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Ontogeny, Sociality & Preferences

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Introduction

At first glance, the concept of play seems to be rather intuitive to us humans, as probably most of us are able to recognize playful behaviour in our conspecifics. It is commonly referred to as simply 'having fun' or to 'not take things too seriously', and is sometimes even accompanied with a somewhat negative connotation for being 'the opposite of work' (Bateson, 2014). However, provided that other animals also show extensive play behaviour, this raises suspicions that there might be a lot more to it than initially assumed. But before addressing the concept of play directly, it is crucial to understand the fundamentals of another important behaviour inseparably associated with play: exploration. This derives from the assumption that play basically builds upon the motivations and proximate mechanisms of exploratory behaviours, as play usually incorporates exploration (Pellis & Burghardt, 2017).

It is widely accepted that exploratory behaviour primarily serves the gathering and basic processing of information about a subject's diverse environment and the resulting acquisition of novel skills to effectively exploit it (Mettke-Hofmann et al., 2002; Reader & Laland, 2003; Kendal et al., 2005; Miller et al., 2015). Whilst an animal's underlying motive to explore does not derive from the goal to satisfy any urgent physiological needs, it seems that the main driving force stems from an intrinsic motivation to actively search and investigate novelty in its surroundings (Immelmann & Beer, 1989; Greenberg & Mettke-Hofmann, 2001; Mettke-Hofmann et al., 2002; O'Hara & Auersperg, 2017). The subsequent interaction with the unknown then leads to a habituation process resulting in a shift from novelty towards familiarity, as a consequence of associative and latent learning (Thorpe, 1956; Renner, 1988; Greenberg & Hofmann, 2001). Subconscious and intrinsically motivated forms of knowledge acquisition, such as latent learning, could potentially play an important role in young individuals in particular. Oftentimes, juveniles show pronounced exploration behaviour at specific sensitive ages. This is supported by various findings addressing more extensive exploratory behaviours shown by young individuals of different primate species when compared to their adult conspecifics (see Miller et al., 2015 for an overview). But the picture is neither that clear, nor universal it seems, since Kendal et al. (2005) also found a positive correlation between age and exploratory behaviour in callitrichid monkeys (Callitrichidae), as a contrasting example.

Another study revealed that the propensity for exploratory behaviour can be highly affected by a species' preference for specific ecological factors, such as habitat and diet complexity, as observed in several parrot species (Psittacidae) (Mettke-Hofmann et al., 2002). Accordingly, it is argued that the early and efficient acquisition of exploitative skills seems to be of particular importance to the young of dispersing species and feeding generalist utilizing wide ranges of varying and moderately changing habitats, as common in several corvid species, like carrion crows (*Corvus corone*), common ravens (*Corvus corax*), or the Australian Magpie (*Gymnorhina tibicen*) (Pellis, 1981; Goodwin, 1986; Heinrich, 1995; Winkler & Leisler, 1999; Mettke-Hofmann et al., 2002; Reader & Laland, 2003). Such skills may be developed based on information about the distribution and quality of food, the existence of potential predators and mating partners, or territory availability and its possible defence, aiming to increase one's general flexibility.

However, the actual exploratory interaction of an individual with its environment is additionally modulated by its species-specific personality traits, such as neophobia and neophilia. Neophobia can be summarized as the general initial fearful response and sceptical attitude towards novel objects, often resulting in increased hesitance to approach, or even in complete avoidance. In contrast, neophilia describes the exact opposite behavioural tendency (Greenberg & Mettke-Hofmann, 2001). In corvids for instance, this is of particular interest, as in principle, they are both neophilic and neophobic at the same time (Heinrich, 1995; Greenberg & Mettke-Hofmann, 2001). Based on previous studies, there is broad consensus on its ultimate functions. Since quality and quantity of exploration seemingly stand in direct association with an individual's ecological factors, neophobia and neophilia can be seen as flexible adaptations to environmental changes. This serves the avoidance of high risks and negative trade-offs in unknown territory, without missing valuable opportunities (Greenberg, 1990a & 1990b; Greenberg & Mettke-Hofmann, 2001). These highly flexible adaptations not only lead to differences between species, but also within species. This relates to age and ontogenetic effects in particular, with juveniles usually being bolder and more strongly attracted to novel objects, and generally more playful compared to their older conspecifics (Ortega & Bekoff, 1987; Heinrich, 1988; Heinrich, 1995; Miller et al., 2015). Conclusively, it can be stated that the complexity of the ecological environment forms the basic framework in which various exploratory behavioural outputs can occur.

Driven by variable innate curiosity, highly adaptive exploration behaviour then leads to the successful acquisition of adequate exploitative skills, that directly benefit the chances of survival.

The resulting fitness consequences of explorative behaviours highlight their general importance, thus raising the question of the specific connection between exploration and play. Especially the added value of the latter is of particular interest, given the fact that playful behaviour is based upon the principles of exploration. One might argue that any gathered information, e.g., about the basic physical properties of a novel object via exploratory behaviour, is simply motivated by an individual's intrinsic drive to familiarize with its functional characteristics (Mettke-Hofmann et al., 2002). Building on this, play extends beyond and additionally serves as a potential enhancer of learning processes and enforces the acquisition of explicit knowledge about how to creatively use an individual's surroundings, like the creative manipulation of specific objects (Bjorklund & Gardiner, 2010; Auersperg, 2015; O'Hara & Auersperg, 2017). In order to ensure a conceptual distinction between exploration and play, it is necessary to determine the diverging features of playful behaviour. To do so, Gordon Burghardt (2005) proposed five criteria to define play, which have to be fulfilled simultaneously to accurately identify playful behaviour (see also Bateson, 2014 and O'Hara & Auersperg, 2017). In a nutshell, play is an [1] intrinsically motivated [2] generator of novelty [3] without an immediate goal or benefit, [4] performed repeatedly and voluntarily [5] by healthy individuals under relaxed conditions. Furthermore, play has to be carried out in an obvious positive mood and has 'to be fun', to be considered as playful per se. This last criterion is certainly difficult to assess across most species not using human language. Therefore, the majority of scientific studies on play primarily relate to the first five play defining criteria.

It is possible to distinguish between three main types of play, which imply different behavioural components: social play, locomotor-rotational play and object play (Ficken, 1977; Fagen, 1981; Bekoff & Byers, 1981; Ortega & Bekoff, 1987; Burghardt, 1998; Burghardt, 2005; Bateson, 2014; O'Hara & Auersperg, 2017). Firstly, social play is usually performed by two or more individuals of the same species in a safe space, and it describes the playful interaction over behaviours being typically shown in other social contexts, such as mating and predation, cooperative and competitive behaviour, or personal and territory defence, while fulfilling the above stated criteria (Bekoff, 2001). This form of play

is considered being linked to the acquisition of basic social skills in a species' social system. It allows notably young individuals to learn how to interact adequately with others without the potential risks and consequences associated with social contexts, e.g., competition and aggression (Bekoff, 2001). Secondly, while performing locomotor play, an individual is, in principle, independent of the involvement of external variables, such as interaction partners in a social context or the manipulation of specific objects. This type of play is centred around repetitive actions exclusively performed with an animal's own body (Burghardt, 1998). This involves all possible forms of locomotion physically available to an individual performed under the provisions of the play concept (Ortega & Bekoff, 1987). It is argued that this type of play could benefit the acquisition and training of physical abilities, such as basic motor skills, coordination, and overall dexterity (O'Hara & Auersperg, 2017). Finally, object play comprises all physical manipulations directed towards an inanimate object, performed by an individual whilst in a play situation (Bekoff & Byers, 1981). It is possible to distinguish between primary and secondary manipulations, representing two different levels of complexity (Torigoe, 1985). Whereas, primary manipulations represent the basic physical use of an object (e.g., holding, dropping), secondary manipulations describe more creative interactions by sensibly combining it with its environment and/or other objects. Such manipulations are very common in tool-using species, like primates (see O'Hara & Auersperg, 2017 for an overview), or New Caledonian crows (*Corvus moneduloides*) (Kenward et al., 2011).

Usually, playful behaviours are exclusively shown in one of the above-mentioned categories. However, their boundaries can be somewhat blurry in species with higher cognitive skills. This relates to the tendency that play might actually become more diverse in animals that are socially more complex and express advanced cognitive abilities (Bateson, 2014). In these species, the demonstration of playful behaviour might also become increasingly independent from the type of play or the context. Corroborating this, in bottlenose dolphins (*Tursiops truncatus*), juveniles can show more than thirty different play patterns (Kuczaj et al., 2006). In chimpanzees (*Pan troglodytes*), Kahlenberg & Wrangham (2010) described a special form of pretend play of sub-adult females, during which sticks or other pieces of wood are cradled and cared for as if it is their actual offspring. Compatible with this, Smith (2010) investigated the sophisticated role-playing abilities of young humans by the use of spoken language. In these three

mammalian species, the incidence and complexity of play is considered to be associated with the relative size of their cerebral cortex, additionally supporting the assumed connection between play and cognition (Fagen, 1981). However, this relation needs to be further examined, particularly in non-mammalian species equally displaying complex social systems and high cognitive abilities, following a comparative approach.

