians, birds, and dinosaurs. Birds are living dinosaurs and form, together with the extinct dinosaurs, the clade Dinosauria.

Archosauria originated around 250 MYA. During the Late Triassic, crocodile-line archosaurs (crurotarsans) were dominant over bird-line archosaurs including dinosaurs (avemetatarsalians) in diversity and abundance. However, in the Early Jurassic, dinosaurs achieved their role as dominant terrestrial vertebrates (Brusatte, Benton, et al., 2010). Dinosaurs were inhabiting the Earth for approximately 163 MY throughout the Mesozoic (Fastovsky & Weishampel, 2016)) until going extinct during the Late Cretaceous, around 66 MYA (Renne et al., 2013).

Within Dinosauria, one generally distinguishes between Ornithischia and Saurischia. These two groups differ from each other regarding their pelvis structures. In ornithischian ("bird-hipped") dinosaurs, at least a part of the pubis is rotated backwards, lying parallel to the ischium. In saurischian ("lizard-hipped") dinosaurs, on the other hand, the pubis is directed anteriorly. Ornithischia comprises a variety of herbivorous dinosaurs, such as *Triceratops* and *Stegosaurus*. Saurischia consists of Sauropodomorpha and Theropoda - the latter including modern birds (Fastovsky & Weishampel, 2016).

Within the theropod dinosaurs, Maniraptora includes the closest relatives to modern birds. Maniraptoran theropods exhibited true pneumaticity with extensive air sacs, highly efficient unidirectional breathing, and hollowed bones. Maniraptora comprises the oviraptorosaurs, deinonychosaurs, and Avialae. Deinonychosaurs and avialans together represent Paraves. The non-avian paravians will be mentioned frequently throughout this thesis as this group includes the most "bird-like" dinosaurs.

Finally, Avialae includes *Archaeopteryx*, Aves (the extant birds), and all the evolutionary steps in between. These steps led towards increased flight proficiency through for example flight feathers, a rigid trunk, increased encephalization and flight musculature. The extant representatives of Aves still inhabit this planet today in form of modern birds (Fastovsky & Weishampel, 2016).

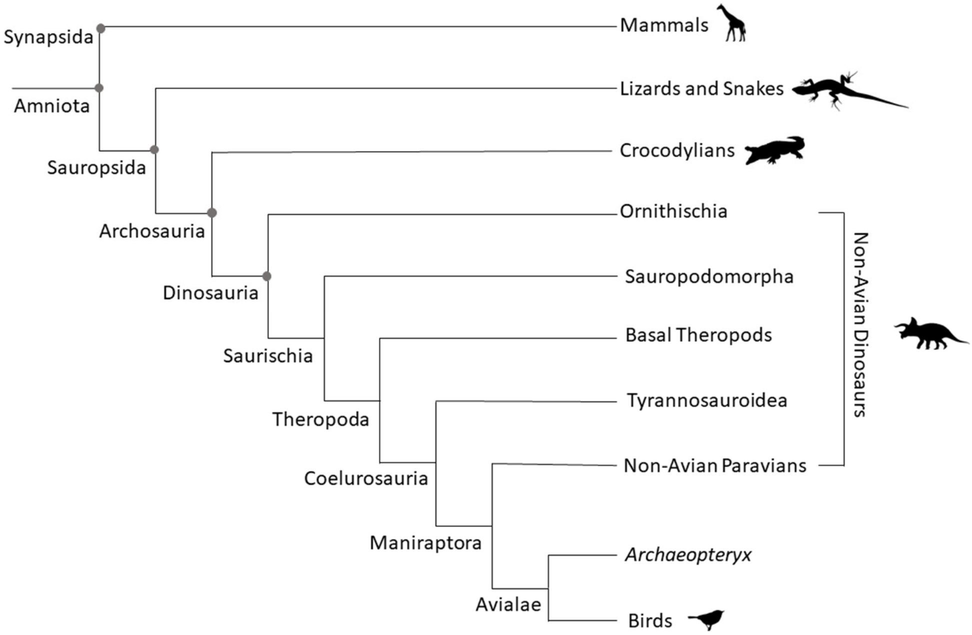

Figure 1: A phylogenetic tree of amniotes (drawn by CZ, silhouettes from PhyloPic, based on Brusatte, Nesbitt, et al., 2010).

2 Dinosaurs

2.1 Why study dinosaurs?

According to the most recent estimate, there are currently around 8.7 million eukaryote species inhabiting the Earth (Mora et al., 2011). However, to obtain a better understanding of the principles of cognitive evolution, it is of special interest to study extinct species to gain insights into the emergence of cognitive traits, the selective pressures they are underlying, and possible relaxations of evolutionary constraints.

Comparative psychologists have for the longest time focused their research predominantly on primates, primarily with the aim of uncovering the origins of our own cognitive capacities. The field has since broadened, but studies are still biased towards mammals and some large-brained bird species, such as corvids and parrots.

However, when trying to unveil the evolution of cognition, it is crucial to study a wide variety of distantly related species (Matsubara et al., 2017). Comparisons of performances on the same task of species occupying key phylogenetic positions are needed to trace how specific traits have changed in evolutionary time. Further knowledge is gained if the results of such studies are subsequently correlated with species' socio-ecologies, brain anatomies, and various other factors.

Birds are of special interest when trying to understand evolutionary trends in cognition for two reasons. Firstly, birds have demonstrated cognitive capacities matching or even surpassing that of many mammals. Corvids and parrots even appear to exhibit cognitive levels on par with great apes. They have among other things been shown to possess complex problem-solving skills (Huber & Gajdon, 2006), manufacture and use tools (Auersperg et al., 2012), pass a mirror-self-recognition test (Prior et al., 2008), and plan for the future (Kabadayi & Osvath, 2017).

Despite their similarities in cognitive output, avian brain morphology differs drastically from that of mammals. Birds lack a neocortex – the brain region commonly associated with higher cognitive functions in mammals. Instead, the avian cerebrum is organized in pallial aggregations. Additionally, birds have evolved an equivalent to the mammalian prefrontal cortex – a part of the neocortex associated with executive functions, such as working memory and planning. The functional equivalent in the avian brain is called the nidopallium caudolaterale (Güntürkün & Bugnyar, 2016).

Mammals and birds shared their last common ancestor around 325 MYA, possibly even further in the past (Ford & Benson, 2020). Despite their long, separate evolutionary paths and their different neuroanatomical outcomes, the achieved cognitive output appears to be very similar. This is one reason why it is important to compare avian and mammalian cognitive capacities: to find functional similarities, but also uncover differences and limitations of different neuroanatomies.

The second motive to study avian cognition is that they represent a direct window to extinct species – the dinosaurs. We know today that birds are not descendants of the dinosaurs; they are in fact living theropod dinosaurs. This, in combination with extensive palaeontological research providing a wealth of knowledge about dinosaurs, allows for glimpses into the behaviour and cognition of early birds and to an extent dinosaurs. Through studying cognition in extinct species, we can draw inferences on the cognitive capacities of animals living at that time and can trace back the emergence of certain cognitive traits.

In the following, the current state of knowledge regarding dinosaur brains and their evolution will be explained together with methods of studying cognition in extinct species.

2.2 Dinosaur brains

Due to advances in the field of palaeontology and the extensive fossil record of dinosaurs, we today know a great deal about the brains of these extinct animals. As this thesis concerns the evolution of avian cognition, we will focus here on theropod brains.

One might ask how it is possible to gain information about the brains of extinct species, as soft tissue rarely fossilizes (but see for example Brasier et al., 2017). Fossilized skulls, however, can shed light on brain anatomies. Palaeontologists create 3D-models of dinosaur brains through generating endocasts of the endocranial cavity - the cavity in the skull that houses the brain. In earlier times, the braincase of a fossil specimen was for that purpose filled with successive layers of latex (Hurlburt et al., 2013). New technological advances allow for the generation of digital endocasts through high-resolution X-Ray Computed Tomography (HRCT), a completely non-destructive method. The endocasts represent a proxy for the actual brain shape depending on its brain-to-endocranial cavity (BEC) index of the respective specimen, i.e.,to which extent the brain was filling the braincase (Balanoff & Bever, 2017).

BEC differs significantly between animal species. The brains of ancestral vertebrates only filled a very small proportion of the braincase and even those of extant reptiles only fill about half of their braincase (Hurlburt et al., 2013). Consequently, endocasts from such species are poor estimates for their brain morphology.

Nevertheless, they can be used to estimate the relative size of the brain. Hurlburt and colleagues (2013) compared the encephalization quotients (brain mass to body mass ratio; EQ) of several theropod species, including tyrannosaurids, allosaurids, and *Archaeopteryx* to extant bird and non-avian reptile species. They thereby differentiated between bird EQs (BEQs) and reptile EQs (REQs). The authors found that the relative brain size of most theropod dinosaurs falls well within the range of extant non-avian reptiles of their body-mass, with the highest value for *Tyrannosaurus rex* with an EQ comparable to that of extant crocodylians. The EQ of *Archaeopteryx lithographica* was found to lie above the mean REQ, placing it at the lower end of the BEQ range. The only theropod dinosaurs falling within the bird EQ-range were late Cretaceous small theropods (*Bambiraptor*, *Ornithomimus*, *Troodon*). This indicates an evolutionary shift in relative brain size from earlier theropod dinosaurs to theropods from the late Cretaceous, such as the coelurosaurs and maniraptorans.

In fact, Osmólska (2004) discovered imprints of intracranial vascular channels on the skull roof of an oviraptorid theropod (*Ingenia yanshini*). It was inferred from this finding that the brain surface must have been closely appressed to the bone, indicating that the brain was filling the braincase to a high degree in this species. This, combined with similar observations in ornithomimids, troodontids and dromaeosaurids (Russell, 1972; Osmólska, 2004) led to the conclusion that all maniraptoran theropods exhibited this feature.

Oviraptorosaur brains were later shown to not only have filled the braincase, but were moreover the first ones to exhibit an inflation of the forebrain, resulting in a sigmoidal shape of the brain and a lateral displacement of the optic lobes (Balanoff et al., 2014). Despite this, their forebrain was not yet large enough to close the gap to the cerebellum, as found in extant birds. Furthermore, oviraptorosaur brains exhibited a reduction of olfactory tracts and bulbs.

Finally, the Neornithes - the clade containing the extant bird groups Neognathae and Palaeognathae – diverged. Neornithes established during the Cretaceous but experienced an explosive radiation after the end-Cretaceous extinction (K-Pg boundary). Mesozoic birds from the Lower Eocene have been found to already have possessed essentially modern avian brains, with ventrolaterally displaced optic lobes due to an expanded telencephalon (to a much higher degree than in *Archaeopteryx*), and a hyperpallium (formerly called "Wulst") that is commonly regarded as the primary visual processing area of the avian brain (Medina & Reiner, 2000).

However, some features of these early birds were differing from modern avian brains. Their olfactory lobes were relatively large, and their hearing sensibility was increased due to a long cochlear duct. These features represent a sensory adaptation that paralleled and even exceeded that of extant birds. Moreover, the cerebellar expansion of these early birds had not reached the extent of modern birds (Milner & Walsh, 2009; Walsh & Milner, 2011)

In general, four evolutionary steps can be identified from the brains of non-maniraptoran theropods to that of extant birds (Torres et al., 2021). Basal non-maniraptoran theropods, such as *Tyrannosaurus*, retained the ancestral, linear arrangement of neuroanatomical regions (Bever et al., 2011). The brains of non-avialan maniraptorans, such as *Zanabazar*, showed first expansions of both the cerebrum and the cerebellum, causing a ventral displacement of the midbrain (Balanoff et al., 2014). Shortly after the divergence of Avialae, for example in *Archaeopteryx,* the cerebrum and cerebellum further expanded until they pushed into contact. This caused a complete ventral displacement of the midbrain. Finally, extant birds have further increased relative brain size and cerebrum size (Balanoff et al., 2013).

2.3 Avian brain evolution

While palaeontological studies have mainly used relative brain sizes estimated through endocasts as measures for the cognitive capacities of extinct dinosaurs, more recent approaches have shed new light on avian brain evolution. These new studies have increasingly focused on neuronal numbers as measures of cognitive performance rather than relative brain size. This approach has various advantages over more conservative methods. Firstly, distantly related brains can have vastly differing numbers of neurons in the entire brain, as well as in specific brain areas of the same mass (Herculano-Houzel, 2017; Němec & Osten, 2020). Macaques, for example, have similar numbers of pallial neurons compared to corvids, despite them having an almost seven times larger brain than their avian counterparts (Olkowicz et al., 2016).

Moreover, the causal relationship between relative brain size and cognitive capacity has been challenged. Evidence is accumulating suggesting that number of neurons – the computational units of the brain – is a better predictor of cognitive performance than relative brain size (Striedter, 2004; Roth & Dicke, 2005; Herculano-Houzel, 2011; Dicke & Roth, 2016).

Through collecting a comprehensive dataset of neuronal numbers of extant species, Kverková and colleagues (2022) recently shed new light on avian brain evolution. This study found that over time, both mammals and birds have convergently evolved towards increased total and relative brain sizes, as well as higher neuronal numbers. This increase is disproportionately bigger than in reptiles, resulting in significantly lower neuronal numbers for a given body size in this group compared to mammals and birds. Within the overall increase of neuronal numbers, primates and core land birds (hawks and eagles, owls, falcons, songbirds, and parrots) subsequently experienced an additional increase in telencephalic neurons compared to other mammal and bird species.

Interestingly, this study found that proportionally, the biggest increase of neurons in the avian brain is accounted for by the cerebellum. Until now, the telencephalon has been regarded as the centre of higher cognitive function. These new findings, however, indicate a bigger role of the cerebellum in the evolution of complex cognition than previously thought. This is in line with accumulating evidence of an involvement of the cerebellum in various cognitive functions, such as executive control, language, working memory, learning, pain, emotion, and addiction (e.g. Strick et al., 2009; Barton, 2012; Smaers et al., 2018).

Kverková and colleagues (2022) moreover argued that the transition to endothermy was key to enabling the dramatic increase of neuronal numbers. This has new implications for dinosaur brains. A recent study (Wiemann et al., 2022) argued for a dinosaur-origin of endothermy. The authors investigated traces of advanced lipoxidation end-products (ALEs) in the bones, teeth, and eggshells from all major amniote radiations. ALEs are a by-product of metabolic stress caused by the physiological heat underlying endothermy. Based on this method, the authors determined that stem archosaurs were ectothermic, but that all ornithodirans (pterosaurs, dinosaurs, and their last common ancestor) were endothermic with increasing rates along the avian lineage. According to this study, ornithischian dinosaurs secondarily reduced their metabolic rate back to ectothermy.

Though very interesting, the results of this study should be handled carefully. The authors made inferences for all extinct amniote species based on data from 30 fossil specimens, of which only six were ornithischian and seven saurischian dinosaurs. These are quite small sample sizes to make broad phylogenetic assumptions. Nevertheless, it is today commonly accepted that at least the non-avian paravian dinosaurs were endothermic (e.g. Legendre et al., 2016; Rezende et al., 2020).

As noted above, endothermy is closely related to increases in neuronal numbers (Kverková et al., 2022). Endothermy is metabolically costly (Else & Hulbert, 1981; Nagy et al., 1999), as are neurons (Hyder et al., 2013). Through shifting to endothermy, the cost of neurons might have relatively decreased, while simultaneously paying off through improved cognitive capacities. Endothermy in non-avian paravian dinosaurs thus suggests that these dinosaurs might already have had increased neuronal numbers. What cognitive capacities these neuronal numbers brought about remains, however, unclear to date. How it is possible to study the cognition of extinct dinosaurs will be explained in the following.

2.4 How to study social cognition in dinosaurs

Social behaviours are inherently difficult to preserve in the fossil record. Consequently, gregariousness in dinosaurs can only be inferred from communal bonebeds (e.g. Funston et al., 2016), trackways (e.g. Lockley & Matsukawa, 1999) and nesting sites (e.g. Horner & Makela, 1979). While such trace records can stimulate hypotheses about sociality in dinosaurs, they can often be explained in alternative ways.

An assembly of animals in one area is commonly the result of other circumstances than sociality. Firstly, members of a species are expected to be found in similar environments as they are foraging for the same food sources and have the same ecological requirements to their habitats. Even group movements, that have been proven through trackways of many members of the same dinosaur species moving in the same direction, can be explained by migrations, or simply the lack of an alternative route. Moreover, seasonal abundances of food can lure many individuals to the same location, as can for example be seen in extant grizzly bears (*Ursus arctos horribilis*) that assemble during periods of salmon migration. If these animals were to suddenly die in this location, it would likely be assumed from the fossil record that they were representatives of a social species. For these reasons, the conclusions that can be drawn on dinosaur sociality based on trace records are limited.

Even if trail records were to shed light on the sociality of extinct species, they fail to provide insights into the cognitive abilities these animals exhibited to navigate their social lives. At first glance, it might appear impossible to study non-fossilizing features of dinosaurian lives, such as cognition. However, palaeontologists commonly use a trick to overcome this issue: the so-called extant phylogenetic bracketing (Witmer, 1995).

This approach is based on the assumption that shared traits in extant members of a clade are derived from a common ancestor. Dinosaurs form, together with their extant descendants (the birds) and their closest relatives (the crocodylians) the clade Archosauria. Within this group, the lineage leading to birds, i.e., the theropod dinosaurs, can be bracketed, as closely as possible, by modern birds and crocodylians.

Crocodylians have had slow evolutionary rates (Green et al., 2014) with ancestral brain morphologies resembling those of basal archosaurs (Brown et al., 2020), and therefore represent an optimal neurocognitive model for stem archosaurs. On the other side of the phylogenetic bracket are the modern birds. Within Aves, one group is of special importance as a neurocognitive model for extinct dinosaurs: the palaeognath birds.

Paleognathae includes the flightless ratites (ostriches, rheas, kiwi, emus, and cassowaries), and the volant tinamous (Widrig & Field, 2022). Palaeognathae and Neognathae split around 110 MYA, before the end-Cretaceous extinction (Yonezawa et al., 2017). Consequently, they existed at the same time as the non-avian dinosaurs.

These birds constitute the best neurocognitive model for the closely related non-avian paravian dinosaurs, such as dromaeosaurids and troodontids. Palaeognaths exhibit the least derived number of pallial neurons (Olkowicz et al., 2016) and share numerous homologies with the non-avian paravian dinosaurs, including scaling relationships and morphology of the brain (Balanoff et al., 2013; Ksepka et al., 2020).

Moreover, maniraptoran dinosaurs – the clade including the oviraptorosaurs and paravians - displayed a variety of complex social behaviours such as paternal care and brooding of communal nests similar to reproductive strategies of palaeognath birds (Varricchio et al., 2008; Varricchio & Jackson, 2016). These findings, in combination with the above-mentioned shared brain features, suggest similar socio-cognitive capacities in non-avian paravian dinosaurs and palaeognath birds.

Taken together, by studying social cognition in extant crocodylians and palaeognath birds, it is possible to draw inferences about the cognitive abilities of early birds and the most “bird-like” dinosaurs, the non-avian paravians.

2.5 Species in this thesis

This thesis revolves around six species. To phylogenetically bracket extinct dinosaurs, we chose three representatives of Palaeognathae: emus (*Dromaius novaehollandiae*), greater rheas (*Rhea americana*), and elegant-crested tinamous (*Eudromia elegans*). These three palaeognath species occupy different phylogenetic nodes, are representatives of different socio-ecologies, and some are flightless, while others are volant (e.g. Yonezawa et al., 2017). We moreover included one plesiomorphic neognath species that served as an outgroup: red junglefowl (*Gallus gallus*). This species belongs to the lineage Galloanserae that already diverged from other large group of neognaths (Neoaves) before the end-Cretaceous extinction. As a representative of the crocodylians, we chose American alligators (*Alligator mississipiensis*). On the other hand, we studied common ravens (*Corvus corax*), one of the most large-brained avian species that has proven its complex cognitive capacities in many cognitive experiments (for pictures of each species, see Figure 2).

Emus and greater rheas are representatives of the flightless ratites. Emus are the second largest birds in the world (after ostriches), and can be found in most parts of continental Australia, except for sandy deserts and dense forest. In the wild, emus are mainly solitary, but can form pairs and small groups. Males incubates the nest by themselves and guard the chicks for five to seven months after hatching (Folch et al., 2020).

Greater rheas are one of two species of Rheidae. The other species is the Lesser rhea or Darwin's rhea (*Rhea pennata*). Greater rheas inhabit open areas in eastern and southern South America. Males are usually solitary, while females live in small flocks. During breeding season, males gather small harems around them. Like in emus, the males perform parental care including incubation of nests and chick guarding for six to eight months after hatching (Winkler et al., 2020).

Elegant-crested tinamous are representatives of the tinamous, a group of small, ground-dwelling birds of South America. Elegant-crested tinamous inhabit shrublands of southern Chile and Argentina, where they form mixed-sex flocks. Tinamous are volant, though their flight proficiency is rather poor, and they can only fly for short distances. Typically for many palaeognath species, the males incubate the eggs and rear the young (Bohl, 1970).

Red junglefowl are wild ancestors of the domestic chicken. These birds can be found in most areas of Southeast Asia and parts of South Asia. They usually live in flocks of one or a few roosters with several females. The females incubate and rear the chicks (McGowan & Kirwan, 2020).

Common ravens are found all over the Northern hemisphere in a variety of habitats. Subadult ravens live in large fission-fusion flocks, but form pair-bonds when reaching sexual maturity. The pair raises their offspring together. The chicks fledge around 35 days old, but stay with their parents for up to six months (Boarman & Heinrich, 2020).

American alligators are one of two species of alligator, the other one being the Chinese alligator (*Alligator sinensis*). American alligators can be found in freshwater marshes, swamps, rivers, and lakes of the southern and eastern US. These crocodylians are commonly tolerant and can aggregate in basking groups, during droughts, and in breeding groups. Females protect their nest, carry the young to the water after hatching, and guard them for up to one year (Grigg & Kirshner, 2015).

Figure 2: Species in this thesis: Top row (from left to right): Emu, greater rhea, elegant-crested tinamou. Bottom row: American alligator, red junglefowl, common raven. Photo credit: Ivo Jacobs, Helena Osvath.

For a comparison of neuronal numbers of these species, see Table 1. The only crocodylian species with available data on neuronal numbers is the Nile crocodile (*Crocodylus niloticus*), which will be used as a representative for other crocodylian species here.

The neuronal numbers shown in this table are in line with the above-described pattern of avian brain evolution. The birds generally have more neurons in their brains compared the Nile crocodile. The relatively biggest increase took place in the cerebellum. While an emu has approximately 15.75 times as many neurons in the telencephalon as a Nile crocodile, it has about 20.5 more neurons in the cerebellum.

Ravens have almost twice as many neurons in total compared to the larger palaeognaths (emus and rheas), though their numbers of cerebellar neurons are comparable. This reflects the secondary drastic increase in neuronal numbers in the telencephalon of core land birds. Indeed, the telencephalon of a raven houses approximately 2.8 times more neurons than that of an emu.

Table 1: Neuronal numbers of species in this thesis (numbers from Olkowicz et al., 2016; Kverková et al., 2022)

Species	**Brain mass [g]**	**#Neurons total [x10^7]**	**#Neurons telencephalon [x10^7]**	**#Neurons cerebellum [x10^7]**
Nile crocodile	5.8	8.2	3	4
Elegant-crested tinamou	2	21.8	6	13
Greater rhea	21.3	103	36.7	61.1
Emu	21.8	133.5	47.2	81.5
Red junglefowl	2.8	22.1	7.4	11.4
Common raven	14.1	217.1	135.5	75.4

3 Social information and the evolution of social cognition

Social group living has many advantages for animals. It can serve as protection against predators and provide reproductive advantages (Shettleworth, 2010). Moreover, and of special significance to this thesis, it provides animals with opportunities for receiving and transferring social information (Brown & Laland, 2003).

Sociality in animals can take many different forms, ranging from pair-bonds to fission-fusion societies. It can be argued that very few species are truly solitary, as most of them as a minimum meet to mate – at least those that are sexually reproducing. Being able to read and interpret others is thus a useful skill for many species.

This chapter explains how animals acquire and use social information and how the special challenges connected to dealing with social relationships have been suggested to have impacted brain evolution.

3.1 Social information

Animals require information about their environment to be able to make informed inferences about for example the location of food and predators, the reproductive status of possible mates, or the strength of a rival (Giraldeau et al., 2002). Such information is hence used to reduce uncertainty about variable environments (Carter et al., 2016).

Two types of information are accessible to animals: personal information - information animals acquire through interacting with their environment - and social information – information that is acquired by observing others (Dall et al., 2005). Animals can extract personal information from markers in the environment such as landmarks, the sun, or the geomagnetic field (Dall et al., 2005). Social information, on the other hand, can either be shared intentionally through visual or vocal signals, or it can be conveyed inadvertently (Morand-Ferron et al., 2010). Every choice an animal makes sends inadvertent information to others. For example, a gazelle's choice of grazing in a certain patch of grass can inform other gazelles about the abundance and quality of food in that area.

Three steps are involved in the use of social information: acquisition, application, and exploitation (Carter et al., 2016). All three steps underly different phenotypic constraints, and do not necessarily predict each other. In other words, the acquisition of social information does not predict subsequent exploitation of that information. Three-spined sticklebacks (*Gasterosteus aculeatus*), for example, have been observed to discover a foraging task quicker when observing conspecifics solving the task, but did subsequently not solve it quicker themselves (Atton et al., 2012). In chacma baboons (*Papio ursinus*), interest in the acquisition of social information, did not predict the ability to use such information. In other words, the time spent observing a demonstrator was not correlated with subsequent improvements in solving the observed task (Carter et al., 2014).

Such constraints in exploiting social information can operate on an individual level, with individuals varying, for example, in their social competencies, cognition, rank and age, but also on a species level (Carter et al., 2016). Different species undergo varying selective pressures favouring social information use and are equipped with diverse cognitive capacities. These capacities allow for increased attention towards social cues and subsequently improved processing of such information.

The first step of social information use refers to the acquisition of social information. This step requires paying attention to others and their actions. One way of gathering information is to attend to what others are looking at – gaze following. This topic will be discussed at length in *Chapter 4*.

In the next two steps, social information is applied and exploited. Such a sequence could for example look as follows: A young monkey observes a conspecific shaking a branch, which leads to fruit falling (information acquisition). The monkey then climbs up a tree and starts shaking a branch itself (information application). As the fruit falls, it collects and eats it (information exploitation).

This example represents a classic social learning scenario. Other areas of social information use are public information use and social eavesdropping (Bonnie & Earley, 2007). Public information use refers to the use of inadvertently conveyed information such as resource quality, while social eavesdropping informs animals about others' relationships through witnessing their interactions.

Social information has many advantages over personal information, as it allows for quicker, and less costly gathering of information compared to personal information gathering based on trial-and-error (Clark & Mangel, 1984, 1986; Giraldeau et al., 1994; Giraldeau, 1997; Galef & Giraldeau, 2001). It moreover enables the receiver to optimize decisions beyond their personal knowledge, making the ability to use such information adaptive (Morand-Ferron et al., 2010). However, social information can also be unreliable, especially when observed individuals are misinformative, or when information is quickly outdated (Dall et al., 2005).

Nevertheless, the use of social information is generally adaptive, and has therefore been favoured by selective forces throughout evolution. The complex challenges animals face when living in social groups have even been hypothesized to be one of the main drivers of the evolution of large brains and complex cognition. This is called the social intelligence or social brain hypothesis (Jolly, 1966; Humphrey, 1976). These hypotheses will be explained in the next section.

3.2 The social intelligence hypothesis

The social intelligence hypothesis (SIH) has first been proposed by Jolly (1966), and later brought forth again by Humphrey (1976). This hypothesis suggests that the complex cognitive demands of social group living are the main drivers of the evolution of complex cognition in primates and consequently the evolution of large brains (social brain hypothesis; Shettleworth, 2013).

This hypothesis has been inspired by two observations. Humans and non-human primates have larger brains than expected for their body size (Byrne, 1994). They moreover exhibit a number of exceptionally complex cognitive skills. For these reasons, the SIH proposes that these traits have evolved to better anticipate, understand, and manipulate others' behaviour in the complex social groups of primates (Humphrey, 1976). Alternatively, but closely related, the "Machiavellian" intelligence hypothesis (Whiten & Byrne, 1988) suggests that the roots of primate intelligence lie in tactical deception and manipulation of others.

The SIH has found a lot of support by researchers working on primate cognition. Indeed, a correlation between relative brain size and social complexity measured by group size has been identified for many primate species (Dunbar, 1998).

However, the SIH has also received a lot of criticism over time. Firstly, the parameters it is based on are problematic. Some ungulates, for example, live in enormous herds, but they are predominantly anonymous and don't engage in complex social behaviours (Pérez-Barbería et al., 2007). Consequently, group size is not an ideal measure for social complexity. Moreover, the relationship between brain size and cognitive complexity is not fully understood and thus speculative (e.g. Logan et al., 2018).

Additionally, there are a range of phenomena that the SIH cannot account for. Its original formulation disregards non-primate species. However, distantly related groups, such as corvids have demonstrated complex cognitive capacities on par with apes in many cognitive experiments (e.g. Kabadayi et al., 2016; Kabadayi & Osvath, 2017; Pika et al., 2020), even though their brain morphologies differ substantially from those of primates (Güntürkün & Bugnyar, 2016). Birds moreover do not appear to exhibit the same correlational relationship between group size and relative brain size as primates. On the contrary, avian species forming monogamous pair-bonds have larger brains than those with complex mating systems (Emery et al., 2007).

On the other hand, there are species living in similarly complex social structures as primates that have not evolved comparable cognitive skills. Spotted hyenas (*Crocuta crocuta*), for example, live in so-called clans – a social system comparable to troops in baboons. Nevertheless, they have not evolved the same cognitive capacities as primates (Holekamp, 2007).

Finally, even within primates, innovation, tool use, and frequency and sophistication of social learning vary between species independent of their group size (e.g. Reader & Laland, 2002).

For these reasons, alternative explanations for the increase in brain size of primates have been put forth. In fact, a number of other, non-social factors, such as feeding ecologies and foraging techniques could explain brain expansion just as well (Whiten, 2000). The so-called foraging theory of intellect proposes that challenges animals encounter during foraging select for higher cognitive skills (Shettleworth, 2010). Similarly, the ecological intelligence hypothesis states that challenges caused by variable environments such as changing climatic conditions and food sources have driven the evolution of cognition (e.g. Barton, 1996).

A recent study (Hooper et al., 2022) brought up criticism for both the social and the ecological intelligence hypothesis. The authors found several problems in correlational studies of this kind. Estimates of a species' brain size vary significantly between datasets. The same applies to body size estimates used to calculate relative brain sizes. Brain and body size measures are either estimated from one individual or averaged across several individuals. Nevertheless, depending on the sample, this might yield different results in various datasets due to large intraspecific variation. They moreover showed that model specifications, such as the combination of variables included in statistical models and their source significantly impact the results of such correlational studies. The authors found, depending on the models they were choosing, evidence supporting several contradicting theories. Basing entire evolutionary hypotheses on correlational analyses that are susceptible to variation depending on the used dataset or model specification is hence a problematic method.

The ultimate causes of the evolution of complex cognition remain elusive. While some support has been found for both the social and the ecological intelligence hypothesis, it is not fruitful to regard the two as contradictory. The drivers of cognitive evolution are likely variable environmental conditions – which include both the social *and* the ecological environment. The challenges animals are facing due to their social environment are undoubtedly numerous, complex, and extremely important for the survival of a species. Just imagine animals that are not capable of recognizing suitable mating partners or maintaining good relationships with other group members. Such individuals would likely not be able to reproduce successfully. The social environment is thus expected to be an important driver for the evolution of cognition, but most likely not – as stated by the social intelligence hypothesis – the only one.

4 Gaze following

Animals have evolved various mechanisms of gathering social information. One effective way of acquiring such information is by attending to what others are looking at. Co-orienting with others' gaze directions – gaze following - is a fast, easy, and effective way of gathering information about the location of food, predators and third-party relationships (Tomasello et al., 1998; Emery, 2000).

Gaze following is a fundamental socio-cognitive skill due to the many benefits of utilizing social gaze as a source of social information. It moreover has direct implications for the development and evolution of other socio-cognitive components in humans as well as animals. The fundamental character of gaze following becomes apparent in its phylogenetic ubiquity.

65 species across 4 vertebrate classes have been tested for their ability to either co-orient with observed gaze or to find hidden food based on gaze cues. Traditionally, the study of gaze following has focused on primates and some social mammals, limiting evolutionary interpretations to few and closely related lineages. However, in recent years, new studies have emerged, trying to broaden the understanding of gaze following skills in the animal kingdom. These new studies have mainly focused on birds, but also on some reptiles, and fishes. Nevertheless, over time, many different methodologies have been introduced, once again hampering phylogenetic comparisons. Moreover, gaze following studies have often disregarded a number of factors potentially influencing the results of such studies. We have reviewed methodologies, limitations, and new advances in the field of gaze following in PAPER II.

4.1 Gaze following and its implications for human infants

Gaze following was first studied in 1975, when Scaife and Bruner tested co-orientation of human infants with an experimenter's gaze direction. Human infants start to spontaneously follow gaze between three and six months (Butterworth & Jarrett, 1991), but are sensitive to others' gaze directions already as new-borns (Batki et al., 2000; Farroni et al., 2002). A more detailed description of the development of gaze following skills in humans can be found in PAPER II.

The development of gaze following has direct implications for the development of other socio-cognitive skills of humans, such as theory of mind (Brooks & Meltzoff, 2015), joint attention (Carpenter et al., 1998), and language acquisition (Baldwin, 1991; Schafer & Plunkett, 1998; Houston-Price et al., 2006). These developmental connections demonstrate the fundamental role of gaze following in the development of human social cognition.

This becomes even clearer when investigating children with deficiencies in their socio-cognitive skillsets such as individuals with autism spectrum disorder (ASD). Children with ASD are impaired in their ability to detect and attend to social stimuli, such as gaze (Dawson et al., 1998; Dawson et al., 2004), and in initiating joint attention (Mundy et al., 1986; Mundy & Sigman, 1989).

Though delayed, children with ASD develop a sensitivity to directional cues conveyed through gaze at two years old (Chawarska et al., 2003). The absence of gaze following in early developmental stages could according to the authors of this study be explained by difficulties in disengaging attention from their current fixation point or by a lack of salience of social cues to these children. Indeed, studies have found that children with ASD respond better when combining multiple cues, instead of exclusively using gaze cues to redirect the children's attention (Presmanes et al., 2007; Thorup et al., 2016).

