

MASTERARBEIT | MASTER'S THESIS

Titel | Title

The mirror response of juvenile common ravens (*Corvus Corax*)
within their family structure

verfasst von | submitted by

Nicole Kanta BSc

angestrebter akademischer Grad | in partial fulfilment of the requirements for the degree of
Master of Science (MSc)

Wien | Vienna, 2025

Studienkennzahl lt. Studienblatt |
Degree programme code as it appears on the
student record sheet:

UA 066 878

Studienrichtung lt. Studienblatt | Degree
programme as it appears on the student
record sheet:

Masterstudium Verhaltens-, Neuro- und
Kognitionsbiologie

Betreut von | Supervisor:

Univ.-Prof. Mag. Dr. Thomas Bugnyar

Acknowledgments

First and foremost, I would like to express my gratitude to Univ.-Prof. Mag. Dr. Thomas Bugnyar for his trust and for sparking my interest in the research on ravens. A special thanks also goes to Lisa-Claire Vanhooland, PhD, for her unwavering support. Your tireless help during all the troubleshooting sessions and your readiness to help me with advice and encouragement have been invaluable. I would also like to extend my sincere thanks to the entire team at the Haidlhof research station.

Additionally, a special acknowledgment goes to my boss, Univ.-Prof. Manuela Schmidt, PhD, and the team of “AG Schmidt”, who have always supported and motivated me throughout this journey. Dr. Sabrina Grundtner, thank you so much for your mental support and for always being there when I needed it most.

A special thanks also to my parents and family for supporting my choices throughout my life. Last but certainly not least, I want to express my deepest gratitude to my husband, the best person by my side, for his unconditional support throughout all these years. Without you, I would not have been able to achieve this. Thank you for always believing in me and standing by me every step of the way.

Table of content

Abstract.....	5
Zusammenfassung.....	6
1 Introduction.....	7
2 Methods and Material.....	13
2.1 Subjects and housing.....	13
2.2 Experimental Apparatus.....	15
2.3 Procedure and Time Frame	15
2.4 Data collection	17
2.5 Data Analysis	19
3 Results	20
3.1 Exploration behaviours and time in zone 1 of juvenile ravens	20
3.2 Social behaviours of juvenile ravens.....	24
3.3 Comparison juvenile and adult ravens	25
3.4 General object exploration (wood sessions)	31
4 Discussion.....	34
5 Conclusion	38
References	39
Appendix	45

Abstract

A wide range of behavioural responses, from social interactions to mirror-guided self-directed behaviours, can be elicited by mirror exposure. Although ravens (*Corvus corax*) do not exhibit self-recognition in mirrors, they show a strong preference for them, engaging responses like exploratory and social behaviours. This study investigated how juvenile ravens respond to the mirror within the context of their family structure. Juvenile ravens, together with their parents, were exposed to either a mirror or a wooden board in experiments over multiple years (2017, 2019, 2020). In contrast to their parents, who displayed more social behaviour, juvenile ravens showed higher exploratory rates and spent more time near the mirror than adults, consistent with their neophilic tendencies. Exploration behaviours and time spent in front of the mirror increased further as juveniles grew older. Even though behaviour differed significantly between ravens from different family sizes, no consistent trend was observed. Sex, parental exploratory tendencies, and prior experience with the apparatus had no significant impact on the behaviour of juvenile ravens. This study supports previous findings and sheds new light on mirror responses in birds and contributes to the understanding of the social and exploration behaviour.

Zusammenfassung

Durch die Auseinandersetzung mit Spiegelbildern können eine Vielzahl von Verhaltensreaktionen hervorgerufen werden, die von sozialen Interaktionen bis hin zu spiegelgesteuerten, selbstbezogenen Verhaltensweisen reichen. Obwohl Kolkrahen (*Corvus corax*) keine Selbsterkennung im Spiegel zeigen, haben sie eine starke Vorliebe für Spiegel und zeigen exploratives und soziales Verhalten. Diese Studie untersucht die Reaktionen auf Spiegel junger Kolkrahen innerhalb ihrer Familienstruktur, wobei der Schwerpunkt auf explorativem und sozialem Verhalten lag. Juvenilen Raben wurde, zusammen mit ihren Eltern, in mehrjährigen Experimenten (2017, 2019, 2020) entweder ein Spiegel oder ein Holzbrett präsentiert. Im Gegensatz zu ihren Eltern, die mehr soziales Verhalten zeigten, wiesen Jungvögel ein höheres Explorationsverhalten auf und verbrachten mehr Zeit in der Nähe des Spiegels als Erwachsene, was mit ihrer neophilen Tendenz übereinstimmt. Das Explorationsverhalten und die vor dem Spiegel verbrachte Zeit nahmen mit zunehmendem Alter der Jungvögel weiter zu. Das Verhalten von Raben aus Familien unterschiedlicher Größe unterschied sich deutlich, es konnte jedoch kein einheitlicher Trend beobachtet werden. Das Geschlecht, das Explorationsverhalten der Eltern und deren frühere Erfahrungen mit dem Apparat hatten keinen signifikanten Einfluss auf das Verhalten der Jungvögel. Die Ergebnisse dieser Untersuchung bestätigen bisherige Studien und liefern neue Einblicke in das Verhalten von Vögeln im Spiegeltest. Sie leisten einen Beitrag zum Verständnis sozialer und explorativer Verhaltensweisen.

1 Introduction

Exploration of novel objects plays a crucial ecological role by enabling individuals to gather information about sources of danger and habitat resources (Reader, Kendal & Laland 2003, Miller et al. 2015, Schaden 1993). Two distinct types of exploratory behaviours can be identified based on the underlying motivation: extrinsic and intrinsic exploration. Exploration for essential resources such as food and water or warmth and shelter, but also sexual partners or a chance to escape is driven by extrinsic motivation (Tinbergen 1951, Welker 1957, Hughes 2007). In contrast, intrinsic exploration behaviour is defined as an act that is pursued for its own sake and is also known as novelty-seeking or stimulus-seeking (Hughes, 1997). Alongside the classification into extrinsic and intrinsic exploration, Berlyne (1960) postulated the existence of three categories of exploratory responses. The first category comprises orienting responses, which can be defined as alterations in the orientation of the sense organs. The second, locomotor exploration, involves changes in the location of the entire animal. Lastly, the third category comprises investigatory responses and describes changes in stimulus objects caused by the exploring subject, such as manipulation.

Mirrors can be considered as a stimulus object that may elicit various forms of exploratory behaviours (Plotnik, de Waal, Reiss 2006). Humans have been using mirrors as a reflective, functional surface already for around 8000 years (Enoch, 2006). The mirror is not only used by people to look at the reflected image of themselves but has also attracted the attention of science. In children under 2 years of age, there is an age-dependent development when they are confronted with a mirror. Children from 6–12-month show sociable reactions and recognize a playmate in the mirror image. At the age of 14 month, the children start to respond to the mirror with avoidance behaviour, are embarrassed or afraid. Mirror self-recognition appears in children aged 18-24 months (Amsterdam, 1972; Rochat, 2003) and is independent of whether they have had previous experiences with a mirror or not (Priel, de Schonen, 1986). To investigate the capacity for self-awareness, Gallup Jr. (1970) introduced the mark test for chimpanzees, later used by Amsterdam (1972) for infants (i.e. the Rouge test). In

this test, the individual is marked in a location on its body that can only be seen by the individual when it uses the reflection of the mirror. Researchers then observe whether the animal uses the mirror to investigate the mark by touching it (Gallup Jr., 1970; Plotnik, De Waal & Reiss 2006). In animals, experiments with mirrors have captured the attention of researchers to learn more about their behaviour, perception and cognitive skills. Different species have been widely used in terms of response to mirrors. These studies have shown that non-human animals, can go through various stages of mirror understanding, from perceiving the mirror image as “another” to complete self-recognition (Rochat, 2003). If animals are able to recognize themselves in a mirror, they typically go through four stages (Gallup Jr., 1970; Plotnik, De Waal, Reiss 2006). The first stage involves a social response, where the mirror image is mistaken for a conspecific. This often causes social behaviours such as vocalizations, visual displays or aggressive reactions. Physical mirror inspection is the second stage. Here, the reflection is apparently no longer perceived as another individual, but the mirror is physically explored, or the animal looks behind the mirror. These behaviours shows that the animal is trying to find out the physical properties of the reflecting apparatus (Plotnik, de Waal, Reiss 2006). Animals that do not recognize themselves in a mirror typically do not progress beyond the first or second stage (Shaffer, Renner 2002; Hyatt, 1998). The behaviour in the third stage indicates that the animal is starting to understand the mirror and is named repetitive mirror-testing behaviour. In this phase, for example, the head or body is moved quickly in one direction while observing the mirror image. The individual may start to recognize a connection between its own movements and the reflection in the mirror (Plotnik, De Waal, Reiss 2006). In the fourth and final stage, the animals begin to examine parts of their bodies that they would not be able to see without a mirror. Self-recognition in the reflective surface occurs and can be verified with the mark test (Gallup Jr., 1970; Plotnik, De Waal & Reiss 2006). The ability for self-recognition might be influenced by factors such as the degree of encephalization or the extent of cortical connectivity (Marino, 2002). So far, mirror self-recognition has been reported in chimpanzees (Gallup Jr., 1970; Povinelli et al., 1993), orangutans (Lethmate & Dücker, 1973), bonobos (Walraven et al., 1995), elephants (Plotnik et al., 2006), bottlenose dolphins (Reiss & Marino, 2001), cleaner wrasses (Kohda et al. 2019), magpies (Prior et al., 2008), Indian house crow (Buniyaadi,