In birds, the common raven (*Corvus corax*) is a well-fitting representative to investigate playful behaviour and its development, as this species generally meets all stated requirements. Ravens are known to be socially complex animals inhabiting very broad and diverse habitats as feeding generalist (Goodwin, 1986; Heinrich, 1989 & 1995). They form long-term monogamous pair bonds and their social structure is organised by affiliative relationships and a steep hierarchy dominated by adults and males (Boucherie et al., 2022). They possess relatively large, cognitively high-functioning brains, allowing them to execute sophisticated forms of learning (Stettner, 1974; Emery & Clayton, 2015), and fulfilling the basic physical requirements for exploratory behaviour and play (Ortega & Bekoff, 1987). Along with the majority of other avian species, ravens show each of the above mentioned three categories of play due to their broad behavioural repertoire (Ficken, 1977). Especially object play is exceptionally widespread amongst corvid species, supposedly due to their strong reliance on visual cues for orientation (Ficken, 1977; Ortega & Bekoff, 1987; Heinrich, 1995), whilst in direct association with their respective feeding ecology (O'Hara & Auersperg, 2017). When investigating the quantitative occurrence of locomotor and social play in birds, Ortega & Bekoff (1987) revealed a difference in general propensity to either engage in one or the other, depending on the degree of autonomy of a species' offspring. They proposed that avian species raising altricial young tend to display higher amounts of social play, whereas, the results showed the exact opposite for species with precocial offspring, as they predominantly performed locomotor play. According to this, in ravens, who are altricial and show extensive parental care, social play should be equally predominant as object play. Based on these assumptions, the specific expressions of object play and its respective social components are of high interest.

It is known that, in corvids, a prevalent form of object play is the caching of inedible objects (Heinrich & Smolker, 1998; Burghardt, 2005; Jacobs et al., 2014). Here, the properties of preferred items vary across species, as some primarily cache objects that

resemble physical features of their food (Clayton, 1993 & 1994), whereas others are attracted to the general novelty of an object, as frequently seen in common ravens (Heinrich, 1995; Bugnyar et al., 2007b; Jacobs et al., 2014). Though, in addition to the acquisition of exploitative skills, object play and play caching seem to take major roles in social contexts too. It can notably be used for the formation and maintenance of social relationships and as information-gathering in competitive settings (Bekoff, 1984; Stöwe et al., 2006; von Bayern et al., 2007; Bugnyar et al., 2007a; Pika & Bugnyar, 2011). In turn, the social context can also influence exploration and play behaviour. For instance, Miller et al. (2015) revealed a positive correlation between the propensity to explore novel objects and the presence of conspecifics in juvenile common ravens and carrion crows (*Corvus corone*, *Corvus cornix*). Additionally, not only the presence but also the identity of the bystander may play a role, notably its status, rank, dominance and general affiliative relationship to the potential explorer (Stöwe et al., 2006). In common ravens, it was shown that individuals prefer to cooperate with their affiliates (Asakawa-Haas et al., 2016), especially in situations where close proximities between actors are crucial and unavoidable (Boucherie et al., 2019), as tolerating others within a subject's personal space plays an important role in pair-bonding processes (Fraser & Bugnyar, 2010; Bugnyar, 2013). Such interactions in close proximity are also assumed to enhance social learning (Coussi-Korbel & Frigaszy, 1995). Interestingly, since ravens seemingly prefer to interact with novel objects while in presence of an affiliate conspecific, like a sibling, which results in a quantitative enhancement of exploratory behaviour, the latencies to approach the novel objects also tend to increase (Stöwe et al., 2006). This might be due to synchronization processes among the interacting individuals, referred to as 'socially-induced neophobia' (Miller et al., 2015). Here, emotional contagion between interaction partners could play an important role to facilitate the within-group synchronization in terms of explorative behaviour (Osvath & Sima, 2014). Conclusively, it can be stated that the presence of affiliates either enhances explorative behaviour and associated learning processes in particular ways, as seen in common ravens (Stöwe et al., 2006; Schwab et al., 2008; Bugnyar, 2013), or it may entail the exact opposite effect, like in other bird species (Coleman & Mellgren, 1994; Mainwaring et al., 2011). Therefore, the species-specific characteristics of the social system (Miller et al., 2015) and concluding adaptations to the ecological environment (Coleman & Mellgren, 1994) must certainly be beared in mind

when investigating play behaviour. Here, it is further important to examine its ontogeny, to better understand the adaptive values at various life-stages and age-related changes in explorative behaviour. This is contextually associated with the exceptional combinatory variations of neophobic and neophilic tendencies in corvid species. Unfortunately, holistic scientific work on this is quite scarce, especially in terms of developmental processes.

Generally, in common ravens, the quantity of play is considered being negatively correlated with age. The amount of playful behaviour will usually strongly decline at the onset of sub-adulthood, while accompanied with increasing levels of neophobia (Heinrich, 1995; Greenberg & Mettke-Hofmann, 2001; Miller et al., 2015; O'Hara & Auersperg, 2017). Though, before becoming around six months old, object play tends to drastically increase with age, in juvenile ravens (Heinrich, 1995; Jacobs et al., 2014). The development of individual cognitive competences is assumed to directly affect the propensity of playful behaviour and the predominance of a certain type of play, as briefly mentioned before. For instance, object play and in particular caching seem to be directly associated with the acquisition of object permanence within the first few months of life (Pollok et al., 2000; Bugnyar et al., 2007a). Thus, it is essential to consider age and individual development when studying play. In summary, all of the above-mentioned behaviours and their continuous adjustments can be understood as essential learning tools to acquire and develop crucial skills that are necessary for sub-adult ravens when dispersing into the wild. Specifically, this involves variations in exploration, changes in object play complexity and its social components, as well as adaptations in behavioural synchronization and cooperation. To better understand each of these processes and how they variably interact in the play context, it seems reasonable to establish a longitudinal scientific approach.

Therefore, this study aims to provide further insight into the ontogeny of object play and its exploratory fundamentals, in consideration of the varying social context in which it occurs and its reactional impact in juvenile ravens. To do so, I investigate the development of object play behaviour in an experimental setting, in the early life phases of juvenile ravens. I also examine the potential prevalence of novel object preferences, and adaptations in social interactions while expressing object play. In order to assess varying age differences in play behaviour at specific times during development, collected data is additionally compared between juveniles and their adult conspecifics.

Methodologically, this is realized by repeatedly providing familiar as well as novel inedible objects to raven families during defined periods within a seven-week time frame. Participating families respectively consist of an adult breeding pair with one to three chicks each. The test subjects are able to freely interact with the objects and spontaneously express exploratory and play behaviour. Shown behaviours of interest, such as frequencies and latencies of object approaches, as well as numbers and durations of (social) object play, are scored on an individual basis. The statistical analyses follow a within-subjects, as well as a between-subjects design, to investigate development effects and differences between adults and juveniles at given times. According to this and based on the presented findings of preceding scientific work, this study's hypotheses and their respective predictions read as follows.

Hypotheses

- I. There will be ontogenetic effects on the number of initial approaches for the test objects and their respective latencies in juvenile ravens.
- II. The individual's age will affect the duration of object play behaviour.
- III. The novelty of an object will determine the individual's propensity to interact with it.
- IV. The individual's motivation to engage in social object play will underly ontogenetic effects.

Predictions

- I. The number as well as the latencies of initial approaches for the playground will increase in juvenile ravens throughout this experiment.
- II. Juvenile ravens will show an increasing duration of object play over time.
- III. Ravens of both age groups will generally prefer to interact with novel objects over the familiar ones.
- IV. The quantity of social object play will increase in juvenile ravens throughout this experiment, whereas, there will be no such effect in adult birds.

Methods

Subjects & Housing

The experiment was conducted on six common raven families between May 2019 and July 2019. Individual families were composed of three to five subjects each (parents and chicks). In total, I thus worked with 26 subjects including 12 adults and 14 post fledged chicks (Tab. 1). All ravens were individually identifiable by color-coded rings around one of their legs. Males ($n = 12$) and females ($n = 14$) were almost evenly distributed among the experimental group (Tab. 1). Adult birds were over three years old and already experienced with raising offspring. Juvenile ravens' age ranged from about six to eight weeks in the beginning of the experiment, to around 13 to 15 weeks at the end.

The six raven families were held in captivity in large outdoor aviaries separately at three different locations in Austria: The Haidlhof Research Station, Bad Vöslau, Lower Austria, the Tiergarten Schönbrunn in Vienna, and the Konrad Lorenz Research Station (KLF) in Grünau (Tab. 1). Size and vegetation of the respective aviaries varied depending

on their location. The two enclosures at Haidlhof Research Station were about 12 x 7 x 5 m (length-width-height) in size each, the one at Tiergarten Schönbrunn was even bigger with more vegetation, whereas, the aviaries at KLF were more rounded in shape and partly higher. Regardless of such variations, all aviaries provided enough space for proper flying in all directions, they were equipped with numerous perching possibilities at different heights and diverse substrate on the ground, like soil, gravel and bark. In general, all aviaries fulfilled highest housing conditions for ravens. For the duration of this experiment, birds were fed a balanced diet twice a day and they had ad libitum access to water. All ravens participated on a voluntary basis, since they always had the possibility to withdraw into their nest or the roofed experimental compartment, or to just simply ignore the provided objects. The birds' health status was checked regularly by the professional staff on site and veterinary care was provided at any times needed.