Children with ASD are moreover often impaired in their language acquisition (e.g. Charman et al., 2011) and about 25% of autistic children remain completely non-verbal (Kim et al., 2014). Children with ASD produce their first words on average at 38 months, while neurotypical children start talking between 8 and 14 months (Howlin, 2003).

When combining the early development of gaze following in human infants with its connection to the development of other socio-cognitive skills and the deficits in children with impairments in joint attention, including the use of gaze cues, it becomes clear that gaze following is a fundamental part of the socio-cognitive repertoire of humans. It is thus a skill that is also expected to be central to animals.

4.2 Modes of gaze following

The comparative cognition literature commonly distinguishes between two levels of gaze following. This dichotomy has been introduced by Povinelli and Eddy (1996) that proposed a high- and low-level interpretation of gaze following. According to this theoretical framework, low-level gaze following entails reflexive co-orientations with observed gazes that do not involve an attribution of mental states. High-level gaze following, on the other hand, requires the representation of others' visual perspectives.

These two modes are tested in two distinct experimental paradigms: gaze following into the distance and geometrical gaze following. Gaze following into the distance tests for low-level gaze following skills. In this experimental setup, a demonstrator is gazing either up or to the side. An observer with low-level gaze following skills is expected to co-orient with the observed gaze direction. In geometrical gaze following experiments, a demonstrator is lured to gaze to a location that is concealed by a barrier from the observer's viewpoint. A subject capable of high-level gaze following is expected to relocate itself around the barrier to identify the gaze target. This requires a representation of others' visual perspectives through generalising between allo- and egocentric space.

Geometrical gaze following is thus diagnostic of visual perspective taking, i.e., the ability to predict others' visual experience (Michelon & Zacks, 2006). In this context one traditionally distinguishes between level I and level II knowledge, that allow for the prediction of two different types of information (Flavell et al., 1981). Level I refers to an understanding of *what* the other can see, i.e., which objects are visible from the other's viewpoint. Level II includes an understanding of the visual aspects from the predicted viewpoint, i.e., *how* the scene looks to the other.

Geometrical gaze following can only reveal level I knowledge of others' visual perspectives, while it does not signify level II perspective taking. It has, however, been proposed as an embodied precursor for the development and evolution of such perspective taking skills (Kessler & Rutherford, 2010). Through repositioning themselves around the barrier, subjects experience the other's visual perspective, which might later be used in mental simulations of others' visual experiences.

Geometrical gaze following does hence not require an attribution of mental states, but in human children, grasping others' visual perspectives is crucial for the development of an understanding of others' mental states. Brooks and Meltzoff (2015), for example, found that children exhibiting improved gaze following skills at 10.5 months (both in speed and accuracy) were subsequently producing more mental-state words at 2.5 years, i.e., words of cognition, desire and emotion. At 4.5 years, the same children performed better on a theory of mind test battery including diverse desires, knowledge acquisition, false belief, diverse beliefs, hidden emotions, and false beliefs.

Low-level gaze following skills, i.e., gaze following into the distance, appear to be phylogenetically widespread and have to date been found in all tested amniote species including a variety of mammals (e.g. Schaffer et al., 2020) and birds (e.g. Nawroth et al., 2017), some reptile species (e.g. Wilkinson et al., 2010), and possibly even one fish species (Leadner et al., 2021). High-level gaze following, i.e., geometrical gaze following, on the other hand, appears to have evolved in parallel in mammals (e.g. Met et al., 2014) and some songbirds (e.g. Bugnyar et al., 2004; for a review see PAPER II).

Additionally, low-level gaze following has been described to precede the development of high-level gaze following skills in the ontogeny of several distantly related species (e.g. humans: Butterworth & Jarrett, 1991; ravens: Schloegl et al., 2007; wolves: Range & Virányi, 2011).

The differences in phylogenetic distribution and development of the two modes of gaze following indicate different neurocognitive underpinnings of the two behaviours. Indeed, neuroscientists have identified two distinct neurobiological pathways in line with a low- and high-level of gaze following. These pathways will be described in the following.

4.3 Neurocognitive mechanisms of gaze following

Despite the abundance of studies on gaze following in human psychology as well as comparative cognition, the underlying neurobiological processes remain puzzling. Nevertheless, neurobiological studies suggest two distinct pathways: one fast, yet crude pathway, and one more sophisticated, cortical pathway that allows for visual perspective taking. The neurocognitive mechanisms guiding gaze following have been summarized in PAPER II but will be explained in more detail below.

4.3.1 The subcortical pathway

The fast and reflexive nature of gaze following (Deaner & Platt, 2003) suggests an evolutionary old, conserved subcortical pathway (Sewards & Sewards, 2002; Johnson, 2005). This pathway allows for fast, yet unrefined gaze following responses. In the mammalian brain, it runs from the retina to the superior colliculus, the pulvinar, and to the amygdala (Morris et al., 1999; Johnson, 2005; Jiang & He, 2006). Every step of the pathway is interconnected with cortical areas responding to social stimuli, such as the fusiform gyrus (face perception and recognition: Johnson, 2005), the exastriate body area (visual processing of the body: Downing et al., 2001) and the superior temporal sulcus (functions explained in 4.3.2; Shepherd, 2010).

The superior colliculus represents the principal visual processing centre that - together with the pulivnar nucleus of the thalamus – guides attention and organizes head and eye orientation (Platt et al., 2003). The brains of fishes, amphibians, reptiles, and birds have a homologue of the superior colliculus - the optic tectum. The remaining pathway is the same as in mammals.

The amygdala is involved in emotional processing (Hoffman et al., 2007; Adolphs, 2010), and moreover controls social attention through direct connections to reward cortices involved in the initiation of social interactions (Schilbach et al., 2010; Pfeiffer et al., 2014). It has for that reason also been proposed to play a role in the development of autism (Schultz, 2005).

Several neuroimaging studies in humans and monkeys have demonstrated the involvement of the amygdala in gaze detection (Kawashima et al., 1999; Adams et al., 2003; Hoffman et al., 2007; Hadjikhani et al., 2008; Sauer et al., 2014). Lesions of the amygdala lead to a disruption of gaze responses in humans through reduced fixation of the eyes (Adolphs et al., 2005; Spezio et al., 2007; Gamer et al., 2013). A recent study on live interactions between monkeys found a dual function of the amygdala. A subset of neurons exhibits short latency responses to mutual gaze, possibly to detect eye contact. Another group of amygdala neurons were activated towards the end of eye fixations. These neurons might regulate gaze timing through disrupting fixations and initiating gaze shifts (Gilardeau et al., 2021).

4.3.2 The cortical pathway

High-level gaze following, i.e., spatially sophisticated behaviours such as geometrical gaze following, is unlikely guided by the subcortical pathway alone. The subcortical pathway is thus proposed to be interconnected with cortical networks in mammals. How more complex gaze following is processed in other vertebrates lacking cortical structures remains unclear.

The superior temporal sulcus (STS) has been found to play a central role in cortical gaze perception in humans (Puce et al., 1998; Hoffman & Haxby, 2000) and non-human primates (Tsao et al., 2003; Kamphuis et al., 2009). This cortical area is particularly active when viewing faces and following others' gazes (Tsao et al., 2006; Kamphuis et al., 2009). Transformations of the face such as changes in colour or size have no impact on the activation of face-sensitive neurons. Scrambling of facial features, however, diminishes the cells' activation (Perrett et al., 1982).

Cells reacting to different facial orientations have been identified in the anterior and middle part of the STS of rhesus macaques (Bruce et al., 1981; Perrett et al., 1982; Desimone et al., 1984; Rolls, 1984; Baylis et al., 1985; Perrett et al., 1985; Hasselmo et al., 1989; Perrett et al., 1992; Eifuku et al., 2004; De Souza et al., 2005).

Facial orientation is encoded through neurons responding differently to various views of the face. The activation of some cells decreases the more the face is rotated away, others are more reactive to profile views of a face. In the same way, some of these neurons respond stronger to vertical head movements, i.e., turning the face up or down (Perrett et al., 1985; Perrett et al., 1992). These neurons hence encode other's visual attention as they are sensitive to face orientation rather than identity (Perrett et al., 1985; Perrett et al., 1990).

Of the face-sensitive neurons in the macaque STS, a subpopulation is sensitive to the direction of eye gaze. While most of these cells respond strongest to congruent head and eye directions, some are specifically activated when head and eye direction are incongruent (Perrett et al., 1985). Again, different neurons encode different eye orientations. Some eye-sensitive neurons only respond to direct gaze, while others are activated by averted gaze (Yamane et al., 1988). Furthermore, an ablation of the banks and floor of the STS has been found to impair the ability to discriminate between direct and other angles of eye gaze (Campbell et al., 1990).

To successfully follow gaze, the detected direction of the face and eyes needs to further be processed to shift one's own attention. The upper bank of the STS projects directly onto the intraparietal cortex in macaques (Harries & Perrett, 1991). The lateral part of this structure - the lateral parietal area (LIP) - is involved in maintaining attention (Schiller & Tehovnik, 2001; Ben Hamed & Duhamel, 2002), as well as in overt (Thier & Andersen, 1998) and covert attentional shifts (Colby & Goldberg, 1999; Bisley & Goldberg, 2003).

Shepherd and colleagues (2009) even identified "gaze mirror neurons" in the LIP that might bring about attentional shifts. These neurons fire both when gazing towards a location and when observing someone else looking at the same location, similar to the functioning of motor mirror neurons (Rizzolatti et al., 2009). Simultaneously, other neurons of the LIP act inhibitory, possibly to supress other behaviours while continuing to fixate on the face. In this way, LIP neurons might contribute to shifts in attention when detecting gaze cues.

Furthermore, the LIP is part of the dorsal attention network (in humans: dorsal & ventral frontoparietal attention systems) that detects and orients attention toward stimuli in the environment (Gitelman et al., 1999; Corbetta & Shulman, 2002). Other parts of this network are the supplementary and frontal eye fields (Seltzer & Pandya, 1989) that elicit eye movement and control gaze shifts (Tehovnik et al., 2000). Together, the attention network judges the cost and benefit of attentional shifts and redirects attention based on these cost-benefit calculations (for a review see: Klein et al., 2009).

Studies on cortical gaze processing have exclusively been conducted on humans and macaques. However, social processing areas are proposed to be homologous among primates (Tootell et al., 2003; Rosa & Tweedale, 2005) and possibly other mammalian species (Kendrick et al., 2001). The neurocognitive mechanisms mediating high-level gaze following in other taxa lacking cortical structures, such as birds and reptiles, remain unclear.

4.4 Gaze following in Archosauria

Gaze following studies have traditionally lacked a phylogenetic focus, leaving a patchy picture of the distribution and evolutionary principles of this socio-cognitive skill. To partly fill this gap, in PAPER I, we studied the gaze following repertoires of five archosaur species. Subjects to this study were respectively six individuals of three palaeognath species (emus, greater rheas, and elegant-crested tinamous), one plesiomorphic neognath species (red junglefowl), and one crocodylian species (American alligators). These species were tested over the course of three experiments following the high- and low-level distinction of gaze following. Experiment 1 and 2 tested for gaze following into the distance upwards and to the side. Experiment 3 investigated geometrical gaze following, i.e., gaze following behind a barrier.

Experiment 1 and 2 revealed low-level gaze following skills in all five tested species. It should, however, be noted that alligators followed gaze at significantly lower rates than birds. Future studies are needed to address whether this discrepancy is caused by differences in the neuroanatomy or the social ecologies of the species.

The presence of low-level gaze following in all tested species in combination with evidence of gaze following into the distance from many species of various taxa suggests roots in deep evolutionary time. This is in line with the above-described conserved subcortical pathway shared among all vertebrates. The exact emergence of gaze following into the distance, though, remains unclear. It could have evolved when vertebrates moved onto land – around 365 MYA - and visual cues became more important, or possibly even earlier than that. More studies on non-amniote vertebrates such as amphibians and fishes will be needed to pinpoint the emergence of low-level gaze following skills. To date, no studies on amphibian gaze following exist, and only one study described sensitivity to directional cues of conspecifics in archerfish (Leadner et al., 2021). It is from that study, however, not clear whether this represents a species-specific adaptation to their hunting style – shooting water jets at moving objects – or whether this capacity is shared among all fishes.

Our experiments yielded different results with respect to geometrical gaze following. Alligators did not track conspecifics' gazes around barriers, while all four bird species successfully followed their conspecifics' gazes geometrically. The performance of alligators is in line with the results of a study on central bearded dragons (*Pogona vitticeps*), that were found to follow the gaze of a conspecific into the distance, but not geometrically (Siviter et al., 2017). It should, however, be noted that this is the only other study testing geometrical gaze following in a reptile. For that reason, it is not clear whether reptiles generally do not follow gaze geometrically, or if this is an artefact of the low number of studies.

With respect to birds, geometrical gaze following had to date only been reported in corvids (Bugnyar et al., 2004; Schloegl et al., 2008) and one other songbird, the European starling (*Sturnus vulgaris*; Butler & Fernández-Juricic, 2014). Our new findings suggest geometrical gaze following and the connected visual perspective taking skills as a universal socio-cognitive component of all birds. Despite this, it should be noted that one study reported negative results for geometrical gaze following in Northern bald ibises *(Geronticus eremita*; Loretto et al., 2009). In that study, the authors reported that subjects looked significantly more often *at* the barrier in test compared to control trials. This suggests that subjects detected and co-oriented with the gaze cue. The absence of relocations around the barrier could be the result of three factors. Firstly, the ibises might lack an understanding of others' visual perspectives. Secondly, birds were placed in compartments next to each other and not facing each other. This might have distorted the subjects' predictions of the demonstrator's visual perspective, i.e., the subject might have interpreted the gaze cue as a sideways look rather than a look behind the barrier. Thirdly, subjects might have understood the demonstrator's visual perspective, but might not have been willing to move around the barrier. To look behind the barrier, subjects would have had to walk through a relatively narrow space between the barrier and the mesh dividing them from the demonstrators. This could have been avoided by the subjects due to spatial confinements as well as the closeness to the demonstrator bird. The authors claim that the birds were comfortable with moving around the barrier. However, it remains unclear whether this was also tested with the mesh divider and the demonstrator bird present.

Future studies will need to establish whether Northern bald ibises are indeed not capable of geometrical gaze following. Moreover, more studies on a variety of distantly related avian species will be needed to support our hypothesis that visual perspective taking is a shared cognitive trait among all birds.

The presence of geometrical gaze following in birds, but its absence in alligators and other reptiles, suggests a later evolution of this skill compared to gaze following into the distance. This further supports the hypothesis that geometrical gaze following involves more complex neurocognitive mechanism than gaze following into the distance as suggested by Povinelli and Eddy (1996).

Our findings indicate two different evolutionary patterns of the two gaze following modes. Gaze following into the distance likely has a shared evolutionary root for all vertebrates, though the exact point of emergence of this skill is not clear without more research on other vertebrate classes. Geometrical gaze following, on the other hand, likely evolved parallelly in mammals and birds, while being absent in other groups.

4.5 Checking back and the role of the cerebellum

Apart from our findings on gaze following in PAPER I, we observed that all tested bird species, but not the alligators, were "checking back" with their demonstrators. In other words, after following the indicated gaze direction, they looked back at the demonstrator. Such gaze alternations could occur repeatedly within one trial. This is the first description of checking back in any bird species.

This behaviour has first been discovered in human infants by Scaife and Bruner (1975). The authors observed that children were looking back at the experimenter when they could not identify anything of interest in their line of sight. Children first engage in such double looks at 8 months old (Scaife & Bruner, 1975). Developmental psychologists commonly associate this behaviour with an understanding of the deictic nature of gaze, i.e., that it is pointing towards a target in the environment. This hypothesis has been strengthened by reports of infants pointing at an object after following experimenters' gazes before checking back with them (Butterworth & Cochran, 1980). This can be interpreted as a form of double-checking the correctness of the gaze target.

In animals, checking back has first been described by Call and colleagues (1998) in chimpanzees (*Pan troglodytes*). They defined it as a subject looking back to the experimenter "when there were no interesting objects in the human's line of sight" (Call et al., 1998, p. 90). Checking back has since been described in all other great ape species: bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla*), and orangutans (*Pongo pygmeaus*; Bräuer et al., 2005; Okamoto-Barth et al., 2007), gibbons: pileated gibbons (*Hylobates pileatus*; Horton & Caldwell, 2006), and some Old World monkeys: Diana monkeys (*Cercopithecus diana*; Scerif et al., 2004), and long-tailed macaques (*Macaca fascicularis*; Goossens et al., 2008). No evidence of checking back has been found in two species of New World monkey: spider monkeys (*Ateles geoffroyi*) and capuchin monkeys (*Cebus apella*; Amici et al., 2009), though this might have been a methodological artefact due to two reasons.

Firstly, in that study, checking back was defined as subjects following the demonstrator's gaze direction, looking back at them, and then looking in the gaze direction again. However, the experimenter held up a piece of food while they were presenting their gaze cue. While this most likely caught the subject's attention at the beginning of the trial, it might have been problematic for checking back. When looking back at the experimenter, the food might have attracted the subject's attention and might have kept it from retracking the experimenter's gaze direction. Moreover, the authors reported that one spider monkey repeatedly checked back, suggesting the presence of this behaviour in these animals.

In primates, checking back is commonly interpreted in the same way as in human children. In line with this interpretation, several reports describe more instances of checking back in situations where gaze cue and target referred to different locations (Scerif et al., 2004; Horton & Caldwell, 2006), i.e., where the expectancy of detecting a gaze target is violated.

Okamoto-Barth and colleagues (2007) designed an experiment to test great apes' understanding of others' visual perspectives through checking back. They investigated subjects' checking back responses in a "meaningful" and "meaningless" condition. In the meaningful condition, the demonstrators' line of sight was obstructed by a barrier. Thus, their gaze had no target. Subjects were expected to check back more often in this condition, as a sign of their surprise about the lack of a gaze target. In the meaningless condition, the barrier had a window through which the demonstrator (and the subject) could see an object. The apes were expected to check back less often in this condition, as they could easily detect the gaze target in the demonstrator's line of sight. Chimpanzees and bonobos were acting according to the experimenters' predictions. Orangutans and gorillas, however, appeared insensitive to the differences in the conditions. This indicates that there are different levels in the understanding of others' visual perspectives even among closely related species. Future studies should follow similar experimental designs to obtain a better understanding of their subjects' perspective-taking skills in the presence of checking back behaviours.

Different levels of perspective-taking capacities might impact the level of surprise animals experience when facing an expectancy violation. In PAPER I, we propose an explanation for the surprise in gaze following situations causing checking back behaviours. The surprise could be caused by the violation of social predictions. Animals might check back due to a discrepancy between a social prediction – to find a target in the other's line of sight - and the sensory feedback – not finding anything interesting in the observed gaze direction.

The results of PAPER I suggest that birds can form social predictions based on social cues, while alligators, representatives of the crocodylians, failed to do so – at least they exhibit no behavioural signs of the violation of such a prediction. This difference is likely caused by differences in neuroanatomical features between birds and crocodylians. As described above (see 2.3), avian brains have evolved significantly higher numbers of neurons compared to non-avian reptiles. The biggest proportional increase in neurons thereby took place in the cerebellum (Kverková et al., 2022).

The function of the cerebellum has long been believed to primarily lie within motor control. However, the past decades have accumulated evidence that this structure is involved in a variety of cognitive processes, such as executive control, language, working memory, learning, pain, emotion, and addiction (Strick et al., 2009). The cerebellum is interconnected with the cerebral cortex through parallel loops. Through these loops, it simultaneously receives input from and sends projections to the cerebrum (Welniarz et al., 2021). This highly regular cytoarchitecture indicates one single underlying mechanism to its numerous functions (Diedrichsen et al., 2019).

One theoretical framework proposed as such a unifying mechanism are so-called internal forward models. These models are top-down processes, i.e., they anticipate behavioural outcomes based on prior information. Forward models allow for quick updating through error processing as they do not underly feedback control (Wolpert et al., 1998). A reliance on feedback would lead to time delays of 50 and 300 ms between motor command and sensorimotor feedback (Wolpert & Flanagan, 2001). Instead, forward models rely on predictions and are subsequently updated in the case of a prediction error (e.g. Roth et al., 2013). Such models continuously strive to minimize the discrepancy between prediction and feedback. This discrepancy is also called variational free energy (Friston et al., 2017).

An example of an internal forward model from a grasping situation could look as follows: the motor system generates a motor command, while the forward model receives an efference copy of this command. The motor system controls the action, while the forward model forms a prediction about the outcome of the action. The sensory feedback of the motor system is subsequently compared to the predicted sensory feedback of the forward model. In the case of a discrepancy between the two, a prediction error is detected and the forward model is updated (Nowak et al., 2013). Updating can either be achieved through changing one's beliefs about the situation, i.e., changing the prediction, or through changing the world to match the prediction. Taking action to align the world with the prediction is called active inference (Friston et al., 2017).

The theoretical framework of internal forward models can be applied to our findings on checking back in birds. When observing a demonstrator gazing towards a location in the environment, an internal forward model forms a prediction about discovering a gaze target in the observed gaze direction. A mismatch between the prediction and the sensorimotor feedback from the eyes is registered when no gaze target is detected. Checking back could thus represent an attempt to update the model through active inference by retracking the gaze direction.

Taken together, in PAPER I, we for the first time describe that birds exhibit a gaze following repertoire on par with apes, including low- and high-level gaze following, visual perspective taking and checking back. We moreover propose an explanation for the presence of these sophisticated skills in birds in light of their neuroanatomy. More nuanced studies will be needed to fully understand birds' understanding of others' visual perspectives (similar to the study by Okamoto-Barth et al., 2007), as well as the involvement of the cerebellum in social predictions of birds.

4.6 The development of gaze following

Human infants begin to follow others' gaze directions very early. Similarly, low-level gaze following has been shown to develop early in the ontogeny of mammals (e.g. rhesus macaques and chimpanzees: Tomasello et al., 2001; wolves: Range & Virányi, 2011) and birds (e.g. ravens: Bugnyar et al., 2004; rooks: Schloegl et al., 2008; greylag geese: Kehmeier et al., 2011).

Few studies have focused on the development of gaze following skills in animals, and most of these studies have used human experimenters as demonstrators. However, this practice might be problematic, as gaze following skills arguably evolved to facilitate information transfer between conspecifics. It is thus expected that young animals are initially more attuned to conspecific gaze cues. This might cause differences in the development of con- and allospecific gaze following.

Moreover, our findings on checking back in all tested bird species of PAPER I raised questions about the presence, development, and sophistication of this behaviour in other avian species. Ravens are an interesting species in the field of comparative cognition, as their cognitive skills have been shown to match those of great apes despite their significantly smaller brains (e.g. Kabadayi & Osvath, 2017; Pika et al., 2020) and vastly differing neuroanatomy (Güntürkün & Bugnyar, 2016).

In PAPER III, we compared the development of gaze following into the distance, with human and conspecific demonstrators, as well as the presence, development, and impact of different demonstrators on checking back in juvenile common ravens (*Corvus corax*).

We did not find ontogenetic differences in the onset of con- and allospecific gaze following. Both developed between 5.5 and 8 weeks and thus after fledging. However, it took ravens significantly longer to co-orient with humans compared to conspecifics. This suggests that the gaze following system is indeed attuned to conspecifics. In a follow-up study it would be interesting to investigate whether this discrepancy diminishes over time or whether the same pattern is present in adult ravens.

Additionally – and quite extraordinarily – we found checking back as early as 30 days old, when ravens first started to occasionally co-orient with their siblings. Applying the above-mentioned theoretical framework of internal forward models (see 4.5) this result implies that the capacity to form social predictions already develops prior to fledging in ravens.

In comparison, human children only start to check back at 8 months old (Scaife & Bruner, 1975). The only other account of the ontogeny of checking back stems from great apes (Bräuer et al., 2005). All four great ape species only began to check back as juveniles, between 5 and 10 years old. This implies that the ability to form social predictions develops significantly earlier in at least one bird species compared to great apes. As ravens are somewhat outstanding in their cognitive capacities, more studies will be needed to investigate the development of this behaviour in other avian species.

Additionally, ravens check back significantly more often with conspecifics than humans. This further supports our argument that the gaze following system is attuned to conspecifics and that ravens generally exhibit heightened social attention towards other ravens. It could also suggest that ravens form more robust and/or different social predictions about their conspecifics than about humans. What exactly causes the differences in social predictions about con- and allospecific demonstrators is unclear from our data. Again, it would be interesting to investigate whether this changes throughout the ontogeny of ravens.

Taken together with the findings of PAPER I, this study strengthens our argument that birds possess extraordinary visual socio-cognitive skills. We now have gathered evidence from five distantly related avian species exhibiting checking back behaviours. This suggests a shared behavioural trait among birds. Our results indicate that birds form robust social predictions about conspecifics – likely based on internal forward models. They develop this skill significantly earlier than great apes and even human infants. In other words, gaze following skills in birds are not only sophisticated, but also develop extraordinarily early.

Kehmeier and colleagues (2011), for example, found that greylag geese were following the gazes of conspecifics as early as 10 days old. This is to our knowledge the earliest account of gaze following in any animal. The authors explained this very early onset with the precociality of this species that requires early predator avoidance strategies.

Future studies would benefit from starting developmental gaze following experiments even earlier than our study in PAPER III, while birds are still in the nest. Moreover, more studies on species with different life histories, such as precocial and altricial species, are needed to understand differences in ontogenetic onsets of gaze following responses.

5 Play

While play can be a solitary behaviour, it often involves several individuals and can represent a considerable proportion of a species' social repertoire. The proclivity of a species to play socially can thus provide insights into its social behaviours and the accompanying socio-cognitive capacities.

The past century has accumulated evidence of play from all vertebrate classes. Despite this, the functions of this behaviour remain unclear. A variety of theories have been brought forward over the years, ranging from juveniles practicing "serious behaviours" (Thompson, 1998) to burning off excess energy (Spencer, 1872). While many of these theories likely explain a part of the adaptive value of play, none of them has been able to explain it fully.

To gain an understanding about the evolution of play and its functions, it is important to study species in key phylogenetic positions. As described above, palaeognath birds occupy such a position due to their shared features with early birds and to a degree dinosaurs (see 2.2). In PAPER IV, we provide the first ever systematic description of play in a palaeognath bird, the greater rhea, and use our findings to hypothesize about the evolution of play and its connected socio-cognition.

5.1 Definitions of play

Play is an unusual behavioural state. Despite its apparent lack of function, play behaviours have been observed in all vertebrate classes, including mammals (e.g. Byers, 1999; Lewis, 2000; Himmler et al., 2016), birds (e.g. O'Hara & Auersperg, 2017), reptiles (e.g. Dinets, 2015), and fishes (e.g. Burghardt, 2015).

Before the ultimate functions of play can be discussed, one needs to define what this term entails. It might seem like humans can intuitively recognize play, raising the question for the need of a definition. However, especially in those species that are not classically labelled as "playful", such as reptiles and fishes, it can be difficult to recognize play. When, for example, observing a Komodo dragon (*Varanus komodoensis*) tossing around a bucket (as described in Burghardt et al., 2002), it is not immediately clear whether this is a case of play, object exploration, or misguided aggression.

As play can take on many different forms, one single definition might be too narrow to fully capture the phenomenon. For that reason, Burghardt (2001) determined five criteria that need to be fulfilled for a behaviour to be classified as play. The first criterion of play is that the behaviour is not fully functional. Secondly, the behaviour appears spontaneously, voluntarily and is pleasurable or rewarding to the player. Thirdly, the behaviour differs structurally from the serious performance. It is, for example, exaggerated or modified. The fourth criterion is that the behaviour appears repeatedly, but not stereotypically. Finally, the fifth criterion postulates that the animal performing the behaviour must be healthy and free from stress.

Behaviours classified as play through these criteria, are additionally commonly divided into three categories: locomotor, object, and social play. Locomotor play describes all play behaviours revolving around locomotor movements. It often includes exaggerated forms of running or leaping. Object play refers to manipulations of non-novel objects, such as mouthing, pawing, or tossing. Social play describes play behaviours directed towards other individuals (Burghardt, 2005). Common forms of social play include chasing, play fighting, and nipping.

By dividing play behaviours into these three categories, some aspects of the behaviour might get oversimplified. Chimpanzees, for example, have been found to engage in object play with sticks. However, young males engage in play resembling agonistic interactions, while juvenile females interact with sticks in a “maternal” way, resembling the way human infants interact with dolls (Kahlenberg & Wrangham, 2010). To label both as object play diminishes the complexity of these behaviours. Furthermore, play categories are often combined, such as co-manipulations of an object that are both object and social play. Nevertheless, dividing play into three categories is a useful method when first describing a species’ play repertoire. To this end, in PAPER IV, we adhered to these three categories and Burghardt’s five criteria to identify and describe play in greater rheas.

5.2 Archosaurian play

All vertebrate classes, including the archosaurs, play (Burghardt, 2005). Crocodylians have been found to be surprisingly playful. All three categories of play have been described in a variety of species (Dinets, 2015). With respect to locomotor play, subadult American alligators have been observed to repeatedly slide into water (Burghardt, 2005), and a hatchling broad-snouted caiman (*Caiman latirostris*) repeatedly let itself be drifted across a pool through the current of an outflow pipe (Dinets, 2015). Accounts of social play are exclusively anecdotal, though Dinets (2015) lists personal communications and observations of behaviours indicative of chasing, play fighting, and riding on each other's backs. Object play appears to be the predominant mode of crocodylian play. A Cuban crocodile (*Crocodylus rhombifer*) has, for example, been observed pushing around a large floating ball (Burghardt, 2005), and American alligators have been seen playfully interacting with a water stream through snapping at it and moving their heads in and out of the water (Dinets, 2015).

Object play appears to generally be the predominant play category of reptiles, as described in Komodo dragons (Burghardt et al., 2002), Nile soft-shelled turtles (*Trionyx triunguis*; Burghardt et al., 1996), and sea turtles (*Caretta caretta* and *Chelonia mydas*; Mann & Mellgren, 1997). Many reptilian species are solitary for the majority of their lives, which explains the rarity of social play. Moreover, energy constraints caused by ectothermy might cause the infrequency of locomotor play. This could also explain why most of the described examples of locomotor play are predominantly passive, i.e., letting water or gravity move the body.

The other extant archosaurs – the birds – play too. Some species have even been identified as some of the most vigorous players in the animal kingdom (e.g. ravens: Ficken, 1977; Heinrich & Smolker, 1998). However, one avian group that has to date been completely overlooked in the study of play are the palaeognath birds. Though some reports suggest that palaeognaths engage in play (Franz Sauer, 1969; Bohl, 1970; Hallager, 2010; Timothy, 2019), it has never been formally studied. To partly mend this gap, in PAPER IV, we provide the first systematic study of play behaviours in a palaeognath bird, the greater rhea.

We found that juvenile rheas initiate play significantly more often than adults, which is common among animals and humans (Burghardt, 2005). In contrast to non-avian reptiles, the predominant category was locomotor play in the form of play running. Despite locomotor play being a form of solitary play, the observed play running bouts exhibited were characterized by a considerable component of sociality. The majority of play bouts were contagious, i.e., elicited play in siblings.

Moreover, during these contagious play running bouts, one third of the times, the birds did not all move in the same direction but ran into individually different directions. Osvath & Sima (2014) introduced a theoretical framework stating that if one category of play elicited a different category of play in others it is indicative of emotional contagion, i.e., a spread of a playful mood rather than behavioural synchronization. Emotional contagion is a building block of empathy as it requires the recognition and matching of emotional states (Preston & De Waal, 2002). While locomotor play in our study elicited the same category of play, the different directions suggest an involvement of processes beyond mere behavioural contagion. In the case of behavioural contagion, it would be expected that the birds all move in the same direction. Nevertheless, alternative explanations for this observation exist. Running in different directions might serve as training for anti-predatory responses through practicing unpredictable behaviours (Humphries & Driver, 1970), or might represent a form of self-handicapping (Spinka et al., 2001).

Moreover, juvenile greater rheas actively engaged in social play, though to a smaller degree as locomotor play. They pecked each other playfully, wrestled, and bumped into each other. Social play only started when the birds were around 10.5 weeks old, while locomotor play was already present at study onset around 6 weeks old. Despite this ontogenetic discrepancy, social play still developed relatively early in the rheas' ontogeny compared to the species' sexual maturity at 20 to 24 months (Sales, 2006).

Our findings about social components in the play behaviours of these birds are suggestive of the species' socio-cognition. Firstly, the presence and early ontogeny of social play indicates an important role of sociality in their lives. Indeed, greater rheas live in mixed flocks, while forming harems with one male and several females during breeding season (Sales, 2006). Consequently, it is expected that this species possesses socio-cognitive skills allowing them to navigate social group living. As shown in PAPER I, greater rheas are capable of visual perspective taking and form social predictions about their flock mates. Additionally, our observations on play suggest primitive forms of emotional contagion in these birds implying the capacity for recognition and matching of others' emotional states. Future studies on greater rheas should explicitly focus on these aspects of their social cognition to confirm our hypotheses about their cognitive capacities.

PAPER IV includes the first description of play in adult and juvenile representatives of a palaeognath species. More studies on a variety of palaeognath birds of different ecologies, such as solitary cassowaries or volant tinamous, will be needed to identify whether this is a common play pattern in this group and how it relates to the socio-cognitive capacities of different species.

5.3 Functions of play: Predictive processing

The ultimate functions of play remain unclear. The theories brought forward over the years are diverse, but many hypotheses revolve around practicing serious behaviours in the juvenile period.

Despite many attempts to test for such training effects of play, many studies have failed to empirically prove this hypothesis. For example, one study on domestic cats (*Felis silvestris catus*), that were exposed to one prey item as kittens, did not show improved predation on other prey items as adults (Caro, 1980). A different study on meerkats (*Suricata suricatta*) found no effect of play fighting in juveniles on their fighting success later in life (Sharpe, 2005).

However, it should be noted that some studies suggest an effect of play in the juvenile period on some social behaviours in adults. Blumstein and colleagues (2013), for example, found a correlation between the outcome of play fights in juveniles and later dominance relationships in yellow-bellied marmots (*Marmota flaviventris*). Maternal territorial behaviour and reproductive success of Belding's ground squirrels (*Urocitellus beldingi*) have been found to depend on juvenile social play (Nunes, 2014). Play fighting with same-sex litter mates influences reproductive success in male mouse lemurs (*Microcebus murinus*; Perret, 2021). These examples show that at least in the social domain, the so-called "practice hypothesis" has found some support. Nevertheless, no support for this hypothesis has been identified in other categories, such as object and locomotor play.