Taufique & Kumar, 2020) and a borderline case in Clark's nutcrackers (Clary & Kelly, 2016). The mark test was thought to be something that birds were unable to pass as it was assumed that they only expressed social behaviours in front of mirrors (Gallup Jr. & Capper, 1970; Kraft et al., 2017; Ryan, 1978; Stout, Wilcox, & Creitz, 1969; Vanhooland, Bugnyar & Massen 2020). Even though birds, apart from magpies (Prior et al., 2008) the indian house crow (Buniyaadi, Taufique & Kumar, 2020) and clark's nutcrackers (Clary & Kelly, 2016), do not recognize themselves in a reflective surface, they still show interest in mirrors, e.g. finches (Ryan, 1978), sparrows (Watanabe, 2002), jackdaws (Soler, Pérez-Contreras, & Peralta-Sánchez, 2014) or crows (Vanhooland, Bugnyar & Massen 2020). Jungle crows also respond to a mirror image with social behaviours such as pecking or wing flapping. As mentioned, common ravens do not pass the mark test (Baciadonna et al., 2022; Vanhooland et al., 2023). However, Vanhooland *et al.* (2023) described that ravens exhibit a strong preference for mirrors and display social responses as well as exploratory and self-directed behaviours in front of them. Since mirrors provide social feedback, but only visually, they differ from objects animals typically encounter in nature (Stout et al. 1969; Vanhooland, Bugnyar, Massen 2020). Gallup Jr. and Capper (1970) reported that mirrors can function as a “supernormal social stimulus,” since animals often respond to their reflection with social behaviours such as aggression or territoriality. However, the mirrored image can only reproduce movements, not sounds, which makes it an incomplete imitation. Consequently, mirrors can serve as a tool for studying different types of behaviour, such as explorative behaviour, social responses or mirror self-recognition, depending on an individual's level of understanding of the mirror (Gallup Jr., 1970; Plotnik, De Waal, Reiss 2006; Vanhooland, Bugnyar, Massen 2020). Furthermore, previous studies have shown that exploratory behaviour in ravens differs across age. They have demonstrated that juvenile ravens exhibit a propensity towards neophilia, characterized by curiosity and exploration of novel objects. This tendency stands in contrast to the neophobic behaviour typically exhibited by adult ravens (Greenberg & Mettke-Hofmann, 2001). The behavioural shift from neophilia to neophobia is observed to occur during the process of ontogeny when the juveniles become independent from the parents (Heinrich 1995, Miller et al, 2015). In addition to this shift, previous studies have shown that mirror self-recognition increases during

development, peaks in adolescence, and then declines with age (Povinelli et al., 1993). Therefore, it is interesting for this study to investigate juvenile ravens as their neophilia and curiosity allow unique insights into exploratory behaviour towards a mirror. In addition, when conducting a mirror experiment over a period of time, a habituating effect may occur, as the interaction of organisms with their environment leads to stimuli losing their novelty effect through repeated stimulation (Harris 1943, Hughes 2007). Building on the findings of these studies, it is essential to consider individual development and age when investigating mirror responses.

Further, studies have shown that the group size influences the social experiences of juveniles, as larger groups provide more social partners and diverse interactions, which can promote the development of behaviours as they can learn through observing others (Heyes, 1994; Wild & Hoppitt, 2018). Juveniles raised in larger groups may be better equipped to handle social challenges, as the increased social complexity provides them with more opportunities to develop appropriate behaviours (Branchi, 2009; Fischer et al., 2015). In addition, the exploratory behaviour of ravens towards new objects is influenced by social relationships. When familiar conspecifics are present, ravens are more courageous and explore new objects more quickly (Miller et al. 2015). However, in the presence of less familiar individuals, they are more hesitant. Therefore, social support and trust are crucial factors in overcoming uncertainty. Also, dominant individuals are more likely to be the first to explore new objects, indicating a link between social rank and exploratory behaviour (Stöwe et al., 2006). Loretto *et al.* (2012) studied the ontogeny of social relationships in ravens and demonstrated how social bonds and interactions evolve throughout development. Juvenile ravens first form close bonds with their siblings and parents. Raven parents jointly raise their offspring, with mothers providing equal investment to all chicks, while fathers selectively invest more in heavier sons (Ersoy et al., 2021). Studies in human children have shown that differences in rearing practices affect behaviours in the context of mirror self-recognition (Broesch et al., 2011; Keller et al., 2005). Early social bonds and parental investments may have an influence when it comes to exploring novel objects. In addition, sibling relationships influence social learning in juvenile ravens. For instance, they learn more effectively new behaviours by observing their siblings.

Siblings showed higher levels of social spacing and coordination in manipulating standard aviary equipment than non-siblings (Schwab et al., 2008). Furthermore, interesting patterns can be observed when examining sex-specific differences in behaviour. In ravens, sex-specific differences were shown when manipulation of objects were observed. Males exhibited a higher degree of manipulative behaviour and in addition the latency to approach an object were shorter in males than females (Range et al. 2006). Therefore, male and female ravens were examined in this study to investigate potential sex differences.

Common ravens (*Corvus corax*) share characteristics such as complex social organization and a high brain-to-body ratio with self-recognizing species (Güntürkün & Bugnyar, 2016). They demonstrate elements of social cognition that suggest an understanding of others' perspectives (Bugnyar, Heinrich 2005). Young ravens are influenced by experience through social interactions and are aware of their social environment and the gaze of conspecifics, for example when they cache food (Bugnyar, Stoewe, Heinrich 2007). This awareness of their surroundings may also play a role in exploratory behaviour as juveniles could adjust their level of exploration depending on the presence of other family members (Miller et al., 2014). Examining the interplay between individual traits, group dynamics, and parental influence could provide valuable insights into the cognitive and social development of ravens, highlighting how environmental and social factors shape exploratory behaviour. However, existing literature lacks comprehensive studies on how these elements may interact with mirror exploration, particularly in the context of group dynamics and familial influences.

This study investigates the behaviour of juvenile ravens in response to mirrors within their family structure over multiple years (2017, 2019 and 2020) compared to wooden boards. The study examines whether mirrors elicit stronger social and exploratory behaviour than wooden boards, how factors such as age, sex and family size shape these interactions, and whether parental experience with mirrors influences juvenile behaviour. Building on the knowledge gained from studies on the exploration of novel objects (like a mirror or wooden board), ontogenetic development, group size and

family interactions, this experiment aims to investigate how these factors affect the behaviour of juvenile ravens when confronted with a mirror (Povinelli et al., 1993, Hughes, 1997, Schwab et al., 2008, Bugnyar & Kotrschal, 2002, Massen et al. 2014).

Questions & Predictions

(Q1) Is there a difference in the behaviour raven chicks show, when they explore a mirror or a wooden board?

(P1) The wooden board will elicit less exploration, while the mirror will cause an increased exploration behaviour.

(Q2) Is there an age and sex effect in the exploration behaviour?

(P2) Juveniles will interact more frequently and spend more time at the object than their parents. Males will exhibit more exploration behaviour than females. The exploratory behaviour of juveniles will be more frequently at the beginning but diminishes over time as the mirror loses its novelty.

(Q3) Will the group size have an effect on the exploration of the mirror?

(P3) Larger groups expected to show higher exploration frequency and more time spent at the object.

(Q4) Parents already have experience with the mirror: will the exploration behaviour of the parents have an effect on the juveniles?

(P4) Juvenile ravens with parents who exhibit high exploration behaviour frequencies and already have experience with the apparatus will also exhibit high exploration behaviour.

2 Methods and Material

2.1 Subjects and Housing

A total of 42 parent-raised common ravens (*Corvus corax*) were tested (see **Table 1**), aged between 7 and 11 weeks at the beginning of the experiment. The sample contained 19 females and 19 males. The sample consisted of 16 families with the following distribution of family sizes: four families of size 3, six of size 4, three of size 5, two of size 6, and one of size 7. The data collection started after the chicks had fledged (in May) until they gained independence from their parents (mid-July). During this experiment, the offsprings were housed with their family units (i.e. with their parents and siblings) in large outdoor aviaries. For individual differentiation of the birds, they were marked with different coloured rings on their legs.

Table 1: List of tested individuals ($n = 46$) including family composition, sex, year of data collection, condition and location.

Parents (male - female) $n = 16$	Juveniles $N = 38$	Sex	Year of Data Collection	Group	Location
Horst - Astrid	Masala	female	2017	Test	Haidlhof
	Sichuan	male	2017	Test	Haidlhof
	Basil	female	2017	Test	Haidlhof
	Terragon	male	2017	Test	Haidlhof
	Rosemary	female	2017	Test	Haidlhof
Rocky - Joey	Laphroaig	male	2017	Test	Haidlhof
Laggie - Bobby	Johnny	male	2017	Test	Grünau
	Jacky	female	2017	Test	Grünau
Arthus - Martha	Yarrow	male	2017	Test	Grünau
	Ivy	female	2017	Test	Grünau
	Clove	female	2017	Test	Grünau
	Dandelion	female	2017	Test	Grünau
Rocky - Joey	Hamlet	male	2019	Test	Haidlhof
	Juliet	female	2019	Test	Haidlhof
	Othello	male	2019	Test	Haidlhof

George - Nobel	Hickory	female	2019	Control	Haidlhof
	Hazel	female	2019	Control	Haidlhof
Rufus - Munia	Toma	male	2019	Test	Schönbrunn
Tom - Heidi	Cleo	male	2019	Test	Grünau
	Genghis	male	2019	Test	Grünau
	Xerxes	male	2019	Test	Grünau
Arthus - Martha	Summer	female	2019	Test	Grünau
	Winter	female	2019	Test	Grünau
Horst - Astrid	Nyx	female	2020	Control	Haidlhof
Paul - Aramis	Eragon	male	2020	Test	Haidlhof
	Saphira	female	2020	Test	Haidlhof
Rocky - Joey	Ebony	male	2020	Control	Haidlhof
	Inky	female	2020	Control	Haidlhof
George - Nobel	Maple	female	2020	Test	Haidlhof
	Oak	male	2020	Test	Haidlhof
Rufus - Munia	Ginza	male	2020	Test	Schönbrunn
	Shiba	female	2020	Test	Schönbrunn
	Asakusa	male	2020	Test	Schönbrunn
	Ueno	male	2020	Test	Schönbrunn
Tom - Heidi	Tango	female	2020	Control	Grünau
Arthus - Martha	Cirrus	female	2020	Control	Grünau
	Cumulus	male	2020	Control	Grünau
	Nimbus	male	2020	Control	Grünau

The subjects were housed in outdoor aviaries in three locations: the Haidlhof research station in Bad Vöslau, Austria, the Konrad Lorenz Research Station in Grünau im Almtal, Austria and the Zoo Schönbrunn in Vienna, Austria. Each family was housed in a separate aviary and these aviaries ranged in size from 80 m² to 160 m² and measured between 5 and 7 m in height.

The aviaries at all locations were equipped with enrichment, trees, perches and branches. The substrate consists of a combination of grass, sand and gravel. The enclosure's compartments were fitted with roofing and walls, which offered protection against harsh weather and low temperatures. The birds' diet included fruits, vegetables, cereals, yogurt, eggs and meat and they were fed twice a day. They always had access to fresh water, for drinking as well as for bathing.

2.2 Experimental Apparatus

The experimental apparatus we used consisted of a wooden frame measuring 60 cm x 60 cm x 5 cm. Either a 50 x 50 cm mirror or a wooden board of the same size could be placed in this frame (see **Figure 1**). To allow habituation, the apparatus was placed in the aviaries without the wooden board or mirror approximately two weeks prior to the start of the experiment. The empty apparatus remained in the enclosures throughout the experiment. The apparatus stood stable on the floor and the positioning ensured that the birds could easily inspect it from all sides. The experimenter had clear visibility of both the apparatus itself and the surrounding area.