Table 1. Composition of the experimental group on which this study was conducted (n = 26), divided into adult and juvenile *C. corax*. The housing locations of the families and individuals' sexes are given in brackets respectively (f – female, m – male).

Family	Adults (n = 12)	Juveniles (n = 14)
NG (Haidlhof)	Nobel (f) – George (m)	Hickory (f) – Hazel (f)
JR (Haidlhof)	Joey (f) – Rocky (m)	Hamlet (m) – Othello (m) – Juliet (f)
HT (KLF)	Heidi (f) – Tom (m)	Cleo (f) – Genghis (m) – Xerxes (m)
ML (KLF)	Matte (f) – Lellan (m)	Ganymed (f) – Io (f) – Kallisto (m)
MA (KLF)	Martha (f) – Arthus (m)	Summer (f) – Winter (f)
MR (Schönbrunn)	Munia (f) – Rufus (m)	Toma (m)

Time Schedule

Data were collected throughout a seven-week time frame, composed of one week of testing followed by a two-weeks break. This block was repeated three times over the seven-week period to investigate development effects. Additionally, a three-days habituation phase was carried out right before starting the first experimental week to let the ravens get used to the provided material and the observation process (Fig. 1). Within each of the testing week, the experimental procedure was conducted on every raven family twice a day – once in the morning and once in the afternoon – for a period of four consecutive days, resulting in 48 trials per week, or 144 in total for all 12 testing days. The experimental conditions were predefined and equal for all families.

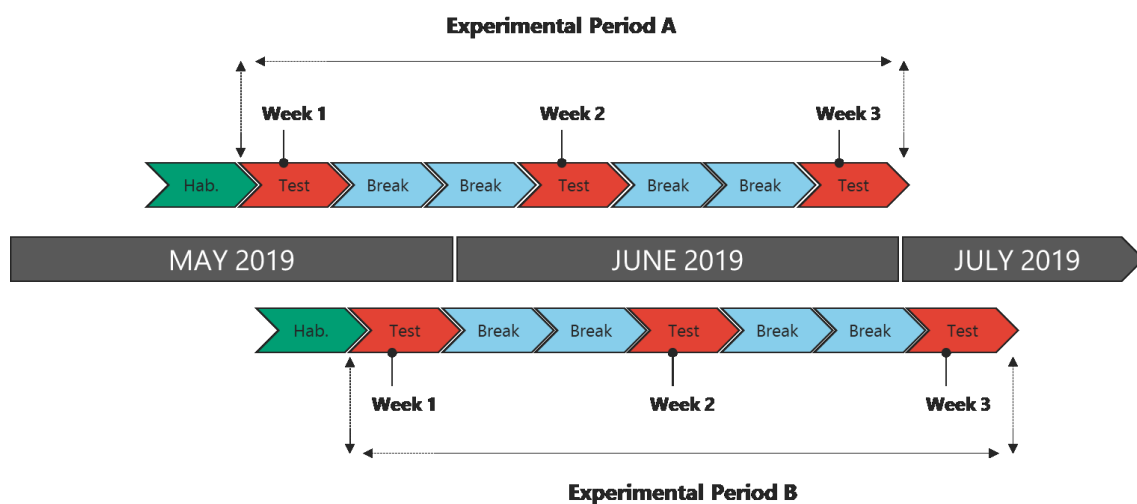


Figure 1. Time line of the experimental procedure. Each coloured section represents a one-week time frame of either habituation (Hab. – blueish green), testing (Test – vermilion), or pausing (Break – sky blue). Week 1, 2 and 3 mark the chronological order of test phases, which are important in relation to the investigation of potential developmental effects. Experimental Period A represents the time frame for the following raven families: NG, JR, HT and ML. The beginning of Experimental Period B was postponed for one week and applied to the families MA and MR.

Material

Boards & Objects

To experimentally elicit object manipulations and (social) object play, families were provided with a 'playground' at the beginning of each trial. The playground was composed of two handcrafted wooden boards with attached coloured objects. The boards were about 40 x 15 x 3 cm (length-width-height) in size. The wooden objects were attached in two different ways, either irremovably by fixing them with blunt screws, or by loosely plugging them onto wooden pins so that they could be removed and carried away by the test subjects. The number of objects on each board matched the number of ravens within each family. For odd-numbered groups, movable objects outmatched the fixed ones by +1. The attached objects were painted in the following non-poisonous, harmless (DIN EN 71-3 certified) colours: dark green, white, yellow, transparent, brown, red, pink, violet, blue and light green. The shapes of the test objects varied between balls, cubes, t-shapes and pyramids, however, their size was roughly the same with about 4 x 4 cm, or 4 cm in diameter respectively (Fig. 2).

Familiar vs. Novel Boards

Every trial started with the provision of the playground. During the pre-experimental habituation phase, and all subsequent experimental trials one board with dark green balls was provided to the families, henceforth referred to as the familiar board/objects. On the second board (novel), the test objects were changed every day. Each type of novel board was thus presented twice per family throughout this study. Boards did not differ with regard to the movability of attached objects, or their respective numbers. The novel object introduced each day was the same for all families (Fig. 2).

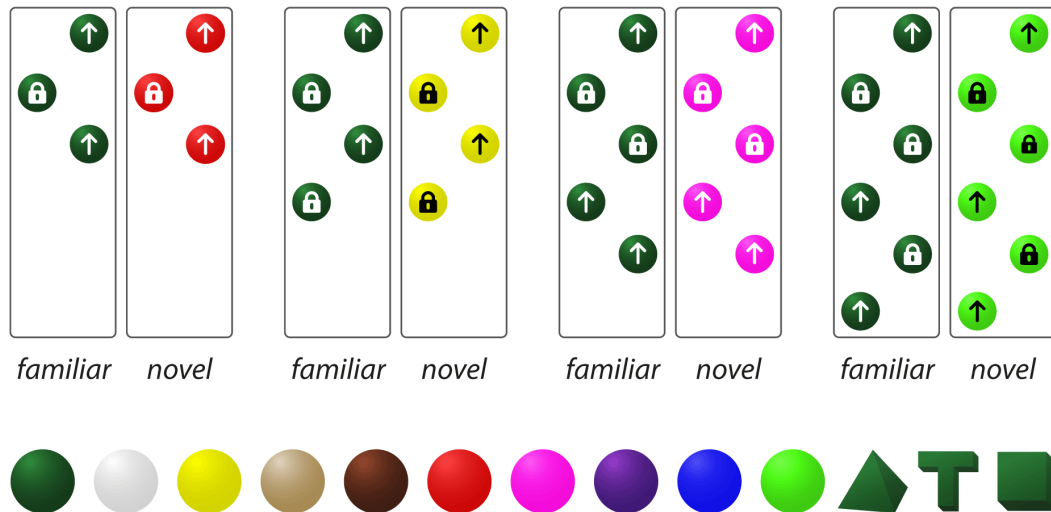


Figure 2. Schematic representation of the test material, which comprised familiar and novel objects, as well as their associated boards. Basic features of novel boards, like number and movability of objects, mirrored those of the familiar ones. The number of objects attached to the boards always matched the number of members in the respective raven family (see examples for group sizes of 3, 4, 5 and 6 individuals). The movability of objects is indicated either by an arrow (detachable) or a lock (fixed). The balancing of movable vs. fixed objects followed the formula $(n + 1) / 2$ in favour of the movable ones. Below the schematic representation of familiar and novel boards, the whole palette of used objects is given. Familiar boards were always composed of dark green balls, therefore, novel objects differed either in colour, or in shape.

Observation & Data Collection

Every experimental trial started with a 15-minutes baseline during which no objects were provided to the ravens, to collect behavioural data under neutral conditions. Afterwards, the 15-minutes test phase was initiated by the introduction of the playground (the familiar and the daily novel board) to the birds in a standardized way. The boards were put down flat on the ground, parallel to each other with a distance of about 50 cm between them. Every aviary had a given spot for the deposition of the boards to avoid any position related biases between trials. The midpoint of both boards now defined the centre of the playground, which again was divided into two respective zones. Playground zone 1 comprised a circular region of one meter in diameter around the boards, whereas,

playground zone 2 was defined by an area with a diameter of three meters around the boards' midpoint (Fig. 3). Ravens were free to interact with the material. At the end of each testing period, the boards as well as the objects were removed from the aviary again to avoid any unwanted habituation effects.

Both phases were videotaped using either one or two camcorders simultaneously (Canon Legria HF G25, 720p, 60 fps). For baseline recordings, only one camera was used to maintain a global shot of the aviary by using an as wide as possible viewing angle (Global camera). In addition to the global cam, a second camcorder was installed for the test recordings focussing on the boards whilst capturing the whole playground area at the same time (Focal camera) (Fig. 3). In addition to the visual data being collected this way, the respective trials were accompanied by live commentary in relation to various events, such as positioning of individuals at the playground, changes in proximities, quantity and quality of object manipulation, or prosocial and agonistic behaviour. After finishing data collection, global and focal recordings of the respective test phase as well as the audio file with the live commentary were put together using DaVinci Resolve 16 by Blackmagic Design, creating a single 15-minutes multiple-view video for each experimental trial. These multiple-view videos served as a basis for subsequent behaviour analyses.