New evidence from studies on rats and hamsters suggests that play in the juvenile period positively influences the development of executive functions mediated by the prefrontal cortex (e.g. Bell et al., 2010; Baarendse et al., 2013; Burleson et al., 2016; Schneider et al., 2016; Stark & Pellis, 2020). Thus, play in the juvenile period might improve emotion regulation, attention, information tracking and decision making (Vanderschuren & Trezza, 2013; Pellis et al., 2014). This hypothesis contradicts the "practice hypothesis" of play, as it suggests that the benefits that adult animals engaging in play as juveniles experience are not caused by practice, but by improved cognitive skills.

Recently, Andersen and colleagues (2022) used a neurocognitive framework to explain the adaptive value of play, the predictive processing framework (PP). PP generally describes the brain as constantly striving to minimize the error between predictions about the environment and its actual state (Friston, 2010; Clark, 2013; Hohwy, 2013). PP can also be applied to play. Andersen and colleagues (2022) argue that when playing, agents are deliberately creating surprising situations. These situations provide players with opportunities to learn about the environment and form predictions about it. Simultaneously, play follows specific rules and constraints (Burghardt, 2005). This suggests that there is a "right" amount of surprise (the authors call it a "sweet spot") in play, that is neither too predictable, nor too chaotic. The authors moreover see an explanation for why play is perceived as pleasurable in this framework. They argue that through creating surprising situations of the "right" amount of uncertainty, agents are reducing prediction error faster than expected. This is inherently perceived as positive and thus fun. This hypothesis was backed up by AI studies that found that error reduction motivates an agent to play and explore (e.g. Oudeyer & Smith, 2016). Play can thus be interpreted as a way of niche construction where players alter their physical and social environment to generate, test and update predictions about the world.

Predictive processing is in line with the previously described internal forward models (see 4.5). Both theoretical frameworks describe top-down processes to minimize prediction errors. In play, these errors are created intentionally, which leads to fast updating of the predictions. Through play, agents can thus practice to form predictions about a variety of situations they might not have encountered naturally.

Hence, predictive processing is a neurocognitive framework that can explain play, but also applies to processes of social information gathering such as gaze following.

6 Implications for social cognition in dinosaurs

The studies in this thesis on socio-cognitive capacities in Archosauria were executed with the overarching goal of providing glimpses into the social cognition of extinct dinosaurs and thereby shedding light on principles of the evolution of social cognition.

Over the course of three empirical studies (PAPER I, III, and IV), we investigated social information gathering and perspective taking, the development of such skills and their attunement to conspecifics and play with its implications for social cognition. The final chapter will discuss what implications these findings have for the social cognition of dinosaurs.

6.1 Gaze following

In PAPER I, we compared the gaze following repertoires of five archosaur species. The findings of this study, that both alligators and all tested bird species followed gaze into the distance in combination with the wealth of studies on other amniotes capable of this skill strongly suggest that dinosaurs were at least capable of low-level gaze following.

The presence of gaze following into the distance in alligators, which represent an optimal neurocognitive model for stem archosaurs, indicate that the common ancestor of crocodylians and birds already shared this trait 325 MYA. However, the capacity to follow gaze into the distance likely emerged even earlier than this, as inferred from the shared subcortical pathway in the brains of all vertebrates mediating fast, reflexive co-orientations with observed gaze directions (for a more detailed discussion see 4.4). Experimental evidence from mammals, reptiles, and birds implies that at least all amniotes are capable of low-level gaze following. More studies on amphibians and fishes are needed to broaden this argument to all vertebrate classes. Nevertheless, it can be safely assumed that dinosaurs followed each other's gazes into the distance.

Geometrical gaze following diagnostic of level I visual perspective taking, on the other hand, was only found in birds, but not in alligators. In Chapter 4.4 we argue that this skill has likely evolved in parallel in birds and mammals but was not present in stem archosaurs. When exactly high-level gaze following skills evolved within Dinosauria is hence difficult to pinpoint. This is partly due to our lack of knowledge about brain structures mediating spatially sophisticated gaze following in birds.

Assuming from the many shared features of the brains of palaeognath birds and non-avian paravian dinosaurs, such as dromaeosaurids and troodontids (see 2.4), it is, however, likely that these dinosaurs possessed a gaze following repertoire comparable to that of palaeognath birds. That would place the evolution of such skills in the Middle Jurassic, around 174-163 MYA.

Alternatively, the evolution of the avian hyperpallium ("Wulst"), a structure central to visual and somato-sensory integration (e.g. Reiner et al., 2005; Gold et al., 2016), might have paved the way for the emergence of visual perspective taking. The timing of the evolution of this structure remains unclear. As it can be found in the brains of both palaeognaths and neognaths, it must have latest evolved before the split of these two groups around 110 MYA (e.g. Yonezawa et al., 2017). More studies on avian neuroanatomy will be needed to confirm the involvement of the hyperpallium in visual perspective taking, along with paleontological studies working on pinpointing the emergence of this structure.

Whether checking back evolved earlier or later than geometrical gaze following is at the present time unclear. It is, however, to be expected that an understanding of the referentiality of gaze is a prerequisite for visual perspective taking. If the observer did not expect to find a gaze target behind the barrier, it would not have an incentive to move around it. Indeed, in human infants, checking back develops at 8 months, and thus considerably earlier than geometrical gaze following that only emerges around 18 months (Butterworth & Cochran, 1980; Butterworth & Jarrett, 1991). PAPER I and III are the first accounts of checking back in birds, but it appears that at least in ravens, this behaviour develops, just as in humans, earlier than geometrical gaze following. In this case, checking back is expected to have evolved earlier than geometrical gaze following and the accompanying visual perspective taking skills. More studies focussing on the phylogenetic distribution, development, and complexity of checking back are needed to allow for more robust hypotheses about the evolution of this behaviour.

In mammals, visual perspective taking has only been described in some primates (apes and Old World monkeys) and canids (wolves and dogs); lineages that diverged after the end-Cretaceous extinction. This points towards an earlier evolution of such skills in Sauropsida than in Synapsida. As briefly described in PAPER I, an earlier evolution of such skills in Sauropsida would not be surprising due to the excellent visual skills of birds. Vision is a central sensory system to birds as they use it for navigation and migration, foraging, to avoid predators, and social behaviours (Shimizu & Bowers, 1999). The importance of vision is evident from birds' excellent visual acuity, colour vision, discrimination ability, and visual memory (Donovan, 1978; Hodos, 1993; Wasserman, 1995).

Many bird species are tetrachromates, i.e., they have four different types of cones in their retina. Additionally, they have coloured oil droplets that filter light before it hits the cones. This way, the number of functional spectral sensitivities could be even higher than the number of different cones (Güntürkün, 2000). In contrast, most mammals only have two types of cones, rendering most mammalian species only capable of dichromatic colour vision. Only some diurnal primates and marsupials have evolved a third cone allowing for foraging based on vision (Heesy & Ross, 2001; Arrese et al., 2002).

Birds moreover possess a fovea; some even have two. This structure contains photoreceptors enabling high visual acuity. The retina of most mammals does not contain this structure. Only some diurnal primates (tarsiers, monkeys, apes) have evolved a fovea (Bringmann et al., 2018). However, the density of ganglion cells in the avian fovea exceeds that of even the most visual mammals, such as humans and other primates (Güntürkün, 2000).

The refinement of the visual systems of primates with colour vision and fovea represent adaptations to a diurnal life, while early mammals were nocturnal and thus did not exhibit such adaptations. Simultaneously, primates have the most complex gaze following skills with visual perspective taking and checking back. These parallels suggest that a refined visual system is needed to evolve visual perspective taking skills. This offers a plausible explanation for an earlier evolution of such skills in Sauropsida.

Firstly, reliance on visual cues is more sensible in diurnal species rather than in nocturnal ones. A visual system adapted to nocturnal vision has high light sensitivity, but, as a trade-off, has a low resolution (Martin, 2017). Nocturnal species can thus not attend to as much detail in the environment as diurnal ones. Secondly, the proclivity to attend to others is higher in animals with improved visual skills, as head and eye movements are easier to detect. Lastly, the value of social information from an individual with enhanced vision is higher, as such an individual can attend to more details in the environment. An animal with poor vision cannot provide reliable information about, for example, the location of food, as it can itself not find a food source based on its vision.

Additionally, the sophistication of the primate visual system co-evolved with an increase of cerebellar neurons (Barton, 2012; Barton & Venditti, 2014), similar to the increase in avian brains (Kverková et al., 2022). This supports the connection we have earlier established between a refined gaze following repertoire and internal forward models. The improved visual skills and connected ability to extract social information likely allowed for more robust social predictions, allowing primates comparable visual socio-cognitive capacities as birds, while other mammals have not evolved such skills.

More studies on mammalian species are needed to establish the ability to generate internal forward models in this group.

6.2 Play

In PAPER IV, we found that one species of palaeognath bird, the greater rhea, plays at least in their juvenile period with a noticeable component of sociality. This was apparent in social play bouts, but also in the high rate of play contagion in locomotor play. For the sake of being able to hypothesize about extinct dinosaurs, we will in the following assume that all palaeognaths play in a comparable manner.

Play is commonly connected to parental care. Extensive postnatal parental care is widespread among the most playful species, such as humans and non-human primates, but also birds (Burghardt, 2005). Palaeognaths exhibit a relatively rare parental care system. In nearly all species, males incubate the eggs and single-handedly care for their offspring. Only in ostriches, females and males take turns in incubating the eggs – the lightly coloured females during the day, the black males during the night. After hatching, the dominant female is sometimes involved in parental care. Similarly, in kiwi, females have been observed to sometimes assist in parental care. For the rest of Palaeognathae, incubation and chick-rearing is exclusively performed by males (Valdez, 2022).

The paternal care system of palaeognath birds likely has its origins in dinosaurs. Several lines of research are supporting this hypothesis. Firstly, fossils of adult oviraptorosaurs and troodontids – both maniraptoran theropods - have been found on top of nests in brooding positions, indicating that these dinosaurs were incubating their eggs (Norell et al., 1995; Varricchio et al., 1997). Moreover, histological analyses revealed that these individuals were likely male (Varricchio et al., 2008). Female archosaurs resorb calcium and phosphorous from their skeletons during egg formation (Simkiss, 1967; Wink & Elsey, 1986). The incubating fossils, however, did not have residual medullary bone or resorption cavities, and were thus most likely male. Lastly, the clutch size of maniraptoran theropods is equivalent to that of extant species with biparental care or that of palaeognaths (Varricchio et al., 2008). Considering the above-mentioned similarities with palaeognath parental care systems, it is more plausible that these large clutch volumes are the result of several females laying their eggs into communal nests, like in some palaeognaths, such as greater rheas. It is thus likely that the parental care system observed in Palaeognathae has been retained from maniraptoran dinosaurs.

This implies that juvenile maniraptorans grew up under comparable socio-ecological circumstances as palaeognath birds, with several clutchmates and under the supervision of a male. This creates an ideal environment not only for extensive play in general, but more specifically for social play. Considering the likely presence of comparable socio-cognitive skills in these dinosaurs and palaeognath birds, it would not be surprising if juvenile maniraptorans played in a similar fashion as the juvenile greater rheas. That would entail a noticeable social component in their play, including frequent play contagion, but also social play bouts.

6.3 Evolutionary roots of predictive minds

The findings of this thesis suggest that early birds and likely non-avian paravian dinosaurs exhibited complex visual socio-cognitive skills, making them proficient social information gatherers. They moreover likely developed these skills early in their ontogeny and supported the development of executive functions through social play in the juvenile period.

What unifies these findings is the evolution of predictive power in the avian brain. We found behaviours suggestive of internal forward models and play as a means of developing predictions involved in these models. Such predictive skills were found in all tested bird species, but not alligators.

This implies an evolutionary trend towards more robust predictive processing throughout avian brain evolution. Internal forward models are suggested to be governed by the cerebellum. Avian brains have dramatically increased numbers of neurons in this brain structure compared to crocodylians. This implies that this increase and consequently the emergence of predictive processing capacities took place somewhere within Dinosauria. It is difficult to pinpoint this evolutionary step exactly, but due to at least non-avian paravian dinosaurs likely being endothermic (e.g. Rezende et al., 2020) and increases in neuronal numbers being closely related to endothermy (Kverková et al., 2022), it is possible that the brains of non-avian paravian dinosaurs already had increased numbers of cerebellar neurons.

However, predictive processing is beneficial to many different species and is most likely not an exceptional cognitive capacity only found in cognitively advanced animals. On the contrary, complex predictive processing, such as planning, most likely evolved progressively from simpler error correction circuits, such as the release of a hormone in response to the detection of a certain physiological state like hunger. These circuits likely evolved very early in the evolution of brains and cognition as they are imperative to the survival of an animal. Throughout evolutionary time, predictions and error corrections likely became more complex, allowing animals to apply predictive processing not only to physiological processes, but also to their physical and social environment (Pezzulo et al., 2021).

The gradual improvement of predictive processing underlies genetic constraints, as well as the selective forces of new challenges animals are facing. Such challenges could for example be more complex bodies and ecological niches. Arguably, one big step towards such new situations including novel environmental challenges was when vertebrates became land dwellers around 365 MYA.

A common theme in the evolution of more complex predictive models, such as internal forward models, is the duplication of simpler error correction circuits building multiple, parallel sensorimotor loops. This means that predictive models consist of several smaller models that are specialized in particular behaviours. Early brains might hence have possessed multiple, replicated sensorimotor circuits (Pezzulo et al., 2021).

This pattern can still be recognized in the ganglia-thalamocortical circuits of modern brains, as well as in the parallel loops of the cerebellum. This evolutionary remnant further strengthens our argument about the involvement of the cerebellum in the formation of internal forward models. The drastic increase in cerebellar neurons of birds and possibly already non-avian paravian dinosaurs might be diagnostic of an evolutionary step towards higher predictive power within this lineage. More studies are needed to compare the evolution of predictive brains in mammals and birds to identify evolutionary trends and their remains in modern brains. Higher predictive power could be one of the reasons why dinosaurs were successful for such a long time and why some of their living descendants are among the cleverest animals on this planet.

In the light of principles of cognitive evolution, an evolutionary trend towards increased predictive power and error reduction appears to be a more sensible driver for cognitive evolution than social group living as proposed by the social intelligence hypothesis. Animals undoubtedly face complex challenges when living in social groups. However, these challenges can be, like other uncertainties in the environment, be solved through constantly striving for a minimization of prediction error. The findings of this thesis support predictive processing as a possible underlying principle of cognitive evolution, as it explains various factors investigated in this work, such as social information gathering and play.

7 Concluding remarks

This thesis represents some of the first attempts at studying dinosaur cognition. When drawing inferences about non-fossilizing traits of extinct species, one must be cautious. In this thesis, we phylogenetically bracketed dinosaurian cognition as closely as possible by studying aspects of the social cognition of extant archosaurs.

Even though the species chosen for this thesis are the best neurocognitive models of non-avian paravian dinosaurs that we have, they are still only that: a model - although a true and living one. Future studies will need to compare a wider range of palaeognath and crocodylian species to establish whether the skills and behaviours described in this thesis are shared among members of their respective clade.

Simultaneously, we drew many parallels to mammals and their evolutionary trajectories. It is thus just as important to study these topics more deeply in mammals. This would aid in manifesting the notion that primates are distinct from other species in their cognitive skillset. Secondly, the study of neurocognitive models of ancestral species, such as marsupials and monotremes, would serve a similar purpose as studying palaeognath birds and crocodylians – to obtain an understanding of ancestral cognitive capacities within a group. In fact, they would even yield stronger results compared to our studies, as we used crocodylians as a model for the earliest ancestors of dinosaurs, though they are members of a sister-taxon. Marsupials and monotremes are both mammalian taxa and are thus even better neurocognitive models for ancestral mammals.

Finally, I would like to propose that more studies focus on connecting their findings to neurocognitive measures, such as neuronal numbers. By using this method, it is possible to uncover evolutionary steps enabling cognitive capacities and draw parallels to other lineages.

We are only at the beginning of the quest of shedding light on the evolution of cognition. By joining forces with neuroscientists, palaeontologists, and developmental psychologists, we have a good chance at solving the puzzle of cognitive evolution.

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Paper I

Gaze-following in Archosauria – alligators and palaeognath birds suggest dinosaur origin of visual perspective taking

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Abstract

Taking someone else's visual perspective marks an evolutionary shift in the formation of advanced social cognition. It enables using others' attention to discover otherwise hidden aspects of the surroundings and is foundational for human communication and understanding of others. Visual perspective taking has also been found in some other primates, a few songbirds, and some canids. However, despite its essential role for social cognition, visual perspective taking has only been fragmentedly studied in animals, leaving its evolution and origins uncharted. To begin to narrow this knowledge gap, we investigated extant archosaurs by comparing the neurocognitively least derived extant birds – palaeognaths – with the closest living relatives of birds, the crocodylians. In a gaze-following paradigm, we showed that palaeognaths engage in visual perspective taking and grasp the referentiality of gazes, while crocodylians do not. This suggests that visual perspective taking originated in early birds or non-avian dinosaurs – likely earlier than in mammals.

Keywords: gaze_1, evolution_2, social cognition_3, perspective taking_4, archosaurs_5

1. Introduction

The advent of visual perspective taking represents a key event in the evolution of social cognition. It marks the transition from a unidirectional to a multidirectional frame of reference in social situations, providing information about the world that would otherwise remain out of reach, and offering new beneficial ways of navigating social environments. Among other things, perspective taking lays the foundation for so-called referential communication, where one refers to a jointly perceived object or event. It also forms the bedrock for ascribing beliefs and mental states to other individuals. However, the most basic form of perspective taking, upon which further skills rely, is the generalization from an egocentric to an allocentric visual viewpoint. Put simply: appreciating that someone else can see what you cannot, and consequently being able to recognize what the other one is attending to. This ability can be identified in the ways humans and other animals follow the gazes of others. Visual perspective taking is revealed in the most advanced form of gaze-following, where the gaze target of the other is blocked from the onlooker's view, causing the onlooker to reposition itself to see what the other is seeing. The ability to take someone else's visual perspective in this way, is known as geometrical gaze-following (e.g. Tomasello et al., 1999).

Despite its foundational role in social cognition, studies on visual perspective taking have largely lacked a phylogenetic focus, leaving a patchy understanding of cognitive evolution in general. To date, geometrical gaze-following has only been found in apes, monkeys, wolves (and dogs), corvids and starlings (Bugnyar et al., 2004; Bräuer et al., 2005; Burkart & Heschl, 2006; Range & Virányi, 2011; Butler & Fernández-Juricic, 2014) – diverse lineages that all have arisen after the end-Cretaceous extinction, a period witnessing extensive neurocognitive evolution (Kverková et al., 2022). Hence, we are currently uninformed about one of the major transitions in social cognition. Considering the growing evidence that mammals and birds – separated by 325 million years – have evolved similar cognitive repertoires independently (Güntürkün & Bugnyar, 2016), and the fact that geometrical gaze-following has only been found in few mammalian and avian species, there are good reasons to assume that visual perspective taking has arisen separately multiple times. It is essential to study each lineage in deep time to better understand the principles of socio-cognitive evolution. Such studies, in combination with research on brain evolution, may shed light on the timing, selective pressures, and possible relaxations of evolutionary constraints.

To begin establishing when visual perspective taking arose in Sauropsida (the lineage including reptiles and birds but not mammals), we used the paleontological inference method of extant phylogenetic bracketing (Witmer, 1995). By comparing the gaze-following repertoire of crocodylians with that of palaeognath birds, we phylogenetically bracketed the dinosaur lineage leading to birds as closely as possible. Crocodylians are the closest living relatives of birds. They have had slow evolutionary rates (Green et al., 2014), and seem to have largely retained an ancestral brain morphology (Brown et al., 2020). Palaeognath birds, on the other hand, are the most neurocognitively plesiomorphic extant birds, making them in this regard more similar to non-avian paravian dinosaurs than any other bird taxa (Olkowicz et al., 2016; Kverková et al., 2022).

The study of gaze-following has its roots in developmental psychology and comprises an extensive research program, which has been successfully adopted by animal researchers. Early on, gaze-following was divided into two qualitatively different levels, a high and a low level (Povinelli & Eddy, 1996). The high level affords the aforementioned geometrical gaze-following, while low level gaze-following is an almost reflexive co-orientation with the visual direction of the other individual (Deaner & Platt, 2003). The low level does not require prior expectations to find anything in the gaze direction, or representations of the referentiality of the gaze, but is an adaptive reaction that leads to noticing objects or events that could otherwise have been missed. Such gaze-following is mediated by conserved sub-cortical structures (Sewards & Sewards, 2002; Johnson, 2005). Low level gaze-following is commonly tested through gaze-following into the distance experiments, where a demonstrator is lured to gaze either up or to the side. An onlooker capable of this skill is expected to co-orient with the gaze direction of the demonstrator. Low level gaze-following develops far earlier in children than high level gaze-following, with an onset between 3 and 6 months of age (e.g. Butterworth & Jarrett, 1991; Perra & Gattis, 2010). Gaze-following into the distance has so far been found in all studied amniotes, ranging from mammals to birds and reptiles (e.g. Wilkinson et al., 2010; Nawroth et al., 2017; Schaffer et al., 2020).

As mentioned, high level gaze-following, on the other hand, is a notably more advanced form. It presupposes expectations of finding something in the other's line of gaze, and that this gaze reference can only be found if one changes one's own perspective. This is the reason it is tested in the geometrical gaze-following paradigm, with barriers blocking the view, that must be circumvented. Unsurprisingly, this form of gaze-following is suggested to be mediated by various cortical areas (Shepherd & Cappuccio, 2011); although the avian homologues for such gaze-following still need to be determined. In children, high-level gaze-following, i.e., geometrical gaze-following, is not seen until the age of 18 months (Butterworth & Jarrett, 1991).

Another central gaze-following behavior, that thus far has only been reported in humans, apes, and Old World monkeys (e.g. Scaife & Bruner, 1975; Bräuer et al., 2005; Goossens et al., 2008) is the so-called "checking-back"-behavior. This behavior is instigated when no object of interest is identified in the other's line of gaze, or when the gaze direction and its target are incongruent. The observer will then look back at the other in an apparent attempt of re-tracking the gaze direction. The "checking-back"-behavior is regarded as an essential diagnostic behavior for the onlooker's representation of the referentiality of the other's gaze, i.e., that it is pointing towards something (Okamoto-Barth et al., 2007). "Checking-back" thereby reveals a violation of the expectancy to find a gaze target in the observed gaze direction.

Visual perspective taking, as displayed in geometrical gaze-following, does not imply the representation of others' epistemic or perceptual states. Rather, it is a form of functional representation, leading to behaviors that correspond to the fact that the other has a different perspective and that its gaze refers to an object.

Furthermore, visual perspective taking is traditionally divided into a level I and II (Flavell et al., 1981). Level I enables taking into account *what* (or that "something") lies in the line of gaze of the other, or in other words, what the other can or cannot perceive. In children this level develops between 18 and 24 months (e.g. Moll & Tomasello, 2004; Moll & Tomasello, 2006; Moll et al., 2007). Level II, on the other hand, requires the adoption of the spatial viewpoint of the other, and hence taking into account *how* the world is perceived from that perspective. One understands that the same thing oneself sees, is perceived differently from the angle of the other. This is considerably more advanced, and does not develop in children until the age of 4-5 years (e.g. Gzesh & Surber, 1985). It has been suggested that while geometrical gaze-following cannot reveal level II perspective taking, it forms the embodied pre-cursor to develop or evolve it. Repositioning the body provides an experience of the other's perspective, which in turn can be used in mental simulations of one's own body positions to understand others (Kessler & Rutherford, 2010). Taken together: geometrical gaze-following is a sophisticated embodied sensory-motor process that anchors the most advanced forms of social cognition.

To investigate potential level I visual perspective taking skills in extant archosaurs, which phylogenetically bracket the extinct Dinosauria, we tested 30 individuals from five archosaur species (six per species) for their ability to follow conspecific gaze: emus (*Dromaius novaehollandiae*), greater rheas (*Rhea americana*), elegant-crested tinamous (*Eudromia elegans*), red junglefowl (*Gallus gallus*), and American alligators (*Alligator mississippiensis*). The three palaeognath species represent different phylogenetic nodes within that group, and different socio-ecologies, as well as flightlessness and volant flight (e.g. Yonezawa et al., 2017). The red junglefowl were added as an outgroup of plesiomorphic neognaths, belonging to the lineage Galloanserae that diverged from Neoaves (the other large group of neognaths) before the end-Cretaceous extinction. The animals were tested in three gaze-following experiments: following gaze into the distance up and to the side, and geometrically behind a barrier (for experimental setups see Figure 1). The potential presence of “checking-back”-behavior was studied in all three experiments.

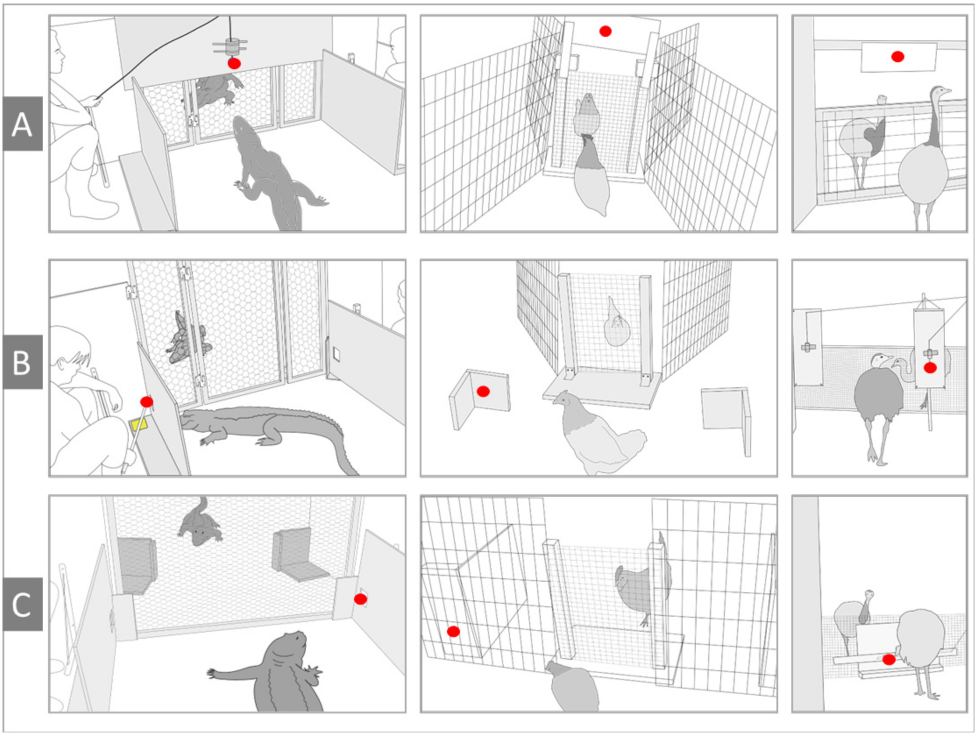

Figure 1: All experimental setups (from left to right) for alligators, small birds (red junglefowl and elegant-crested tinamous), and large birds (emus and rheas). Row A) Setups for Experiment 1 (gazing up). Row B) Setups for Experiment 2 (gazing to the side). Row C) Setups Experiment 3 (geometrical). Red dots depict stimuli used to lure demonstrators’ gazes (for more information about stimuli see Supplementary Material).

2. Results

Gaze-following into the distance and geometrical gaze-following

All tested species followed conspecific gazes into the distance. In Experiment 1 (gazing up), all birds performed at a comparable level (see Figure 2). However, the alligators did not respond by looking up, but instead turned around and looked behind themselves at a significant level (see Figure 2).

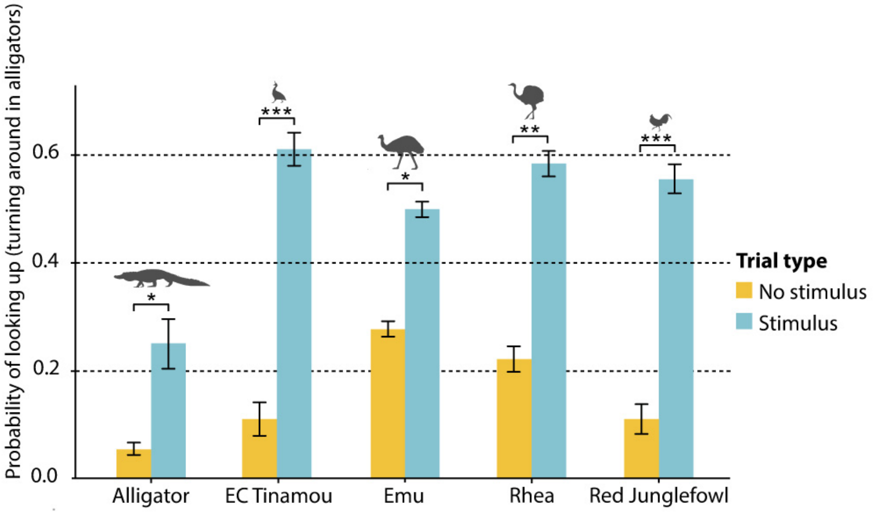

Figure 2: Gaze-following into the distance: Up. Probability of looking up (turning around in alligators) in demonstrator condition of Experiment 1. All bird species looked up significantly more often in trials with a stimulus present (a demonstrator gazing up) compared to trials with no stimulus (likelihood ratio test, $\chi^2 > 4.55$, df = 1, $p<0.033$). Alligators reacted by turning around and looking behind themselves. They did so significantly more often in trials with a stimulus present (likelihood ratio test, $\chi^2 = 5.77$, df = 1, p = 0.016).

In Experiment 2 (gazing to the side), all birds passed the test at similar rates. The alligators also passed, but with a notably lower rate than any bird species (see Figure 3).

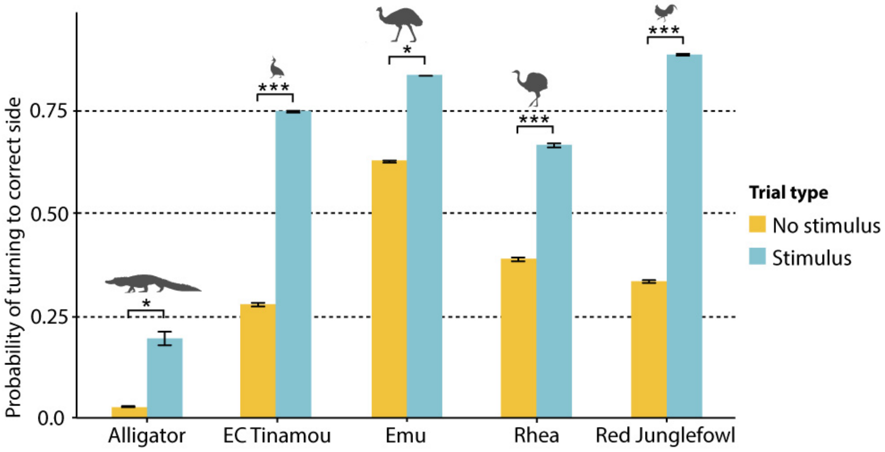

Figure 3: Gaze-following into the distance: Sideways. Probability of turning to correct side in demonstrator condition of Experiment 2. All bird species turned more to the correct side in trials with a stimulus present (likelihood ratio test, $\chi^2 > 3.88$, df = 1, $p<0.049$). No significant difference in gaze-following rate between bird species was found. Alligators followed gaze at significantly lower rates compared to birds (likelihood ratio test, $\chi^2 = 15.055$, df = 4, p = 0.0046). EC Tinamou = elegant-crested tinamou.

There is a clear difference in the frequency of gaze follows into the distance (Experiment 1 and 2) between alligators and birds (see Figure 4), even when regarding the turning around behavior by the alligators in Experiment 1 as a gaze-following response. There is no significant difference between the different bird species.

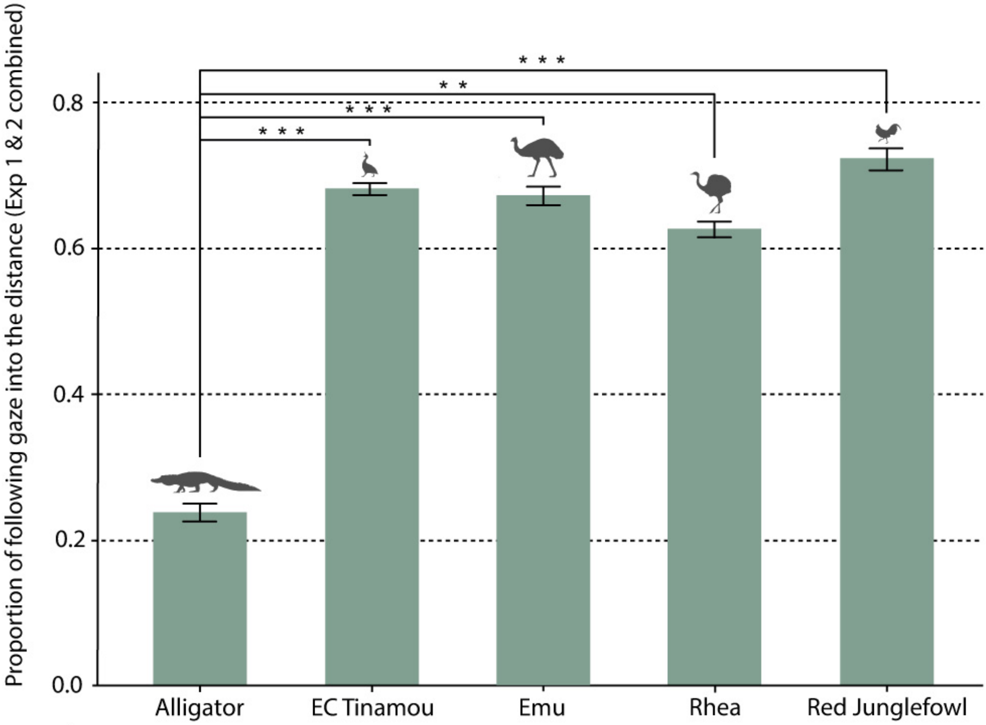

Figure 4: Proportions of gaze-following into the distance. Species had a significant effect on probability of gaze-following (likelihood ratio test, $\chi^2 = 26.407$, df = 4, $p<0.001$). Gaze-following proportions were significantly higher for birds (elegant-crested tinamou; in this graph "EC Tinamou": 0.68, emu: 0.67, rhea: 0.63, red junglefowl: 0.72) compared to alligators (0.24).

All bird species followed gaze geometrically, and at comparable rates (see Figure 5). The alligators, however, did not reveal any geometrical gaze-following in the test.