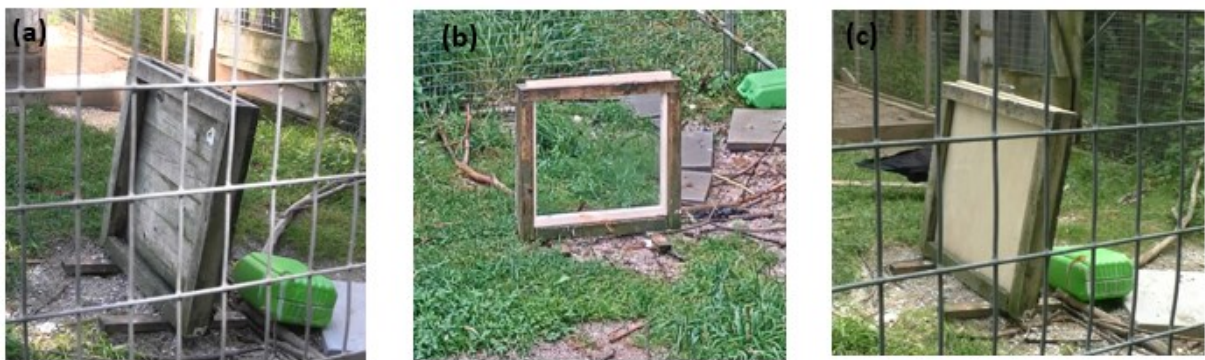


Figure 1 Example of the apparatus constellations (a) apparatus without the wooden board or mirror, (b) apparatus including mirror and (c) apparatus including the wooden board. (©Kanta, 2025)

2.3 Procedure and Time Frame

At the beginning of the experiment, families were divided into test and control groups. The test groups were exposed to both the mirror or the wooden board throughout the experiment. The control groups were only confronted with the wooden board in all their sessions. Before the start of each session, either the mirror or the wooden board was placed in the apparatus. Then treats (quarters of Frolic, 1 Frolic per individual in the family) were placed in front of the apparatus and a timer was started. The experiment was filmed and observed from outside so that it could be stopped immediately if should

any indication of distress was detected in an animal. All subjects were free to move around the entire aviary and visit the apparatus voluntarily and *ad libitum* or stay away from it completely. At the end of the session, the mirror or wooden board was removed. The sessions were usually scheduled from Monday to Friday between 9:00 a.m. and 4:00 p.m. The experiments were done once or twice a day. When done twice a day, the individuals received one session in the morning and the second session in the afternoon with at least 2 1/2 hours between sessions. The session length normally lasted 20 minutes, but due to technical difficulties (e.g., camera failure), this was not achieved in 11 videos. The shortest recording ended after about 9 minutes. The adult animals gained experience with the apparatus over the years (see **Table 2**). Since they were not presented with the apparatus every year, we calculated a value for each year by averaging the experience of both parents for the respective year. However, at the beginning of the experiment, all juvenile ravens were naive to the mirror or wooden board.

Table 2: Parental experience across years: participation in the experiments (indicated by ✓) or non-participation (indicated by X)

Name Parent	Parental experience year						
	2014	2015	2016	2017	2018	2019	2020
Astrid	X	✓	✓	✓	✓	✓	✓
Horst	✓	X	✓	✓	✓	✓	✓
Joey	X	X	✓	✓	✓	✓	✓
Rocky	X	X	✓	✓	✓	✓	✓
Rufus	✓	X	X	X	✓	✓	✓
Munia	X	X	X	X	✓	✓	✓
Tom	✓	X	✓	X	✓	✓	✓
Heidi	X	✓	✓	X	✓	✓	✓
Arthus	X	X	X	✓	X	✓	✓
Martha	X	X	X	✓	X	✓	✓
Matte	X	✓	X	X	X	✓	✓
Lelan	X	✓	X	X	X	✓	✓
George	✓	X	X	X	X	✓	✓
Nobel	✓	X	X	X	X	✓	✓
Laggy	X	X	X	✓	X	X	X
Bobby	X	X	X	✓	X	X	X
Paul	✓	X	X	X	X	X	✓
Aramis	X	X	X	X	X	X	✓

2.4 Data Collection

The sessions were recorded from two perspectives: one zoomed in to the apparatus and its immediate surroundings and a global view covering approximately 2m around the apparatus. Recordings were conducted either with camcorders (Canon Legria HF G25, 720p, 60 fps) or overhead dome cameras, which were permanently installed in the aviaries. In 2019, the videos were assembled by Milena Holzer into multiview-videos using the program DaVinci Resolve 16 /Blackmagic Design. After recording, the videos were uploaded to the server and to the coding program Loopy (loopbio gmbh, Vienna, Austria). The coding of all the videos was done using Loopy. The videos from 2019 were recorded and coded together with my colleague Milena Holzer as part of “300656 UE Lernexperimente 2019S”.

We measured the individuals approach latency to the apparatus, as well as the time they spent in front of or in close proximity to the apparatus. To determine the distance of the raven to the apparatus, spatial zones were defined and coded: Zone 1 = 0m – 0.5m, Zone 2 = 0.5m – 1m, Zone 3 = 1m – 1.5m, Zone 4 = 1.5m – 2m (see **Figure 2**). Zones 2 to 4 were pooled for the analysis. Furthermore, we coded for explorative behaviours, self-directed behaviours, social behaviours towards the apparatus and conspecifics (see **Table 11**, ethogram for detail of the behaviours coded).

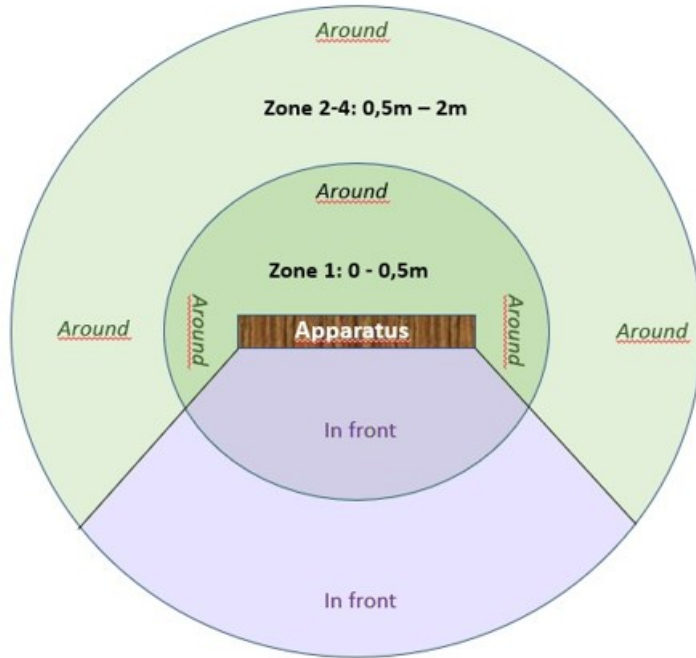


Figure 2 Apparatus zones around and in front, zone 2-4 was pooled

For my analysis, I focused on three categories and pooled them. The first category was social behaviours towards the apparatus (frequency), namely attack, SAD (Self-assertive-Display), submissive display and threat. The second category was exploration behaviour towards the apparatus (frequency) and included bite frame, peck frame, bite surface, peck surface, clawing frame, clawing surface, look down from on top, look behind and look under. Lastly the category showing the amount of time spent in zone 1 in front of the apparatus (duration).

A duration rate was calculated to standardize the time the individual spent in zone 1, as the sessions did not all have the same length. The duration rate was determined by dividing the total duration spent in zone 1 (in seconds) by the session length (in seconds). Similarly, the behaviour rate was calculated by dividing the total frequency of the observed behaviours by the session length (in seconds). This measure allowed us to account for differences in session length and ensure comparability between sessions.

2.5 Data Analysis

The statistical analysis and plots were done using RStudio, PBC, R version 4.4.1 (R Core Team, 2025). The data were analysed by fitting generalized linear mixed models using the glmmTMB package (Brooks et al., 2017). The overall significance of the predictors was evaluated by comparing the full model to a null model (containing the random effects) using a likelihood ratio test. This test was conducted using the anova function with the test “chisq” using the car package (Fox & Weisberg, 2019). Post-hoc pairwise comparisons were performed with the emmeans package (Lenth, 2025). The data was visually represented using the R packages ggplot (Wickham, 2016).

Exploration behaviours and time in zone 1 of juvenile ravens

To investigate the effects of the variables on the mirror responses of juvenile ravens, the model analysis included exploration behaviours toward the apparatus as well as the time juvenile ravens spent in zone 1 front of the apparatus as response variables. The fixed factors included in the model were condition (mirror/wood), age of the juvenile ravens at the session date (in days), size of the family (3-7), sex (female/male), parental experience with the apparatus, exploration rate of the parents, and the time the parents spent in zone 1 in front of the apparatus. The random factors included individual and family.

Social behaviours of juvenile ravens

Due to the small number of recorded social behaviours of juvenile ravens involving the apparatus, a simplified model was used for the analysis of social behaviour. This reduced model incorporated the predictors condition (mirror/wood), age of the juvenile ravens at the session date (in days), size of the family (3-7), sex (female/male), and parental experience with the apparatus and individual as random factor.

Comparison juvenile and adult ravens

To compare the behaviours of juvenile and adult ravens, the analysis focused on three variables: social behaviours, exploration behaviours, and the time spent in zone 1 in front of the apparatus. The predictors included age category (juvenile/adult), condition (mirror/wood), family size (3-7), and sex (female/male). The random factors included individual and year.

General object exploration

To investigate also the ontogeny and group effects on general object exploration behaviours, the analysis focused on data from the wood sessions. The analysis included exploration behaviours and the time spent in zone 1. The predictors were age of the juvenile ravens at hatching (in days), group (test or control), size of the family (3-7), family, and sex (female/male) and the random factors included individual, year and family.

3 Results

3.1 Exploration behaviours and time in zone 1 of juvenile ravens

Exploration behaviours:

The factors in the model had an effect on the exploration behaviours of juvenile ravens (full-null model comparison: $\chi^2 = 54.353$, $df = 10$, $p < 0.001$). Among the predictors, the age of the juveniles on the testing day had a significant positive effect on the rate of exploration behaviour (Est. = 2.01, 95% CI [1.64, 2.48], $p < 0.001$), with older individuals exhibiting higher exploration rates (see **Figure 3**). No significant effects were observed for the other predictors (see **Table 3**).

Table 3 Model results for exploration behaviours of juvenile ravens (estimates, 95% confidence interval and *p*-values).