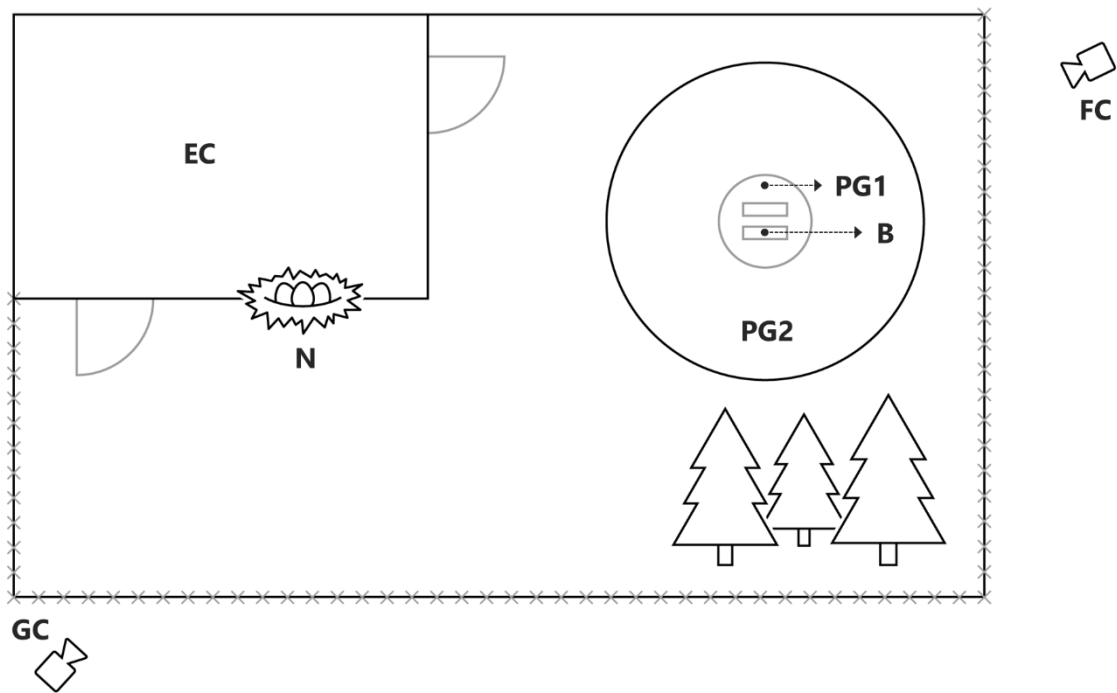


Figure 3. Schematic representation of the experimental set-up for the aviary of the raven family NG at Haidlhof Research Station to record (social) object play and object approaching behaviour in *C. corax*. B – Boards, EC – Experimental compartment, FC – Focal camera, GC – Global camera, N – Nest, PG1 – Playground zone 1, PG2 – Playground zone 2.

Behaviour Analyses

All multiple-view video material was coded using the quantitative video analysis tool Loopy (loopbio gmbh, Vienna, Austria). After defining the ravens' behaviours of interest in an ethogram created exclusively for this study, respective behavioural outputs within the playground area were coded and scored for each individual.

During scoring, the focus was on the following behaviours: Number of initial playground approaches and approach latencies, durations of object play in total and considered individually for familiar and novel objects, as well as number and duration of social object play behaviours. An initial playground approach was fulfilled, as soon as the overall first contact of an individual with the provided material took place during a single test trial. Therefore, only one initial approach was possible per experimental conduction. Approach latencies were defined as the time between the onset of the experimental trial and the first contact of the respective individual with the test material. Object play was

specified as target-oriented physical manipulation of the test material, which comprised the provided familiar and novel objects as well as the associated boards. Social object play was based on the requirements for object play behaviour, but with the addition that manipulations were performed in proximity to at least one other conspecific (70 cm or closer) (see Tab. 3 in appendix for detailed information).

Statistics

Mean scores were calculated for the introduced behavioural response variables of each individual for the three testing weeks separately. Shapiro-Wilk and Levene's-tests were conducted to test the data for normal distribution and homoscedasticity respectively. None of the results revealed normally distributed data in the first place, therefore, non-parametric tests in the form of Generalized Linear Mixed Models (GLMM) were applied – with one exception. In addition to Shapiro-Wilk tests, Kolmogorov-Smirnov tests were modelled, and the dataset was graphically analysed in relation to specific distributions of the data, like gamma, Weibull, Poisson, or log-normal. The results showed a log-normal distribution of social object play durations, which lead to a logarithmic transformation and a subsequent application of a Linear Mixed Model (LMM), since these data followed a normal distribution after treatment. In both cases, predictor variables comprised data referring to test week, age group or object quality. Linear models were conducted following a between-subjects as well as a within-subjects design, to reveal potential group differences and development effects. Every model comprised subject as a random factor and trials were nested within fixed effects, or predictor variables respectively. Best fitting models were selected by comparing Akaike information criteria (AIC). In case linear models showed significant results, Holm-Bonferroni corrected multiple comparisons in the form of Z-tests or T-tests respectively were applied as post-hoc tests, to reveal significant differences at group levels. All statistical analyses were modelled and calculated using RStudio, PBC, Version 1.4.1106. All reported p-values are two-tailed, with α set to 0.05.

Results

Descriptive Statistics

Approaching the Playground

At least one member of the adult and juvenile classes approached the playground every testing week (eight test sessions). The overall number of initial approaches per bird ranged from none to seven in a one-week time frame. The longitudinal observations revealed no case, in which each and every tested subject initially approached the playground within a single testing week. The number of initial approaches peaked in the third week of the experiment for juveniles, with a total of nine individuals (64 %) interacting with the playground first, and in the second week for adults. Here, ten individuals showed an initial approach for the playground, meaning that 83 % of all adults went for the testing material first at least once. (Tab. 2).

In adults, a mean approach latency of 212 seconds (180–229) was measured for the three weeks of testing. In comparison, juveniles showed a mean latency of 227 seconds (154–291). The highest numbers of individuals interacting with the playground were observed in the second and the third week of testing. All adult ravens interacted with the testing material in the second week. Similarly, all juveniles approached the playground in the second and third week, at least once (Tab. 2).

Object Play

On average, adult ravens spent 324 seconds (251–445) interacting with the test material per testing week, whereas, juvenile birds spent 419 seconds (260–640). During the second week only, all of the test subjects manipulated the provided objects (Tab. 2), meaning that individuals did not systematically interact with the playground.

Adults manipulated the familiar objects for 99 seconds (75–112) on average, and spent 225 seconds (141–333) interacting with the novel objects. In comparison, juveniles' mean interaction time was 150 seconds (114–198) manipulating the familiar objects, and

280 seconds (145–467) interacting with the novel objects. In week two, all adults interacted with both the novel and the familiar objects, whereas, only novel objects were manipulated by all of the juveniles on that week (Tab. 2).

Social Object Play (SOP)

The average number of SOP interactions was 7 (5–9) in adults, and 15 (10–25) in juveniles per testing week. Like for object play, the highest frequencies of SOP were observed in the second week for both adults and juveniles. In this week all subjects engaged in SOP at least once. The highest frequency of SOP was shown by a juvenile in week three, with a total number of 63 events (Tab. 2).

Adults engaged in SOP for 89 seconds (75–98) on average per testing week. In comparison, juvenile birds spent a mean time of 215 seconds (110–311) manipulating the test objects (Tab. 2).

Table 2. Mean ($\pm$ S.E.) number of initial approaches for the playground and average approach latencies per trial, mean overall object play duration and a division into manipulation times of familiar and novel objects respectively, as well as mean number and duration of social object play interactions for the three weeks of testing among adult and juvenile *C. corax*. The range is given in brackets. Statistically significant differences are highlighted by an asterisk. The second value in brackets shows the number of behaviour-performing individuals.