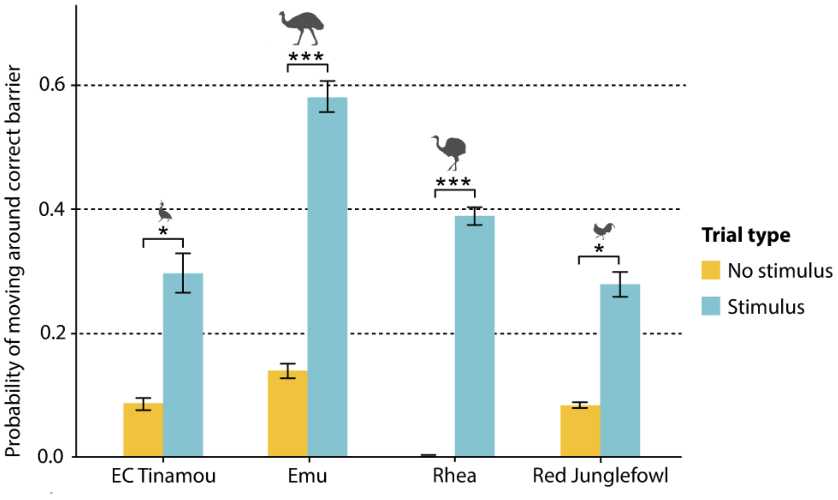

Figure 5: Geometrical gaze-following. Probability of moving around correct barrier in demonstrator condition of bird species (Experiment 3). Alligators did not follow gaze geometrically. Between birds, no significant effect of species was found, but there is a trend for a higher proportion in emus (Z= 1.93, p=0.054). All bird species moved around the correct barrier significantly more often in trials with a stimulus compared to trials without a stimulus (likelihood ratio test, $\chi^2 = 33.74$, df = 1, $p<0.001$). EC Tinamou = elegant-crested tinamou.

"Checking-back"-behavior

All bird species engaged in "checking-back"-behavior, but the alligators did not. There was a significant species effect among the birds on the probability of "checking-back" in Experiment 3, the geometrical gaze-following (likelihood ratio test: $\chi^2 = 9.73$, df = 3, p = 0.021). This difference, however, is likely caused by differences in the experimental setups because of varying body sizes. While the larger birds (emus and rheas) could effortlessly "check back" by lifting their head, the smaller birds (junglefowl and tinamous) had to walk out from behind the barrier to be able to see the demonstrator again, as they were too small to look over it. This is likely the reason why the larger birds were found to "check back" more often in the geometrical experiment, while in the other two experiments, all birds "checked back" at comparable rates. This is evident from the fact that this difference was found *after* relocation, i.e., after birds had looked behind the barrier.

"Checking-back"-behavior will lead to a renewed gaze follow towards the target if the demonstrator is still looking at it. In 27% of the "checking-back" instances, the observer again followed the gaze towards the target. In these instances, the demonstrators' gazes lasted on average 30% (0.73 seconds) longer, indicating that the demonstrator was still gazing towards the target.

3. Discussion

This is the first study on visual perspective taking in palaeognath birds and crocodylians. The palaeognath birds, and the junglefowl, show a gaze-following repertoire on par with apes and some Old World monkeys, including behaviors diagnostic of the expectation of a gaze reference. The alligators' performance is mostly similar to other non-avian reptiles and appears to be restricted to the low-level form of gaze-following into the distance. Collectively, this suggests that visual perspective taking, along with representations of the referentiality of gazes, originated somewhere within Dinosauria. It is also likely that these cognitive skills arose earlier in this lineage than in Mammalia, perhaps due to a sophisticated diurnal vision that yet had to evolve in mammals.

Apart from the current study, only one reptile species – the central bearded dragon (*Pogona vitticeps*) – has been tested for geometrical gaze-following (Siviter et al., 2017). Just as alligators, they did not exhibit these high-level gaze-following skills. However, all previously studied reptiles follow gaze into the distance (Wilkinson et al., 2010; Siviter et al., 2017; Simpson & O'Hara, 2019). This indicates that low level gaze-following skills are a shared attribute among reptiles, but that visual perspective taking might be absent, suggesting a comparable repertoire in ancestral archosaurs.

Interestingly, however, the alligators do not follow gazes upwards, but instead turn around. This contrasts with all tested terrestrial non-avian reptiles, which co-orient with upward gazes (Wilkinson et al., 2010; Siviter et al., 2017; Simpson & O'Hara, 2019). It may reflect crocodylians' adaptation to a life at the water surface, which is apparent in the horizontal arrangement of their sensory organs, and retinal ganglion cells in the eye (Reber, 2020). Perhaps they mainly raise the head to see further ahead over the surface, rather than up, which would then be at a location behind and not above the observer. Turning around would then entail gaze-following outside one's own field of vision, which is a form of geometrical gaze-following. Another interpretation is that turning around is an appeasing response, as snout lifting is a submissive signal (Senter, 2008); however, such a response has never been reported, nor observed by us in any other situation. The turning around is likely a response to gaze, but, as alligators show no geometrical gaze-following in Experiment 3, it could be a taxon-specific response due to its potential adaptive importance at the water surface, or it could represent an evolutionary early form of geometrical gaze-following.

That geometrical gaze-following was shown by all bird species in our study, indicates that it should be within the repertoire of all birds (unless lost secondarily), given that the species studied represent some of the neurocognitively most conserved taxa.

Previously, geometrical gaze-following in birds has only been identified in two corvid species, common ravens *(Corvus corax*; Bugnyar et al., 2004) and rooks (*Corvus frugilegus*; Schloegl et al., 2008) and in one other songbird, the European starling (*Sturnus vulgaris*; Butler & Fernández-Juricic, 2014). On the other hand, only one other study on birds has investigated geometrical gaze-following. A study on the Northern bald ibis (*Geronticus eremita*), did not find such gaze-following, which would counter our prediction or represent a secondary loss (Loretto et al., 2009). However, the results probably reflect methodological limitations. Among other things, and in contrast to most studies (including the current one), the ibis were not facing each other in the geometrical condition but stood next to one another which might have distorted the observer's prediction of the demonstrator's visual perspective. The authors themselves also cautioned against the results, and suggested tests with different methods. The best prediction is still that most birds, from all taxa, have this seemingly conserved ability.

"Checking-back"-behavior, which was found in all birds, has not been reported outside apes and Old World monkeys. However, our findings suggest that "checking-back" is a more widespread behavior than previously thought. It has simply never been described or looked for in other species. The only negative results on "checking-back" stem from two species of New World monkey: black-handed spider monkeys (*Ateles geoffroyi*) and tufted capuchin monkeys (*Cebus apella*) (Amici et al., 2009).

Arguably, "checking-back"-behaviors should be within the repertoire of species capable of geometrical gaze-following, as such gaze-following presupposes the expectation that the other's gaze is directed at something, which cannot currently be seen. "Checking-back" is a behavior signifying such an expectation. The behavior develops earlier in children than the ability to follow gaze geometrically – 8 months versus 18 months (Butterworth & Cochran, 1980; Butterworth & Jarrett, 1991). Indicating that the ability to expect a reference of the gaze, not only precedes, but is a prerequisite for, visual perspective taking. The negative results in the study on New World monkeys, may be experimental artefacts, something the authors also suggested. Indeed, one individual spider monkey in the study was found "checking-back" multiple times.

As mentioned, alligators and birds differed in that the alligators did not reveal visual perspective taking (barring the curious turning around behavior) or any "checking-back"-behavior. But they also differed in another important measure: the sensitivity to the other's gaze, which is seen in the proportions of gaze follows in Experiment 1 and 2 (Figure 4). The birds, on the other hand, had a proportion of gaze follows similar to great apes (e.g. Kano & Call, 2014).

The potential role of differences in cerebellar size

A major neuroanatomical difference between crocodylians and avians is the radically higher density of neurons in birds, leading to much greater neuron numbers in their brains. The main proportional increase of neurons in the evolution from stem archosaurs to birds is found in the cerebellum (Kverková et al., 2022). For example, an emu has 20.5 times as many neurons in the cerebellum as a Nile crocodile (*Crocodylus niloticus*), while having 15.75 times as many neurons in the telencephalon. We suggest that the vastly expanded cerebellum provides insights into why birds, but not crocodylians (or other reptiles), show visual perspective taking with its accompanying representations of gaze reference. While a large cerebellum is not sufficient for advanced gaze-following, it is most likely a prerequisite.

The cerebellum primarily guides motor control, but is involved in a variety of cognitive processes (Strick et al., 2009). This structure is organized in parallel loops through which it simultaneously receives input and sends projections to cortical areas (Welniarz et al., 2021). The highly regular cytoarchitecture suggests a unified mechanism underlying its various functions (Diedrichsen et al., 2019). An influential theoretical framework proposed for this unifying mechanism is that of the so-called internal forward models.

Such models are top-down processes using prior, instead of immediate, information to guide behavior and to predict behaviors of others (Wolpert et al., 1998; Wolpert et al., 2003; Bastian, 2006; Roth et al., 2013). Well-developed sensory-motor predictions allow rapid appropriate actions and update quickly when the model does not match the world. This considerably speeds up behavior, as compared to a system that instead continuously responds only to the feedback from the external world (bottom-up).

We propose that the differences in the gaze-following repertoires of alligators and birds are partly explained by more robust internal forward models in birds. Gaze-following is mediated by top-down processes in various action predictions of others (e.g. Perez-Osorio et al., 2015; Perez-Osorio et al., 2017). The act of gazing can induce the prediction in the observer that the other’s gaze points to “something”. The “checking-back”-behavior clearly shows when such expectations are violated, but also that the system is tuned to updating, which is a hallmark of internal forward models (e.g. Roth et al., 2013). The evolution and development of visual perspective taking, and representing referentiality, is likely an embodied process starting out from building sensory-motor forward models of one’s own behavior, which gets extended to other’s basic behaviors (Friesen & Rao, 2011). Obviously, more robust internal forward models in the cerebellum, making more detailed and fine-grained predictions, will only arise in the presence of well-developed sensory-motors areas in the pallium (or cortex) which they project on, which are something birds have as compared to reptiles. However, we do not know to what extent the enlargement of the cerebellum seen in the maniraptoran theropods (Torres et al., 2021), reflects the existence of other brain areas involved in visual perspective taking.

The origins of visual perspective taking and further research

Palaeognaths are the best available extant neurocognitive models of non-avian – but closely related – paravian dinosaurs, such as dromaeosaurids and troodontids. There are of course differences between the least derived (extant) avian brain and that of extinct non-avian paravians. For example, the presence of the Wulst (hyperpallium), and ventrally deflected optical lobes in birds (Torres et al., 2021), which likely mainly represent adaptations to the visual-motor requirements of flight. Nevertheless, the palaeognath brain is strikingly more similar to a non-avian paravian brain, than to that of a crocodylian. For example, in size, shape, and proportions between areas (e.g. Balanoff et al., 2013; Olkowicz et al., 2016; Kverková et al., 2022). But also in the relationship between body and brain size, where palaeognaths fall within the scaling relationship of non-avian paravians, unlike most other birds (Ksepka et al., 2020). One of the central questions, however, is whether the neuronal density was similar between paravians and palaeognaths, because the number of neurons is currently one of the best neurobiological correlates to cognitive performance (e.g. Herculano-Houzel, 2017; Sol et al., 2022). Palaeognaths have the least derived scaling relationship of neuronal numbers among birds (shared with some neognath taxa), but that still allows about twice as many neurons per volume unit than in a non-primate mammal (Olkowicz et al., 2016; Kverková et al., 2022). It has recently been shown that endothermy is highly associated with the extreme increase of neuron numbers (Kverková et al., 2022). Accumulating evidence from different methodological sources suggests endothermy in at least non-avian paravians (Legendre et al., 2016; Rezende et al., 2020; Wiemann et al., 2022). There are hence reasons to assume that these dinosaurs had neuronal densities more similar to palaeognaths than to extant reptiles.

Despite the lack of studies on structures in the avian brain corresponding to those in mammals that mediate geometrical gaze-following, it may be the case that they existed in non-avian paravians too, given several similarities to palaeognaths. If so, visual perspective taking could have arisen in the non-avian paravians (or perhaps earlier) and may thus have been present by the Middle Jurassic (ca. 174-163 million years ago). However, if the unique avian Wulst, which is an area of visual and somato-sensory integration (e.g. Reiner et al., 2005; Gold et al., 2016), proves central for visual perspective taking, then one would expect that its origin occurred later. There is still no consensus, based on the fossil record, when the Wulst appeared, but since it exists in both palaeognaths and neognaths, which according to molecular analyses diverged in Early Cretaceous (about 110 million years ago; e.g. Yonezawa et al., 2017), it should at least have been present then. There indeed exist projections between the Wulst and the cerebellum (Gutiérrez-Ibáñez et al., 2018). However, the visual and somatosensory requirements of flight likely exceed those of terrestrial mammals and might therefore represent levels of sensory-motor models beyond what is needed for modelling other's occluded lines of gaze. Only further research on brain anatomy and brain function in birds, as well as on brain anatomy in extinct dinosaurs (including avians), will help to better pinpoint the origins of visual perspective taking in dinosaurs.

However, as hinted at earlier, the current evidence from mammalian geometrical gaze-following places the evolution of this attribute in lineages that diverged after the end-Cretaceous extinction: Simiiformes (monkeys and apes) and Canidae (where it is only shown in wolves and dogs). That puts the origin of visual perspective taking considerably later in mammals than in birds – with several tens of millions of years. However, if it was not convergently evolved in simians and canids, it should be found in many taxa that diverged since the split of the common ancestor of Primates and Carnivora, ranging from rodents to bats and a long range of others, and its origins would then be traced well before the end-Cretaceous extinction (Álvarez-Carretero et al., 2022) (but still probably many millions of years after its origins in dinosaurs). More gaze-following studies on mammals are needed to provide better understanding, and to disentangle to what extent these skills evolve convergently within mammals.

It is not surprising if visual perspective taking, with accompanying representations of gazes' referentiality, evolved earlier in dinosaurs than in mammals. The major increase of neurons, which is seen in both mammals and birds – likely as a response to endothermy – might be a prerequisite, but acute vision may be of additional importance. The benefits of gaze-following are likely enhanced by an advanced visual system, where foveae and color vision seem particularly useful, both of which most likely existed already in non-avian dinosaurs as it exists in reptiles and birds (except where lost due to nocturnal adaptations). Following the gaze of someone who can attend to more details in the environment, as well as see further into it, provides more information, given that the gaze follower itself has similar visual capabilities. Mammals were initially, and for a very long time (and a majority still is), primarily nocturnal, and vision had less utility than e.g. olfaction (Hall et al., 2012). The most well-developed gaze-following repertoires in mammals are found in simians, and particularly apes. Primates have readapted their vision to diurnal conditions and regained both foveae and color vision. The refinement of the visual system co-evolved with the relative expansion of the primate cerebellum (Barton, 2012), which proportionally increased even more in great apes (Barton & Venditti, 2014). Arguably, this expansion led to improved visual motor internal forward models for prediction of other's behaviors, perhaps making apes similar to birds in this regard. Studies on other mammals are needed to understand the role of visual acuity for visual perspective taking, and whether differences may lead to convergent evolution of this skill within mammals. But also, more studies are needed investigating to what degree other sensory modalities aid in various forms of perspective taking.

Geometrical gaze-following reveals only the most basic forms of visual perspective taking (level I) and cannot attest to more advanced socio-cognitive skills. Decades of research into animal cognition have focused on various aspects of "mindreading"-abilities. Animals' *mental* perspective taking, such as representations of others' epistemic states, intentions, desires, or other motivational states, has been intensely studied, where apes and corvids show the highest proficiency (Krupenye & Call, 2019). However, much more research is needed on neurocognitively plesiomorphic animals to better understand the evolution of social cognition.

4. Materials and Methods

Experimental Design

We tested 30 subjects of five archosaur species (six per species, for more information on subjects see Supplementary Material) for their ability to follow gazes of conspecifics in three experiments. Testing took place between January 2019 and November 2020. Experiments 1 and 2 tested for gaze-following into the distance upwards (Experiment 1) and to the side (Experiment 2). Experiment 3 investigated geometrical gaze-following, i.e., tracking gaze around a barrier. Due to limited sample sizes, some individuals of each species were used as both demonstrator and subject. Those individuals first finished all demonstrations before serving as subject to minimize the number of potentially biased trials. Demonstrators were selected based on highest responsiveness to gazing stimuli (described below).

Due to the physical differences of the tested species, three different experimental setups were used within each experiment to create optimal testing conditions. Alligators, large birds (emus and rheas) and small birds (elegant-crested tinamous and red junglefowl), received their own setups, respectively (see Figure 1).

A gazing stimulus was used to evoke gazing responses of demonstrators. Demonstrator birds from all bird species, besides red junglefowl, spontaneously reacted by looking towards the red dot of a laser pointer. The demonstrators among the red junglefowl were conditioned to turn towards the dot of a laser pointer in training sessions prior to the experiments. The demonstrators among the alligators were conditioned to turn towards a blue rubber ball. Conditioning was achieved through clicker-training in both species. However, no clicker was used during testing (for a more detailed description, see Experimental Setups).

Every experiment was divided into two conditions: Demonstrator and no-demonstrator. In the demonstrator condition, subject and demonstrator were present, while only the subject was present in the no-demonstrator condition. Half of the subjects started with the demonstrator condition, the other half with the no-demonstrator condition. Each condition was further divided into two trial types: stimulus and no-stimulus. In stimulus trials, the gazing stimulus was presented, whereas no stimulus was shown in no-stimulus trials. Trial types were pseudorandomized.

Every condition (demonstrator or no-demonstrator) consisted of 12 trials, 6 of each trial type. In stimulus trials of the demonstrator condition, the stimulus was presented until a gazing response of the demonstrator was evoked. In no-stimulus trials of the demonstrator condition, no stimulus was presented, so that the demonstrator was simply present. These trials controlled whether the mere presence of a conspecific altered the gazing behavior of subjects.

In stimulus trials of the no-demonstrator condition, only the subject was present while the stimulus was presented for 5 seconds. This served to control if the stimulus was visible from the subject side. In no-stimulus trials of the no-demonstrator condition, no stimulus was shown while only the subject was present. This was done to maintain the same procedure and session length as in the demonstrator condition. In both conditions, the trial lasted for 10 seconds after demonstration (either the demonstrator gazing, or the stimulus being presented without demonstrator present). Only in Experiment 3, alligators were given 1 minute due to the potential amount of walking in this setup.

If a significant difference in orienting responses could be identified between stimulus and no-stimulus trials in the demonstrator, but not the no-demonstrator condition, this difference was most likely caused by the gaze cue of the demonstrator. All trials were video recorded, with one camera behind the subject, and one facing the subject to ensure optimal angles of the heads and eyes of subjects.

Experimental Setups

Experiment 1: Up

In Experiment 1, an opaque screen was mounted on top of the divider that was placed between subject and demonstrator. For alligators, the blue rubber ball that demonstrators were conditioned to turn towards could be lowered into view with a string from an opaque tube attached to this screen on the side facing the demonstrator. For all bird species, the dot of a laser pointer was projected onto the screen on the demonstrator side.

Experiment 2: Side

For alligators, two experimenters seated behind 60-centimeter-high wooden barriers on either side of the demonstrator each had a blue rubber ball mounted on a wooden stick. In stimulus trials, one experimenter presented the ball through a cut-out in the wooden barrier they were seated behind. A small wooden barrier in front of this cut-out prevented the subject from seeing the ball. Sides were counterbalanced; each subject received the same number of trials on either side. A sponge underneath the cut-out ensured that no sounds were made when lowering the balls after presentation.

For small birds, two wooden barriers were placed on the demonstrator side on which the dot of the laser pointer could be presented towards the demonstrator.

Large demonstrator birds (emus and rheas) quickly habituated to the dot of the laser pointer. For that reason, in Experiment 2 and 3, their gazes were lured by showing food. Due to structural differences in the enclosures, this was done in two different ways. For emus, two tall wooden boards were propped up on both ends of the mesh divider on the demonstrator side. Two experimenters stood behind these boards. Each of them held a grape on a stick, which could be shown in a cut-out to lure the gaze of the demonstrator (similar to the alligator setup). For rheas, two wooden boards were hung from poles on each end of the mesh divider. On the side facing the demonstrator, an opaque tube was attached to both boards from which grapes could be lowered into view with a string.

Experiment 3: Geometrical

Alligators were exposed to the same setup as in Experiment 2 (side). However, this time, two wooden barriers were placed approximately one meter in front of the mesh barrier on the subject side. The stick with the target ball was in this condition not only shown in the cut-outs but stuck out of them to make the demonstrator gaze behind one of the two barriers on the subject side. In the presence of geometrical gaze-following, the subject would have to walk up to the barriers and turn around the indicated one. The barriers were slightly angled, which prevented the subject from seeing behind both barriers simultaneously when placing itself between them.

For small birds, two barriers were placed on the subject side. The dot of the laser pointer was directed to the back of the barrier, so that it was only visible to the demonstrator. In this way, an orientation of the demonstrator towards that barrier looked to the subject as if the demonstrator was looking behind that barrier.

For large birds, a wooden barrier was placed between demonstrator and subject. On the demonstrator side, a contraption was installed on ground level from which a grape could be shown by pulling it out from an opaque tube with a string. By showing the grape, the gaze of the demonstrator was lured towards the ground behind the barrier. A successful subject would be expected to lean over the barrier to identify the gaze target. The experimental setups for all three experiments are depicted in Figure 1.

Coding Definitions

All videos were coded using Solomon Coder (Péter, 2017). When coding trials of all three experiments, we coded "target location" and "checking-back". "Target location" had different definitions depending on the experiment, but generally referred to the location where the gazing stimulus was shown. In Experiment 1, the target location was the panel above the divider. We coded "target location" every time a subject looked up towards that panel. For alligators, we additionally coded "turning around", which was defined as the subject turning more than 90° away from its initial position. In Experiment 2, the target location was the side where the stimulus was shown, or the side the demonstrator looked towards. In no-stimulus trials, we pre-determined "correct" sides randomly and coded "target location" if the subject turned towards that side. We only scored first orientations of subjects in this experiment. The same method was applied to Experiment 3 of the small birds and alligators. Experiment 3 of the large birds did not include sides, but only had one "target location": the ground behind the barrier. "Target location" was only coded when subjects relocated themselves around barriers (or looked over the barrier in large birds) and not when they looked towards that location. Additionally, we coded the latency of "target location" for each experiment, either from trial onset in no-stimulus trials, or from the onset of the stimulus (the gazing stimulus in the no-demonstrator condition, or the gaze of a demonstrator in the demonstrator condition). We coded "checking-back" when a subject looked towards the target location and then back at the demonstrator. We moreover recorded whether the subject looked to the target location again after "checking-back". 10 percent of the videos were coded for inter-observer reliability, and intraclass correlation was good (ICC = 0.85, F= 12.6, $p<0.001$).

Statistical Analysis

The data were analysed with generalized linear mixed models (GLMMs) in RStudio (Version 1.4.1717; RStudio Team, 2020). For every experiment, a model for each of the two conditions was created. The models were fitted with a binomial distribution, and individual identity of the observer was added as a random factor with session nested within. Head movements towards a target served as the response variable; species and trial types (luring stimulus present/not present), as well as their two-way interaction, were fixed factors. We reduced these full models, using the Akaike Information Criterion (AIC), to find those explaining the most variance. These final models were subjected to likelihood ratio tests to assess the effect of remaining factors (for values of final models, see Supplementary Material). If trial type with the lure stimulus present had no significant effect in the *no-demonstrator* condition, but a significant effect in *demonstrator* conditions, this was interpreted as gaze-following. Subsequently, we ran the same models for each experiment but used "checking-back" as the response variable.

Acknowledgements

This work was supported by Swedish Research Council grants 2019-03265 and 2021-02973. We thank Nina Thierij, Mark Kernkamp, Mathias Andersson, Morgan Luce, Simon Grendeus, Thomas Rejsenhus Jensen, Ola Oscarsson, and Ivo Jacobs for their practical help. We are grateful for Helena Osvath for the creation of figures. We thank Steve Brusatte, Pavel Němec and Lawrence Witmer for helpful comments on the manuscript. We are also grateful to Ystad Zoo.

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Supplementary Materials for

Gaze-following in Archosauria – alligators and palaeognath birds suggest dinosaur origin of visual perspective taking

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1. Ethical statement

All animals participated on voluntary basis and could leave the set-up, that was installed in a part of their home enclosure, whenever they chose to. No force of any kind was used. Sometimes animals were given food rewards. Both the observer and the demonstrator were familiar group members with no known antagonistic history. All animals were housed in either zoos or at private owners that met the legal requirements, as well as Lund Universities ethical standards. The research did not include so-called procedures under the EU-directive 2010/63/EU, and did not qualify for ethical approval, which is also true according to the stricter Swedish legislation (SJVFS 2019:9, chapter 2, § 22).

2. Subjects & housing

Table 1: Test subjects. Subjects within a species marked in the same color were housed together as a social group.

Species	Subject	Sex	Age	Role
Alligator mississippiensis	Toke	female	subadult	Demonstrator& Subject
Alligator mississippiensis	Ivar	male	subadult	Demonstrator& Subject
Alligator mississippiensis	Bestla	male	subadult	Subject
Alligator mississippiensis	Sigi	female	subadult	Subject
Alligator mississippiensis	Kåra	female	subadult	Subject
Alligator mississippiensis	Gudrun	female	subadult	Subject
Dromaius novaehollandiae	Snow	female	adult	Demonstrator& Subject
Dromaius novaehollandiae	Tufty	male	adult	Demonstrator& Subject
Dromaius novaehollandiae	Uncrowned	female	adult	Demonstrator& Subject
Dromaius novaehollandiae	Crowned	male	adult	Demonstrator& Subject
Dromaius novaehollandiae	Judy	female	adult	Demonstrator& Subject
Dromaius novaehollandiae	Harry	male	adult	Demonstrator& Subject
Rhea americana	Nox	male	adult	Demonstrator& Subject
Rhea americana	Hamilton	male	adult	Demonstrator& Subject
Rhea americana	Yvette	female	adult	Subject
Rhea americana	Salsa	female	adult	Demonstrator& Subject
Rhea americana	Lucia	female	adult	Demonstrator& Subject
Rhea americana	Arroz	female	adult	Subject
Eudromia elegans	Alicio	male	adult	Demonstrator& Subject
Eudromia elegans	Sleepy Genius	male	adult	Demonstrator& Subject
Eudromia elegans	Pretty Boy	male	adult	Demonstrator& Subject
Eudromia elegans	New Tinamou	male	adult	Subject
Eudromia elegans	Jon Snow	male	adult	Subject
Eudromia elegans	Sandy	female	adult	Subject
Gallus gallus	Yellow	female	adult	Demonstrator& Subject
Gallus gallus	Pink	female	adult	Demonstrator& Subject
Gallus gallus	Red	female	adult	Subject
Gallus gallus	White	female	adult	Subject
Gallus gallus	Green	female	adult	Subject
Gallus gallus	Rooster	male	adult	Subject

3. Housing

3.1. Alligators

Subjects were six seven-year-old American alligators (*Alligator mississippiensis*; 2 males and 4 females) that were group-housed in an indoor facility consisting of a 42 m^2 pool area and a 26.5 m^2 land area. Subjects were tested on land by dividing the pool from the land area with opaque screens that didn't allow for visual contact with the rest of the group, but they could still hear each other.

3.2. Small birds

Small birds in this study were six adult elegant-crested tinamous (*Eudromia elegans*, 1 female and 5 males) and six adult red junglefowl (*Gallus gallus*, 1 male and 5 females), living in one social group, respectively. Elegant-crested tinamous were group-housed in an outdoor aviary during the experimental period, while red junglefowl had access to an indoor and outdoor aviary. Elegant-crested tinamous were tested in their outdoor aviary, while red junglefowl were tested indoors.

3.3. Large birds

Large birds in this study were six adult emus (*Dromaius novaehollandiae*, 3 females and 3 males) and six adult greater rheas (*Rhea americana*, 2 males and 4 females). Emus were all pair-housed, i.e., the experiments took place in three different locations. Rheas were from two different mixed-sex groups, housed at two different locations. Both species were tested in their outdoor enclosures.

4. Statistical models

Table 2: Results of likelihood ratio test performed on the final Generalized Linear Mixed Models (lowest AIC). VCO = visual co-orientation; TA = turning around; CB = checking back.

Model	Response variable	Distribution	Coefficient	Chisq	df	p
Proportions gaze following into distance	VCO	Binomial	Experimental Condition	9.71	1	0.0022**
			Species	25.80	4	<0.001***
Experiment 1, birds, no-demonstrator condition	VCO	Binomial	Species	3.19	3	0.36
			Test Condition	0.12	1	0.73
Experiment 1, birds, demonstrator-condition	VCO	Binomial	Species	4.47	3	0.21
			Test Condition	16.33	1	<0.001***
			Species*Test Condition	4.40	3	0.22
Experiment 1, alligators, no-demonstrator condition	TA	Binomial	Test Condition	1.86	1	0.17
Experiment 1, alligators, demonstrator condition	TA	Binomial	Test Condition	5.77	1	0.01*
Experiment 2, birds, no-demonstrator condition	VCO	Binomial	Test Condition	3.61	1	0.05
Experiment 2, birds, demonstrator condition	VCO	Binomial	Species	9.26	3	0.03*
			Test Condition	14.73	1	<0.001***
			Species*Test Condition	5.67	3	0.13
Experiment 2, alligators, no-demonstrator condition	VCO	Binomial	Test Condition	1.39	1	0.24
Experiment 2, alligators, demonstrator condition	VCO	Binomial	Test Condition	4.09	1	0.04*
Experiment 3, birds, no-demonstrator condition	VCO	Binomial	Species	3.96	3	0.27
			Test Condition	3.44	1	0.06
Experiment 3, birds, demonstrator condition	VCO	Binomial	Species	4.88	3	0.18
			Test Condition	33.74	1	<0.001***
Checking back birds	CB	Binomial	Experimental Condition	4.65	2	0.098
			Species	9.72	3	0.021*
			Experimental Condition*Species	13.75	6	0.033*

Paper II

Gaze following: A socio-cognitive skill rooted in deep time

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Abstract

Social gaze has received much attention in social cognition research in both human and non-human animals. Gaze following appears to be a central skill for acquiring social information, such as the location of food and predators, but can also draw attention to important social interactions, which in turn promotes the evolution of more complex socio-cognitive processes such as theory of mind and social learning.

In the past decades, a large number of studies has been conducted in this field introducing differing methodologies. Thereby, various factors influencing the results of gaze following experiments have been identified. This review provides an overview of the advances in the study of gaze following, but also highlights some limitations within the research area.

The majority of gaze following studies on animals have focused on primates and canids, which limits evolutionary interpretations to only a few and closely related evolutionary lineages. This review incorporates new insights gained from previously understudied taxa, such as fishes, reptiles, and birds, but it will also provide a brief outline of mammalian studies.

We propose that the foundations of gaze following emerged early in evolutionary history. Basic, reflexive co-orienting responses might have already evolved in fishes - which would explain the ubiquity of gaze following seen in amniotes. More complex skills, such as geometrical gaze following and the ability to form social predictions based on gaze, seem to have evolved separately at least two times and appear to be correlated with growing complexity in brain anatomy such as increased numbers of brain neurons. However, more studies on different taxa in key phylogenetic positions are needed to better understand the evolutionary history of this fundamental socio-cognitive skill.

Keywords: gaze$_1$, evolution$_2$, social cognition$_3$, social information$_4$, orienting$_5$

Summary Box:

- Studies on gaze following and object choice have traditionally lacked a phylogenetic focus.
- Comparisons between species are especially difficult due to different methodologies used over time.
- A variety of often disregarded factors can potentially impact the results of gaze following experiments.
- To form hypotheses about the evolutionary roots of gaze following, it is crucial to compare this skill in distantly related species.
- Gaze following into the distance appears to be a conserved cognitive trait shared among at least all amniotes, possibly even all vertebrates.
- Geometrical gaze following seems to have evolved convergently in mammals and birds.
- More sophisticated gaze following skills appear to be the result of increased neuronal numbers.
- Non-avian dinosaurs likely already followed others’ gaze directions.

1. Introduction

Sociality in non-human animals takes many forms, ranging from solitary species that meet only to mate, to species living in complex societies. Truly solitary species are rare, as a minimal degree of sociality can be found in many species – at least in the sexually reproductive ones. Species with varying degrees of sociality face different challenges. Consequently, species vary in their socio-cognitive repertoires.

Social interactions rely on the transfer and use of social information. Such information can either be conveyed intentionally through communicative signals or be produced inadvertently. For example, an individual's presence in a certain location can inform others about food sources and risk of predation. Social information enables the receiver to optimize decisions, and therefore the ability to use such information is adaptive (Morand-Ferron et al., 2010).

Due to the value of social information, various functions have evolved to facilitate its use. One way of acquiring social information is to observe what others are looking at. In this way, one can use others' visual attention to gather information about the surroundings that would have otherwise remained elusive. The ability to co-orient with others' gaze directions is called gaze following (Butterworth & Jarrett, 1991).

The advantages of following others' gazes are numerous and range from gathering information about the location of predators or food sources, to drawing attention to important social interactions (Tomasello et al., 1998). Eavesdropping on social interactions promotes knowledge of third-party relationships and can be used in tactical deception or observational learning (Emery, 2000). Arguably, observational learning would be difficult without gaze following, as the gaze draws attention to central affordances in a task.

Gaze following is an important fundamental skill to study, when uncovering some of the evolutionary roots of social cognition. The presence of gaze following in various distantly related species implies an origin in deep evolutionary time. This quick and easy way of gathering social information might have been the starting point for the evolution of more complex socio-cognitive skills such as empathy and theory of mind (Emery, 2000; Shepherd & Platt, 2008).

Despite gaze following appearing to be a widespread skill, the majority of animal studies have focused on primates and canids. This limits evolutionary interpretations. To better understand the evolution of social cognition, and of gaze following in particular, it is necessary to expand research efforts to more distantly related lineages. In recent years, the interest in such taxa has increased and a number of new studies - especially on reptiles and birds – provide insights into the evolution of gaze following.

This review describes general ideas and methodologies of the research field. It also discusses limitations and describes various factors potentially impacting the results of gaze following studies in non-human animals with the aim of improving future experimental designs.

With respect to the evolution of gaze following, this review highlights recent advances in the research on the Sauropsida lineage (reptiles and birds). Though still scarce, new evidence from this lineage is important for understanding deep evolution. We also provide an outline of studies on mammals, including human and non-human primates.

2. The roots of gaze following research: Developmental psychology

Co-orienting with others' gazes is a fundamental part of human social cognition. A classic example is when someone in a crowd suddenly looks up and scans the sky. People around will shortly start looking up as well, seeking for the object of interest.