Exploration behaviours, juvenile ravens			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.00	0.00 – 0.12	0.003
Condition [Wood]	0.84	0.57 – 1.23	0.365
Age at Session Date	2.01	1.64 – 2.48	<0.001
Size Family [4]	25.92	0.26 – 2625.86	0.167
Size Family [5]	0.03	0.00 – 3.18	0.137
Size Family [6]	0.10	0.00 – 24.22	0.415
Size Family [7]	3.76	0.01 – 1862.86	0.676
Sex [Male]	1.08	0.59 – 1.96	0.805
Parental Experience with the Apparatus	7.37	0.60 – 91.28	0.120
Parents in Zone 1	1.07	0.79 – 1.44	0.677
Parental Exploration	0.69	0.47 – 1.02	0.061

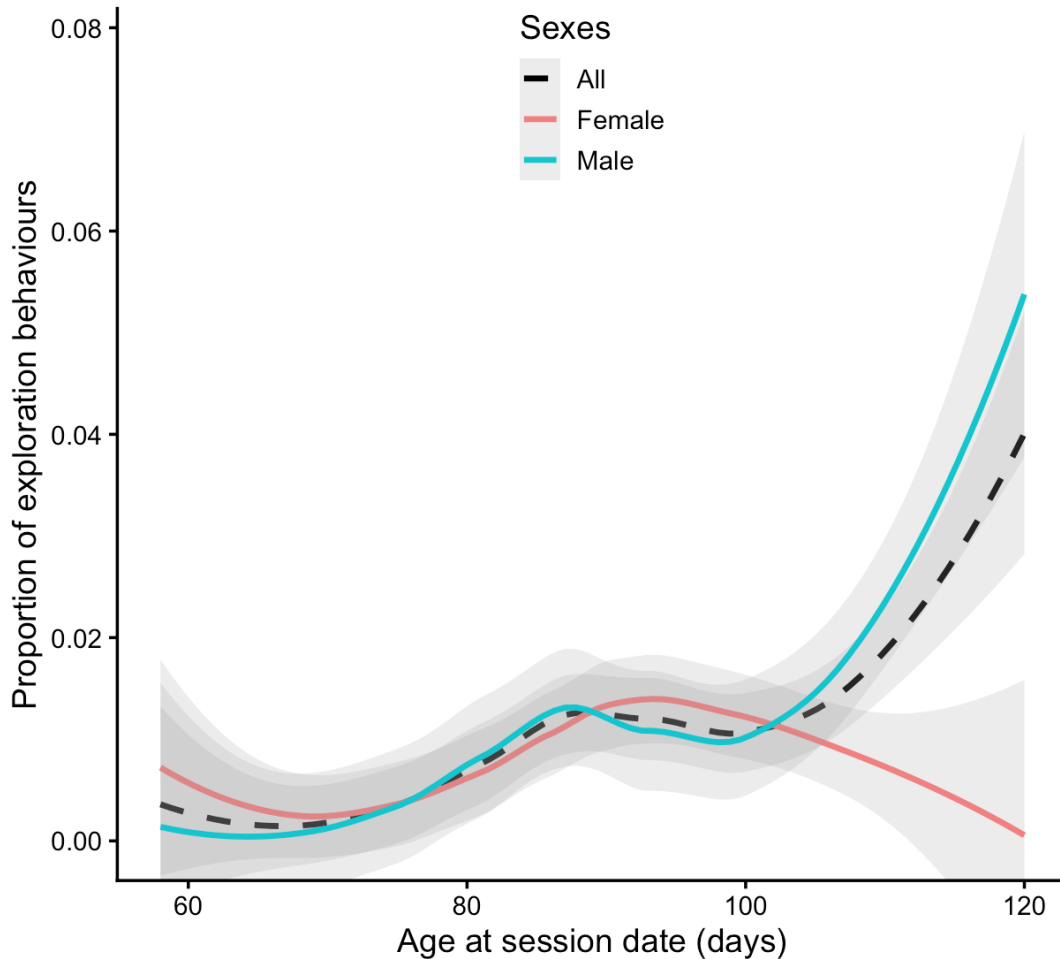


Figure 3 Smoothed curves (loess) illustrating the age at session date (in days) and the exploration rate of juvenile ravens for males (turquoise), females (coral), and all individuals combined (black, dashed). Shaded areas represent 95% confidence intervals (CI).

Time in zone 1

The time juvenile ravens spent in zone 1 was affected by the factors of the model (full-null model comparison: $\chi^2 = 84.208$, $df = 10$, $p < 0.001$). It was found that the condition and the age that the juvenile ravens had at the session date had an influence on the time spent in front of the mirror. Individuals spent more time in zone 1 when confronted with a mirror than with the wooden board (Est. = 0.54, 95% CI [0.40, 0.71], $p < 0.001$, see **Figure 4**). Besides the condition, age at session date was also significant (Est. = 1.92, 95% CI [1.63, 2.26], $p < 0.001$), indicating that older individuals spent more time in zone 1. None of the other predictors showed significant effects (see **Table 4**).

Table 4 Model results of time spent in front of the mirror in zone 1 of juvenile ravens (estimates, confidence interval and *p*-values).

Time spent in zone 1, juvenile ravens			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.07	0.01 – 0.87	0.039
Condition [Wood]	0.54	0.40 – 0.71	<0.001
Age at Session Date	1.92	1.63 – 2.26	<0.001
Size Family [4]	0.93	0.08 – 11.63	0.958
Size Family [5]	0.15	0.01 – 2.28	0.174
Size Family [6]	0.22	0.01 – 3.34	0.277
Size Family [7]	1.33	0.06 – 30.30	0.857
Sex [Male]	0.80	0.36 – 1.77	0.581
Parental Experience with the Apparatus	1.93	0.72 – 5.15	0.188
Parents in Zone 1	0.95	0.76 – 1.18	0.638
Parental Exploration	0.85	0.65 – 1.12	0.251

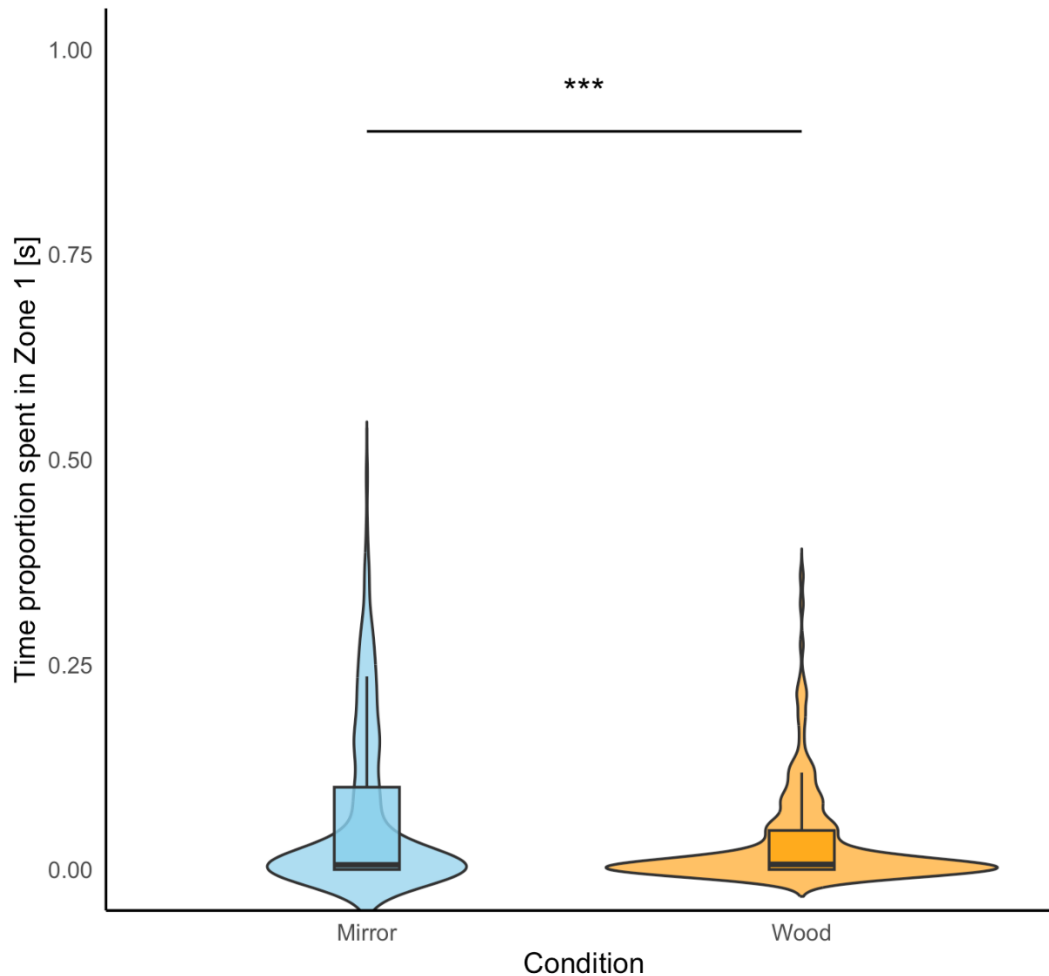


Figure 4 Time spent in zone 1 (duration rate) by juvenile ravens in the mirror and wood conditions. Violin plots with inserted box plots (median, interquartile range) are shown.

3.2 Social behaviours of juvenile ravens

When observing the effects of the variables on the mirror responses of juvenile ravens, a total of 73 exhibitions of social behaviours involving the apparatus were recorded. The factors in the reduced model had an effect on the social behaviours of juvenile ravens (full-null model comparison: $\chi^2 = 21.348$, $df = 8$, $p = 0.006$). There is a significant effect of the condition, but not of the session date, size of the family, sex or the parental experience with the apparatus. Juvenile ravens exhibited higher exploration rates in the mirror condition than in the wood condition (Est. = 0.04, 95% CI [0, 0.54], $p < 0.016$, see Table 5).

Table 5 Model results social behaviour of juvenile ravens (estimates, 95% confidence interval and p-values).

Social behaviours, juvenile ravens			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.00	0.00 – Inf	1.000
Condition [Wood]	0.04	0.00 – 0.54	0.016
Age at Session Date	1.07	0.99 – 1.15	0.070
Size Family [4]	0.00	0.00 – Inf	0.999
Size Family [5]	0.01	0.00 – Inf	1.000
Size Family [6]	0.00	0.00 – Inf	1.000
Size Family [7]	0.00	0.00 – Inf	1.000
Sex [Male]	0.98	0.03 – 38.08	0.992
Parental Experience with the Apparatus	4.06	0.00 – Inf	1.000

3.3 Comparison juvenile and adult ravens

Exploration behaviours

The factors in the model had an effect on the exploration behaviour in comparison between juvenile and adult ravens (full-null model comparison: $\chi^2 = 64.257$, $df = 7$, $p < 0.001$). The condition, age category and family size influenced the exploration behaviours towards the apparatus. Juveniles and adults exhibited significantly more exploration behaviours towards the mirror condition than the wood (Est. = 0.58, 95% CI [0.43, 0.49], $p = 0.001$, see **Figure 5**). Post-hoc pairwise comparisons revealed, families of size 3 exhibited significantly higher exploration rates compared to families of size 5 (Est. = 1.918, SE = 0.528, $p = 0.003$) and size 6 (Est. = 1.377, SE = 0.506, $p = 0.051$). Similarly, families of size 4 showed significantly higher exploration rates

than families of size 5 (Est. = 2.348, SE = 0.420, $p < 0.001$) and size 6 (Est. = 1.807, SE = 0.583, $p = 0.017$). In contrast, families of size 7 exhibited significantly higher exploration rates than families of size 5 (Est. = -2.535, SE = 0.885, $p = 0.034$) and size 6 (Est. = -1.994, SE = 0.717, $p = 0.043$). No significant differences were found between other family size pairs or sex (see **Table 6**).