Variable	Adult			Juvenile		
	Week 1	Week 2	Week 3	Week 1	Week 2	Week 3
Initial Approaches *	3 $\pm$ 0.75 (0–7; 8)	2 $\pm$ 0.55 (0–5; 10)	1 $\pm$ 0.23 (0–2; 5)	0 $\pm$ 0.10 (0–1; 2)	1 $\pm$ 0.44 (0–6; 7)	2 $\pm$ 0.62 (0–6; 9)
Approach Latency (sec) *	180 $\pm$ 25 (1–693; 10)	228 $\pm$ 31 (2–889; 12)	229 $\pm$ 39 (5–879; 11)	291 $\pm$ 62 (2–898; 7)	235 $\pm$ 29 (8–866; 14)	154 $\pm$ 24 (5–886; 14)
Object Play: Overall Duration (sec) *	445 $\pm$ 109 (122–1124; 9)	251 $\pm$ 42 (58–517; 12)	276 $\pm$ 125 (5–804; 6)	260 $\pm$ 151 (5–800; 5)	357 $\pm$ 103 (12–1542; 14)	640 $\pm$ 216 (9–1442; 8)
Object Play: Familiar Duration (sec) *	112 $\pm$ 36 (16–330; 9)	110 $\pm$ 27 (4–279; 12)	75 $\pm$ 40 (2–261; 6)	114 $\pm$ 64 (3–332; 5)	138 $\pm$ 37 (32–510; 13)	198 $\pm$ 59 (2–379; 7)
Object Play: Novel Duration (sec) *	333 $\pm$ 77 (106–795; 9)	141 $\pm$ 20 (50–239; 12)	201 $\pm$ 89 (1–542; 6)	145 $\pm$ 87 (2–468; 5)	229 $\pm$ 69 (12–1031; 14)	467 $\pm$ 169 (9–1175; 8)
Social Object Play: Interactions *	5 $\pm$ 1.50 (0–11; 7)	7 $\pm$ 0.79 (3–14; 12)	9 $\pm$ 4.65 (0–27; 4)	10 $\pm$ 5.19 (0–23; 3)	10 $\pm$ 1.62 (1–21; 14)	25 $\pm$ 8.14 (0–63; 8)
Social Object Play: Duration (sec)	95 $\pm$ 31 (2–213; 7)	75 $\pm$ 17 (8–192; 12)	98 $\pm$ 43 (5–208; 4)	224 $\pm$ 105 (20–368; 3)	110 $\pm$ 20 (11–234; 14)	311 $\pm$ 128 (8–961; 8)

Inferential Statistical Analyses

Effect of Development on Object-Approaching Behaviour

The analyses of the number of initial approaches for the playground revealed a significant effect of age and week number (development effect; Wald Chi-Squared Test: $\chi^2(2, N = 26) = 26.35, p < 0.001$), with adults showing significantly more initial approaches than juveniles in the first week of testing, but juveniles performing significantly higher numbers than adults on the third week (Adult 1 – Juvenile 1: Z-Test, $z(25) = 3.26, p = 0.015$; Adult 3 – Juvenile 3: Z-Test, $z(25) = -2.75, p = 0.048$). Over time, adults showed a significant decrease in the number of initial playground approaches from the second to the third testing week (Adult 2 – Adult 3: Z-Test, $z(25) = 2.91, p = 0.041$). In contrast, juveniles significantly increased the number of their initial approaches within the same time frame (Juvenile 2 – Juvenile 3: Z-Test, $z(25) = -2.79, p = 0.047$) (Fig. 4).

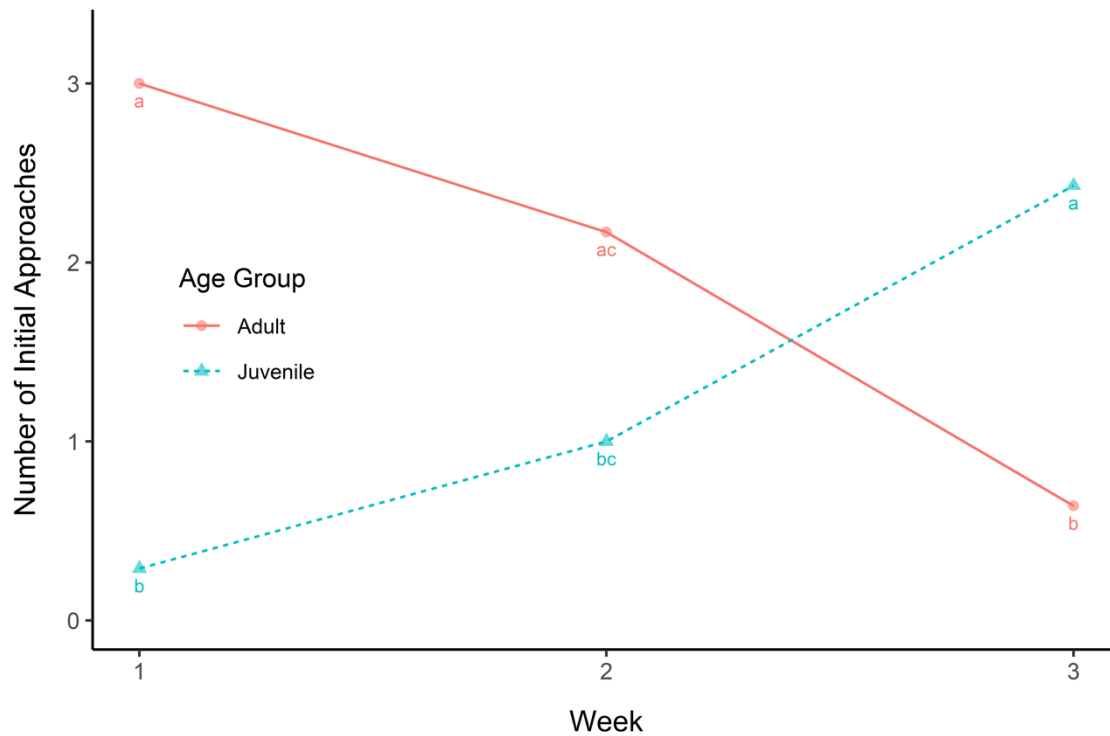


Figure 4. Mean number of initial playground approaches for the three testing weeks among adult and juvenile ravens shown in a multiple regression model. Significant differences between and within subjects are indicated by different letters respectively. The regression lines' deviation from their horizontal parallelism indicate potential interaction effects, describing the relationship between the timepoint of testing and the mean number of initial playground approaches per individual depending on its age.

The statistical analyses of approach latencies also revealed a significant development effect of week number (Wald Chi-Squared Test: $\chi^2(2, N = 26) = 14.36, p < 0.001$). From week two to week three, latencies to approach the objects significantly decreased in juveniles (Juvenile 2 – Juvenile 3: Z-Test, $z(25) = 3.20, p = 0.019$), whereas, there were no significant differences between age groups. Also, approach latencies remained somewhat stable between 180 and 229 seconds in the adult ravens' group and revealed no effect of time (Fig. 5).

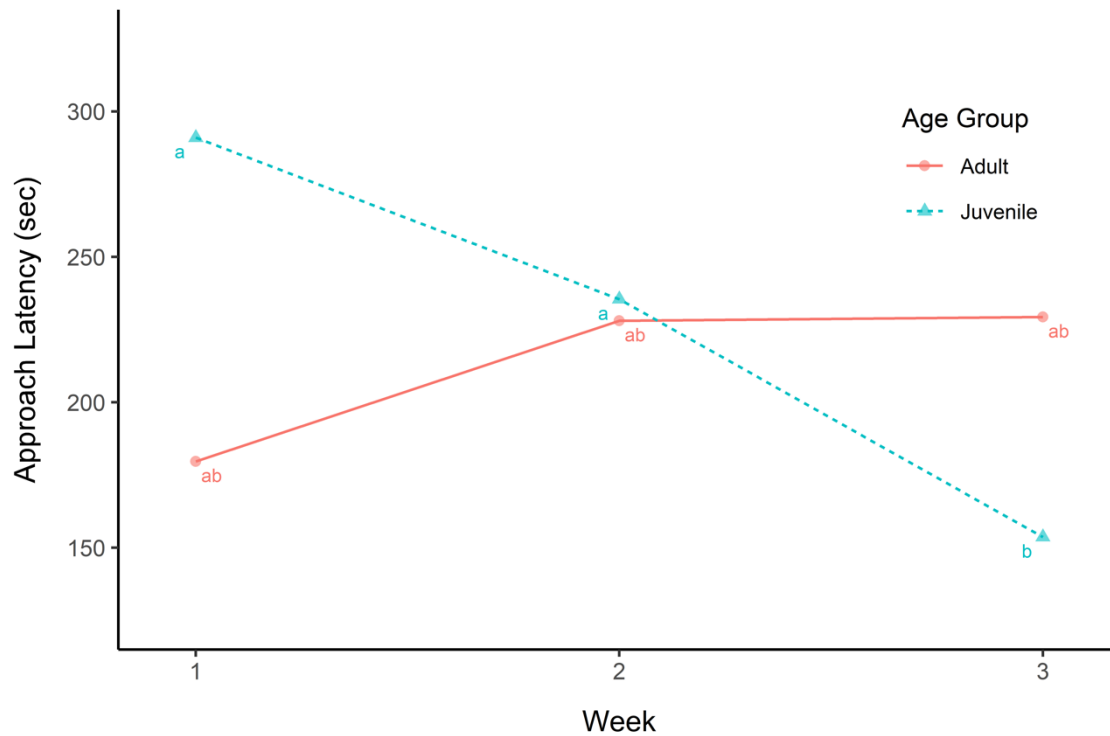


Figure 5. Mean latency to approach the playground for the three testing weeks among adult and juvenile ravens shown in a multiple regression model. Significant differences between and within subjects are indicated by different letters respectively. The regression lines' deviation from their horizontal parallelism indicate potential interaction effects, describing the relationship between the timepoint of testing and the mean latency of an individual to approach the playground depending on its age.