Humans are skilled gaze followers from an early age. In fact, the study of gaze following began in developmental psychology. The earliest insights stem from a study by Scaife and Bruner (1975) that found that human infants start following head directions at 2-4 months, and that all children have developed this ability by 11 months.

It was later shown that already newborns are sensitive to others' gazes (Batki et al., 2000; Farroni et al., 2002) and have a preference for direct gaze (Farroni et al., 2002). Gaze cueing, where observers orient towards an object in the direction of another's gaze, also appears to be present in newborns (Farroni et al., 2004).

The ontogenetic onset of gaze following has later been pushed back to 3 – 6 months (e.g. Butterworth & Jarrett, 1991; Perra & Gattis, 2010). The extent to which infants can modulate their early gaze following responses remains unclear. Senju and Csibra (2008) showed that gaze following of 6 -month-old infants depends on ostentive signals such as eye contact or addressing the child. Gredebäck and colleagues (2018), however, found that infants of the same age responded to gaze cues with and without ostentive signals. More recently, Ishikawa and Itakura (2019) demonstrated that arousal facilitates infants' gaze following responses, which can in turn be heightened through ostentive signals. It should, however, be noted that the children in this study were between 9 and 10 months old. The ability to modulate gaze following responses based on arousal might thus develop later than spontaneous co-orientations.

Early gaze following responses are, however, not very precise. Infants can only reliably identify the target of observed attention at 12 months (Farroni et al., 2004; Moore, 2008). Moreover, children younger than 10 months follow the head direction of a demonstrator with open and closed eyes without distinction, implying a developmental shift in understanding referentiality of looking around that time (Woodward, 2003; Brooks & Meltzoff, 2005; Csibra & Volein, 2008; Senju et al., 2008). Gaze following abilities are fully developed at 18 months, when the infants follow gazes outside their immediate visual field and behind themselves (Butterworth & Jarrett, 1991; for a recent review see Del Bianco et al., 2019).

The development of gaze following in human infants plays a central role in the development of other socio-cognitive skills, such as theory of mind (Brooks & Meltzoff, 2015), joint attention (Carpenter et al., 1998), and language acquisition (Baldwin, 1991; Schafer & Plunkett, 1998; Houston-Price et al., 2006), illustrating its fundamental role in human social cognition.

3. Neurocognitive mechanisms of gaze following

The neurocognitive mechanisms underlying gaze following are not fully understood. The consensus is, however, that two distinct pathways guide co-orientations with observed gaze directions. Fast, reflexive co-orientations (Deaner & Platt, 2003) are mediated by an evolutionary conserved subcortical pathway (Sewards & Sewards, 2002; Johnson, 2005) providing fast, yet crude co-orienting responses to gaze. In mammals, the subcortical pathway is proposed to run from the retina to the superior colliculus, the pulvinar, and finally to the amygdala (Morris et al., 1999; Johnson, 2005; Jiang & He, 2006). In fishes, amphibians, reptiles, and birds, the optic tectum represents the homologue of the superior colliculus, while the rest of the pathway remains the same.

This subcortical pathway is, however, likely insufficient to mediate spatially sophisticated gaze following, such as tracking others' gazes around barriers. Thus, the subcortical pathway is most likely interconnected with more nuanced cortical networks in mammals, such as the fusiform gyrus (face perception and recognition: Johnson, 2005), the exastriate body area (visual processing of the body: Downing et al., 2001) and the superior temporal sulcus (functions explained below; Shepherd, 2010). The cortical homologues responsible for more complex gaze following skills in other vertebrates remain unknown.

The superior temporal sulcus (STS) of humans and non-human primates has been found to contain cells reacting to different facial orientations (e.g. Perrett et al., 1982) and some are specifically sensitive to the direction of eye gaze (Perrett et al., 1985; Yamane et al., 1988). Hence, this structure might be important in the detection of others' visual attention.

The STS projects onto the parietal intraparietal cortex in macaques (Harries & Perrett, 1991). The lateral part of this structure (lateral parietal area, LIP) houses "gaze mirror neurons", i.e., neurons that fire both when looking at a specific location and when watching someone else gazing toward the same location (Shepherd et al., 2009). Such neurons might cause attentional shifts through matching the observed gaze direction with one's own visual attention, similar to the functioning of mirror neurons of the motor system (Rizzolatti et al., 2009). Visuosocial areas of the fusiform gyrus and STS are moreover interconnected with an extended face processing network that might further modulate gaze following responses (Ishai et al., 2005; Vuilleumier & Pourtois, 2007).

Data on cortical pathways of gaze following stem exclusively from humans and macaques. Nevertheless, it has been proposed that social processing areas might be homologous in all primate (Tootell et al., 2003; Rosa & Tweedale, 2005) and possibly other mammalian species (Kendrick et al., 2001). How other taxa, such as birds, achieve spatially sophisticated gaze following skills remains unclear and will need to be addressed in future studies.

4. Factors influencing gaze following

A variety of animal species have been tested for their capacity to follow others' gaze directions. While in human studies, a distinction is often made between following the direction of the head and shifts of eye gaze alone, most studies on animals use a head directional cue in their gaze following studies. In this review, when speaking of gaze following, we refer to co-orientations with head directions. For a more detailed discussion of this topic, see 4.3.

Within the great number of animal gaze following studies, many factors and methodologies can significantly impact subjects' performances. Two experimental paradigms are used when studying how animals use social information conveyed through gaze: (1) visual co-orientation, and (2) object choice. In the former, the animal is presented with a demonstrator looking toward a specific location in the environment and the observer's co-orientation with the line of gaze is recorded. In object choice, subjects are tested for their capacity to use gaze cues to identify the location of food. For an overview of species tested in different experimental paradigms, see Table 1.

Many different factors can influence a species' performance in gaze following experiments. Realistically, it is difficult to take all of the following issues into account. Nevertheless, this summary should provoke researchers to closely familiarize themselves with the species and subjects they are testing. These considerations should further be taken into account when designing gaze following experiments.

4.1 Experimental paradigms

4.1.1 Visual co-orientation

Visual co-orientation is commonly tested in two ways, in line with Povinelli and Eddy's low- and high-level model of gaze following (1996). According to this first account of gaze following in chimpanzees (*Pan troglodytes*), low-level gaze following is a simple co-orienting reflex that does not require any mentalistic attributions. High-level gaze following, on the other hand, requires a representation of others' visual perspectives.

To test these models, two different experimental setups are used: gaze following into the distance (from here on GFD) and geometrical gaze following (from here on GGF). In the former, a demonstrator is gazing either up or to the side while co-orientations of the observer are recorded. This is considered to only require only low-level cognitive abilities without an attribution of mental states. GGF refers to tracking gazes around barriers. It is elicited by a demonstrator gazing toward a location behind a barrier that is not seen from the subject's location. If an observer were to simply co-orient with the demonstrator, one would expect it to look at the barrier. An observer capable of GGF, though, moves around the barrier to inspect the target of the demonstrator's gaze. This is regarded as high-level gaze following as it is believed to require an understanding of visual perspectives (Bräuer et al., 2005).

Most studies on gaze following in animals have focused on GFD. GGF has been tested in primates (Bräuer et al., 2005; Amici et al., 2009; Bettle & Rosati, 2019), canids (wolves: Range & Virányi, 2011; domestic dogs: Met et al., 2014), birds (Corvids: Bugnyar et al., 2004; Schloegl et al., 2007; Schloegl, Schmidt, et al., 2008; Northern bald ibises: Loretto et al., 2009; European starlings: Butler & Fernández-Juricic, 2014), and two reptile species (Bearded dragons: Siviter et al., 2017; American alligators: Zeiträg et al., 2022, Preprint).

4.1.2 Object choice

In the object choice paradigm, an experimenter indicates the location of a hidden piece of food through a cue such as pointing, tapping, or gazing. In this review, we focus exclusively on gaze cues and their use in locating food. Several variations of the object choice paradigm exist: classic object choice, competitive object choice, food theft competition, and the guesser-knower task, which will be explained below.

4.1.2.1 Classic object choice

In the classic object choice paradigm, an experimenter is cueing the subject towards one of two objects that is baited with food. These objects are usually small containers such as cups. When the animal has chosen one object, the remaining one is removed from access of the subject.

In experiments where gazes are used as cues, a distinction is made between *gaze* - referring to a shift of both head and eye direction - and *glance* - referring to a shift of the eyes alone (e.g. Neiworth et al., 2002; Scheumann & Call, 2004; Burkart & Heschl, 2006). Surprisingly, most tested species struggled with this paradigm and failed to use gaze to locate food (Anderson et al., 1995; Schloegl, Kotrschal, et al., 2008; Giret et al., 2009). The disparity between the seemingly ubiquitous gaze following, but poor results in object choice experiments, suggests a difference in the mental processing of gaze direction and its use in finding food.

Call et al. (2000) argued that there is a functional disparity between following gaze and foraging, and that chimpanzees do not seem to apply their elsewhere proven gaze following skills in foraging contexts. In the same study the authors found that vocalizations and other behaviors, such as approaching the baited object, significantly increased performance. The authors argued that these additional behaviors drew the subjects' attention towards the demonstrator's head direction which was then used to locate the hidden food. They called this the *attention boosting hypothesis.*

However, this hypothesis does not explain why animals follow gaze at all, as they seemingly cannot use it for locating food. Therefore, one must disentangle whether gaze following takes place in foraging contexts at all, or whether many species are unable to infer the location of food from observed gaze directions.

One study on common marmosets (*Callithrix jacchus*) showed that the monkeys followed the experimenter's gaze to the correct container, but were unable to find the hidden food (Burkart & Heschl, 2007). Call et al. (2000) argued in their study that chimpanzees did not understand the communicative and informative intent of the human experimenter. That would also explain why adding vocalizations can enhance object choice performance, as it might convey and emphasize the communicative intent of the situation to the subject. Similarly, Hauser and Wood (2011) found improved performances of rhesus macaques (*Macaca mulatta*) in an object choice task when using ”communicative gaze gestures”, i.e., wide open eyes and jerking the head several times towards the target object. However, Burkhart and Heschl (2007) provide an alternative explanation for their marmosets’ behavior: looking at an object might be interpreted as an indication of ownership and lead to avoidance of that object. While this explanation seems reasonable for the cooperatively breeding marmosets, it does not explain the behavior of competitive species such as chimpanzees.

In fact, two lemur species, black lemurs (*Eulemur macaco*) and brown lemurs (Eulemur fulvus), have been reported to react in a contrary manner as common marmosets (Ruiz et al., 2009). In an object choice experiment, the lemurs were more likely to locate hidden food after they had successfully followed the gaze direction from a conspecific’s photograph. The poor performance of many species in object choice experiments is according to this study caused by low gaze following rates. The authors called this effect *gaze priming*, i.e., an increase of saliency of an object or location through following gaze direction. However, it should be noted that this is, to our knowledge, one of only two studies using conspecific demonstrators (even though just photos) in an object choice experiment, which might have significant effects on subjects’ behaviors (for a study on ravens, see: Schloegl, Kotrschal, et al., 2008).

Unfortunately, object choice studies rarely report whether subjects had followed the demonstrator’s gaze toward the correct object or not. More of these reports are needed to understand the reasons behind the poor performance of many species in the object choice paradigm. Nevertheless, two factors have been identified to improve subjects’ performance. Chimpanzees have been found to perform better when leaving the experimental area after each trial, and having to approach the experimenter at the beginning of each new trial (Barth et al., 2005). This indicates an attentional issue in “classic” object choice setups, where subjects stay in the same place between trials. Secondly, chimpanzees perform better when the food is hidden in, or behind, an object that allows visual access to the experimenter, but blocks the subject’s view (Call et al., 1998). This is the case with, for example, tubes or barriers, where the experimenter can see the hidden food while cueing its location to the subject. It could be argued that animals do not perceive an experimenter as knowledgeable of the food’s location when they cannot see the hidden food at the time they are giving cues to the subject (for alternative explanations see Call et al., 1998).

Though many species struggle with object choice experiments, it seems as though changes to the setup can significantly improve subjects’ performances. For that reason, alternative versions of the classic object choice paradigm have been introduced.

4.1.2.2 Competitive object choice

One alternative explanation for the poor performance of many species in object choice experiments could be that informing others about the location of hidden foods does not come naturally to many animals. Several authors have argued that especially competitive species such as chimpanzees would hardly ever inform conspecifics about hidden food, making the experimental setup much less relevant to them. For that reason, Hare et al. (2000) invented the competitive object choice paradigm. This experiment has, to our knowledge, only been conducted on primates. In the competitive object choice setup, two individuals, one dominant and one subordinate, are observing an experimenter placing two food items in an experimental room. One of the food items is visible to both participants, while another is only visible to the subordinate. Once the food is placed, both individuals are released into the experimental room. If the subordinate understood the visual perspective of the dominant, it would be expected to first go and collect the hidden piece of food to avoid competition with the dominant. A variety of primate species appeared to demonstrate an understanding of others' visual perspective in the competitive object choice paradigm (see below).

In an additional condition in this paradigm, Hare et al. (2000) introduced a delay to the release of the dominant in relation to the subordinate in order to rule out that the choice made by the subordinate would be influenced by the approach and choice of the dominant competitor, i.e., that the subjects were simply choosing the food item that the dominant was *not* choosing.

Chimpanzees appeared to take visual access of the dominant into account by choosing the food item only visible to them over the one visible to both. Subordinates were still choosing the food item only visible to them when being released with a head start. The same behavior was found in common marmosets (Burkart & Heschl, 2007) and long-tailed macaques (*Macaca fascicularis*; Overduin-de Vries et al., 2014). Subordinate capuchin monkeys (*Cebus apella*) also displayed a preference for the hidden food (Hare et al., 2003). This preference, however, broke down when granting the subordinate a head start into the arena.

Using cross-correlations of subordinates' and dominants' behaviors, Hall and colleagues (2014) showed that subordinate chimpanzees rarely follow the dominant's gaze in a competitive object choice setup. This supports the hypothesis that subordinates are not simply choosing based on the other's behavior. Dominants, on the other hand, were following subordinates' gazes and were adapting their foraging technique to that of the conspecific with privileged knowledge about the location of food.

To further control for behavior-reading, Overduin-de Vries et al. (2014) introduced a one-way mirror in their study on long-tailed macaques that allowed the subordinate to see the dominant, creating the illusion of a competitive situation. The dominant, however, could not actually see the subordinate or the food, excluding the possibility of giving behavioral cues about which food item they will be choosing to the subordinate. Interestingly, in this setup fast subordinates were often observed collecting both food items. In those instances, subjects were going for the visible food item first, before collecting the food only visible to them. Slower individuals more often only chose the food item that was not visible to their competitor.

4.1.2.3 Food theft competition

In the food theft competition, the subject's choice of object is mediated by its gaze sensitivity in a competitive setting. Two food items are placed in the experimental room, with an experimenter monopolizing one of the items through closer proximity or visual orientation to the item. If the subject chooses the object by the experimenter, the object is immediately removed from access and the trial ends. If the subject chooses the object not contested by the experimenter, it may eat the food item.

A variety of primate species have been successful in this paradigm, including gibbons (Sánchez-Amaro et al., 2020), Old world monkeys (Vick & Anderson, 2003; Flombaum & Santos, 2005), and one species of lemur (three other species failed in this study; Sandel et al., 2011)

In a more complex setup, chimpanzees could reach for a banana either through an opaque or a transparent tunnel (Melis et al., 2006). Chimpanzees preferred to conceal their actions through choosing the opaque tunnel. Orangutans did not show a preference in a replication of this experiment, failing to show an understanding of visual access (Gretscher et al., 2012).

4.1.2.4 Guesser-knower task

In this object choice paradigm, the subject's understanding of a demonstrator's visual access is tested. The standard setup involves a subject and two demonstrators. Food is then hidden outside the visual access of the subject, while one demonstrator has visual access to the baiting process (the knower), and the other demonstrator does not (the guesser). This can be achieved through the guesser being absent (e.g. Maginnity & Grace, 2014), turned away (e.g. Call et al., 2000), or having their eyes closed (Proops & McComb, 2010) during baiting. Both demonstrators (or one demonstrator in different trials) subsequently perform a cue towards one of two objects. A subject with an understanding of visual access should prefer the object indicated by the informed demonstrator.

Two primate species have been successful in this paradigm: chimpanzees (Call et al., 2000) and capuchin monkeys (Defolie et al., 2015). Moreover, some domesticated species could infer visual access of humans: domestic dogs (*Canis familiaris*; Virányi et al., 2004; Maginnity & Grace, 2014; Catala et al., 2017), domestic horses (*Equus caballus*; Proops & McComb, 2010; Ringhofer et al., 2021), and domestic pigs (*Sus scrofa domesticus*; Byrne et al., 2001).

Only one bird species has been subject to the guesser-knower task: Common ravens (*Corvus corax*; Bugnyar, 2011). Ravens were watching a human experimenter cache food in the presence of two conspecifics: a guesser, whose view was obstructed during caching, and a knower, that could witness the caching process. After releasing the subject and either of the two conspecifics (the guesser or the knower) into the arena, subjects were pilfering the caches quicker when in competition with an informed conspecific, showing that they were taking others' visual access into account.

4.2 Demonstrators

The experimental study of gaze following requires a gaze cue by a demonstrator. Such a demonstrator should on command gaze towards a specific location. To ensure controlled testing conditions, the majority of studies – especially on primates – have used human demonstrators (for an overview see: Rosati & Hare, 2009). This allows for controlling parameters such as looking time, specific target of gaze, and the disentanglement of head direction and eye-gaze alone. While it is doubtless beneficial to keep testing conditions as controlled as possible, the relevance of human gaze cues to animals, especially non-primates, has been debated.

The large body of literature on gaze following in a variety of species indicates that many animals can indeed follow the gaze of a human demonstrator - even around barriers. That, however, does not mean that the frequency and sophistication are representative of the species' socio-cognitive potential. Though commonly brought up in discussions, few studies have directly addressed this topic.

One study on cotton-top tamarins (*Saguinus oedipus oedipus*), for example, showed that the monkeys did not follow the gaze of humans, but only of conspecifics (Neiworth et al., 2002). Contrarily, other primate studies have reported comparable responses to human and conspecific demonstrators (Tomasello et al., 1998; Hare & Tomasello, 2004; Herrmann et al., 2007). However, Byrnit (2004) described that non-enculturated orangutans, i.e., parent-raised, failed to use human gaze cues to identify a target object. Similarly, only enculturated chimpanzees have been found to be sensitive to visual attentive states of human experimenters in a guesser-knower task (Call et al., 2000).

If previous exposure to humans indeed impacts animals' sensitivity to human gaze cues, the ability to follow human gazes might vary significantly depending on age and experience. To our knowledge, only one observational account of such a developmental effect exists from common ravens (Schloegl et al., 2007). The authors observed the first spontaneous co-orientations of raven nestlings with their conspecifics approximately 7 weeks before they started to react to the gaze of a human experimenter.

Previous exposure to humans could also explain the excellent performance of domestic dogs using human gaze cues in object choice tasks (e.g. Miklósi et al., 1998; Hare & Tomasello, 1999; Agnetta et al., 2000; Soproni et al., 2001). It has been argued that this is the result of their long history of domestication and exposure to humans. A direct comparison of dogs and chimpanzees in an object choice task revealed that dogs indeed outperform chimpanzees when using communicative cues given by human experimenters, such as pointing and gazing. Chimpanzees, on the other hand, were better at inferring the location of the hidden food from causal cues such as the sound produced when shaking the baited container or the shape of a board that is slanted because of food being hidden under it (Bräuer et al., 2006). This further supports the hypothesis that the poor performance of chimpanzees in object choice tasks is not caused by a lack of understanding, but rather because they do not recognize the communicative intent of the human experimenter and therefore fail to use it as a cue.

Hattori and colleagues (2010) compared the responses of humans and chimpanzees to con- and allospecific gaze cues and found that chimpanzees follow human gazes significantly less often compared to conspecific gazes and moreover look longer at faces of other chimpanzees than of humans. Interestingly, humans were equally sensitive to gazes of both demonstrator species.

Taken together, these findings indicate that some enculturated individuals and domesticated species might respond stronger to human compared to conspecific gaze cues. However, a recent study on gaze following in domesticated ungulates found that even domesticated species preferred to follow conspecific gazes (Schaffer et al., 2020). This suggests that for the majority of species, the use of conspecific demonstrators would be beneficial and that many studies might not have revealed the full gaze following potential of their tested species.

To keep experimental conditions controlled while using conspecific demonstrators, some studies have used photographs and even videos of conspecifics to induce gaze following responses. This seems to work surprisingly well. Primates such as rhesus macaques (Lorincz et al., 2000), Diana monkeys (*Cercopithecus diana diana*; Scerif et al., 2004), and two lemur species (Ruiz et al., 2009) followed the gaze direction of a photograph of a conspecific to an object. Several primate species have also been found to co-orient to videos of conspecifics, such as chimpanzees, bonobos, orangutans (Kano & Call, 2014) and rhesus macaques (Emery et al., 1997).

However, not only primates have been found to co-orient with artificial stimuli. Bearded dragons (*Pogona vitticeps*) followed the video of a conspecific gazing up and towards the side (Siviter et al., 2017), and even archerfish co-oriented themselves with a photograph of a conspecific (Leadner et al., 2021). Butler and Fernández-Juricic (2014) have gone as far as creating a robot version of a European starling (*Sturnus vulgaris*) to test for GGF skills in this species. The subjects followed the robot's gaze behind barriers, suggesting that artificial demonstrators can even be used in GGF studies.

4.3 Eye morphology

One problem when interpreting gaze following is knowing exactly where an animal is looking. Birds, for example, can switch from lateral to binocular vision, therefore the target of their gaze cannot be deduced from their eye orientation (Dawkins, 2002). In animal studies, the target of gaze can only be inferred. This is usually done by extrapolating postural indicators such as beak or snout direction.

Similarly, when using conspecifics as demonstrators, they usually orient their bodies or at least the head toward that location. In the presence of a co-orienting response, it is therefore difficult to discern which cue the observer has been following, the direction of the body, the head, or the eyes alone. Some studies on primates have started to disentangle these cues, but again with human demonstrators to specifically control the body parts orienting toward the target (e.g. Anderson et al., 1996; Neiworth et al., 2002; Burkart & Heschl, 2006).

Differences in the accuracy of gaze tracking might be caused by varying eye morphologies. It has long been believed that human eyes are unique in their salience through the contrast between the white sclera and the dark central iris. This eye morphology has been thought to allow for accurate identification of the target of the conspecifics' gaze, and has been an explanation for the ability of humans to use eye gaze alone, in comparison to non-human primates that rely on head direction to track gaze directions (Tomasello et al., 2007). This has been called the *cooperative eye hypothesis*. However, a recent study found that despite the differences in scleral pigmentation, the contrast between sclera and iris is comparable for great apes and humans (Perea-García et al., 2019). Thus, the contrast of the eyes alone is not sufficient to explain the differences in the sophistication of gaze following between humans and non-human primates.

Kano and colleagues (2022) recently shed new light on this question. Humans and chimpanzees were asked to choose one out of three pictures of faces of humans and chimpanzees. The task was to pick the face with averted eyes. In different conditions, parameters of the eyes, such as brightness and size were manipulated. Humans and chimpanzees were both better at discriminating the human's eye direction and this effect was most prevalent in visually challenging conditions, i.e., when the pictures were shaded or small. The authors argued that the uniformly white sclera of humans, rather than the contrast of sclera and iris, is responsible for human gaze following skills as it makes it easier to follow eye movement alone rather than head direction.

Other animals, however, do not possess such an eye morphology and need to rely on other directional cues, such as head directions. While it seems likely that the evolution of a conspicuous eye morphology in humans has refined the ability to extract social information from the eyes alone, it does not mean that other animals lacking this morphology cannot follow others' gaze directions. They, however, need to rely on different directional cues. In ravens, for example, the direction that the beak is pointing towards is a clearer indicator of others' visual attention than a shift of the small, dark, and evenly coloured eyes.

The phylogenetic ubiquity of co-orientations in combination with evidence for an evolutionary conserved subcortical pathway guiding gaze following responses moreover indicate that the evolutionary roots of this skill run deeper than the evolution of human eye morphologies. It is, hence, more likely that uniquely human abilities' in extracting directional cues from shifts of eye directions alone are a species-specific extension of the gaze following capacities of other animals rather than a separate, more sophisticated way of extracting directional information.

4.4 Emotions

Another factor influencing gaze following are the emotions associated with attentional shifts. Goossens and colleagues (2008) have studied this effect in long-tailed macaques through a human experimenter accompanying their gaze shifts with mimicked facial expressions representing different emotional states for the monkeys, namely aggression, submission and affiliation. The authors reported that long-tailed macaques were more likely to follow gaze when the attentional shift was accompanied by facial expressions of fear and submission. This could be an indication that gaze following can be employed flexibly in socially meaningful situations.

Teufel and colleagues (2010) found that facial expressions generally facilitated gaze following in Barbary macaques (*Macaca sylvanus*), starting from the ontogenetic onset of the behavior. A learning process can therefore be excluded. This effect, however, wore off when the individuals got older, indicating an impact of experience on modulating gaze following behavior. In this study, monkeys reacted strongest to ”commenting” facial expressions, i.e., facial expressions that are used when observing third-party interactions. The authors therefore argued that this effect might have evolved to facilitate the acquisition of social knowledge through drawing attention towards social interactions. In humans, negative facial expressions, such as disgust and fear, have been shown to cause quicker gaze following responses compared to happy or neutral faces (e.g. Pecchinenda et al., 2008; Matsunaka & Hiraki, 2014). In contrast, a similar study on pigtail macaques (*Macaca nemestrina*) did not find evidence for an effect of facial expressions on gaze following performances (Paukner et al., 2007).

These experimental setups are limited, firstly, to emotions that are visible in facial expressions, and secondly to species exhibiting facial expressions, which is mainly the case in primates. This however does not mean that other animals are not affected by observing facial expressions. Horses have, for example, been shown to follow human gaze less frequently when the experimenter expressed disgust, indicating an interspecies interpretation of facial expressions (Baba et al., 2019).

Not only the emotional state of the demonstrator can impact gaze following performances, but also the emotional state of the subject. Putnam and colleagues (2016), for example, found that rhesus macaques were more likely to follow gaze in response to videos of a conspecific after inhaling intranasal oxytocin. The oxytocin might enhance the motivation for social interactions through receptors projecting onto social cortical regions, such as the STS.

4.5 Social dynamics

Social dynamics, i.e., the relationship between the demonstrator and the observer, can affect the likelihood of gaze following. For example, in rhesus macaques, social status impacts gaze following (Shepherd et al., 2006). While low-status males followed the gazes of all familiar conspecifics, high-status males exclusively followed the gazes of other high-status individuals. For low-ranking individuals, it might be crucial to monitor the behavior of their conspecifics to avoid aggressive encounters, while high-ranking individuals are only threatened by other high-ranking monkeys. This shows that gaze following responses may be modulated by social context to optimize gathering of relevant social information. Contrarily, in Barabary macaques, the social status of the demonstrator does not influence gaze following responses (Teufel et al., 2010).

But status, or even kinship, is not always the most important social factor in gaze following. In crested macaques (*Macaca nigra*), such factors had no influence, but instead strong positive bonds between individuals facilitated quicker responses in gaze following (Micheletta & Waller, 2012). The authors argued that social information from friends might be more relevant due to shared interests and motivations. Also, when locating resources such as food, the competition might be reduced between affiliates. The different motivation to follow a friend's gaze could be to monitor social interactions involving affiliates to offer support in conflicts or provide post-conflict affiliation.

Social dynamics also play a role when using human demonstrators. This effect was reported in a study on object choice in jackdaws (von Bayern & Emery, 2009). The birds only responded to gaze cues by a familiar experimenter. Similar to the crested macaques, familiarity might make it easier for jackdaws to predict the other's actions, especially in a competitive situation.

4.6 Sex differences

Lastly, an effect that has rarely been tested in animals, is the impact of sex on gaze following. In humans, women show a stronger gaze cueing effect, i.e., they are more likely to follow others' gazes (Bayliss et al., 2005). They moreover react quicker to gaze cues than men. Interestingly, this sex-difference was correlated with self-reported empathy levels (Alwall et al., 2010).

The only reports of such an effect in animals stem from rhesus and Barbary macaques. Both studies found that females were more likely to follow gaze (Paukner et al., 2007; Rosati et al., 2016). In contrast, a different study on Barbary macaques found that sex had no effect on gaze following rates (Teufel et al., 2010). More studies are needed to understand sex differences in gaze following and their connections to empathy in animals.

5. Gaze following in mammals

Primates play a central role in the study of gaze following as most experimental methods have been developed in primate studies (see sections above), with chimpanzees being the first animal species to be tested in this paradigm. Here, we provide a brief overview of the current state of knowledge of gaze following in primates (for more detailed reviews see: Emery, 2000; Zuberbühler, 2008; Rosati & Hare, 2009; Shepherd, 2010).

To date, reports of GFD of at least some members from all major primate radiation exist: Apes, including great apes (e.g. Bräuer et al., 2005) and gibbons (Horton & Caldwell, 2006), Old World monkeys (e.g. Emery et al., 1997), New World monkeys (e.g. Neiworth et al., 2002), and lemurs (e.g. Shepherd & Platt, 2008; but see Ruiz et al., 2009).

The number of GGF studies is lower. Evidence for gaze following around barriers exists from all major primate radiations besides the lemurs: Great apes (e.g. Bräuer et al., 2005), Old World monkeys (e.g. Goossens et al., 2012) and one species of New World monkey (common marmosets: Burkart & Heschl, 2006).

Many primates have been found to struggle with using gaze cues to find food in the classic object choice task (e.g. Anderson et al., 1995; Neiworth et al., 2002; Burkart & Heschl, 2006). It seems unlikely that primates are incapable of locating food based on experimental cues. It rather appears that they fail to understand the communicative intent of a human experimenter. A competitive version of this experiment improved the performance of some species, in that they avoided food items that dominant conspecifics were looking at (chimpanzees: Hare et al., 2000; capuchin monkeys: Hare et al., 2003; common marmosets: Burkart & Heschl, 2007; long-tailed macaques: Overduin-de Vries et al., 2014). Successful performances in this task are usually interpreted as an understanding of visual access in the tested species, though close attention needs to be paid to exclude the possibility of solving the task through behavior-reading.

Few more primate species have been tested in other variations of the object choice paradigm: food theft competition and guesser-knower task. Many primates seem successful in a food theft competition task (olive baboons: Vick & Anderson, 2003; rhesus macaques: Flombaum & Santos, 2005; chimpanzees: Melis et al., 2006; ringtailed lemurs: Sandel et al., 2011; gibbons: Sánchez-Amaro et al., 2020), which supports the hypothesis that a competitive setting is more relevant to a variety of species. Two species have moreover been found to infer visual access of human experimenters in a guesser-knower task, namely chimpanzees (Call et al., 2000) and capuchin monkeys (Defolie et al., 2015).

Other than primates, the largest body of literature on the use of gaze cues in mammals stems from domestic dogs. Dogs successfully use variations of gaze to locate hidden food, making them significantly better at this task than any tested primate species (Hare et al., 1998; Miklósi et al., 1998; Agnetta et al., 2000; McKinley & Sambrook, 2000; Soproni et al., 2001; Bräuer et al., 2006). The cues in these studies include gazing, gaze alternations, glancing, different numbers of objects to choose from, and different distances between experimenter and object, i.e., the cue was performed by an experimenter standing close to or far away from the baited container. In a guesser-knower task, dogs moreover demonstrated an understanding of visual access by preferring the cue of the knower over the one of the guesser (Maginnity & Grace, 2014; Catala et al., 2017) and by begging more from a human facing the dog compared to one with their back turned (Virányi et al., 2004).

Interestingly, the results are less clear when it comes to GFD. It has been reported that dogs do not spontaneously follow human gaze into distant space (Agnetta et al., 2000). Their performance improved, though, when the target of gaze was clearly defined, or when the communicative intent was made clear through ostensive cues, such as calling the dog's name (Téglás et al., 2012; Werhahn et al., 2016; Duranton et al., 2017). In a comparison with pack-living domestic dogs and wolves (*Canis lupus*), wolves actually followed human gaze more frequently, while both species followed their packmates' gaze at comparable rates (Werhahn et al., 2016).

An explanation for this phenomenon could be that dogs are overly focused on humans and struggle with directing their attention away from them to a location in the environment. Wallis and colleagues (2015), for example, reported that even a short training of dogs to seek eye contact with humans disrupted their gaze following responses. With respect to GGF, dogs seemed capable of tracking human gazes around visual barriers, and even more so in a foraging context, i.e., when they were aware of food being hidden (Met et al., 2014). This suggests that domestication might favor the use of gaze cues to locate food but might simultaneously hinder spontaneous gaze following responses.

Other canids tested are wolves, dingoes (*Canis lupus dingo*) and silver foxes (*Vulpes vulpes*). Hand-raised wolves followed both human and conspecific gaze into the distance and around barriers. They were found to follow human gazes into distant space at 14 weeks, while GGF only developed after 6 months (Range & Virányi, 2011). Dingoes failed to locate hidden food using gaze cues given by a human experimenter (Smith & Litchfield, 2010). Domesticated silver fox kits performed comparable to dogs in an object choice tests with gaze cues and significantly better than their feral counterparts (Hare et al., 2005). Only one study on domestic cats (*Felis silvestris catus*) in an object choice paradigm exists. Cats were able to use human gazes to locate hidden food even without ostensive cues (Pongrácz et al., 2019). These studies support the hypothesis that previous exposure to humans and domestication drastically improve animals' interpretations of experimenter-given cues.

A variety of farm animals have been subject to gaze following studies. Visual co-orientation has been tested in a number of ungulates: domestic goats (*Capra hircus*), llamas (*Lama glama*), guanacos (*Lama guanicoe*), and mouflons *(Ovis orientalis*

orientalis; Kaminski et al., 2005; Schaffer et al., 2020). All these species, except for the guanacos, followed human gazes into distant space. In an object choice task, however, goats failed to use experimenter-given gaze cues to find hidden food (Kaminski et al., 2005). In a follow-up study, Nawroth and colleagues (2015) showed that dwarf goats (*Capra aegagrus hircus*) have an understanding of visual attention of humans through increased anticipatory behaviors when a human was facing them compared to when they were not. However, they did not – just as many primate species - apply these skills in an object choice task.

In contrast, juvenile domestic pigs could find hidden food using a human's head and body orientation, but interestingly did not follow head direction into distant space (Nawroth et al., 2014). In a guesser-knower task, pigs could choose to follow an informed or uninformed conspecific into one of two corridors, of which one has been baited with food before (Byrne et al., 2001). One pig successfully solved this task. These findings indicate that negative results from one testing paradigm do not necessarily predict a species' performance in another paradigm.