Table 6 Model results of the comparison of exploration behaviour between juvenile and adult ravens (estimates, 95% confidence interval and p -values).

Exploration behaviours, juvenile-adult comparison			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.00	0.00 – 0.00	<0.001
Condition [Wood]	0.58	0.43 – 0.49	0.001
Age Category [Juvenile]	6.35	2.65 – 15.24	<0.001
Sex [Male]	0.99	0.45 – 2.18	0.976
Size Family [4]	1.54	0.62 – 3.82	0.355
Size Family [5]	0.15	0.05 – 0.41	<0.001
Size Family [6]	0.25	0.09 – 0.68	0.007
Size Family [7]	1.85	0.50 – 6.93	0.359

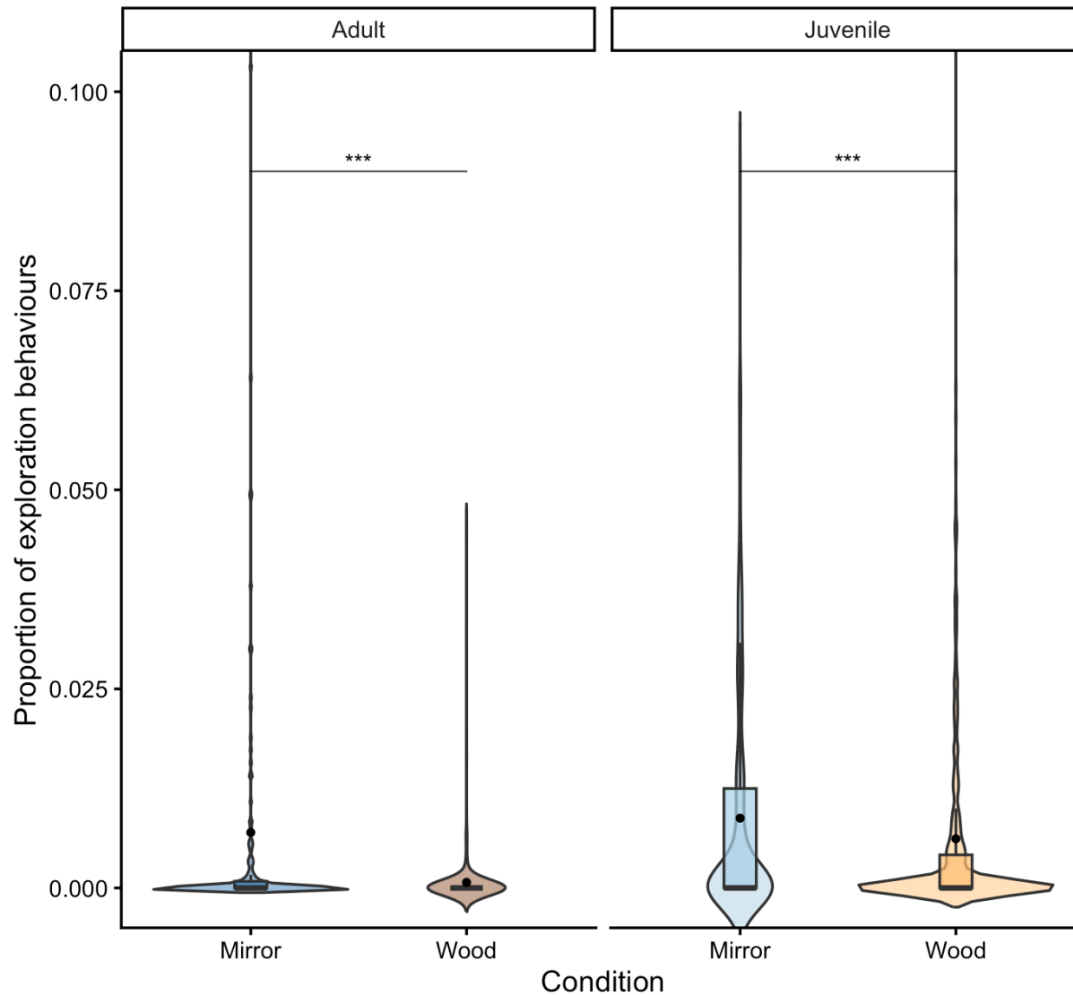


Figure 5 Violin plots with inserted boxplots illustrating the rate of exploration behaviour of ravens across conditions (mirror vs. wood) and age categories (adults vs. juveniles). The violin plots display the distribution of individual data points, while the embedded boxplots highlight the median and interquartile range; black dots indicate the mean values.

Time in zone 1

The time the birds spent in zone 1 in comparison of juvenile and adult ravens was influenced by the factors in the model (full-null model comparison: $\chi^2 = 213.42$, $df = 7$, $p < 0.001$). The condition and the size of the family had an effect on the time spent in zone 1. Juveniles and adults spent more time in the zone 1 during the mirror than the wood condition (Est. = 0.36, 95% CI [0.30, 0.43], $p < 0.001$). Post-hoc pairwise comparisons showed, families of size 3 spent significantly more time in zone 1 compared to families of size 5 (Est. = 1.414, SE = 0.226, $p < 0.001$) and size 6

(Est. = 1.648, SE = 0.252, $p < 0.001$). Similarly, families of size 4 spent significantly more time in zone 1 than families of size 5 (Est. = 1.577, SE = 0.210, $p < 0.001$) and size 6 (Est. = 1.811, SE = 0.275, $p < 0.001$). Families of size 7 spent significantly more time in zone 1 compared to families of size 5 (Est. = -2.037, SE = 0.349, $p < 0.001$) and size 6 (Est. = -2.272, SE = 0.362, $p < 0.001$, see **Table 7**, **Figure 6**).

Table 7 Model results for exploration behaviours comparing juvenile and adult ravens (estimates, 95% confidence interval and p -values).

Time in zone 1, juvenile-adult comparison			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.04	0.02 – 0.09	<0.001
Condition [Wood]	0.36	0.30 – 0.43	<0.001
Age Category [Juvenile]	1.58	0.83 – 3.03	0.165
Sex [Male]	1.00	0.55 – 1.81	0.990
Size Family [4]	1.18	0.76 – 1.83	0.469
Size Family [5]	0.24	0.16 – 0.38	<0.001
Size Family [6]	0.19	0.12 – 0.32	<0.001
Size Family [7]	1.87	1.04 – 3.34	0.036

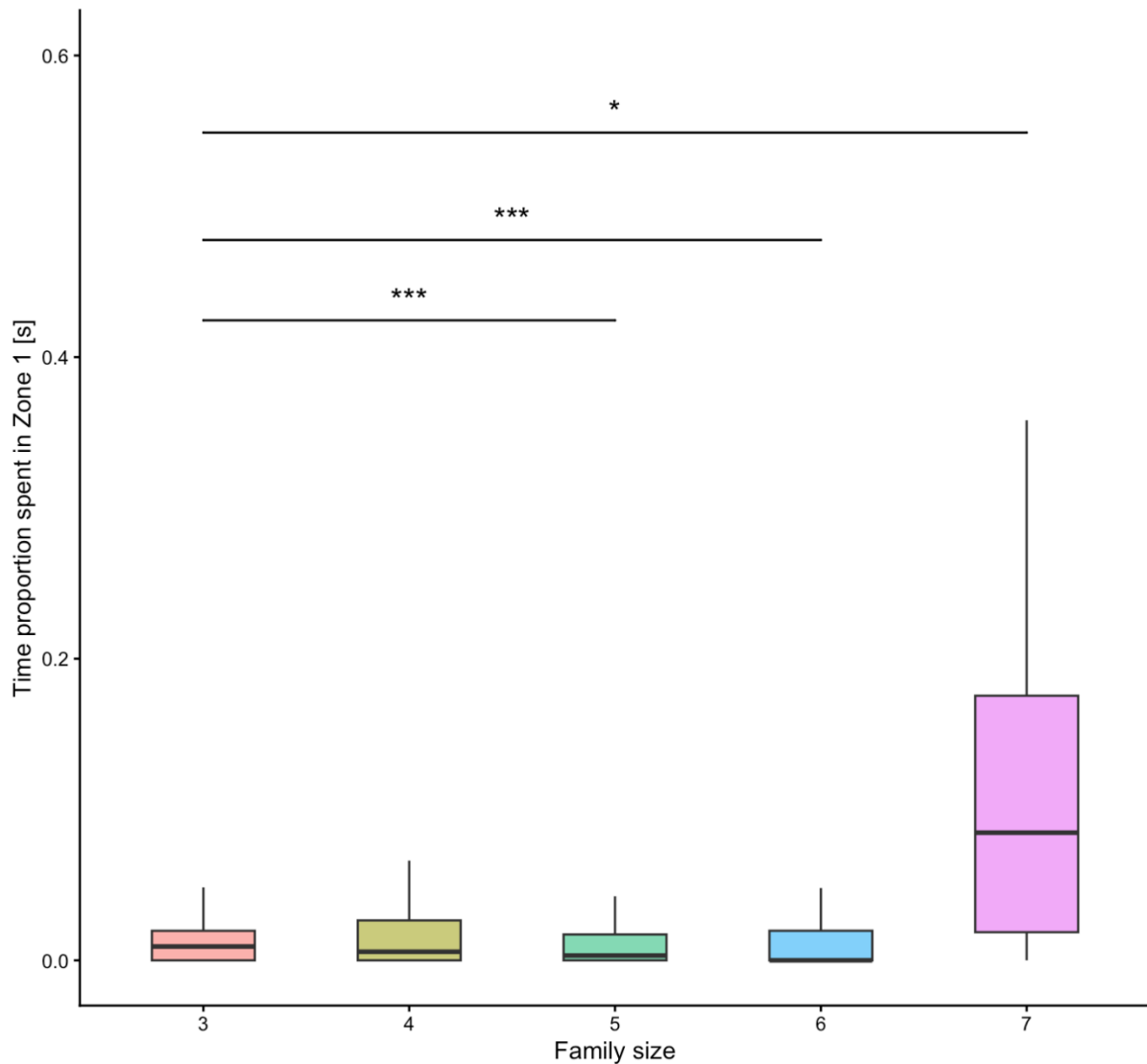


Figure 6 Time spent in zone 1 by juvenile and adult ravens, grouped by family size. Boxplots show the median (central line) and interquartile range (box), with whiskers representing the range of the data within 1.5× the interquartile range.