Familiar vs. Novel Objects – Preferences & Ontogenetic Effects

The analyses of object manipulations revealed significant differences in object play duration between adults and juveniles, as well as development effects within these groups (Wald Chi-Squared Test: $\chi^2(2, N = 26) = 23.87, p < 0.001$). The main age effect was found in the third week, with juveniles showing significantly higher durations of object manipulation than adults (mean manipulation time: 640 versus 276 seconds, respectively; Adult 3 – Juvenile 3: Z-Test, $z(25) = -2.88, p = 0.048$). Over time, adult birds' duration of object play significantly decreased from week one to week two (Adult 1 – Adult 2: Z-Test, $z(25) = 3.05, p = 0.030$) and remained stable afterwards, whereas,

juveniles showed a significant increase from the first until the third week of testing (Juvenile 1 – Juvenile 3: Z-Test, $z(25) = -3.10$, $p = 0.027$) (Fig. 6).

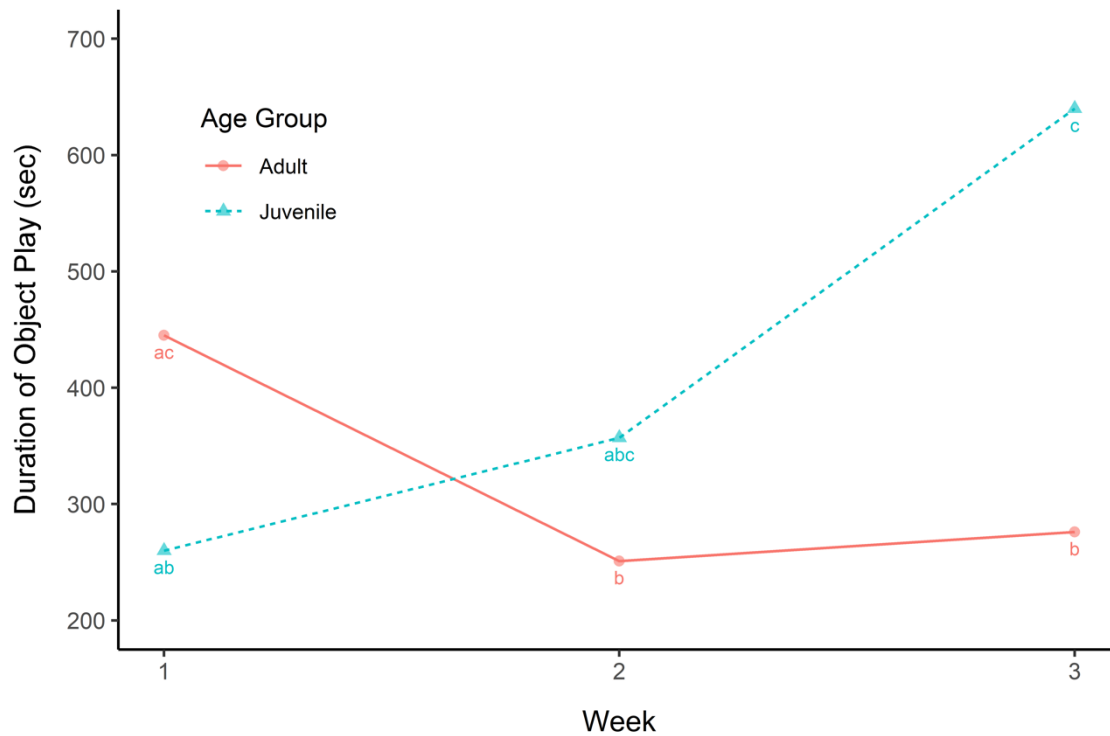


Figure 6. Mean overall object play duration for the three testing weeks among adult and juvenile ravens shown in a multiple regression model. Significant differences between and within subjects are indicated by different letters respectively. The regression lines' deviation from their horizontal parallelism indicate potential interaction effects, describing the relationship between the timepoint of testing and the mean duration of object play depending on the individual's age.

Also, a significant difference in object play duration between familiar and novel objects was found (Wald Chi-Squared Test: $\chi^2(1, N = 26) = 37.04$, $p < 0.001$) for ravens of both age classes, who both preferentially manipulated the novel objects compared to the familiar ones (Adult Familiar – Adult Novel: Z-Test, $z(25) = -4.42$, $p < 0.001$; Juvenile Familiar – Juvenile Novel: Z-Test, $z(25) = -4.20$, $p < 0.001$) (Fig. 7).

This difference was confirmed between novel and familiar objects on a weekly basis (Adults – Wald Chi-Squared Test: $\chi^2(1, N = 12) = 36.38$, $p < 0.001$; Juveniles – Wald Chi-Squared Test: $\chi^2(1, N = 14) = 9.03$, $p = 0.003$). In particular, adults manipulated novel

objects significantly longer than familiar ones in week one and week three, but not in the second week (Familiar 1 – Novel 1: Z-Test, $z(11) = -3.49$, $p = 0.004$; Familiar 3 – Novel 3: Z-Test, $z(11) = -4.84$, $p < 0.001$) (Fig. 8).

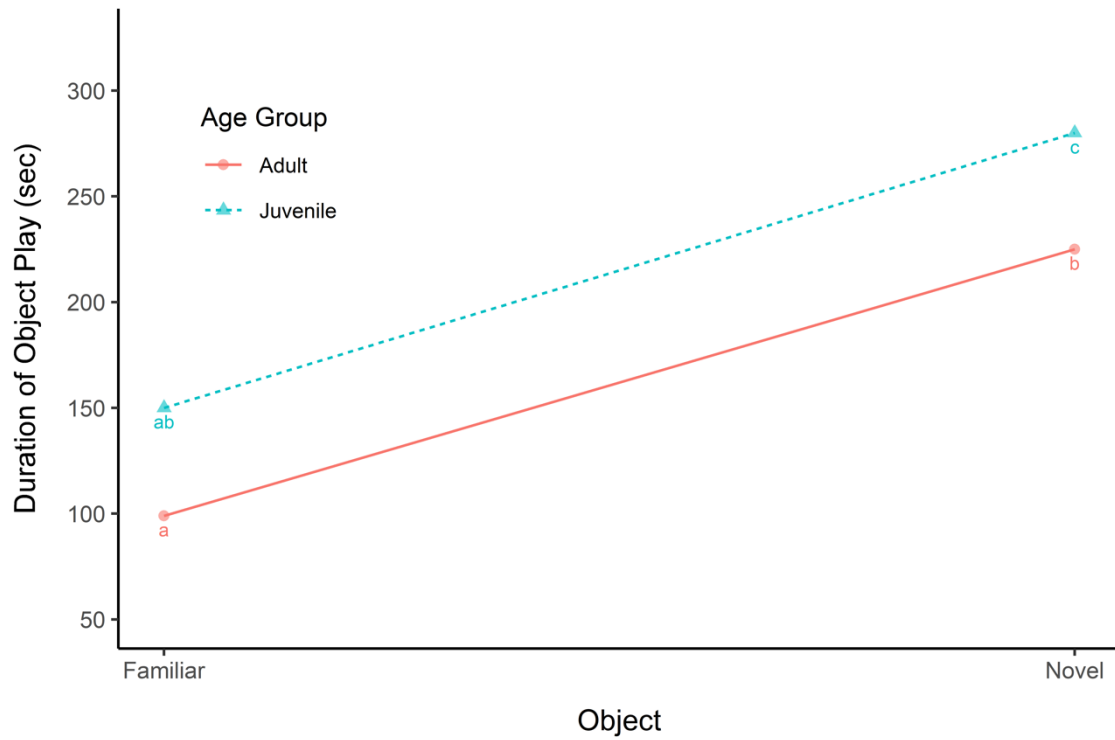


Figure 7. Mean overall object play duration for familiar and novel objects among adult and juvenile ravens shown in a multiple regression model. Significant differences between and within subjects are indicated by different letters respectively. The regression lines' deviation from their horizontal parallelism indicate potential interaction effects, describing the relationship between the object's characteristic and the mean duration of object play depending on the individual's age.