Domestic horses identified a visually attentive experimenter over an inattentive one to approach for food, using body and head orientation as well as open or closed eyes as cues for visual attention. However, when the attentional cues were mixed, the horses' performance broke down (Proops & McComb, 2010). They moreover passed a guesser-knower task and thus demonstrated sensitivity to visual attention of human experimenters (Ringhofer et al., 2021). In an object choice task, however, horses could not use alternating gaze as a cue to find hidden food (Proops et al., 2010).

Finally, some other mammalian species have been tested in object choice experiments. Asian elephants (*Elephas maximus*) did not use any human-given cues to locate food (Ketchaisri et al., 2019). Bottlenose dolphins (*Tursiops truncatus*) were able to use static and dynamic gaze to identify the correct object but failed with eye gaze alone (Tschudin et al., 2001; Pack & Herman, 2004). South African fur seals (*Arctocephalus pusillus*) used human gaze with head direction to identify the correct location of food (Scheumann & Call, 2004), while Gray seals (*Halichoerus grypus*) failed to do so (Shapiro et al., 2003).

The above-presented studies show a large variety in gaze following abilities and the use of gaze in locating food within mammals. The majority of studies have focused on object choice paradigms, which appears inherently difficult to many animals. Gaze following studies in mammals are rare, limiting inferences of the status of this socio-cognitive skill within the mammalian clade.

6. Gaze following in birds

After mammals, birds have been subject to most gaze following studies, especially corvids. This group is generally regarded among the most cognitively complex animals. Within the corvids, the common raven has been most extensively studied. Ravens follow the gaze of a human experimenter into distant space and geometrically around barriers (Bugnyar et al., 2004). While ravens already followed the experimenter's look-ups as fledglings, GGF occurred only after 6 months. The same developmental trajectory was found in another corvid species, the rook (*Corvus frugilegus*; Schloegl, Schmidt, et al., 2008).

Both studies provided similar explanations for the development of gaze following skills, namely different ecological valences of the two modes of gaze following. Scanning the sky might serve as anti-predatory response and would therefore be a crucial cue already for fledglings. Looking around barriers, on the other hand, might serve as a cue to food sources, which is not important to fledglings due to parental care. Moreover, the emergence of GGF coincides with the time when ravens first start hiding behind barriers to conceal their caching (Bugnyar et al., 2007), indicating a developmental milestone in the understanding of visual perspectives around that time.

The same developmental pattern has been found in primates and other mammals, where GFD emerges early in the development (e.g. rhesus macaques: Ferrari et al., 2000; chimpanzees: Tomasello et al., 2001; wolves: Range & Virányi, 2011), and GGF develops significantly later (e.g. human infants: Scaife & Bruner, 1975; chimpanzees: Okamoto et al., 2004; wolves: Range & Virányi, 2011). A more likely explanation, thus, is that the two modes of gaze following require different cognitive processes that develop at different times. The gap in the development of the two modes indicates more complex cognitive processes involved in GGF that the early developing brain is not yet capable of. Gaze following skills appear to develop at comparable rates and in the same pattern in birds and mammals, even though their brain morphologies differ drastically.

Ravens were moreover found to habituate quickly to look-ups, but not to geometrical visual cues of an experimenter (Bugnyar et al., 2004; Schloegl et al., 2007). To solve the habituation problem, Schloegl and colleagues (2007) introduced a new experimenter when the ravens stopped reacting to gaze cues of the familiar experimenter. This increased gaze following responses, though the subjects did not respond as strongly as in initial demonstrations. This increase, however, subsided quickly, indicating a rapid generalization between experimenters. The authors explained the lack of habituation in the geometrical experiment by the natural tendency of ravens to cache food. When tracking gaze behind a barrier and not finding an interesting object there, ravens might expect the object to be hidden and that a continuous search could be advantageous. As a comparison, chimpanzees do not habituate to gaze cues without an interesting target until adulthood (Tomasello et al., 2001).

Ravens have also been tested in an object choice experiment. Schloegl and colleagues (2008) investigated whether ravens can locate a hidden piece of food through a variety of experimenter-given cues. The ravens did not seem to use gaze cues, not even when the experimenter was kneeling closely to the target object while gazing at it. Interestingly, the ravens also did not respond to a conspecific giving gazing cues towards one of two locations. The authors explained this negative result with the argument that the functional value of GGF is to use visual barriers to cache food outside of view from competitors rather than to locate the caches of conspecifics. While this seems to be a reasonable explanation for the evolution of GGF in ravens, it does not explain its presence in other non-caching birds and mammals.

In a comparative study on caching rooks and non-caching jackdaws (*Corvus monedula*; Schloegl, Schmidt, et al., 2008), only the rooks followed the gaze of a human experimenter into distant space as well as geometrically. The authors found only weak evidence for gaze following in jackdaws even when using a conspecific demonstrator perhaps due to a higher vigilance in these birds rendering the detection of gaze follows difficult.

In an object-choice situation, jackdaws identified the correct food location using cross-distal pointing and alternating gazes of their caretaker. They did not respond to static cues such as static gaze or head direction and did not respond to cues from an unfamiliar human (von Bayern & Emery, 2009). The authors argued that the dynamic nature of the used cues - in contrast to the static cues - conveyed the communicative intent of the gaze. Furthermore, these findings suggest that the negative results on gaze following in jackdaws in the above-mentioned study (Schloegl, Schmidt, et al., 2008) were likely due to methodological artefacts.

The ability to use experimenter-given cues in an object-choice task of a fourth species of the corvid family - Clark's nutcracker (*Nucifraga columbiana*) - has been examined (Tornick et al., 2011). These birds are non-social, in contrast to the other tested corvid species. Most subjects immediately used a touch gesture to identify the location of hidden food, which can be explained by local enhancement. Additionally, the birds successfully learned to use point and gaze cues. The gaze cue consisted of both head and eye direction and was dynamic, i.e., the gaze was alternated between the subject and the goal location. Despite methodological differences in studies, it seems like

Clark's nutcrackers perform comparably to social corvid species. This indicates that the social-nonsocial dichotomy is not sufficient to explain the presence of socio-cognitive skills, as they might either be derived from a social ancestor, or might be advantageous without social group living (for a more detailed discussion see: Wilkinson, Kuenstner, et al., 2010).

Outside of the corvid family, GFD with a conspecific demonstrator has been found in Greylag geese (*Anser anser*; Kehmeier et al., 2011), African penguins (*Spheniscus demersus*; Nawroth et al., 2017) and Northern bald ibises (*Geronticus eremita*; Loretto et al., 2009). Only three non-corvid bird species have been tested in GGF. European starlings (Butler & Fernández-Juricic, 2014) and red junglefowl (Gallus gallus; Zeiträg et al., 2022, Preprint) successfully tracked the gaze of a conspecific around a barrier, while Northern bald ibises failed to follow a conspecific's gaze geometrically (Loretto et al., 2009). However, due to the many positive accounts of GGF in other bird species, it is possible that this negative account of GGF is caused by methodological artefacts.

A recent study (Zeiträg et al., 2022, Preprint) reported the first accounts of gaze following in palaeognath birds. These birds are the less neurocognitively derived of the two major bird clades – palaeognaths and neognaths. They have retained many ancestral features from the non-avian dinosaurs (for a more detailed discussion see below). In this study, the authors found that three palaeognath species – greater rheas (*Rhea americana*), emus (*Dromaius novaehollandiae*), and elegant crested tinamous (*Eudromia elegans*) were capable of GFD– both up and to the side – as well as GGF.

The only non-corvid bird species tested in an object-choice experiment is the African gray parrot (*Psittacus erithacus*; Giret et al., 2009). The experimenter-given cues in this study included different pointing cues and distal and proximal gaze cues. Only one parrot spontaneously used a combination of proximal sustained pointing and gazing, a second one was able to learn to use the same gesture. Gaze cues alone were insufficient for any subject to locate the food.

7. Gaze following in reptiles

There are very few studies on gaze following in reptiles, likely because they are considered non-social and thus unsuitable subjects to study social cognition. However, two studies have demonstrated socio-cognitive skills, such as social learning, in non-social reptile species (Wilkinson, Kuenstner, et al., 2010; Kis et al., 2015). Studying reptiles is crucial for understanding the evolution of social cognition in Sauropsida, the clade containing reptiles and birds. Many studies have focused on the cognitive skills of mammals and birds. However, when trying to make inferences about the emergence of cognitive traits – in particular in birds – data from reptiles is needed (Matsubara et al., 2017).

Wilkinson and colleagues (2010) conducted the first study on gaze following in a reptile – the red-footed tortoise (*Geochelone carbonaria*). They showed that this species co-orients with a conspecific's upward gaze. Since then, three more reptilian species have been found capable of GFD: bearded dragons (*Pogona vitticeps*; Siviter et al., 2017), leopard geckos *(Eublepharis macularius*; Simpson & O'Hara, 2019), and American alligators (*Alligator mississippiensis*; Zeiträg et al., 2022, Preprint).

Only two of these studies has additionally investigated GGF. No evidence for GGF was found in neither, bearded dragons (Siviter et al., 2017) nor American alligators (Zeiträg et al., 2022, Preprint). Though only few studies on reptiles exist, the large phylogenetic difference between the tested species indicates that GFD is present in distantly related reptilian radiations. The absence of GGF could be a result of the limited number of studies, or of an actual absence of this skill in reptiles. The brains of mammals and birds have, compared to reptiles, evolved substantially more neurons in their telencephalon and cerebellum – regions commonly associated with higher cognitive capacities (Kverková et al., 2022). This neuroanatomical difference could explain the absence of high-level gaze following in reptiles. However, more studies are needed to verify the absence of this skill in reptiles.

8. Gaze Following in other species

To understand the evolutionary roots of gaze following, data from distantly related animal taxa capable of using gazes of others is needed. However, several taxa are either understudied or have not been investigated at all. No studies on amphibians exist, and research on reptilians has just started to gain more attention.

One recent study investigated the use of attentional cues in archerfish (Leadner et al., 2021). These fish spit water jets at insects above the surface. The subjects in the study were trained to spit water at a target on a computer monitor above their tank. In the test, the fish were confronted with the picture of a conspecific on the screen, oriented toward the right or left. After that, a target appeared on the left or right of the screen – half of the time congruent with the side indicated by the fish on screen. Archerfish were quicker to spit water at the target when it aligned with the demonstrator's orientation. However, fish cannot turn their heads independently of their body. Therefore, the cue was a full-body orientation. It is thus not possible to discern which part of the cue conveyed the direction of attention.

Interestingly, the authors reported an absence of *inhibition of return* (IOR) in archerfish. IOR describes the inhibition of returning attention toward a location that has already been observed after shifting attention elsewhere as a result of peripheral cues (McKee et al., 2007). When following gaze cues though, the IOR is absent in humans as well as the studied archerfish. The authors argued that archerfish – just like humans – might possess neural substrates specialized in processing social cues.

Whether the described co-orienting behavior is a special adaptation of archerfish and their hunting style, or a skill shared among fish species in unknown. As described above, all vertebrates share an evolutionary old subcortical pathway that mediates fast, reflexive shifts in visual attention. More studies on fish and amphibian species are needed to verify whether the presence of this pathway is sufficient for admitting gaze following skills in all vertebrates.

9. The use of social information conveyed through gaze: Social predictions

What animals actually understand about the gaze of others has been debated since Povinelli and Eddy (1996) first introduced the low- and high-level explanation of gaze following (see above). While GGF can be interpreted as an understanding of the referential nature of gaze, very few studies have looked closer into social predictions that animals form based on observed gaze.

In this context, *checking back* (also called *double looks*) is of special interest. Checking back was first described when human children looked back to an experimenter in the absence of a target in their line of sight (e.g. Scaife & Bruner, 1975; Butterworth & Cochran, 1980). Children start this gaze alternation at 8 months, comparably late in contrast to the early onset of visual co-orientation between 3 and 6 months (Butterworth & Jarrett, 1991). Developmental psychologists have interpreted this behavior as a sign of an understanding of the mental aspects of gaze, i.e., that gazing refers to a target in the environment. Through alternating gazes between the gazer and the location they have oriented their gaze towards, infants try to identify the correct gaze target. It has been reported that babies even point at a target and then turn back to the gazer as if to confirm its correctness (Butterworth & Cochran, 1980).

In animals, this behavior has first been described in chimpanzees by Call and colleagues (1998) as the animal looking back to the experimenter in the absence of interesting objects in their line of sight. Since the first description of checking back in chimpanzees, it has been reported in other great ape species like bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*; Bräuer et al., 2005; Okamoto-Barth et al., 2007), pileated gibbons (*Hylobates pileatus*; Horton & Caldwell, 2006), and Old World monkeys – Diana monkeys (Scerif et al., 2004), and long-tailed macaques (Goossens et al., 2008). Interestingly, though specifically studied, no evidence for checking back was found in two species of New World monkey - spider monkeys (*Ateles geoffroyi*) and capuchin monkeys (Amici et al., 2009).

Bräuer and colleagues (2005) found a comparable ontogenetic trajectory of checking back in non-human primates and human infants. All five species of great ape checked back at comparable rates, but age had a significant effect on the number of checking back instances. The behavior was absent in infants, was first observed in juveniles, and occurred most often in adults.

In line with the hypothesis that checking back shows an expectancy violation when demonstrator's gazes are not referring to a target in the environment, pileated gibbons were found to check back more when a target appeared in a location that was incongruent with the location indicated through the gaze direction of a human experimenter or the photograph of a conspecific (Horton & Caldwell, 2006). The same was found in Diana monkeys (Scerif et al., 2004). Long-tailed macaques checked back more often in gaze shifts accompanied by social facial expressions, indicating an overall heightened attention in socially relevant situations (Goossens et al., 2008).

However, the mentalistic interpretation of checking back in infants has received criticism. Corkum and Moore (1995) for example argued that young children only look back at adults to confirm their attention or because they have expectations of the gazer's behavior in the current situation. In an experimental setup such an expectation could be that the experimenter will orient their gaze towards a new location after a brief break. Looking back at the experimenter could therefore be a sign of expecting a new gaze cue.

Call and colleagues argued in their study on chimpanzees (1998) that their subjects might have just returned to their neutral forward orientation. Finding the experimenter still gazing towards a location might have triggered a second, independent co-orientation. However, Bräuer et al. (2005) ruled this alternative explanation out by observing that checking back increased with age, indicating a learning process over time from a simple co-orienting reflex in infants and juveniles to a perspective-taking model in adults.

To experimentally test the functions of checking back, Okamoto-Barth and colleagues (2007) investigated great apes' checking back behaviors in a "meaningful" and a "meaningless" condition. In both conditions, the experimenter was looking towards a target. In the meaningful condition, the experimenter's line of sight was blocked by an opaque barrier. As there was nothing of interest to be seen when following the experimenter's gaze, the authors hypothesized that apes will be more likely to look back at the experimenter in this condition. In the meaningless condition, the barrier between experimenter and target had a window, so that the experimenter and the subject could see the target. In this condition the authors expected less checking back behavior as following the experimenter's gaze would lead the apes to discover the target. The hypotheses were confirmed, as the chimpanzees and bonobos checked back more often in the meaningful condition. Orangutans and gorillas on the other hand seemed insensitive to the differences in the barrier conditions, producing checking back behaviors in both. This insensitivity indicates that the occurrence of checking back alone might not be sufficient to show understanding of visual perspectives and the referential nature of gaze.

Perhaps surprisingly, a recent study discovered checking back in three species of palaeognath and one species of neognath birds (Zeiträg et al., 2022, Preprint). This was the first-ever description of checking back in any bird species, while in the same study, no such behavior was found in American alligators. The discrepancy between the two is likely caused by differences in their neuroanatomy. Birds have significantly more neurons in their brains than crocodylians and non-avian reptiles in general. However, proportionally, the biggest increase of neuronal numbers is accounted for by the cerebellum (Kverková et al., 2022). The higher neuronal numbers in the cerebellum of birds could explain the presence of checking back behaviors as this structure is believed to be involved in the formation of so-called internal forward models. These models are top-down processes using prior information to predict actions and others' behaviors (Wolpert et al., 1998; Wolpert & Flanagan, 2001; Bastian, 2006; Roth et al., 2013). The model is updated in case of a mismatch between the prediction and sensorimotor feedback. Checking back could thus firstly be diagnostic of the violation of a social prediction, and secondly represent an attempt to update the model by retracking the gaze direction. These novel results indicate that the increased number of cerebellar neurons of birds likely allow for the formation of more robust internal forward models and the connected social predictions compared to reptiles.

10. The evolution of gaze following

The ability to visually co-orient with the gaze direction of others has been found in distantly related taxa, suggesting roots in deep evolutionary time. The origin of this skill, however, remains elusive. Perhaps, GFD evolved before vertebrates became land dwellers, or maybe shortly after. The lack of studies on non-amniotes, such as amphibians and fishes, makes it difficult to pinpoint the emergence of this skill. What speaks for a very old origin, is the conserved subcortical pathway in the vertebrate brain, involved in fast, reflexive co-orientation responses to the gaze of others. At least one fish species appears sensitive to body orientations of others, though this could be an adaptation to the species' hunting style (see above). Based on evidence for GFD from all tested amniotes (mammals, reptiles, and birds), it is likely that this skill was present in the stem amniote, about 325 million years ago (Ford & Benson, 2020).

The ability for GGF, on the other hand, appears to have evolved in parallel, or convergently, in Synapsida (the lineage including the mammals) and Sauropsida (the lineage including the reptiles and birds), as this skill has to date only been found in mammals and birds. Decades of research in this area seem to have confirmed that GFD and GGF represent two distinct skills, as already suggested by Povinelli and Eddy (1996). This implies that GGF relies on more complex, and hence later evolved, neurocognitive structures.

Two lines of evidence support this assumption. Firstly, in all species where the ontogeny of GGF has been studied, its onset clearly succeeds the development of GFD. Secondly, and perhaps more importantly, the two lineages exhibiting GGF skills – mammals and birds – have over time drastically increased their total and relative brain sizes, as well as their neuronal numbers. This disproportionally large increase left them with significantly more neurons relative to body size than reptiles (Kverková et al., 2022). The heightened computational power connected to more neurons in the brain might equip mammals and birds with the capacity for visual perspective taking, while the lower neurons numbers of reptiles might not allow for sophisticated visual socio-cognitive skills. However, more studies are needed to verify the absence of GGF in reptiles and to better understand the correlational relationship between neuronal numbers and GGF.

It is still unclear when GGF arose in the two different lineages. Mammals are the last extant representatives of the Synapsida. Thus, any comparisons with animal groups outside mammals, but within the synapsids, are not possible. However, within mammals, monotremes and marsupials have to our knowledge not been tested in gaze following. Monotremes are egg-laying mammals that diverged long before marsupial and placental mammals and are as close as we can get to the earliest mammals today. Marsupials are more derived, but their brains have retained more ancestral features compared to placental mammals (Ashwell, 2010; Álvarez-Carretero et al., 2022; Flannery et al., 2022; Kverková et al., 2022). Studies on these neurocognitively distinct groups would substantially support our understanding of the timing of the emergence of GGF in mammals, or to show that it might have even evolved before mammals.

In Sauropsida the picture is somewhat clearer. As GGF is not found in reptiles, it likely evolved somewhere within the dinosaur lineage. At least it seems to have existed in the first birds around 150 million years ago. But it is not unlikely that GGF existed in non-avian dinosaur taxa. The Maniraptora is the group of theropod dinosaurs from which the birds derived, and its members show overlapping traits with birds, in particular with palaeognaths. Their brains had morphologies comparable to modern palaeognaths (Balanoff et al., 2014). Moreover, they had comparable scaling relationships of body and brain size (Ksepka et al., 2020). Even some social behaviors connected to reproductive strategies were similar, such as the parental care system, where the male incubates the eggs from several females and provides care of the chicks (Varricchio et al., 2008; Varricchio & Jackson, 2016). That said, GGF might have been present even deeper into the non-avian dinosaurs. However, to better understand its origin, more studies on the neurocognition of GGF in birds are needed. Finally, more palaeontological neuroanatomy studies will help to shed light on the evolution of GGF.

Gaze following – with its different levels – appears to be an important fundament for social cognition. This can, for example, be seen in the crucial role it plays for a developing human mind. Without gaze following, a wealth of information is lost, and the opportunities to evolve essential skills, such as perspective taking and social predictions, are hampered. Considering the likely cardinal function this fundamental and underlying social behavior has, it is surprisingly understudied from an evolutionary perspective.

Table 1: Overview of the species tested in different gaze following paradigms and corresponding references. GFD = Gaze following into distance, GGF = Geometrical gaze following, GFBS = Gaze following behind subject, OC = Object choice using gaze cues, COC = Competitive object choice, FTC = Food theft competition, GKT = Guesser-knower task, CB = Checking back, ✓ = succeeded in this paradigm, ✗ = failed in this paradigm, ✓/✗ = conflicting findings, - = not tested in this paradigm

Species	GFD	GGF	GFBS	OC	COC	FTC	GKT	CB	References
BIRDS **Corvids**									
Clark's nutcracker (*Nucifraga columbia*)	-	-	-	✓	-	-	-	-	Tornick et al., 2010
Common raven (*Corvus corax*)	✓	✓	-	✗	-	-	✓	-	Bugnyar et al., 2004; Bugnyar, 2011; Bugnyar et al., 2016; Schloegl et al., 2007; Schloegl et al. 2008a; Schloegl et al. 2008b
Jackdaw (*Corvus monedula*)	✗	✗	-	✓	-	-	-	-	von Bayern & Emery, 2009; Schloegl et al., 2008c
Rook (*Corvus frugilegus*)	✓	✓	-	✗	-	-	-	-	Schloegl et al., 2008c; Schmidt et al., 2011
Fowl									
Red junglefowl (*Gallus gallus*)	✓	✓	-	-	-	-	-	✓	Zeiträg et al., 2022, Preprint
Greylag goose (*Anser anser*)	✓	-	-	-	-	-	-	-	Kehmeier et al. 2011
Ibises									
Northern bald ibis (*Geronticus eremita*)	✓	✗	-	-	-	-	-	-	Loretto et al., 2009
Palaeognaths									
Elegant-crested tinamou (*Eudromia elegans*)	✓	✓	-	-	-	-	-	✓	Zeiträg et al., 2022, Preprint
Emu (*Dromaius novaehollandiae*)	✓	✓	-	-	-	-	-	✓	Zeiträg et al., 2022, Prerpint

Species	GFD	GGF	GFBS	OC	COC	FTC	GKT	CB	References
Rhea (*Rhea americana)*	✓	✓	-	-	-	-	-	✓	Zeiträg et al., 2022, Preprint
Parrots									
African gray parrot (*Psittacus erithacus)*	-	-	-	×	-	-	-	-	Giret et al., 2009
Passerines									
European starling (*Sturnus vulgaris*)	-	✓	-	-	-	-	-	-	Butler & Fernández-Juricic, 2014
Penguins									
African penguin (*Spheniscus demersus*)	✓	-	-	-	-	-	-	-	Nawroth et al., 2017
MAMMALS **Canids**									
Domestic dog (*Canis familiaris*)	✓	✓	-	✓	-	✓	-	-	Hare et al., 1998; Miklósi et al., 1998; Hare & Tomasello, 1999; Agnetta et al., 2000; McKinley & Sambrook, 2000; Soproni et al., 2001; Bräuer et al., 2006; Téglás et al.,2012; Maginnity & Grace, 2014; Met et al., 2014; Wallis et al. 2015; Werhahn et al., 2016; Catala et al., 2017; Duranton et al., 2017; Clark & Leavens, 2021
Wolve (*Canis lupus*)	✓	✓	-	-	-	-	-	-	Range & Viranyi, 2011
Dingo (*Canis lupus dingo*)	-	-	-	×	-	-	-	-	Smith & Litchfield, 2010
Cetaceans									
Bottlenose dolphin (*Tursiops truncatus*)	-	-	-	✓	-	-	-	-	Tschudin et al., 2001; Pack & Herman, 2004
Felids									
Cat (*Felis silvestris catus*)	-	-	-	✓	-	-	-	-	Pongrácz et al., 2019

Species	GFD	GGF	GFBS	OC	COC	FTC	GKT	CB	References
Pinnipeds									
South African fur seal (*Arctocephalus pusillus)*	-	-	-	✓	-	-	-	-	Scheumann & Call, 2004
Gray seal (*Halichoerus grypus)*	-	-	-	✗	-	-	-	-	Shapiro et al., 2003
Proboscids									
Asian elephant (*Elephas maximus)*	-	-	-	✗	-	-	-	-	Ketchaisri et al., 2019
Ungulates									
Domestic horse (*Equus caballus)*	-	-	-	✗	-	✓	-	-	McKinley & Sambrook, 2000; Proops & McComb, 2010a; Proops & McComb, 2010b
Domestic pig (*Sus scrofa domesticus)*	✗	-	-	✓	-	✓	-	-	Byrne et al., 2001; Nawroth et al. 2014
Dwarf goat (*Capra aegagrus hircus)*	✓	-	-	✗	-	-	-	-	Kaminski et al., 2005; Nawroth et al., 2015; Schaffer et al., 2020
Guanaco (*Lama guanicoe)*	✗	-	-	-	-	-	-	-	Schaffer et al., 2020
Llama (*Lama glama)*	✓	-	-	-	-	-	-	-	Schaffer et al., 2020
Mouflon (*Ovis orientalis orientalis)*	✓	-	-	-	-	-	-	-	Schaffer et al., 2020

Species	GFD	GGF	GFBS	OC	COC	FTC	GKT	CB	References
PRIMATES **Great Apes**									
Bonobo (*Pan paniscus)*	✓	✓	-	✓	-	-	-	✓	Bräuer 2005, 2006; Bräuer et al., 2005; Okamoto-Barth et al., 2007; Mulcahy & Call, 2009; Herrmann et al., 2010; Kano & Call, 2014
Chimpanzee (*Pan troglodytes*)	✓	✓	✓	✓	✓/✗	✓	✓	✓	Itakura, 1996; Povinelli & Eddy, 1996a, 1996b, 1997; Call et al., 1998; Itakura & Tanaka 1998; Tomasello et al., 1998, 1999, 2001; Itakura et al., 1999; Hare et al., 2000, 2001; Karin-D'Arcy & Povinelli, 2002; Okamoto et al., 2002, 2004; Bräuer et al.,2005; Melis et al., 2006; Okamoto-Barth et al., 2007; Mulcahy & Call, 2009; Herrmann et al., 2010; Kano & Call, 2014
Gorilla (*Gorilla gorilla*)	✓	✓	-	✓/✗	-	-	-	✓	Peignot, 1999; Bräuer et al., 2005; Okamoto-Barth et al., 2007; Byrnit, 2009; Schmid et al., 2017
Orangutan (*Pongo pygmaeus*)	✓	✓	✓	✓/✗	-	✗	✗	✓	Itakura, 1996; Itakura & Tanaka, 1998; Kaplan & Rogers, 2002; Byrnit, 2004; Bräuer et al., 2005; Okamoto-Barth et al., 2007; Mulcahy & Call, 2009; Gretscher et al., 2012; Kano & Call, 2014
Gibbons									
Hoolock gibbon *(Hoolock leuconedys)*	-	-	-	-	-	-	✓	-	Sanchez-Amaro et al., 2020
White-handed gibbon (*Hylobates lar)*	✓	-	-	✓	-	-	-	✗	Inoue et al., 2004; Liebal & Kaminski, 2012
Pileated gibbon (*Hylobates pileatus*)	✓	-	-	-	-	-	-	✓/✗	Horton & Caldwell, 2006; Liebal & Kaminski, 2012
Siamang (*Symphalangus syndactylus*)	✓	-	-	-	-	-	-	✗	Liebal & Kaminski, 2012
Silvery gibbon (*Hylobates moloch*)	✓	-	-	-	-	-	✓	✗	Liebal & Kaminski, 2012; Sanchez-Amaro et al., 2020

Species	GFD	GGF	GFBS	OC	COC	FTC	GKT	CB	References
Lemurs									
Black-and-white ruffed lemur (*Varecia veriegata*)	×	-	-	-	-	-	×	-	Sandel et al., 2011
Black lemur (Eul*emur macaco*)	✓/×	-	×	✓	-	-	×	-	Itakura, 1996; Anderson & Mitchell 1999; Ruiz et al., 2009; Sandel, 2011
Brown lemur (*Eulemur fulvus*)	✓	-	×	✓	-	-	-	-	Itakura, 1996; Ruiz et al., 2009
Mongoose lemur (*Eulemur mongoz*)	×	-	-	-	-	-	×	-	Sandel et al., 2011
Ringtailed lemur (*Lemur catta*)	✓	-	-	-	-	-	✓	-	Shepherd & Platt, 2008; Sandel et al., 2011
New World monkeys									
Common marmoset (*Callithrix jacchus*)	×	-	-	×	✓	-	✓	×	Burkart & Heschl 2006; Burkart & Heschl 2007
Cotton-top tamarin (*Saguinus oedipus oedipus*)	✓	-	-	✓	-	-	-	-	Santos & Hauser, 1999; Neiworth et al., 2002
Spider monkey (*Ateles geoffroyi*)	-	✓	-	-	-	-	-	×	Amici et al., 2009
Squirrel monkey (*Saimiri sciureus*)	✓	-	×	-	-	-	-	-	Itakura, 1996; Anderson et al., 2005
Old World monkeys									
Barbary macaque (*Macaca sylvanus*)	✓	-	✓	-	-	-	-	-	Teufel et al., 2010; Rosati & Santos, 2017
Crested macaque (*Macaca nigra*)	✓	-	-	-	-	-	-	-	Micheletta & Waller, 2012
Long-tailed macaque (*Macaca fascicularis*)	✓	×	-	-	✓	-	-	✓	Goossens et al., 2008, 2012; Overduin-de Vries et al., 2014

Species	**GFD**	**GGF**	**GFBS**	**OC**	**COC**	**FTC**	**GKT**	**CB**	**References**
Pig-tailed macaque (*Macaca nemestrina)*	✓	-	×	-	-	-	-	-	Itakura, 1996; Tomasello et al., 1998; Ferrari et al., 2000, 2008; Paukner et al., 2007
Rhesus macaque (*Macaca mulatta)*	✓	×	×	✓/×	-	-	✓	-	Anderson et al., 1996; Itakura, 1996; Itakura & Anderson, 1996; Tomasello et al., 1998, 2001; Lorincz et al., 2000; Flombaum & Santos, 2005; Shepherd et al., 2006; Emery et al., 2007; Hauser et al., 2007; Roy et al., 2014; Rosati et al., 2016; Bettle & Rosati, 2019
Stump-tailed macaque (*Macaca arctoides)*	✓	-	×	-	-	-	-	-	Itakura, 1996; Tomasello et al., 1998; Anderson & Mitchell, 1999
Tonkean macaque (*Macaca tonkeana)*	-	-	×	-	-	-	-	-	Itakura, 1996
Pigtail macaque (*Macaca nemestrina)*	✓	-	-	-	-	-	-	-	Ferrari et al., 2000, 2008; Paukner et al., 2007
Capuchin monkey (*Cebus apella)*	✓	✓	×	×	×	✓	-	×	Anderson et al., 1995; Itakura, 1996; Vick & Anderson, 2000; Hare et al., 2003; Anderson et al., 2005; Amici et al., 2009; Defolie, 2015
White-faced capuchin (*Cebus capucinus)*	-	-	×	-	-	-	-	-	Itakura, 1996
Diana monkey (*Cercopithecus diana diana)*	✓	-	-	-	-	-	-	✓	Scerif et al., 2004
François' langur (*Trachypithecus francoisi)*	✓	-	-	-	-	-	-	-	Chen et al., 2017
Golden snub-nosed monkey (*Rhinopithecus roxellana)*	✓	-	-	-	-	-	-	-	Chen et al., 2017
Olive baboon (*Papio anubis)*	✓	-	-	-	-	-	✓	-	Parron et al., 2016; Vick & Anderson, 2003

Species	GFD	GGF	GFBS	OC	COC	FTC	GKT	CB	References
Sooty mangabey (*Cercocebus atys torquatus)*	✓	-	-	-	-	-	-	-	Tomasello et al., 1998
REPTILES **Crocodylians**									
American alligator (*Alligator mississippiensis)*	✓	×	-	-	-	-	-	-	Zeiträg et al., 2022, Preprint
Lizards									
Bearded dragon (*Pogona vitticeps)*	✓	×	-	-	-	-	-	-	Siviter et al., 2017
Leopard gecko (*Eublepharis macularius)*	✓	-	-	-	-	-	-	-	Simpson & O'Hara, 2019
Tortoises									
Red-footed tortoise (*Geochelone carbonaria)*	✓	-	-	-	-	-	-	-	Wilkinson et al., 2010
FISHES									
Archerfish *(Toxotes chatareus)*	✓	-	-	-	-	-	-	-	Leadner et al., 2021

Acknowledgments

This work was supported by Swedish Research Council grants 2021-02973 and 2019-03265, and the LMK Foundation. We thank Steve Brusatte for his comments on the manuscript.

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Paper III

Differential responses to con- and allospecific visual cues in juvenile ravens (*Corvus corax*): The ontogeny of gaze following and social predictions

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Abstract

Gaze following refers to the ability to co-orient with others' gaze directions. Ontogenetic studies on gaze following in animals have predominantly used human experimenters as demonstrators. It is, however, likely that developing animals are initially more attuned to individuals from their own species, which might result in differences in the ontogenetic onset of gaze following with human and conspecific demonstrators.

"Checking back" is a signature behaviour in the gaze following repertoires of humans, apes, and some Old world monkeys. It is commonly interpreted as an understanding of the referentiality of gaze. Recently, "checking back" has been discovered in four avian species, suggesting a shared behavioural trait among birds.

To investigate effects of con- and allospecific demonstrators on gaze following responses, we studied visual co-orientations of four hand-raised juvenile common ravens (*Corvus corax*) with human and conspecific gaze cues. Moreover, we for the first time investigated "checking back" in ravens and compared the effects of con- and allospecific demonstrators on this behaviour.

Ravens followed human and conspecific gaze with no apparent differences in ontogenetic onset, but after significantly longer latencies with human demonstrators. Subjects moreover already checked back at 30 days old and did so significantly more often with conspecific demonstrators.

Our findings suggest differences in processing speed and social predictions of human and conspecific gazes, indicating an underlying neurocognitive mechanism attuned to social information gathering from conspecifics. We propose more studies using conspecific demonstrators to reveal the full gaze following potential of a species.