Social behaviours

Overall, the factors in the model influenced the social behaviour of juvenile and adult ravens (full-null model comparison: $\chi^2 = 100.91$, $df = 7$, $p < 0.001$). The condition, age and family size had a significant effect on social behaviours. The ravens showed more social behaviours in the mirror condition compared to the wood condition (Est. = 0.03, 95% CI [0.01, 0.06], $p < 0.001$). Juveniles showed significantly reduced social rates compared to adults (Est. = 0.05, 95% CI [0.00, 0.43], $p = 0.007$), as shown in **Figure 7**.

Post-hoc pairwise comparisons indicated, families of size 3 exhibited significantly higher social rates compared to families of size 6 (Est. = 5.735, SE = 1.511, $p = 0.001$). Similarly, families of size 4 showed significantly higher social rates than families of size 5 (Est. = 2.981, SE = 0.901, $p = 0.008$) and size 6 (Est. = 6.797, SE = 1.720, $p = 0.001$). No significant differences were found between other family size pairs or sex (see **Table 8**).

Table 8 Model results social behaviour, juvenile vs. adult ravens (estimates, 95% confidence interval and p -values).

Social behaviours, juvenile-adult comparison			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.00	0.00 – 0.01	<0.001
Condition [Wood]	0.03	0.01 – 0.06	<0.001
Age Category [Juvenile]	0.05	0.00 – 0.43	0.007
Sex [Male]	0.40	0.05 – 3.16	0.379
Size Family [4]	2.89	0.34 – 24.60	0.331
Size Family [5]	0.15	0.02 – 1.31	0.086
Size Family [6]	0.00	0.00 – 0.06	<0.001
Size Family [7]	0.14	0.01 – 1.94	0.143

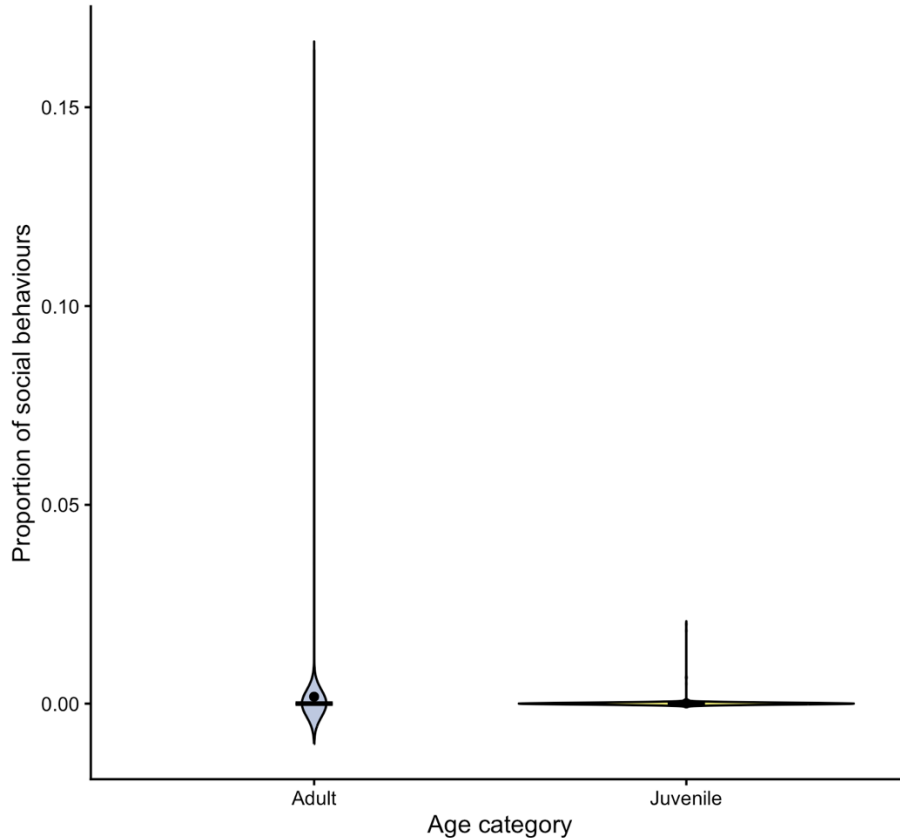


Figure 7 Comparison of the proportion of social behaviours (rate) between adult and juvenile ravens. Violin plots with overlaid boxplots and mean points are shown.

3.4 General object exploration (wood sessions)

Exploration behaviours

The factors included in the model influenced the exhibition of general object exploration behaviours of juvenile ravens (full-null model comparison: $\chi^2 = 59.819$, $df = 7$, $p < 0.001$). The age at session date, group (mirror or wood) and the family size had a significant effect on the exploration behaviour. Older juveniles exhibited higher exploration rates towards the apparatus than younger ones (Est. = 1.04, 95% CI [1.03, 1.05], $p < 0.001$). In addition, it revealed that the test group showed a significant higher exploration rate than the control group (Est. = 2.94, 95% CI [1.63, 5.30], $p < 0.001$). Post-hoc pairwise comparisons identified families of size 3 exhibited significantly

higher exploration rates compared to size 6 (Est. = 1.520, SE = 0.548, $p = 0.044$). Families of size 4 showed significantly higher exploration rates than size 5 (Est. = 1.005, SE = 0.332, $p = 0.021$) and size 6 (Est. = 1.401, SE = 0.454, $p = 0.017$). Finally, families of size 6 exhibited significantly lower exploration rates compared to size 7 (Est. = -1.829, SE = 0.657, $p = 0.043$). No significant differences were found between other family size pairs or sex (see **Table 9**).

Table 9 Model results of general exploration behaviours (only wood) of juvenile ravens (estimates, 95% confidence interval and p -values).

Exploration behaviours, object in general			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.00	0.00 – 0.00	<0.001
Age at Session Date	1.04	1.03 – 1.05	<0.001
Sex [Male]	1.23	0.74 – 2.05	0.426
group [Mirror Exposure]	2.94	1.63 – 5.30	<0.001
Size Family [4]	0.89	0.41 – 1.94	0.764
Size Family [5]	0.32	0.14 – 0.77	0.010
Size Family [6]	0.22	0.07 – 0.64	0.006
Size Family [7]	1.36	0.31 – 5.90	0.680

Time in zone 1

Overall, the factors in the model had an effect on the time juveniles spent in zone 1 in front of the object in general (wood sessions, full-null model comparison: $\chi^2 = 117.38$, $df = 7$, $p < 0.001$). The age at session date and the size of the family had a significant positive effect on the time spent in zone 1. It was found that older juveniles spent more time in zone 1 (Est. = 1.05, 95% CI [1.04, 1.06], $p < 0.001$). Post-hoc pairwise comparisons showed, families of size 3 spent significantly less time compared to families of size 7 (Est. = -1.676, SE = 0.429, $p = 0.001$). Similarly, families of size 4 spent significantly less time compared to families of size 7 (Est. = -1.590, SE = 0.570,

$p = 0.042$). In addition, families of size 6 spent significantly less time compared to families of size 7 (Est. = -3.109, SE = 0.694, $p < 0.001$). No significant differences were found between other family size pairs and none of the other predictors showed significant effects (see **Table 10**).

Table 10 Model results for the time juvenile ravens spent in zone 1 in front of the object in general (estimates, 95% confidence interval and p -values).

Time in zone 1, object in general			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.00	0.00 – 0.00	<0.001
Age at Session Date	1.05	1.04 – 1.06	<0.001
Sex [Male]	1.08	0.78 – 1.48	0.645
Group [Mirror Exposure]	1.51	0.96 – 2.38	0.076
Size Family [4]	1.09	0.48 – 2.45	0.835
Size Family [5]	0.72	0.32 – 1.61	0.424
Size Family [6]	0.24	0.08 – 0.70	0.009
Size Family [7]	5.34	2.30 – 12.40	<0.001

4 Discussion

This study investigated the exploration behaviours of juvenile ravens towards a mirror and a wooden board to examine whether responses differed by condition, individual variation, family size, or the parental exploratory behaviours and prior experience with the apparatus. The results reveal that social behaviours were more frequently expressed in the mirror condition compared to the wood condition, with adults exhibiting these behaviours more than juveniles. Juvenile ravens, while showing fewer social behaviours overall, displayed significantly more exploratory behaviours towards the mirror than the wooden board and spent more time in front of the apparatus in the mirror condition. Exploration behaviour was also age-dependent, with juveniles showing higher exploration rates than adults, and exploration increasing further with age within the juvenile group. Although the family sizes occasionally demonstrated statistical significance, the results did not reveal a clear trend in the analysis of family sizes, as individuals from families with five or six members showed significantly less explorative and social behaviour as well as time in front of the apparatus, while ravens from families with seven members showed significantly more. Neither sex, parental exploratory tendencies, nor prior experience with the apparatus affected the juvenile behaviour significantly.

The results of this study show that, although social behaviours were generally exhibited towards the mirror, adult animals exhibited significantly more of these behaviours than juveniles. Within the juvenile group, no age-related differences in social behaviours were found in the present data. This could be explained by the fact, that juvenile ravens of that age do not yet display the same social behaviour patterns as adults, as their social repertoires are still developing (Boucherie et al. 2020). In contrast, adults, with their already established social repertoire, are more likely to exhibit behaviours typically associated with perceiving the mirror as a potential conspecific (Gallup Jr., 1970; Plotnik, De Waal, Reiss 2006). These findings indicate that mirrors elicit social behaviours, with age playing a crucial role in shaping the type of response displayed. However, it is worth noting that the ravens still exhibit considerably less social behaviour than exploratory behaviour. Furthermore, juvenile ravens in the experiments

demonstrated more exploratory behaviours towards the mirror compared to the wooden board. Comparing adults and juveniles regarding condition preferences, the results show that both preferred the mirror over the wooden board. The results align with the proposed predictions and also with previous reports that ravens exhibit a strong preference for mirrors (Vanhooland et al., 2023). The responses fit within the first two stages of mirror interaction, namely social reactions and physical exploration of the reflective surface (Gallup Jr., 1970; Plotnik, de Waal, & Reiss, 2006).