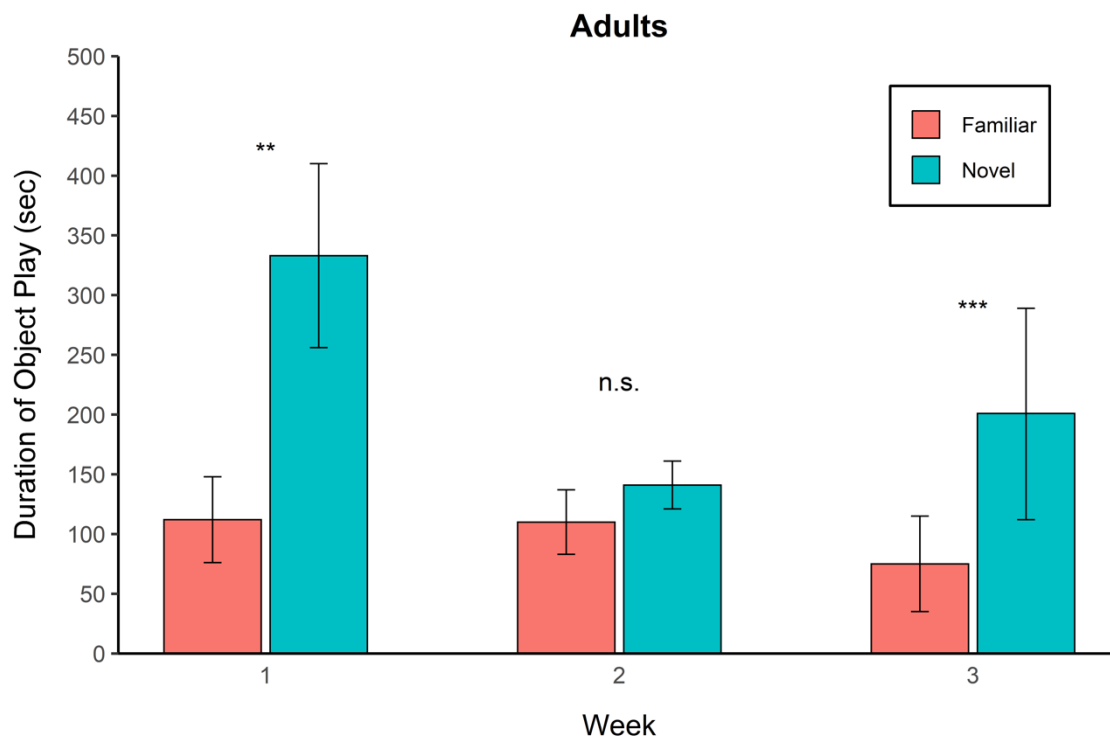


Figure 8. Mean ($\pm$ S.E.) adult raven's object play time for the three testing weeks in consideration of object quality shown in a grouped bar plot. Significant differences between familiar and novel objects within the respective weeks are indicated as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, n.s. = not significant.

Juveniles showed no significant preferences in week one or two, but manipulated novel objects significantly longer in week three (Familiar 3 – Novel 3: Z-Test, $z(11) = -3.57$, $p = 0.005$) (Fig. 9).

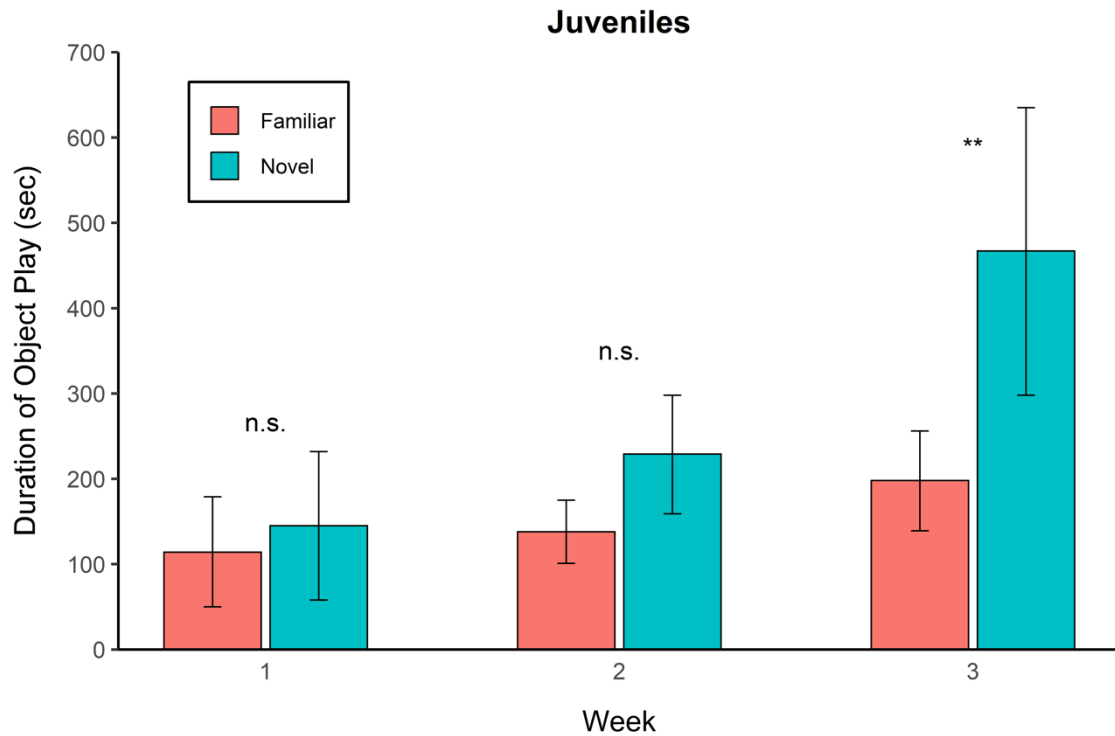


Figure 9. Mean ($\pm$ S.E.) juvenile raven's object play time for the three testing weeks in consideration of object quality shown in a grouped bar plot. Significant differences between familiar and novel objects within the respective weeks are indicated as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, n.s. = not significant.

Social Object Play (SOP) – Ontogeny & Age-Specific Differences

The analysis of SOP frequencies revealed significant development effects for juveniles (Wald Chi-Squared Test: $\chi^2(2, N = 26) = 30.84, p < 0.001$). In the first two weeks of testing, subjects' responses remained somewhat stable and no differences, neither between nor within age classes were found, whereas, the number of SOP interactions significantly increased from week two to week three in juveniles (Juvenile 2 – Juvenile 3: Z-Test, $z(25) = -6.02, p < 0.001$) (Fig. 10).

When considering the duration of SOP, a significant age effect between groups was found (Overall F-Test: $F(1, 15) = 8.12, p = 0.012$). However, the post-hoc comparisons revealed no significant differences, but a strong trend between the two extreme measures – the mean duration of SOP for adults in week two and for juveniles in week three (Adult 2 – Juvenile 3: T-Test, $t(25) = -2.88, p = 0.077$) (Fig. 11).

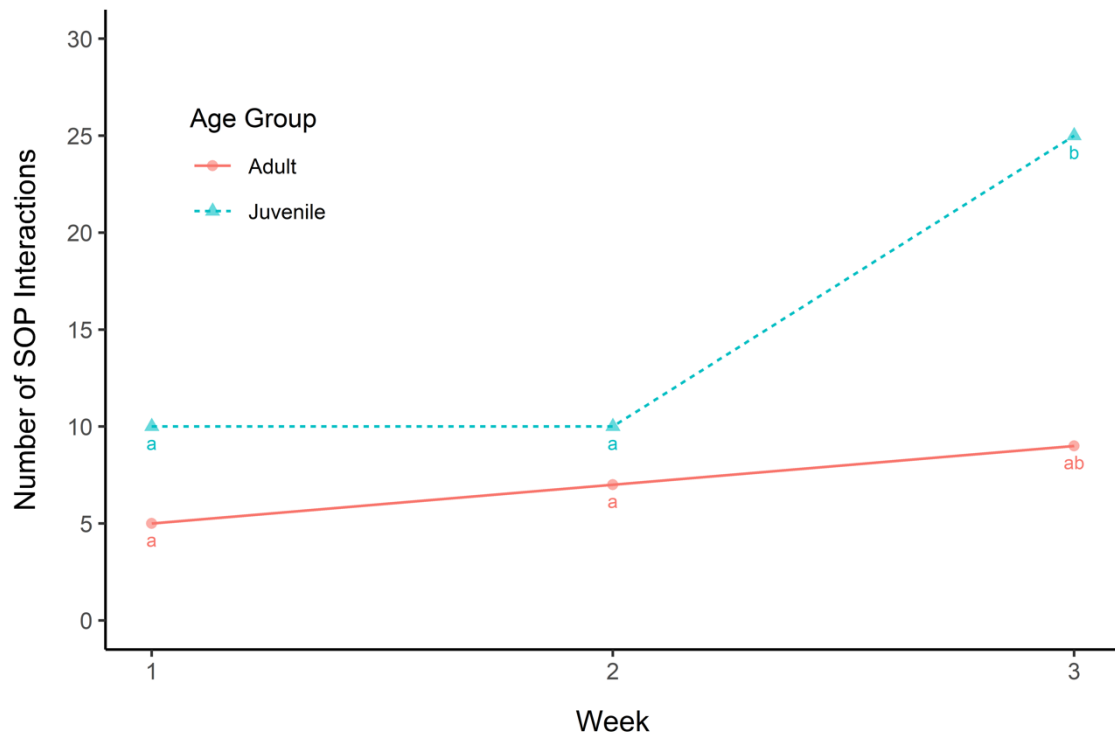


Figure 10. Mean number of social object play (SOP) interactions for the three testing weeks among adult and juvenile ravens shown in a multiple regression model. Significant differences between and within subjects are indicated by different letters respectively. The regression lines' deviation from their horizontal parallelism indicate potential interaction effects, describing the relationship between the timepoint of testing and the number of social object play interactions depending on the individual's age.