Keywords: gaze$_1$, ontogeny$_2$, social cognition$_3$, social predictions$_4$

1. Introduction

The transfer and use of social information is an integral part of sociality (Shettleworth, 2010). One effective way of acquiring such information is to attend to what others are looking at. Co-orienting with others' gaze directions (gaze following) is a fundamental socio-cognitive component of human as well as non-human animals. The advantages of extracting social information from observed gaze are numerous and range from gathering information about food and predators, to drawing attention to social interactions (Tomasello et al., 1998; Emery, 2000). Witnessing others' social interactions can subsequently inform animals about third-party relationships and facilitate social learning.

Human infants are already as new-borns sensitive to others' gaze directions (Batki et al., 2000; Farroni et al., 2002) and spontaneously start co-orienting with gazes between 3 and 6 months (e.g. Butterworth & Jarrett, 1991; Perra & Gattis, 2010). The early ontogeny of gaze following in humans illustrates the fundamental character of this socio-cognitive skill that subsequently has implications for the development of other cognitive capacities. In human children, for example, gaze following affects the development of theory of mind (Brooks & Meltzoff, 2015), joint attention (Carpenter et al., 1998), and language acquisition (Baldwin, 1991; Schafer & Plunkett, 1998; Houston-Price et al., 2006).

Many similarities in the development of gaze following in human infants and young animals have been discovered. Co-orientations with observed gaze directions develop early in the ontogeny of mammals (e.g. rhesus macaques and chimpanzees: Tomasello et al., 2001; wolves: Range & Virányi, 2011) and birds (ravens: Bugnyar et al., 2004; rooks: Schloegl et al., 2008; greylag geese: Kehmeier et al., 2011).

However, it is difficult to draw parallels between developmental studies on humans and animals, as human infants are tested for their ability to follow conspecific gaze, while most animals, so far, have been presented with gaze cues from an allospecific demonstrator – a human experimenter. While this practice is beneficial to keep testing conditions as controlled as possible, gaze following has presumably evolved to facilitate the transfer of social information between conspecifics. Therefore, animals are likely initially more attuned to social signals from conspecifics. Animals might learn to interpret human communicative signals later in their development given enough exposure to humans. Parent-raised orangutans (*Pongo pygmaeus*), for example, fail to use human gaze to locate a target (Byrnit, 2004) and only enculturated chimpanzees (*Pan troglodytes*) are sensitive to visual attentive states of a human experimenter (Call et al., 2000). Consequently, animals might develop the ability to follow human gaze later than conspecific gaze. Only one observational account for such a disparity exists for ravens (Schloegl et al., 2007). The authors observed ravens co-orienting with their conspecifics' gazes shortly after fledging - approximately 7 weeks before reacting to experimental human gaze cues.

Human children develop into increasingly skilled gaze followers throughout their ontogeny. At 8 months, children begin to look back at a demonstrator when following their gaze and not findings anything interesting in their line of sight (Scaife & Bruner, 1975; Butterworth & Cochran, 1980). Developmental psychologists commonly view this "checking back"-behaviour as diagnostic of an expectancy violation: the failure of finding something in the environment that the gazer was expected to look at. Hence, the behaviour reveals an understanding of the referentiality of a gaze. The comparably late ontogenetic onset of "checking back" compared to co-orientations, suggests an involvement of more complex neurocognitive mechanisms, such as the formation of predictions about others' visual perspectives and behaviours.

"Checking back" has later also been observed in apes (Bräuer et al., 2005; Horton & Caldwell, 2006; Okamoto-Barth et al., 2007) and some Old World monkeys (Scerif et al., 2004; Goossens et al., 2008), while still not shown in New world monkeys (Amici et al., 2009). Recently, this behaviour has for the first time been described in birds, namely three palaeognath species (emus, *Dromaius novaehollandiae*, greater rheas, *Rhea americana*, and elegant-crested tinamous, *Eudromia elegans*), and one neognath species (Red junglefowl, *Gallus gallus*) (Zeiträg et al., 2022; Preprint). These new findings raise the possibility of "checking back"-behaviour being a conserved behavioural trait among all birds, though it has to date never been described in any other avian species.

Developmental accounts of "checking back" in animals are hence scarce, though at least in apes, it appears to follow the same developmental pattern as in human children. Bräuer and colleagues (2005) found that in all four ape species infants (1-4 years) did not look back at the demonstrator, but started to show this behaviour as juveniles (5-10 years), and were most likely to check back as adults (10+ years).

To obtain a better understanding of the impact of con- and allospecific demonstrators on gaze following responses of developing animals, we tested four hand-raised juvenile common ravens (*Corvus corax*) for their ability to follow human and conspecific gazes into the distance between the age of 30 and 95 days. We moreover investigated "checking back" in ravens, its ontogenetic development, and the potential effects of different demonstrators on this behaviour.

2. Methods

2.1 Subjects and Housing

We tested four hand-raised juvenile ravens of unknown sex that came from three different (captive) nests, i.e., two of them were siblings. Testing was carried out at Lund University Corvid Cognition Station. All four chicks were initially kept together in an artificial nest, where they were cared for by humans. They were ringed for individual recognition. After fledging, the ravens were moved to an outdoor aviary section of 240 m^2, which was also shared with two adult females, unrelated to the chicks. They were continually hand-fed by humans (and by one of the females), until they could provide for themselves. Time of fledging was used to estimate the ravens' age. The subjects were 30, 38 and 44 days old at study onset. They had been taken into human care at 13, 20 and 17 days of age and had thus been fed and cared for by humans from an early age.

2.2 Experimental Design

The experiment was divided into two demonstrator conditions: a human and a conspecific condition. Each condition had two trial types: control and test trials. In the human condition, a human demonstrator was standing or kneeling in front of the subject so that they were approximately on eye-level. At the beginning of each trial, the human caught the subject's attention through calling or waving. The trial started once the subject was facing the demonstrator. In control trials, the experimenter looked for 5 seconds in the direction of the subject, without directly looking at it. In test trials, the experimenter gazed up for 5 seconds through lifting both head and eyes. Two familiar human experimenters were used that were both involved in hand-raising the ravens.

In the conspecific condition, two ravens were placed on perches facing each other approximately 2 meters apart. The experimenter waited for a moment when both birds faced each other before starting a trial. In test trials, the experimenter lured the gaze of the demonstrator to a board hanging above the birds' heads by reflecting the beam of a laser pointer onto the board on the demonstrator side until the demonstrator reacted by looking up. In control trials, no stimulus was flashed, so that the birds were just facing each other. Subjects served as demonstrators for each other. In all trials of both demonstrator conditions, the reaction of the subject was recorded for 10 seconds after the demonstration in test trials or for 15 seconds in control trials.

We interspersed stimulus controls in a pseudorandomized order. They controlled whether the laser pointer beam was visible to subjects. Stimulus controls were conducted in the same way as conspecific test trials, but without a demonstrator present. For information on dates and trials, see Table 1 (for more detailed information, see Supplementary Material Table 1). All trials were video recorded with two cameras. The experiment was run for 8 weeks, with 2 testing sessions per week in the first 3 weeks and one session per week for the remainder of the experimental period to reduce habituation. We moreover had to stop conspecific trials after 3 weeks, as it became too difficult to engage two juvenile ravens in the experiment, due to higher mobility and increased exploratory behaviours.

Table 1: Trials conducted on each experimental day.

Date	Age [days]	Demonstrator Condition	Test Condition	#Trials
210512	30,37,44,44	Conspecific	Test	8
210512	30,37,44,44	Conspecific	Control	8
210517	35,42,49,49	Human	Test	7
210517	35,42,49,49	Human	Control	7
210517	35,42,49,49	Conspecific	Test	6
210517	35,42,49,49	Conspecific	Control	6
210521	39,46,53,53	Human	Test	8
210521	39,46,53,53	Human	Control	8
210521	39,46,53,53	Conspecific	Test	8
210521	39,46,53,53	Conspecific	Control	8
210524	42,49,56,56	Human	Test	8
210524	42,49,56,56	Human	Control	8
210524	42,49,56,56	Conspecific	Test	8
210524	42,49,56,56	Conspecific	Control	8
210524	42,49,56,56	Conspecific	Stimulus Control	7
210528	46,53,60,60	Human	Test	8
210528	46,53,60,60	Human	Control	8
210528	46,53,60,60	Conspecific	Test	8
210528	46,53,60,60	Conspecific	Control	8
210528	46,53,60,60	Conspecific	Stimulus Control	8
210531	49,56,56,56	Human	Test	6
210531	49,56,56,56	Human	Control	5
210531	49,56,56,56	Conspecific	Test	3
210531	49,56,56,56	Conspecific	Control	4
210531	49,56,56,56	Conspecific	Stimulus Control	7
210607	56,63,70,70	Human	Test	8
210607	56,63,70,70	Human	Control	8
210607	56,63,70,70	Conspecific	Stimulus Control	8
210614	63,70,77,77	Human	Test	8
210614	63,70,77,77	Human	Control	8
210621	70,77,84,84	Human	Test	4
210621	70,77,84,84	Human	Control	4
210628	77,84,91,91	Human	Test	5
210628	77,84,91,91	Human	Control	4
210702	81,88,95	Human	Test	2
210702	81,88,95	Human	Control	1

2.3 Coding and Statistical Analyses

All trials were coded from video recordings using the program Solomon Coder (Version: beta 19.08.02; Péter, 2017). We coded upward looks during predefined trials, including latency and duration of these orientations. Upward looks were inferred from beak orientations. We coded "checking back" every time a subject looked back at the demonstrator after looking up. The latencies and durations of this behaviour were also coded. 10 percent of the videos were coded for inter-observer reliability and intraclass correlation was excellent (ICC = 0.95, F = 36.3 , $p < 0.001$).

Generalized linear mixed models (GLMMs) were used to analyse the data with the glmer function of the lme4 package in RStudio (Version 1.4.1717; RStudio Team, 2020). We created a full model using demonstrator condition (human or conspecific), age, and trial type (test, control, stimulus control), as well as their three-way interaction as fixed effects and upward looks as dependent variable with a binomial distribution. We included subject as random factor. We ran the same model with latency of looking up as response variable with a Gamma distribution. When using latency as response variable, it was transformed by adding 1 to each value to avoid errors due to zero values in the data. We then fitted a third model with the same fixed effects, but "checking back" as response variable with a binomial distribution. For all three models, we reduced the full model using the Akaike Information Criterion (AIC) to determine the best-fitting model. We subsequently used likelihood ratio tests on the final model to reveal the effects of the remaining factors.

3. Results

When analyzing experiments throughout the entire experimental period, we found a significant effect for trial type (test or control; GLMM; $\chi^2 = 11.95$, df = 2, $p = 0.0025$, see Figure 1), but not for demonstrator condition (human or conspecific) on upward looks. The final model explained more variance than a model including age (Δ AIC > 10). Thus, no developmental trend over the course of the experimental period could be identified. Ravens looked up significantly more often in conspecific test trials compared to stimulus control trials (GLMM; $\chi^2 = 5.57$, df = 1, $p = 0.018$), suggesting that they could not see the beam of the laser pointer, but that it was the gaze of the demonstrator that caused the upward orientation.

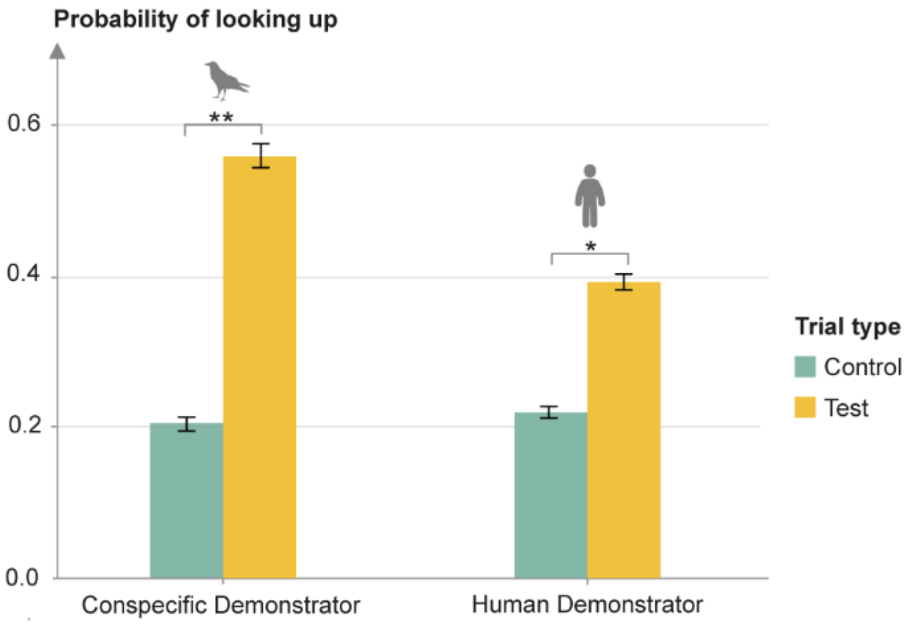

Figure 1: Probability of looking up in control compared to test trials with conspecific and human demonstrators.

When analyzing experimental days individually, we found the first significant difference between test and control trials on day three of the experiment (GLMM; χ^2 = 15.71, df = 2, p= 0.00039), meaning the ravens were 39, 46 and 53 days old. Again, no significant difference between demonstrator conditions was identified. We thus did not detect a difference in ontogenetic onset of con- and allospecific gaze following. As only two subjects were the same age, the exact ontogenetic onsets could not be determined, but both gaze following capacities were present on day three of the experimental period.

When comparing latencies of co-orientation in test trials, ravens looked up significantly quicker with conspecific demonstrators compared to human demonstrators (GLMM; χ^2 = 8.85, df = 1, p = 0.0029, see Figure 2). Based on the difference in mean latencies (1.96 seconds after the onset of gaze demonstration, i.e., the demonstrator looking up, with conspecifics compared to 4.76 seconds with humans), we introduced a 5-second cut-off for upward looks to be scored as gaze follows. This revealed a significant effect of the demonstrator condition (GLMM; χ^2 = 5.20, df = 1, p = 0.023). In fact, when analysing the demonstrator conditions separately with this new criterion, no significant difference between test and control trials could be identified anymore in the human condition (see Figure 3). In the conspecific condition, the effect of trial type became even stronger, as the new criterion removed some upward looks from control trials, but none from test trials (GLMM; $\chi^2 = 13.46$, df = 1, $p = 0.00024$, see Figure 3).

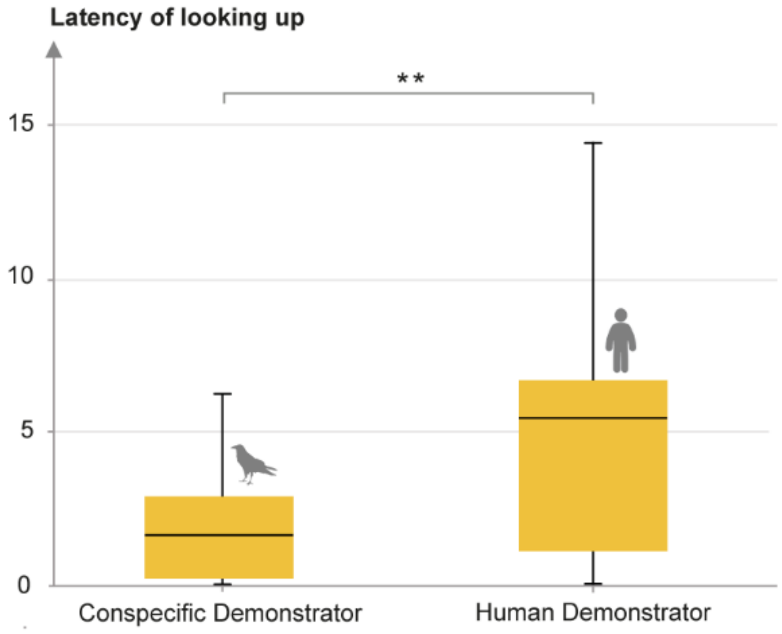

Figure 2: Difference in latency of looking up in test trials with conspecific and human demonstrators.

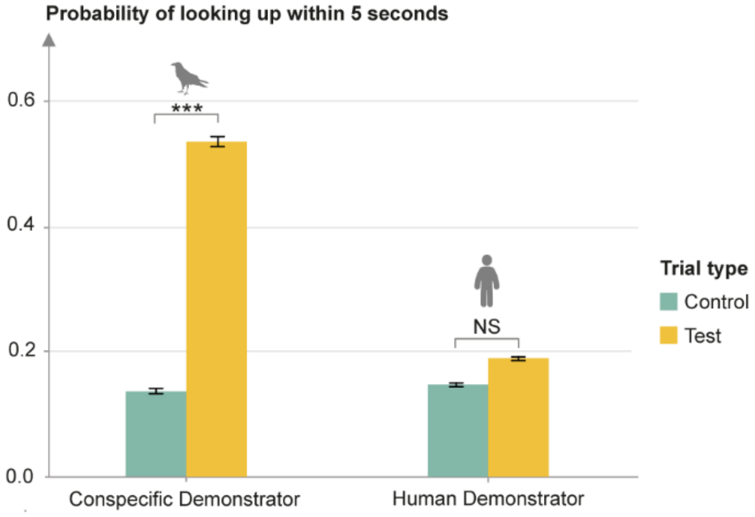

Figure 3: Probability of looking up in control compared to test trials with conspecific and human demonstrators after introducing a 5-second criterion for upward looks to be considered gaze follows.

All four juvenile ravens "checked back" to the demonstrator after following their gaze and did so already from the onset of the study, i.e., as early as 30 days old. Again, the final model excluded age and explained more variance than when including this factor (Δ AIC > 10). Thus, no developmental effect over the experimental period could be identified. However, a significant effect of demonstrator condition on "checking back" was found (GLMM; $\chi^2 = 9.28$, df = 1, $p = 0.0023$). Juvenile ravens checked back significantly more often with conspecific compared to human demonstrators.

4. Discussion

We investigated the development of gaze following in juvenile common ravens and the effect of con- and allospecific demonstrators. The ravens in this study already occasionally co-oriented with conspecifics at study onset, but only started to significantly follow gazes of both human and conspecific demonstrators between 39 and 54 days old (5.5 to 8 weeks). We did not detect a difference in the ontogenetic onset of gaze following between the two different demonstrator conditions. This could, however, be a methodological artefact due to low sample sizes. Our findings are in line with the results of Bugnyar and colleagues (2004), reporting that ravens first started to follow the gaze of an experimenter at 8 weeks.

Only one other study (Schloegl et al., 2007) described the development of conspecific gaze following in ravens and observed first visual co-orientations with siblings "a few days after fledging" (Schloegl et al., 2007, p.772). In the present study, we first recorded visual co-orientations with siblings at 30 days old, and thus even before fledging. These co-orientations were, however, not yet occurring on a statistically significant level. True gaze following skills only developed after fledging.

When analyzing upward looks in the full 10 seconds of the trials, no significant effect of demonstrator condition on overall looking-up rate was identified, indicating co-orientations with both humans and conspecifics. Many species have been found capable of following human gaze, especially primates (for a review see Rosati & Hare, 2009). However, even within primates, cotton-top tamarins (*Saguinus oedipus oedipus*) only follow the gazes of conspecifics (Neiworth et al., 2002). Chimpanzees follow human gazes, but at significantly lower rates compared to conspecifics (Hattori et al., 2010). And even domesticated ungulates prefer to follow the gaze of a conspecific over that of a human experimenter (Schaffer et al., 2020).

Similarly, after introducing a more conservative criterion for gaze follows in our study, i.e., a 5-second cut-off after the onset of the gaze cue for upward looks to be scored as gaze follows, no significant effect of trial type could be identified any longer with a human demonstrator. Juvenile ravens might hence perhaps not follow human gaze at all in this age range.

Nevertheless, two lines of evidence speak against this. Firstly, without the time cut-off, ravens looked up significantly more often in test compared to control trials with human demonstrators. The only difference between the two trial types was the human gaze cue, suggesting that the gaze caused the difference in upward looks. Secondly, we found "checking back"-behaviour in human test trials, implying that co-orientations with humans were indeed incidences of gaze following.

The prolonged time to react to human gaze could be the result of longer processing times to interpret allospecific gaze. To our knowledge, no study has compared latencies of co-orientation with con- and allospecific demonstrators. One should note that in the human demonstrator condition, the human was gazing continuously for 5 seconds, and the subject reacted, on average, after 4.76 seconds. The gaze of a conspecific, though, was a quick spontaneous gaze towards the laser pointer, lasting on average 3.6 seconds, but with several instances only lasting for 1 second. In other words, such quick gazes by a human would probably not have elicited a response in the young ravens.

Finally, we observed "checking back" in juvenile ravens as young as 30 days old and thus even before fledging. That is very early compared to human infants and great apes (Scaife & Bruner, 1975; Bräuer et al., 2005). This finding does not only support the hypothesis that "checking back" is a shared behavioural trait among birds, but also implies that birds form social predictions about others exceptionally early in their ontogeny. Studies with higher sample sizes and even earlier onset will be needed to pinpoint the ontogenetic onset of this behaviour.

We moreover found a difference in "checking back" rates between demonstrator conditions. Juvenile ravens checked back significantly less with humans compared to conspecifics. This discrepancy might be the result of differences in the formation of social predictions about con- and allospecific demonstrators. The quicker responses indicate that ravens are more attuned to conspecific gaze. They might thus have a stronger expectation to find a target in their line of gaze compared to the gaze of a human. The more robust social prediction might cause more surprise when not finding a gaze target, leading to more "checking back" with conspecifics compared to humans.

There are two alternative explanations for this phenomenon. Firstly, the difference in "checking back" with humans and conspecifics might not be caused by more robust social predictions, but by different predictions for humans and conspecifics. Ravens are food cachers. Consequently, when not finding an object in the line of sight of a conspecific, it could be beneficial to continue the search, while they might not have such predictions for human behaviour. However, it should be noted that ravens only start caching approximately 2 months after fledging (though premature forms of this behaviour can already occur shortly after fledging; Bugnyar et al., 2007) – considerably later than the onset of "checking back" in our study. They moreover had never observed adult ravens nor humans cache food. Secondly, an inherent anatomical difference between humans and ravens, such as the pointy beak, might allow for more accurate tracking of gaze directions and thus more robust predictions about the location of gaze targets. More nuanced studies investigating social predictions of ravens based on human and conspecific gaze cues will be needed to understand the differences in "checking back"-behaviours.

Taken together, even though we did not find a difference in the ontogenetic onset of gaze following with con- and allospecific demonstrators, our findings suggest differences in processing speed and social predictions between the two. This indicates different ecological, anatomical, or other valences of con- and allospecific gaze – at least for very young individuals.

It should be noted that the subjects of this study were hand-raised by the human experimenters in this study, and thus had ample exposure and positive experiences with humans. This indicates that the neurocognitive mechanisms involved in gaze following are intrinsically attuned to conspecifics, likely because they have evolved to optimize social information gathering within a social group of conspecifics. Gaze following studies using human demonstrators might thus not have discovered species' full gaze following potentials in terms of speed and rate of co-orientations. Follow-up studies should investigate whether ravens overcome this discrepancy and eventually develop the same gaze following responses towards humans. Indeed, the opposite would be of interest too: do humans note and follow the gazes of ravens to the same extent as ravens do.

Nevertheless, there are disadvantages when using conspecific demonstrators. Length and exact location of gaze cues are less controlled when luring an animal to gaze towards a stimulus. This might, however, make these gazes more realistic and consequently encourage gaze following responses. Due to the above-mentioned advantages and differences in outcomes when using con- and allospecific demonstrators, we propose more studies using conspecific demonstrators to reveal animals' true gaze following potentials.

Acknowledgements

This work was supported by Swedish Research Council grant 2019-03265. We are grateful to Helena Osvath for her help with data collection and the creation of figures. We moreover thank Sofia Haley for her help with video coding.

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Supplementary Materials for

Differential responses to con- and allospecific visual cues in juvenile ravens (*Corvus corax*): The ontogeny of gaze following and social predictions

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1. Ethical statement

All subjects participated voluntarily. Experiments took place in the animals' home enclosure, where they were free to move to a different area. Animals were motivated to participate using food rewards without ever applying force of any kind. All subjects were hand-raised together. Both human demonstrators were involved in the hand-raising process. Thus, both the human and conspecific demonstrators were familiar to the subjects and had no antagonistic history. All animals were housed at Lund University's Corvid Research Station that meets the legal requirements, as well as Lund Universities ethical standards. The research did not include so-called procedures under the EU-directive 2010/63/EU, and did not qualify for ethical approval, which is also true according to the stricter Swedish legislation (SJVFS 2019:9, chapter 2, § 22).

2. Subjects

Table 1: Test subjects

Subject	Age at study onset [days]	Date of collection
Red	30	210425
Blue	37	210426
Yellow	44	210425
White	44	210425

3. Trials

Table 2: Numbers of trials for each condition per experimental session

Date	Subject	Age [days]	Demonstrator Condition	Test Condition	#Trials
210512	Red	30	Conspecific	Test	2
	Red	30	Conspecific	Control	2
	Blue	37	Conspecific	Test	2
	Blue	37	Conspecific	Control	2
	Yellow	44	Conspecific	Test	2
	Yellow	44	Conspecific	Control	2
	White	44	Conspecific	Test	2
	White	44	Conspecific	Control	2
210517	Red	35	Human	Test	2
	Red	35	Human	Control	2
	Red	35	Conspecific	Test	2
	Red	35	Conspecific	Control	1
	Blue	42	Human	Test	2
	Blue	42	Human	Control	2
	Blue	42	Conspecific	Test	2
	Blue	42	Conspecific	Control	2
	Yellow	49	Human	Test	1
	Yellow	49	Human	Control	1
	Yellow	49	Conspecific	Test	1
	Yellow	49	Conspecific	Control	2
	White	49	Human	Test	2
	White	49	Human	Control	2
	White	49	Conspecific	Test	1
	White	49	Conspecific	Control	1
210521	Red	39	Human	Test	2
	Red	39	Human	Control	2
	Red	39	Conspecific	Test	2
	Red	39	Conspecific	Control	2
	Blue	46	Human	Test	2
	Blue	46	Human	Control	2
	Blue	46	Conspecific	Test	2
	Blue	46	Conspecific	Control	2
	Yellow	53	Human	Test	2
	Yellow	53	Human	Control	2

	Yellow	53	Conspecific	Test	2
	Yellow	53	Conspecific	Control	2
	White	53	Human	Test	2
	White	53	Human	Control	2
	White	53	Conspecific	Test	2
	White	53	Conspecific	Control	2
210524	Red	42	Human	Test	2
	Red	42	Human	Control	2
	Red	42	Conspecific	Test	2
	Red	42	Conspecific	Control	2
	Red	42	Conspecific	Stimulus Control	2
	Blue	49	Human	Test	2
	Blue	49	Human	Control	2
	Blue	49	Conspecific	Test	2
	Blue	49	Conspecific	Control	2
	Blue	49	Conspecific	Stimulus Control	1
	Yellow	56	Human	Test	2
	Yellow	56	Human	Control	2
	Yellow	56	Conspecific	Test	2
	Yellow	56	Conspecific	Control	2
	Yellow	56	Conspecific	Stimulus Control	2
	White	56	Human	Test	2
	White	56	Human	Control	2
	White	56	Conspecific	Test	2
	White	56	Conspecific	Control	2
	White	56	Conspecific	Stimulus Control	2
210528	Red	46	Human	Test	2
	Red	46	Human	Control	2
	Red	46	Conspecific	Test	2
	Red	46	Conspecific	Control	2
	Red	46	Conspecific	Stimulus Control	2
	Blue	53	Human	Test	2
	Blue	53	Human	Control	2
	Blue	53	Conspecific	Test	2
	Blue	53	Conspecific	Control	2
	Blue	53	Conspecific	Stimulus Control	2
	Yellow	60	Human	Test	2
	Yellow	60	Human	Control	2

	Yellow	60	Conspecific	Test	2
	Yellow	60	Conspecific	Control	2
	Yellow	60	Conspecific	Stimulus Control	2
	White	60	Human	Test	2
	White	60	Human	Control	2
	White	60	Conspecific	Test	2
	White	60	Conspecific	Control	2
	White	60	Conspecific	Stimulus Control	2
210531	Red	49	Human	Test	2
	Red	49	Human	Control	2
	Red	49	Conspecific	Control	1
	Red	49	Conspecific	Stimulus Control	2
	Blue	56	Human	Test	1
	Blue	56	Human	Control	2
	Blue	56	Conspecific	Test	1
	Blue	56	Conspecific	Control	1
	Blue	56	Conspecific	Stimulus Control	2
	Yellow	63	Human	Test	2
	Yellow	63	Human	Control	2
	Yellow	63	Conspecific	Test	1
	Yellow	63	Conspecific	Stimulus Control	2
	White	63	Human	Test	1
	White	63	Conspecific	Test	1
	White	63	Conspecific	Control	2
	White	63	Conspecific	Stimulus Control	1
210607	Red	56	Human	Test	2
	Red	56	Human	Control	2
	Red	56	Conspecific	Stimulus Control	2
	Blue	63	Human	Test	2
	Blue	63	Human	Control	2
	Blue	63	Conspecific	Stimulus Control	2
	Yellow	70	Human	Test	2
	Yellow	70	Human	Control	2
	Yellow	70	Conspecific	Stimulus Control	2
	White	70	Human	Test	2
	White	70	Human	Control	2
	White	70	Conspecific	Stimulus Control	2
210614	Red	56	Human	Test	2

	Red	56	Human	Control	2
	Blue	70	Human	Test	2
	Blue	70	Human	Control	2
	Yellow	77	Human	Test	2
	Yellow	77	Human	Control	2
	White	77	Human	Test	2
	White	77	Human	Control	2
210621	Red	70	Human	Test	2
	Red	70	Human	Control	2
	Blue	77	Human	Test	2
	Blue	77	Human	Control	2
210628	Red	77	Human	Test	1
	Blue	84	Human	Test	2
	Blue	84	Human	Control	2
	White	91	Human	Test	2
	White	91	Human	Control	2
210702	Red	77	Human	Test	1
	Yellow	95	Human	Test	1
	Yellow	95	Human	Control	1

4. Coding definitions

When coding trials, we first specified subject, demonstrator condition (human or conspecific), and trial type (control or test). In control trials, the subject's behaviour was coded for 15 seconds, and in test trials for 10 seconds after the demonstration. We coded all upward looks, inferred from beak orientation (lifting beak up) and head orientation (tilting the head to orient one eye to the sky), including latency from the onset of demonstration and duration of visual orientation. We moreover coded "checking back", defined as a bird co-orienting with the observed gaze direction and looking back to the demonstrator. Again, we coded latency and duration of this behaviour.

Paper IV

Play in juvenile greater rheas: Different modes and their evolutionary and socio-cognitive implications

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Abstract

Even if there is evidence of play from all vertebrate classes suggesting origins in deep time, descriptions of the evolution of play are surprisingly patchy. To bridge this gap, one must study play comparatively and include taxa from key phylogenetic positions.

This study is the first systematic description of play in greater rheas, and thereby the first such report on any palaeognath bird. Palaeognaths represent a major subgroup of modern-day birds that has retained many ancestral features from their direct ancestors, the non-avian dinosaurs, making them an ideal window into the behaviors of the earliest birds.

We recorded play behaviors of a group of captive rheas, with a focus on the modes and ontogenetic development of their play. Juveniles predominantly engaged in contagious locomotor play, adding a social component to the majority of their play bouts. Interactive social play, such as wrestling, appeared only around the age of 10.5 weeks and was generally rarer. Based on our findings we hypothesize that early birds, and likely also non-avian paravian dinosaurs, played in a similar fashion with a noticeable component of sociality. These hypotheses need to be expanded through more studies on different species of palaeognath birds.

Keywords: play$_1$; palaeognathae$_2$; evolution of play$_3$; dinosaur play$_4$; play contagion$_4$

1. Introduction

Play has captured the fascination of researchers in both biological and social sciences for more than a century. This phenomenon has, however, proven to be surprisingly elusive from an evolutionary viewpoint. While play appears to have deep evolutionary roots, exhibited by mammals (e.g. Byers, 1999; Lewis, 2000; Himmler et al., 2016), birds (e.g. O'Hara & Auersperg, 2017), reptiles (e.g. Dinets, 2015), and fishes (e.g. Burghardt, 2015), it remains unexplained why play – a seemingly unproductive behavioral state – is favored by natural selection. Many hypotheses on the adaptive value of play have been forwarded, ranging from the improvement of sensorimotor control, to supporting cognitive development, and the acquisition of social skills. But most hypotheses have various shortcomings and none of them can fully explain the evolution of play (Burghardt, 2005).

One established method to better understand the evolution of particular traits is to compare species that occupy key phylogenetic positions. Such comparisons often provide insights into how a feature changed in evolutionary time through its expression in various lineages. Further knowledge is gained when the comparative results are correlated with e.g., socio-ecology, brain anatomy, and various other factors. So far, play research has mainly focused on humans, non-human primates, and mammals in general, and has disregarded other species occupying evolutionary key positions (Burghardt, 2005).

The evasiveness of the phenomenon of play is not only apparent from the evolutionary perspective, but also when it comes to defining it. Sometimes, behaviors are intuitively labelled as play that in fact represent serious behaviors, and sometimes it is the other way around such as in leapfrogging fish (e.g. Gudger, 1944) and reptiles tossing around objects (e.g. Burghardt et al., 2002). To tackle this problem, and to avoid a single simple definition which risks to become too narrow, Burghardt (2001) identified five criteria, all of which must be fulfilled for a behavior to be categorized as play.

For a behavior to be play, 1) it must be incomplete in its function in the present context and include elements that do not contribute to current survival, 2) it must be voluntary, rewarding, pleasurable and done for its own sake, 3) it must differ from functional expressions by being incomplete, exaggerated, awkward, or modified, 4) it must be repeated, but not stereotypically, during ontogeny, and 5) it must be initiated only when not under physical or mental stress.

Applying these criteria, one often discriminates between three categories of play: locomotor play, object play, and social play. While this classification might simplify some aspects of play (Pellis et al., 2019), it allows for a first systematic description of play in a species. Locomotor play includes all forms of play that involve often exaggerated locomotor movements, such as running, leaping, or prancing. Object play describes manipulations of non-novel objects such as mouthing, pawing, pushing, or pecking. Finally, social play describes all play that is directed towards another individual. Examples of social play are chasing, play fighting and nipping (Burghardt, 2005). In this study we adhered to Burghardt's criteria and analyzed the modes of play according to the above.

Even though play can be a solitary activity it is often associated with sociality in group living species. Social play contexts often represent a safe space where juveniles can practice social norms under more tolerant conditions. It is not unusual that animals display play signals to mark that the actions are not serious (Bekoff, 1972; Palagi et al., 2015; Byosiere et al., 2016; Palagi et al., 2016). Thus, it is not farfetched to hypothesize that play might have parts of its adaptive value in the social lives of group living animals. This hypothesis is supported by neurobiological findings suggesting that species engaging more in social compared to non-social play have enlarged brain areas associated with play in primates (Graham, 2011), and higher relative brain masses in birds (Kaplan, 2020). Thus, play is an interesting phenomenon when studying the evolution of social cognition.