We expected that juvenile ravens would interact more frequently and spend more time at the object than their parents. Accordingly, juvenile ravens exhibited more exploration behaviour and spent more time in zone 1 in front of the mirror than the adults. These results are in line with previous observations, which indicate that juvenile ravens display neophilic tendencies up to a certain age, actively exploring novel objects (Heinrich, 1995). In contrast, adult ravens tend to be neophobic (Greenberg & Mettke-Hofmann, 2001), which could explain why they spent less time in front of the apparatus. Furthermore, it is known that exploratory behaviour in animals decreases with adulthood, which could also explain why the adult ravens spent less time near the exploration object (Povinelli et al., 1993). Since the parents have already gained experience with the apparatus over the years, it could also be explained by the effect of habituation (Harris 1943, Hughes 2007). We expected that the exploratory behaviour of juveniles will be more frequently at the beginning of the experiments but diminishes over time as the mirror loses its novelty. Over the course of the experiment, the ravens exhibited more exploratory behaviours as they grew older and spent more time in zone 1 in front of the apparatus. It could be linked to the concept of intrinsic exploration behaviour, which is closely associated with stimulus-seeking tendencies (Hughes, 1997). In addition, exploration behaviour is crucial for juvenile ravens, as it enables them to gather essential knowledge about habitat resources and potential dangers (Schaden, 1993). This is particularly important at the stage in their lives, when they are becoming independent from their parents and probably enter new habitats where it is beneficial to be more exploratory (Macri et al., 2002). Consequently, older juveniles may have developed an increased tendency to engage with the mirror or wood across sessions. To examine the ontogeny and group effects on exploratory behaviour in

general, the wood sessions were also analysed. The results showed that, in addition to significant effects of family size and age-related factors, the test groups that were also exposed to a mirror displayed more exploratory behaviour compared to the control group, which was only presented with a wooden board. The increased exploratory behaviour exhibited by the juvenile ravens in the test group during the mirror testing may have fostered an increased tendency to explore the wooden board as well. This observation is supported by extant literature which suggests that diversified exploration is characteristic of individuals seeking novel experiences or an escape from feelings of boredom (Berlyne, 1960). The alternation between stimuli, like mirror and wooden board, could prevent boredom and thus encourage exploration.

We predicted that males would exhibit more exploration behaviour than females. However, the results of this study showed no significant sex differences, although there was a slight trend for males to explore more than females (see **Figure 2**). This effect may potentially become more pronounced with further development, as behavioural patterns continue to emerge during maturation (Miller et al. 2015). Previous research suggested that males can be more manipulative towards objects (Range et al., 2006). Other studies found that object exploration in ravens is influenced by the combination of sexes and social relationships within dyads (Stöwe et al., 2006). For future studies, longitudinal approaches that investigate how social and exploratory behaviours towards mirrors change across developmental stages, by following the same individuals from fledging into adulthood, could provide valuable insights into the ontogeny of mirror responses in ravens. In particular, conducting longitudinal mirror experiments with the ravens from this study could help determine whether the stages they exhibit in mirror self-recognition tests are shaped by their early-life experiences.

The present study did not find a significant effect of parental exploratory tendencies or prior experience with the apparatus on juvenile behaviour. This finding might suggest that exploratory responses toward mirrors are less influenced by parental behaviours and more by the social environment experienced by juveniles within their peer group. This interpretation is supported by the results of earlier studies by Boucherie, Blum, & Bugnyar (2020), which showed that although the rearing environment had no significant influence on the quality of relationships among ravens, early contact with

conspecifics had a considerable impact on social competence. In the context of family size, it was predicted that this factor would influence exploration behaviours. More specifically, that larger groups would exhibit higher exploration frequencies and spend more time at the object. In contrast to this prediction, the results of this study do not show a clear trend. Larger families with the size of 5 or 6 showed significantly reduced exploration. Studies have shown that ravens raised in smaller families are more attentive than those from larger families (Gallego-Abenza, Boucherie & Bugnyar, 2022). This is consistent with the findings of the present study, in which juveniles from families of sizes 5 and 6 were less exploratory and, in contrast to individuals who grew up in families with fewer social partners, may pay more attention to novel stimuli. The results revealed also that ravens from the family with the size of 7 members spent significantly more time with the apparatus, although it should be noted that there was only one family with seven members. In contrast to the findings for family sizes 6 and 5, this may indicate that group size influences the behaviour of ravens, as larger groups offer diverse interactions due to the larger number of social partners (Heyes, 1994; Wild & Hoppitt, 2018). The contradictory results could be due to the fact that we only had a small number of families with larger family sizes (e.g., only one family with seven members). A study reported an interaction between family size and sex in shaping early life experiences, noting that males and females are affected differently by group size (Boucherie et al. 2025). In light of these findings, it is possible that the lack of significant sex differences in exploratory behaviour observed in this study may be also influenced by the relatively small sample size or limited representation of larger family groups. Furthermore, it has been observed in human children that parenting and attachment styles have an influence on cognitive development. Studies have shown that cultural and rearing differences significantly impact behaviours such as mirror self-recognition and problem-solving abilities, independent of empathy or theory of mind capabilities (Broesch et al., 2011; Keller et al., 2005). Applying these insights to juvenile ravens, it is conceivable that the rearing environment, including family size and the quality of social interactions, could influence their cognitive and exploratory behaviours. In summary, these findings suggest that the family size influences behaviour, though the extent of this influence may vary depending on the context. Future studies could not only expand the sample size to include a broader and more

balanced distribution of family sizes, but also investigate the role of rearing conditions. This could involve examining how variations in parental investment, sibling interactions, and early social experiences shape exploratory tendencies and cognitive development. In addition, it would be interesting to define groups of juvenile ravens by sex composition and examine whether sex-specific patterns in exploration emerge more clearly during development.

5 Conclusion

To conclude, both juvenile and adult ravens preferred the mirror over the wooden board. The present study revealed clear age-related patterns in exploration and mirror-directed behaviours in ravens, as well as significant differences in the exploratory tendencies of adults and juveniles. While juveniles showed more exploration behaviour and spent more time in zone 1 than their parents, adults expressed more social behaviours towards the mirror. While the family size has a significant effect, but does not show a clear trend, sex, parental exploratory tendencies, and prior experience with the apparatus have no effect on the exploratory behaviour of juvenile ravens. The results align well with previous findings on exploration patterns and their preference for novel stimuli, such as mirrors. It may encourage future research on the interplay between rearing conditions, social structures, and exploratory behaviours. Furthermore, conducting longitudinal mirror experiments with the ravens from this study could provide insights into whether their later stages of mirror self-recognition are influenced by early-life experiences.

References

- Amsterdam, B. (1972). Mirror self-image reactions before age two. *Developmental Psychobiology: The journal of the international society for developmental psychobiology*, 5(4), 297-305.
- Baciadonna, L., Jerwood, G. M., Farrar, B. G., Clayton, N. S., & Emery, N. J. (2022). Investigation of mirror-self recognition in ravens (*Corvus corax*). *Journal of Comparative Psychology*, 136(3), 194.
- Berlyne, D. E. (1960). Conflict, arousal, and curiosity. McGraw-Hill Book Company
Conflict, Arousal and Curiosity. McGraw-Hill, New York, p. 350.
- Boucherie, P. H., Blum, C., & Bugnyar, T. (2020). Effect of rearing style on the development of social behaviour in young ravens (*Corvus corax*). *Ethology*, 126(6), 595-609.
- Boucherie, P. H., Murari, G., Svitil, E. A., & Bugnyar, T. (2025). Rearing group size in young ravens: stress load or social opportunity?. *Royal Society Open Science*, 12(7), 250479.
- Branchi, I. (2009). The mouse communal nest: investigating the epigenetic influences of the early social environment on brain and behavior development. *Neuroscience & Biobehavioral Reviews*, 33(4), 551-559.
- Broesch, T., Callaghan, T., Henrich, J., Murphy, C., & Rochat, P. (2011). Cultural variations in children's mirror self-recognition. *Journal of Cross-Cultural Psychology*, 42(6), 1018-1029.
- Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., ... & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling.
- Bugnyar, T., & Heinrich, B. (2005). Ravens, *Corvus corax*, differentiate between knowledgeable and ignorant competitors. *Proceedings of the Royal Society B: Biological Sciences*, 272(1573), 1641-1646.

- Bugnyar, T., & Kotrschal, K. (2002). Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it 'tactical' deception?. *Animal behaviour*, 64(2), 185-195.
- Bugnyar, T., Stoewe, M., & Heinrich, B. (2007). The ontogeny of caching in ravens, *Corvus corax*. *Animal Behaviour*, 74(4), 757-767.
- Buniyaadi A, Taufique SKT, Kumar V (2020) Self-recognition in corvids: evidence from the mirror-mark test in Indian house crows (*Corvus splendens*). *J Ornithol* 161:341–350
- Clary, D., & Kelly, D. M. (2016). Graded mirror self-recognition by Clark's nutcrackers. *Scientific Reports*, 6(1), 36459.
- Enoch, J. M. (2006). History of mirrors dating back 8000 years. *Optometry and vision science*, 83(10), 775-781.
- Ersoy, S., Maag, N., Boehly, T., Boucherie, P. H., & Bugnyar, T. (2021). Sex-specific parental care during postfledging in common ravens. *Animal Behaviour*, 181, 95-103.
- Fischer, S., Bessert-Nettelbeck, M., Kotrschal, A., & Taborsky, B. (2015). Rearing-group size determines social competence and brain structure in a cooperatively breeding cichlid. *The American Naturalist*, 186(1), 123-140.
- Fox J, Weisberg S (2019). *_An R Companion to Applied Regression_*, Third edition. Sage, Thousand Oaks CA. <<https://www.john-fox.ca/Companion/>>.
- Gallego-Abenza, M., Boucherie, P. H., & Bugnyar, T. (2022). Early social environment affects attention to social cues in juvenile common ravens, *Corvus corax*. *Royal Society Open Science*, 9(6), 220132.
- Gallup Jr, G. G. (1970). Chimpanzees: self-recognition. *Science*, 167(3914), 86-87.
- Gallup Jr, G. G., & Capper, S. A. (1970). Preference for mirror-image stimulation in finches (*Passer domesticus domesticus*) and parakeets (*Melopsittacus undulatus*). *Animal Behaviour*, 18, 621-624.

- Greenberg, R. & Mettke-Hofmann, C. (2001). Ecological Aspects of Neophobia and Neophilia in Birds. In: Current Ornithology, Vol. 16. Nolan, V. & Thompson, C. F. (eds.), pp. 119–178. Springer, Boston, MA.
- Güntürkün, O., & Bugnyar, T. (2016). Cognition without cortex. Trends in cognitive sciences, 20(4), 291-303.
- Harris, J. D. (1943). Habituated response decrement in the intact organism. Psychological bulletin, 40(6), 385.
- Heinrich, B. (1995). Neophilia and exploration in juvenile common ravens, *Corvus corax*. Animal Behaviour, 50(3), 695-704.
- Heyes, C. M. (1994). Social learning in animals: categories and mechanisms. Biological Reviews, 69(2), 207-231.
- Hughes, R. N. (1997). Intrinsic exploration in animals: motives and measurement. Behavioural Processes, 41(3), 213-226.
- Hughes, R. N. (2007). Neotic preferences in laboratory rodents: issues, assessment and substrates. Neuroscience & Biobehavioral Reviews, 31(3), 441-464.
- Hyatt, C.W. (1998). Responses of gibbons (*Hylobates lar*) to their mirror images. American Journal of Primatology, 45, 307–11
- Keller, H., Ka, J., Borke, J., Yovsi, R., & Kleis, A. (2005). Parenting styles and the development of the categorical self : A longitudinal study on mirror self-recognition in Cameroonian Nso and German families, 29(6), 496–504.
- Kohda, M., Hotta, T., Takeyama, T., Awata, S., Tanaka, H., Asai, J. Y., & Jordan, A. L. (2019). If a fish can pass the mark test, what are the implications for consciousness and self-awareness testing in animals?. PLoS biology, 17(2), e3000021.
- Kraft, F. L., Forštová, T., Utku Urhan, A., Exnerová, A., & Brodin, A. (2017). No evidence for self-recognition in a small passerine, the great tit (*Parus major*) judged from the mark/mirror test. Animal Cognition, 20(6), 1049-1057.
- Lenth, R. (2023). emmeans: Estimated Marginal Means, aka Least-Squares Means_. R package version 1.8. 5.