In this study, we aimed at filling parts of the gap in the comparative literature on play by providing the first systematic description of play behaviors in a palaeognath bird, the greater rhea (*Rhea americana*). Palaeognaths comprise an essential taxon when it comes to understanding avian evolution. Palaeognathae is one of two subgroups of birds and retains many ancestral features that are absent in the other order, the Neognathae. In other words, palaeognaths share more features with the earliest birds on earth and their immediate forebearers: the non-avian dinosaurs (Varricchio et al., 2008; Varricchio & Jackson, 2016; Ksepka et al., 2020). Despite this, their play behaviors have never been studied, though some reports point towards the presence of play in these birds (Franz Sauer, 1969; Bohl, 1970; Hallager, 2010; Timothy, 2019). In the present study, we investigate the presence of all three play categories in greater rheas and analyse mechanisms of play contagion. Furthermore, we describe developmental trajectories of different play categories. Lastly, we use our findings to hypothesize about the evolution of play in early birds.

2. Methods

2.1 Subjects, location, and observational period

In this study, we observed a captive group of greater rheas consisting of two adult males, two adult females and seven parent-raised juveniles (sex unknown) at Ystad Zoo, Sweden. The animals were observed using continuous recording with a video camera to ensure the capture of all play behaviors. Observational sessions took place between 9 am and 4 pm and lasted for 3 to 4 hours per session. The observations were made in the rheas' summer enclosure, a large pasture shared with llamas and capybaras between mid-August and the end of September 2020. Our focus was on the juveniles, but adult behaviors were also recorded to compare frequency of play and play contagion between the two age classes. Individual recognition of the juveniles was not possible. The juveniles hatched around the 9th of July 2020 (day of first sighting) and were thus about 6 weeks old at the study onset. On the last three days of observation, one chick was limping and did not engage in play.

2.2 Video Coding

In total, 42 hours of video material was recorded out of which the subjects were observable for 38.36 hours. An ethogram of all observed play behaviors was created and used in the video coding (for descriptions, see Results and Supplementary Material). 233 instances of play were recorded. All play occurred spontaneously without any interventions from the experimenter. In addition to the play behaviors, we also coded the number of individuals involved, the direction of their movements (congruent or incongruent to observed movement direction) and contagion of play. A play bout was considered contagious when at least one other individual started to play during or within 3 seconds after another individual's play bout. We further noted whether the elicited play category in contagious bouts was congruent with the demonstrated category.

The video material was coded in the software Solomon Coder (Version: beta 19.08.02). Half of the videos were coded by CZ and the other half by TRJ. Interrater reliability was determined by cross-coding ten percent of the other's video material respectively. Agreement was excellent for all coded categories (ICC = 0.963, F = 52.8, $p < 0.001$).

2.3 Statistical Analyses

Statistical analyses were executed using generalized linear mixed models (GLMMs) with the glmer function of the lme4 package (Version 1.1-26) in RStudio (Version 1.4.1717; RStudio Team, 2020). Count data on occurrences of play behaviors were analysed using Fisher's exact test. Six GLMMs were fitted with duration of play bout (model1), latency of contagion (model2), number of individuals joining (model3), direction of movement (model4), contagion (model5), and congruency of demonstrated and elicited play category (model6) as response variable, respectively. Models 1 to 3 were run with a Gamma distribution, while models 4 to 6 were fitted with a binomial distribution. We added category of play and initiator (adult or juvenile) as fixed factors for all models. For model4 we included number of individuals as fixed factor. We added observation session as a random factor for all models to control for daily differences in the birds' behaviors. We reduced the full models using the Akaike Information Criterion (AIC), to identify the models explaining most variance. We used likelihood ratio tests on the final models to determine the effects of the remaining factors.

3. Results

3.1 Systematic description of play behaviors

Two categories of play – locomotor and social play – were observed. Four different types of locomotor play were identified. The most common was *play running*, which is running without any obvious goal direction, i.e., not ending at a location with food or parent, or without any biologically relevant cue for locomotion such as fleeing or following a parent. This type of running was often performed in circles. Moreover, play running was frequently accompanied by *neck swinging*, a snake-like movement of the neck, and *wing display*, wing flapping while running. Play running was seen in both adults and juveniles. Additionally, the juvenile rheas engaged in *leaping*, where they jump straight up, often while throwing their necks from side to side. Play running was moreover highly contagious and thus contained a social component. However, due to the lack of active interactions, this type of play was categorized as locomotor play.

Social play was only observed in juveniles. Only play bouts including an active interaction were categorized as social play, including interactive variants of play running. *Chasing* was a pursuit that ended with reaching another individual during play running in both individuals. During play runs, they were also *bumping*, meaning that they were running into each other in the process of play running. These two behaviors could be accidental, however, both coders independently interpreted them as intentional interactions. Furthermore, the subjects were observed *pecking* one another, mainly in the neck area. This did not appear to be an aggressive interaction as the other individual did not try to avoid being pecked. Pecking was only half of the time reciprocated. The most interactive form of social play observed was *wrestling*. In this behavior, two individuals were lying next to each other on the ground with their necks intertwined, mutually pecking each other in the neck area and pushing against each other as if trying to roll the other one on its side (see pictures of described behaviors in Figure 1).

We only recorded one instance that might be suggestive of object play – an adult repeatedly pecking a detached feather. However, this observation did not fulfil Burghardt's fourth criterion of play: the behavior did not occur repetitively. For that reason, we cannot conclude the presence of object play in greater rheas from our observations. We therefore excluded this category from further analyses.

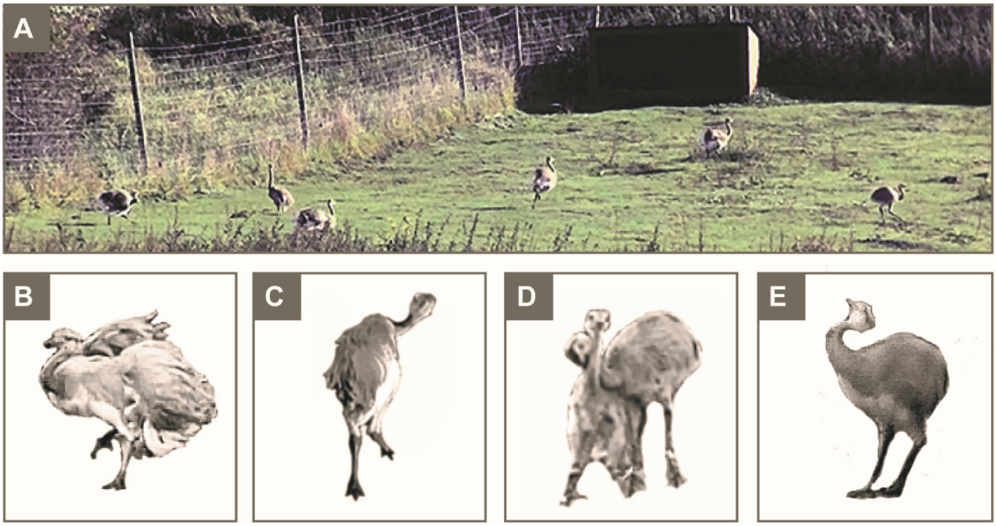

Figure 1. Play behaviors in juvenile greater rheas. (A) A group of juveniles play running. (B) Wing display. (C) Leaping. (D) Wrestling. (E) Neck swinging.

3.2 Statistical Analyses of Play Behaviors

3.2.1 Descriptive Statistics of Play Behaviors

Juveniles initiated play significantly more often than the adults did (adults: 19 times, juveniles: 214 times; Fisher's exact test: $p < 0.001$). Nevertheless, more individuals joined play bouts initiated by an adult compared to a juvenile (GLMM, $\chi^2 = 6.28$, df = 1, p = 0.012).

The average play bout lasted 9.92 seconds. The predominant category of play was locomotor play (89.7%, 208 instances), followed by social play (10.3 %, 24 instances; for more descriptive statistics of play categories see Table 1 and Figure 2).

Table 1: Descriptive statistics of recorded play bouts.

Category	Mean duration (sec)	Min duration (sec)	Max duration (sec)	SD
All	10. 64	0. 4	110	15
Locomotor play	9. 72	0. 4	110	14. 84
Social play	18. 47	2. 6	58. 2	14. 71

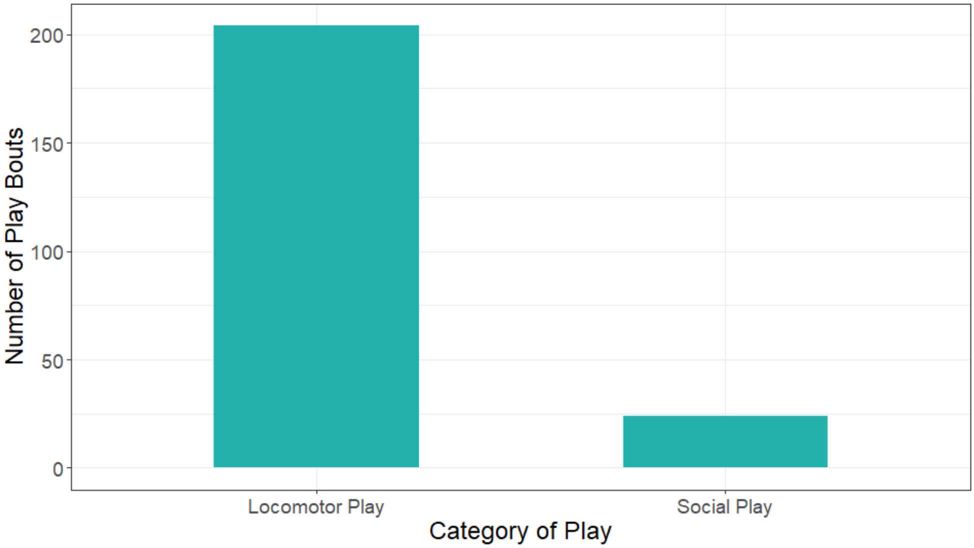

Figure 2. Number of occurrences of the two observed categories of play.

As described above, contagious play running was rated as locomotor play due to a lack of interaction. Locomotor play could thus either occur solitarily (43% of locomotor play bouts, 90 instances) or was contagious (57% of locomotor play bouts, 118 instances). In contagious bouts of locomotor play, on average 3.76 individuals joined the initiator. Social play was limited to two participants, except for two incidents where a third individual joined. Thereby, significantly more individuals joined a locomotor compared to a social play bout (GLMM, $\chi^2 = 12.82$, df = 1, $p = 0.00034$). Social play bouts lasted significantly longer than locomotor play bouts (GLMM, $\chi^2 = 18.16$, df = 1, $p < 0.001$, see Figure 3A).

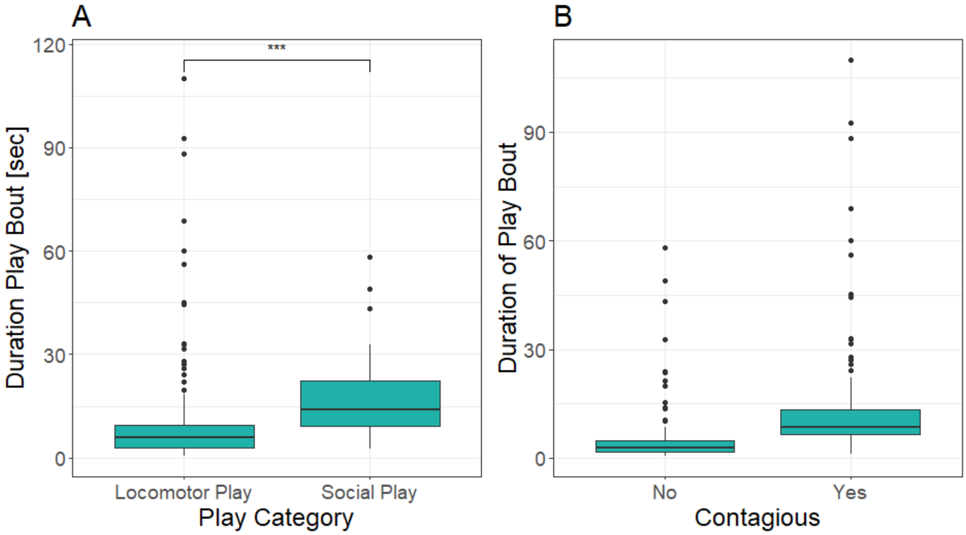

Figure 3. (A) Duration of play bouts by categories. (B) Duration of play bouts by contagiousness.

3.2.2 Contagious Play

56.7% of all observed play bouts were contagious, i.e., they induced play in another individual (132 instances). Other individuals joined on average 2.87 seconds after the play initiation. No significant difference in the latency of contagion was found for play categories (GLMM, $\chi^2 = 1.06$, df = 1, $p = 0.3$) or identity of initiator (adult or juvenile; GLMM, $\chi^2 = 0.04$, df = 1, $p = 0.84$).

Contagious play bouts lasted significantly longer than non-contagious ones (GLMM, $\chi^2 = 38.3$, df = 1, $p < 0.001$, see Figure 3B). No significant effects of play category (GLMM, $\chi^2 = 0.039$, df = 1, $p = 0.84$) or initiator (juvenile or adult; GLMM, $\chi^2 = 0.14$, df = 1, $p = 0.71$) on contagiousness could be identified, meaning that locomotor and social play were equally contagious. The most frequently elicited category of play was locomotor play (90.9%, 120 instances), in the rest of contagious play bouts, social play was elicited (9.1%, 12 instances). Locomotor play was moreover significantly more likely to elicit the same category of play than social play (GLMM, $\chi^2 = 9.98$, df = 1, p = 0.0016, see Figure 4). While 97% of contagious locomotor play elicited locomotor play in conspecifics, only 71% of contagious social play evoked the same category in others. In the other instances, observing siblings play socially induced locomotor play in individuals not directly involved in the social play.

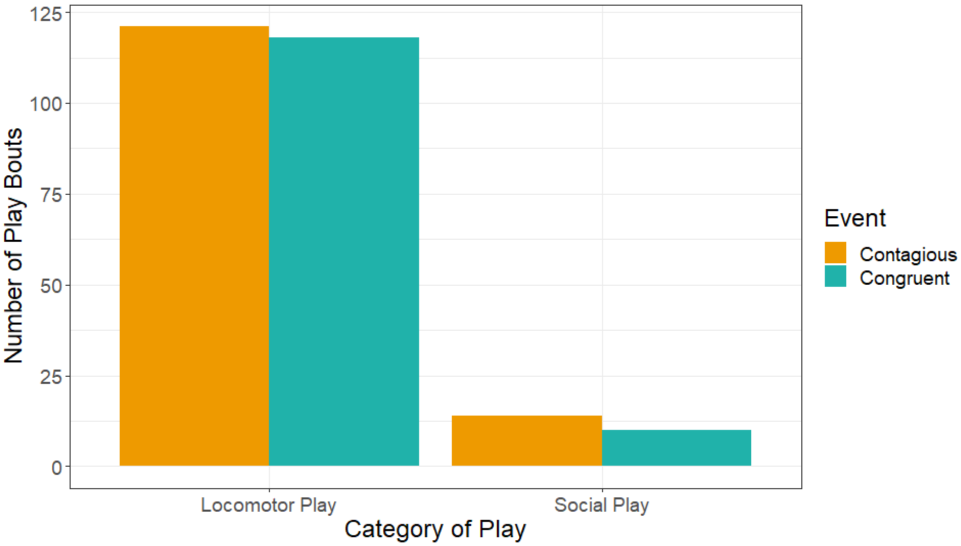

Figure 4. Number of contagious play bouts of locomotor and social play compared to the number of bouts eliciting the same category of play in conspecifics. Of 118 contagious locomotor play bouts, 115 elicited locomotor play in others (97%). Of 14 contagious social play bouts, 10 elicited the same category in conspecifics (71%).

3.2.3 Directions of Play Running

In more than one third of contagious play running bouts, the birds were not all running in the same direction but moving randomly, i.e., in individually different directions (39%, 46 instances). However, no significant effects of initiator (GLMM, $\chi^2 = 1.16$, df = 1, p = 0.28), number of involved individuals (GLMM, $\chi^2 = 0.56$, p = 1, p = 0.46), or duration of bout (GLMM, $\chi^2 = 1.33$, df = 1, p = 0.25) could be identified as influencing the direction of group movement.

3.2.4 Ontogeny of Play

Lastly, an ontogenetic effect on play categories was found. A significant connection could be identified between play category and the subjects' age (Fisher's exact test, p = 0.00046). While locomotor play was observed in every session, social play first occurred one month after the onset of the study period at around 10.5 weeks of age (see Figure 5).

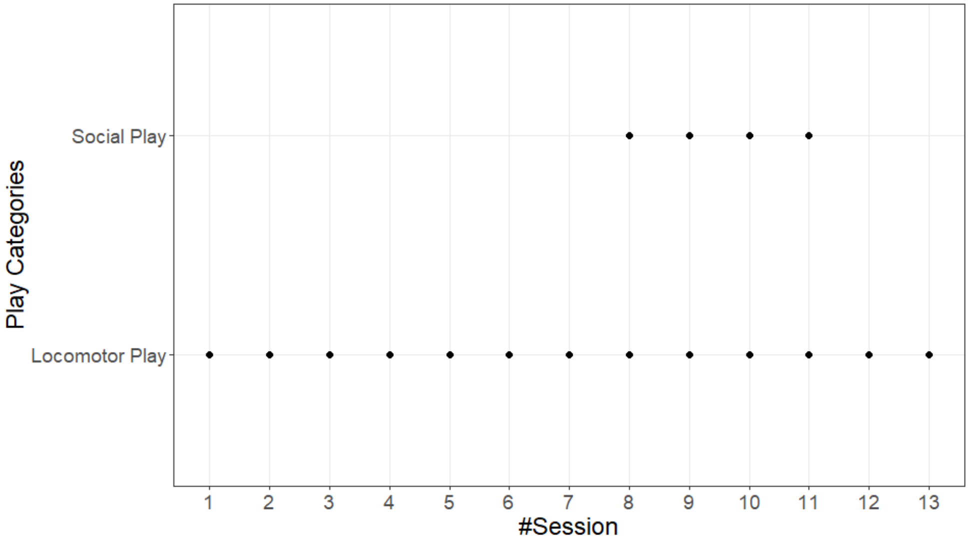

Figure 5. Occurrences of play categories at different ages.

4. Discussion

This study includes the first systematic description of play behaviors in greater rheas and is thereby to our knowledge the first such description of play in any palaeognath bird. These birds exhibit two categories of play: locomotor and social play.

Locomotor play was by far the predominant category of play. Within this category, juvenile rheas engaged in play running while flapping their wings in a wing display, swinging their necks, and leaping. These behaviors are in line with the first report on rhea locomotion that described a static posture of the neck in non-social running, but accompanying neck and wing movements in social contexts (Raikow, 1968). In most neognath birds, locomotor play revolves around flight, such as soaring in Montagu harriers (*Circus pygargus*; Pandolfi, 1996), or play flight in juvenile common ravens (*Corvus corax*; Heinrich & Smolker, 1998). Due to the loss of volant flight in rheas (along with several other palaeognath bird species; Harshman et al., 2008), this obviously does not lie within their repertoire. It is therefore unsurprising that their locomotor play is mainly based on variations of running, similar to many mammalian species such as horses and deer (McDonnell & Poulin, 2002; Carter et al., 2019).

On the first glance, play in juvenile greater rheas appeared to be predominantly solitary in the sense that it was not directed towards another individual. Even though other individuals joined in the majority of locomotor play bouts, direct social interactions during play running were rare and limited to some possibly accidental bumps through running into each other. In human developmental psychology, this type of play is called parallel play, i.e., several children engaging in solitary play in vicinity of each other without interacting (Parten, 1932). Parallel play is commonly categorized as a form of solitary play due to the lack of interaction, even though it takes place in a social setting. In children, this type of play is usually regarded as a developmental stage towards social play (Bakeman & Brownlee, 1980).

Playing parallelly moreover includes an element of contagion where observing another individual play facilitates play in the observer. This effect was clearly seen in our study with almost 60% of play bouts being contagious. At least two possible mechanisms can cause this effect: behavioral synchronization, i.e., the release of species-specific motor patterns triggered by the observation of the latter in conspecifics, or emotional contagion, i.e., matching emotional states through the spread of a playful mood (Niedenthal, 2007; De Waal, 2008). The latter is regarded as a building block of empathy (Preston & De Waal, 2002). Osvath and Sima (2014) suggested that play can be used to disentangle the two phenomena. A match between the category of play that is observed by an individual and the category of play that might thereafter be evoked in this individual would point towards behavioral synchronization, while a mismatch would be an argument for emotional contagion. According to this framework, our findings could not exclude mere behavioral synchronization, as demonstrated and elicited play categories were highly congruent, i.e., observing locomotor play mainly elicited locomotor play in other individuals. Nevertheless, by adopting a different, but related, approach in the analyses, juvenile rheas appear to not merely synchronize their behavior. In a response to e.g. danger through predation, animals exhibit the tendency to collectively move in the same direction (Couzin, 2009). Contrarily, when analysing the direction of running during contagious play bouts in greater rheas, we found that in more than one third of those, the birds moved in individually different directions. This indicates that rather than behavioral synchronization, play running behavior could have been guided by the spread of a playful mood. Alternatively, locomotor play might serve as training for anti-predatory responses. Thus, running in different directions might be a form of protean behavior, i.e., an irregular behavior that prevents prediction by predators (Humphries & Driver, 1970). Moreover, they might practice flight responses through self-handicapping, i.e., instead of moving in the same direction they are trying out individual and less efficient movement patterns (Spinka et al., 2001). More studies specifically targeted towards mechanisms of synchronization are needed to understand the species' behavior and the underlying potential for emotional contagion.

One instance suggestive of object play in an adult was observed. However, this does not necessarily mean that juvenile greater rheas do not engage in object play. It is possible that locomotion is simply easier to observe in a large enclosure with high vegetation, than interactions with objects on the ground. The absence of observations in juveniles might also be caused by a lack of conspicuous objects in the enclosure. In pilot experiments on play behaviors in greater rheas, young adults played intensely when provided with familiar, but unusual, objects (in this case a glove, personal observations of MO). It might thus be possible that object play emerges at a later developmental stage, which could also explain why the only instance was recorded in an adult. It is common for different play categories to develop at different times (for examples, see below). Alternatively, greater rheas might not engage in object play at all. The described instance of object play might represent a case of explorative behavior. More studies on greater rheas will be needed to explore whether object play is part of the species' play repertoire and when it develops.

Social play of juvenile greater rheas mainly consisted of pecking each other on the neck or wrestling movements. Play fighting is defined as the non-serious use of agonistic species-typical behaviors (Pellis & Pellis, 1998). This type of social play is not very common among birds and has only been reported - besides in parrots (e.g. Keller, 1975) and corvids (e.g. Gwinner, 1966) - in two species of hornbills (*Bucorvus leadbeater and Ceratogymna brevis;* Diamond & Bond, 2003), three species of Eurasian babblers (*Turdoides striatus, Turdoides malcolmi, Turdoides squamiceps*; Diamond & Bond, 2003), and Australian magpies (*Gymnorhina tibicen*; Pellis, 1981a). Among those birds that exhibit play fighting, wrestling has been described in keas (*Nestor notabilis*), the above-mentioned hornbills, ravens (Diamond & Bond, 2003), and Australian magpies (Pellis, 1981a). Wrestling in birds can involve beak wrestling, grappling of feet, or jumping onto each other's bodies (Pellis, 1981a; Diamond & Bond, 2003; Bond & Diamond, 2019).

Play fighting is interesting with respect to its role in the development of socio-cognitive skills. It requires social tolerance, self-handicapping for the sake of the game, turn-taking, and role-reversals (Burghardt, 2005). It is thus simultaneously a form of restrained competition and cooperation (Pellis & Pellis, 1998). Awareness of all these social signals and of one's own actions takes time to develop. Play has an ontogenetic trajectory with more complex play behaviors, such as social play, occurring later in the development. The development of social play in rats has been described as an "inversed U-shape" (Panksepp, 1981). The first occurrences have been recorded between day 13 and 17 followed by increasing frequencies up to approximately day 30 to 40 before decreasing towards sexual maturity (Müller-Schwarze, 1966; Thor & Holloway, 1984; Pellis & Pellis, 1990). First occurrences of running and jumping in rats have however already been recorded on days 8 to 12 (Baenninger, 1967). Meerkats (*Suricata suricatta*) first exhibit object play in week 4 before engaging in social play such as wrestling with litter mates in week 5 and then fine-tune their social play skills through learning play-soliciting signals during weeks 9 to 10, which finally leads to a peak in social play with other juveniles and yearlings at 11 to 14 weeks (Doolan & Macdonald, 1999). In cheetah cubs (*Acinomyx jubatus*), the frequency of locomotor play peaks before the frequency of social play. The authors argued that this pattern serves to optimize anti-predatory responses during the most vulnerable developmental periods of the juveniles (Caro, 1995). In the present study, we observed the same developmental pattern within the juvenile greater rheas. They predominantly exhibited locomotor play, perhaps to practice flight responses to predators. Object play was not observed in the juveniles during the study. Social play developed later in the observational period.

However, an alternative strategy has been described for spotted hyena cubs (*Crocuta crocuta*) where social play develops in week 2, while locomotor play only occurred in week 3 and object play in week 4. Interestingly, the cubs are very aggressive in their natal den and the emergence of social play coincides with their move to a communal den. The authors therefore conclude that the development of social play facilitates sociality in the clan (Drea et al., 1996). A similar development has been found in howler monkeys (*Alouatta palliata*; Carpenter, 1934). Ravens already engage in object and social object play (i.e., co-manipulation of objects) in the nest, while locomotor play only develops after fledging (Osvath et al., 2014). Similarly, Australian magpies begin to play with objects in the nest, though their social play only develops after fledging (Pellis, 1981b).

These accounts of different play categories emerging at different developmental stages gives the impression of play functioning as practice at appropriate times in the species' life history. However, as noted above, the functions of play remain unclear. When specifically testing for such training effects, some studies show that social play in juveniles can indeed influence adult social behavior (e.g. Blumstein et al., 2013; Nunes, 2014; Perret, 2021). However, many attempts to prove training effects have failed (e.g. Caro, 1980; Sharpe, 2005). Alternatively, empirical evidence suggests that juvenile social play improves social competence through shaping executive functions governed by the prefrontal cortex (e.g. Bell et al., 2010; Baarendse et al., 2013; Burleson et al., 2016; Schneider et al., 2016; Stark & Pellis, 2020). Thus, play in the juvenile period subsequently improves socio-cognitive skills and emotion regulation (Pellis et al., 2014).

While these studies grant insights into some functions of play, they do not shed light on its evolutionary roots. To achieve this goal, one can turn to reptiles, which belong to the same main lineage as birds (Sauropsida). Studies on play in reptiles are scarce, though the current state of knowledge is that their predominant mode of play is object play, as described in Komodo dragons (*Varanus komodoensis*; Burghardt et al., 2002), Nile soft-shelled turtles (*Trionyx triunguis*; Burghardt et al., 1996) and sea turtles (*Caretta caretta* and *Chelonia mydas*; Mann & Mellgren, 1997). Komodo dragons have moreover been reported to engage in tug-of-war social play with zookeepers (Burghardt et al., 2002). Other descriptions of social play in reptiles include behaviors whose functions are not fully understood and thereby cannot certainly be defined as play, such as wrestling in African chameleons (*Chamaeleo africanus*; Burghardt, 1982), head-bobbing in fence lizards (*Sceloporus undulatus*; Roggenbuck & Jenssen, 1986) and precocial courtship behaviors in emydid turtles (Kramer & Burghardt, 1998). Locomotor play seems to be rare and only some anecdotal reports on a wood turtle (*Clemmys insculpta*) repeatedly sliding down a board into water exist (Burghardt, 2005). Despite the limited literature on reptilian play, it appears that their play differs considerably from our observations on palaeognaths. It therefore appears that play has evolved independently several times in different clades.

Within their own archosaurian lineage however, inferences can be drawn from palaeognath play to non-avian dinosaur play. Palaeognaths retain many features of non-avian dinosaurs. Ksepka and colleagues (2020) discovered that relative brain sizes of theropod dinosaurs and early birds, including palaeognaths, are similar. Moreover, fossil evidence from animals that died on their nests and the associated clutch sizes suggests that the parental care of troodontids and oviraptorosaurs (both maniraptoran dinosaurs) are akin to the reproductive strategies of palaeognath birds with males incubating eggs from several females and taking care of the young after hatching (Varricchio et al., 2008; Varricchio & Jackson, 2016).

Due to evidence for play from both extant archosaurian lineages- crocodylians (Dinets, 2015) and birds (e.g. Diamond & Bond, 2003), one can unproblematically assume that non-avian dinosaurs played too. When trying to infer play behaviors more specifically, the above-mentioned shared features of palaeognaths and non-avian dinosaurs indicate that fundamental behaviors present in these birds might have also been present in their extinct relatives, at least in the clade containing birds and their very closest relatives, like the dromaeosaurids ('raptors') - the paravians. The similar parental care systems indicate comparable social ecologies for juveniles of non-avian paravian dinosaurs. This moreover implies – in contrast to other reptiles – a noticeable component of sociality in their play. This hypothesis is supported by our finding that the studied palaeognaths showed social aspects in their play already from the study onset at about 6 weeks old through extensive play contagion. They moreover exhibited interactive social play at 10.5 weeks old which is relatively early in their development. As a reference, these birds reach sexual maturity at 20 to 24 months (Sales, 2006). Their full potential of social play might therefore not even have completely unfolded at the end of the observational period. For these reasons, probable social play in non-avian paravian dinosaurs can be inferred from both phylogenetically and ecologically close extant species.

To yield more solid hypotheses about early birds and non-avian dinosaurs, more studies on different palaeognath species are needed to infer whether play observed in rheas is representative for this clade. Especially the study of species with different social systems (e.g. solitary species like the cassowary), and ecologies (e.g. flighted tinamous) is crucial to obtain an overview of different play conditions within Palaeognathae. Additionally, data from plesiomorphic neognaths, such as red junglefowl, would allow for more conclusions on the ancestral state of play in birds. Finally, the discovery of species not engaging in play would shed more light on phylogenetic distribution of play and thus the pattern of its evolution.

Acknowledgements

This work was supported by the Swedish Research Council under Grant 2019-03265 and the LMK Foundation. We thank Ystad zoo for supporting and facilitating this research. We are moreover grateful to Helena Osvath for the creation of our figures. Lastly, we thank Steve Brusatte for his comments on the manuscript.

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Supplementary Materials for

Play in juvenile greater rheas: Different modes and their evolutionary and socio-cognitive implications

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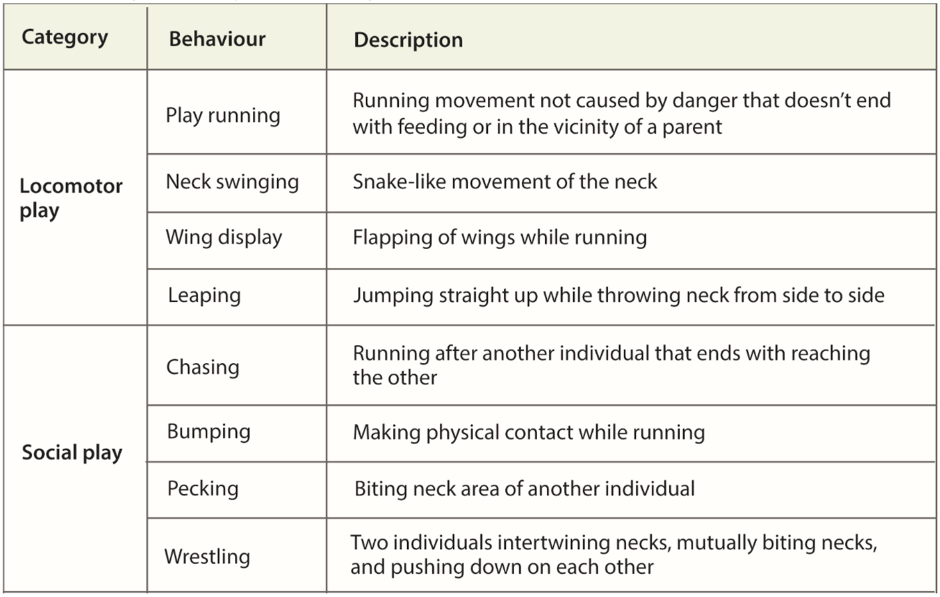
1. Ethogram of Play Behaviors

Table 1: Ethogram of play behaviors in greater rheas.



Category	Behaviour	Description
Locomotor play	Play running	Running movement not caused by danger that doesn't end with feeding or in the vicinity of a parent
	Neck swinging	Snake-like movement of the neck
	Wing display	Flapping of wings while running
	Leaping	Jumping straight up while throwing neck from side to side
Social play	Chasing	Running after another individual that ends with reaching the other
	Bumping	Making physical contact while running
	Pecking	Biting neck area of another individual
	Wrestling	Two individuals intertwining necks, mutually biting necks, and pushing down on each other

2. Coding Definitions

When coding the play behavior, on- and offset of play bouts were marked in the coding sheet to identify the duration of play bouts. A play bout was defined as all play behavious occurring without a break of more than 3 seconds between them. Contagion was defined as at least one individual starting to play either while another individual was playing or within 3 seconds after another individual stopped playing. The 3 second cut-off was determined after viewing the video material, as play bouts were commonly fading away after the chosen interval. Latency of contagion was coded as the latency from the onset of play to the beginning of the next individual's play behavior. Directions of each individual joining the play bout in relation to the initiator of play were coded as "same", "perpendicular" or "opposite" to determine synchronized movements.

This thesis concerns the evolution of social cognition in Archosauria, an animal group that - besides the extant crocodylians and birds - includes the extinct non-avian dinosaurs. Through studying aspects of the social cognition of extant archosaurs, it is possible to draw inferences on the socio-cognitive capacities of extinct dinosaurs. This thesis investigates gaze following and play in five avian and one crocodylian species. The findings are subsequently used to hypothesize about the origins of these skills in non-avian dinosaurs as well as principles of cognitive evolution.

Joint Faculties of Humanities and Theology
Department of Philosophy
Cognitive Science

Lund University Cognitive Studies 184
ISBN 978-91-89415-45-4
ISSN 1101-8453

Printed by Media-Tryck, Lund 2022 NORDIC SWAN ECOLABEL 3041 0903