Lethmate, J., & Dücker, G. (1973). Untersuchungen zum Selbsterkennen im Spiegel bei Orang-Utans und einigen anderen Affenarten 1. Zeitschrift für Tierpsychologie, 33(3-4), 248-269.

Loretto, M. C., Fraser, O. N., & Bugnyar, T. (2012). Ontogeny of social relations and coalition formation in common ravens (*Corvus corax*). International journal of comparative psychology/ISCP; sponsored by the International Society for Comparative Psychology and the University of Calabria, 25(3), 180.

Macri, S., Adriani, W., Chiarotti, F., & Laviola, G. (2002). Risk taking during exploration of a plus-maze is greater in adolescent than in juvenile or adult mice. Animal Behaviour, 64(4), 541-546.

Marino, L. (2002). Convergence of complex cognitive abilities in cetaceans and primates. Brain, behavior and evolution, 59(1-2), 21-32.

Massen, J. J., Szimpl, G., Spreafico, M., & Bugnyar, T. (2014). Ravens intervene in others' bonding attempts. Current Biology, 24(22), 2733-2736.

Miller, R., Bugnyar, T., Pölzl, K., & Schwab, C. (2015). Differences in exploration behaviour in common ravens and carrion crows during development and across social context. Behavioral Ecology and Sociobiology, 69(7), 1209-1220.

Miller, R., Schiestl, M., Whiten, A., Schwab, C., & Bugnyar, T. (2014). Tolerance and social facilitation in the foraging behaviour of free-ranging crows (*Corvus corone corone*; *C. c. cornix*). Ethology, 120(12), 1248-1255.

Plotnik, J. M., De Waal, F. B., & Reiss, D. (2006). Self-recognition in an Asian elephant. Proceedings of the National Academy of Sciences, 103(45), 17053-17057.

Povinelli, D. J., Rulf, A. B., Landau, K. R., & Bierschwale, D. T. (1993). Self-recognition in chimpanzees (*Pan troglodytes*): distribution, ontogeny, and patterns of emergence. Journal of comparative psychology, 107(4), 347.

Priel, B., & de Schonen, S. (1986). Self-recognition: A study of a population without mirrors. Journal of experimental child psychology, 41(2), 237-250.

Prior, H., Schwarz, A., & Güntürkün, O. (2008). Mirror-induced behavior in the magpie (*Pica pica*): evidence of self-recognition. *PLoS biology*, 6(8), e202.

R Core Team (2025). *_R: A Language and Environment for Statistical Computing_*. R Foundation for Statistical Computing, Vienna, Austria. <<https://www.R-project.org/>>.

Range, F., Bugnyar, T., Schölgl, C., & Kotrschal, K. (2006). Individual and sex differences in learning abilities of ravens. *Behavioural processes*, 73(1), 100-106.

Reader, S. M., Kendal, J. R., & Laland, K. N. (2003). Social learning of foraging sites and escape routes in wild Trinidadian guppies. *Animal Behaviour*, 66(4), 729-739.

Reiss, D., & Marino, L. (2001). Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings of the National Academy of Sciences*, 98(10), 5937-5942.

Rochat, P. (2003). Five levels of self-awareness as they unfold early in life. *Consciousness and cognition*, 12(4), 717-731.

Ryan, M. J. (1978). Mirror image versus conspecific stimulation in adult male Zebra Finches. *The Wilson Bulletin*, 90(2), 295-297.

Schaden, G. (1993). Exploration und Neophobie bei Schleiereulen (*Tyto alba guttata*): der Einfluß von Früherfahrung und Vertrautheit. *Egretta*, 36, 67-77.

Schwab, C., Bugnyar, T., Schloegl, C., & Kotrschal, K. (2008). Enhanced social learning between siblings in common ravens, *Corvus corax*. *Animal Behaviour*, 75(2), 501-508.

Shaffer, V. A., & Renner, M. J. (2000). Black-and-white colobus monkeys (*Colobus guereza*) do not show mirror self-recognition. *International Journal of Comparative Psychology*, 13(3).

Soler, M., Pérez-Contreras, T., & Peralta-Sánchez, J. M. (2014). Mirror-mark tests performed on jackdaws reveal potential methodological problems in the use of stickers in avian mark-test studies. *PLoS One*, 9(1), e86193.

Stout, J. F., Wilcox, C. R., & Creitz, L. E. (1969). Aggressive Communication By Lar Us Gla Ucsens Part I. Sound Communication. *Behaviour*, 34(1-2), 29-41.

Stöwe, M., Bugnyar, T., Loretto, M. C., Schloegl, C., Range, F., & Kotrschal, K. (2006). Novel object exploration in ravens (*Corvus corax*): effects of social relationships. *Behavioural processes*, 73(1), 68-75.

Tinbergen, N. (1951). *The study of instinct*. Oxford, U.K.: Oxford University Press.

Vanhooland, L. C., Bugnyar, T., & Massen, J. J. (2020). Crows (*Corvus corone* ssp.) check contingency in a mirror yet fail the mirror-mark test. *Journal of Comparative Psychology*, 134(2), 158.

Vanhooland, L. C., Szabó, A., Bugnyar, T., & Massen, J. J. (2023). A comparative study of mirror self-recognition in three corvid species. *Animal Cognition*, 26(1), 229-248.

Walraven, V., Van Elsacker, L., & Verheyen, R. (1995). Reactions of a group of pygmy chimpanzees (*Pan paniscus*) to their mirror-images: evidence of self-recognition. *Primates*, 36(1), 145-150.

Watanabe, S. (2002). Preference for mirror images and video image in Java sparrows (*Padda oryzivora*). *Behavioural Processes*, 60

Welker, W. I. (1957). "Free" versus "forced" exploration of a novel situation by rats. *Psychological Reports*, 3(1), 95-108.

Wickham, H. (2016). Data analysis. In *ggplot2: elegant graphics for data analysis* (pp. 189-201). Cham: Springer international publishing.

Wild, S., & Hoppitt, W. J. (2018). Social learning. In *Encyclopedia of animal cognition and behavior* (pp. 1-10). Springer, Cham.

Generative AI tools (OpenAI ChatGPT) were used solely to improve phrasing and clarity. All scientific concepts, experimental designs, hypotheses, and project goals were developed by the research team. No synthetic or AI-generated data were included.

Appendix

Table 11 *Ethogram used for coding*

Explorative behaviours	
In front of the apparatus	
Look behind	Bird moves from the front area to the back area of the object (and looks at it)
Look down from top	Bird sits on top of the apparatus and looks down at the surface
Look under	Bird is in front of or behind the apparatus and looks through the gap between the apparatus and the ground
Peek-a-boo	Bird looks repeated in & out of the mirror within 3 to 5 sec.
Jumping Jack	One bird jumps up/back when exploring new environment/object.
Object manipulation	One bird manipulates a non-portable/portable or draggable object in front of the apparatus

Manipulation of the apparatus	
Of the frame	Bird manipulates the frame - pecking, biting, clawing (body contact)
Of the surface	Bird manipulates the surface- pecking, biting, clawing (body contact)

Self-directed behaviours	
Auto-Preening	Bird touches its feathers with its beak
Scratching	Bird scratches any body part with his foot
Shaking	Bird shakes its body
Headshaking	Bird shakes its head
Stretching	Bird stretches its wings/legs in the air
Beak wipe	Bird cleans his beak against something

Social Behaviours Involving Object

Co-manipulate object	Two birds manipulate the same fixed/portable object(s), next to each other (within reaching distance)
Watch ID interact	One bird is in the vicinity of the apparatus and watches another bird interacting with the apparatus
Play	Two birds interact with one another and the apparatus through a wide variety of motor patterns, postures, vocalizations, which do not explicitly express aggressive intentions and appears functionless

Behaviours towards conspecifics

Allo-Preening	One bird touches/runs its beak through the feathers of another bird (for longer than 2 seconds)
Begging	One bird touches another's beak and/or vocalizes with/without wing flapping to request an item
Displace	One bird retreats/moves away in within 1-2s, after another bird enters in its close proximity (from 1m – body contact). With or without vocalization of the emitter/receiver, and with or without physical contact between the two birds.
Supplant	One bird retreats/moves away in within 1-2s, after another bird enters in its close proximity (from 1m – body contact). A conspecific takes the place. With or without vocalization of the emitter/receiver, and with or without physical contact between the two birds.
Peck	One bird pecks another one with its beak. Pecking implies physical contact.
Chase/Charge	One bird pursues / rushes toward another one flying / running
Threat	One bird threatens another one with display “thick head approach” and/or visual threat (the aggressor pecks in the direction of the victim without touching it).
Fight	Two birds hit each other with their feet/beaks, with one/both birds jumping in the air or with one bird down on the ground and one sitting on the top
SAD	Self-assertive-Display, can have many forms

Immobile	The victim of an agonistic interaction /i.e., threat, pack, chase/charge) ignores the behaviour and stays in contact/proximity with its aggressor without reacting.
Retreat	One bird retreats/moves away after receiving an aggression from another bird (i.e., threat, peck, chase/charge), with or without vocalizations.
Submissive Display	One bird protests by posturing after receiving an aggression from another bird (i.e., threat, peck, chase/charge), with or without vocalization.
Avoid	One bird retreats / moves away from an approaching bird before it enters into its contact (approximately before the approaching bird is less 1m away)

Apparatus-directed social behaviours

Threat	One bird threatens the mirror with display "thick head approach" and/or visual threat (the aggressor pecks in the direction of the victim without touching it).
Attack	One bird attacks the mirror with its feet/beak, probably jumping in the air.
SAD	Self-assertive-Display, can have many forms
Submissive Display	One bird protests by posturing after receiving an aggression from another bird (i.e., threat, peck, chase/charge), with or without vocalization.
Vocalizations	
Loud call	e.g. long distance call
Soft call	e.g. grunt, babbling, play call, food/begging, "ha"