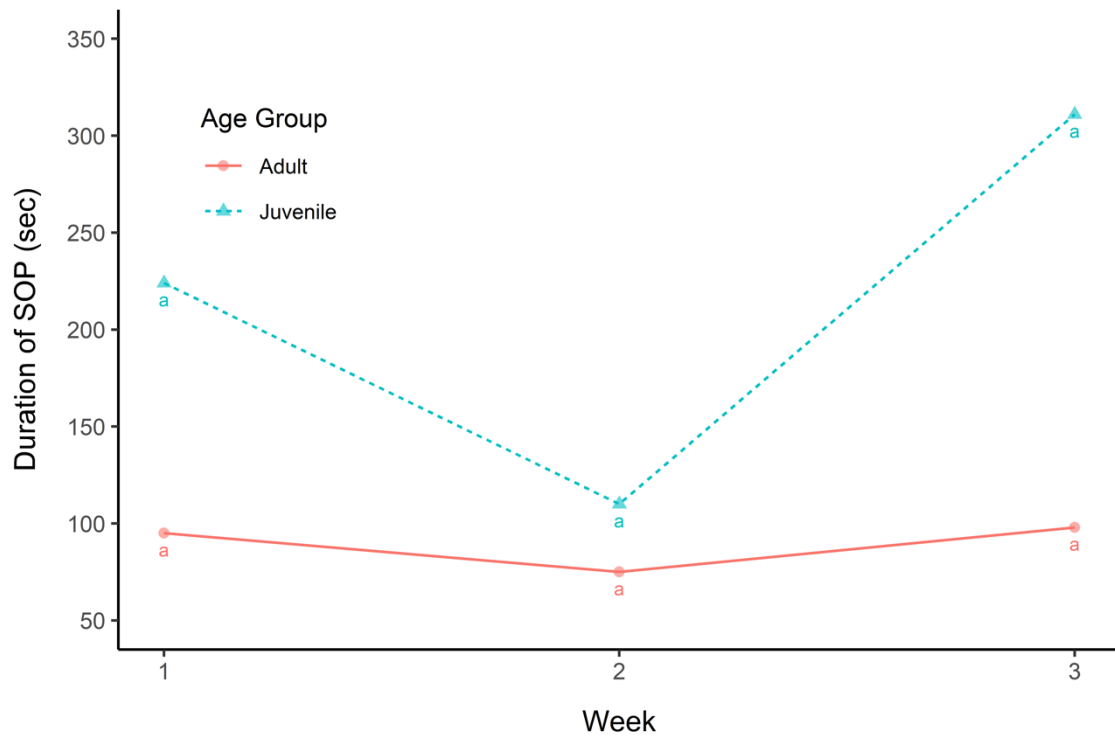


Figure 11. Mean social object play (SOP) duration for the three testing weeks among adult and juvenile ravens shown in a multiple regression model. Significant differences between and within subjects are indicated by different letters respectively. The regression lines' deviation from their horizontal parallelism indicate potential interaction effects, describing the relationship between the timepoint of testing and the duration of social object play depending on the individual's age.

Discussion

Approaching Behaviour as a Proxy for Exploration & Neophobia

Adult and juvenile ravens showed a diametrically opposing temporal development of their interest in object interaction. Over time, juveniles significantly increased the number of initial approaches for the playground, whereas in adults, numbers decreased to an almost equal extent. These findings fit the proposed predictions very well. Specifically, with regard to what is known about the processes of cognitive and physical development in juvenile ravens, which are assumed to be associated with high levels of curiosity and neophilic tendencies (Heinrich, 1995). Since high latency to approach novel objects is considered as an indicative variable for neophobia, which is argued to drastically increase around the onset of sub-adulthood to compensate the strong neophilic tendencies of juvenile ravens (Greenberg & Mettke-Hofmann, 2001), I also expected juveniles to increase their approach latencies, particularly during the third week of testing. The data analyses, however, revealed surprising results. From testing week two to three, juveniles showed a significant decrease in approach latencies, whereas in adults, there were no development effects to be found. When relating these results to the juvenile ravens' rising number of initial approaches, the frequency as well as the latency to approach the objects seem to be mostly driven by a general activity increase. Conclusively, neither the beginning of developing higher amounts of neophobic tendencies, nor the existence of behavioural synchronization processes in relation to 'socially-induced neophobia' (Miller et al., 2015) were found in this group of juvenile ravens.

One explanation for this dominance of neophilic behaviour, or the missing of an emerging neophobic approach respectively, could be simply related to the age factor. Juveniles were still rather young at the time of the third testing period, with an age of about 4 months, and therefore, clearly not at the stage of sub-adulthood. However, this fails to explain the absence of synchronization processes among siblings which could have led to increased hesitance in approaching behaviour, as stated by Miller et al. (2015). In contrast, strong effects of emotional contagion among affiliate juveniles could have actually further facilitated play behaviour and reduced an individual's mean approach latencies (Osvath & Sima, 2014; Wenig et al., 2021). To explore this possibility, future

studies should aim to account for the degree of affiliation between group members on patterns of exploration and play behaviour.

Sexes were almost evenly distributed in this study. However, due to the relatively small sample size it was not possible to investigate potential sex-effects. In previous studies, male ravens were found to approach objects quicker and show higher manipulation times (Range et al., 2006). Future scientific work should thus try to incorporate the possible influence of sex on explorative and manipulative traits when investigating object play behaviour.

Miller et al. (2021) proposed that the main driving forces of neophobia development are primarily due to an individual's predominant socio-ecological factors (e.g., the urbanization and variability of preferred habitats, or social components like flock size). In my experiment, juvenile ravens' specific rearing conditions in captivity provided a rather stable and safe environment, while still living as part of a secure family group with their affiliate siblings (Stöwe et al., 2006). This could have also prevented the development of neophobic traits, as they would probably not provide any major benefits in such a setting (e.g., suspicious hesitance like in unknown foraging contexts to avoid high risks and negative trade-offs). Finally, to assume that neophobia is a flexible behavioural adaptation of individuals to their environment, this raises the question of how efficiently young ravens can actually adapt to abrupt changes in their ecology. According research may contribute to a deeper understanding of the influence of specific (artificially induced) changes in sub-adult ravens' preferred natural environments on their short-term exploration and play behaviour and, eventually, their general survivability.

Ontogeny of Object Play & Object Preferences

I expected a general rise in object play quantity in juvenile ravens throughout this experiment. Accordingly, the sharp increase in mean object play duration in juveniles from the first to the third testing week confirms these assumptions. This finding matches well with the temporal patterns of approach frequencies and latencies. Interestingly, young birds not only extended their general object play time, but simultaneously showed a significant preference for novel objects. This additionally supports the assumption of

high neophilic tendencies at this age and in this specific experimental set-up. These results also fit previous findings, when ravens were found to increase their object play behaviour within the first few months of their lives, eventually leading to a strong attraction towards novelty (Heinrich, 1988 & 1995). Comparing adults and juveniles with regard to object preferences, I found that individuals of both groups preferred to interact with novel instead of familiar objects to the almost exact same extent. These results clearly show that ravens do prefer to explore and play with novel objects regardless of their age. They seemed to be able to detect even small changes in object properties (e.g., dark green balls vs. light green balls), differentiating the novel from the familiar objects. As stated, the assumed general rise in object play at an early age is supported by the consistent increase in overall manipulation times in juveniles after the first week of testing. Adults on the other hand, showed a significant decrease in mean object play duration from testing week one to testing week two before remaining stable. The latter result also suggests that play behaviour might be reinduced in adult ravens by generating novelty in their familiar surroundings – but with a short-lived effect, further re-affirming their ability to quickly adapt to variations in their environment. These patterns are also consistent with previous findings on similar topics (Jacobs et al., 2014).

It is arguable that the provided material itself could have affected the subjects' responses, even though no preferences or complete rejections for specific novel objects were found. There is evidence that ravens might prefer objects with greater sphericity in the context of play caching, compared to elongated stick-like shapes, for example (Jacobs et al., 2014). According to this, it would be quite interesting to define specific features of inedible objects potentially evoking high levels of curiosity in common ravens, as well as properties eliciting the opposite effect. This would be of special interest in urban environments, which are rich of artificial human crafted objects that could possibly be used or rejected by ravens (and other animals) respectively if properly adapted. In this particular study, what seems more reasonable is that the objects' fixation to the boards potentially affected the durations of expressed play behaviour, since some of the test objects were detachable while others were fixed – with the aim to encourage manipulation and object play behaviour, as well as social interactions and cooperation. However, object type (novel, familiar, fixed, detachable) did not vary in position on the respective boards between trials. Therefore, some of the adult ravens might have found

out rather quickly which objects can be removed. This could have facilitated more of an unintended task-solving type of play in adults, with the main aim to efficiently remove the detachable objects and instantly losing interest afterwards, resulting in lower object play durations. Furthermore, this could have also affected certain aspects of juveniles' play behaviour, like duration, sociality, or cooperation.

Development of Social Object Play & Cooperation

I expected that juvenile ravens increase their quantities of social interactions when engaged in object play, based upon previous work on cooperation (Fraser & Bugnyar, 2010; Heinrich, 2011; Asakawa-Haas et al., 2016), social learning (Bugnyar et al., 2007b; Schwab et al., 2008; Braun & Bugnyar, 2012), and behavioural synchronization (Boyd & Richerson, 1988; Osvath & Sima, 2014). But surprisingly, social interactions in this experiment were rather scarce (both prosocial and agonistic behaviours, e.g., sharing, transferring, stealing, or monopolizing objects). Still, juveniles showed a significant increase in the number of social object play interactions – basically incorporating any form of object manipulation while in close proximity to at least one other conspecific – from the second to the third testing week. However, the results showed neither significant development effects, nor differences between age groups in the duration of social object play interactions. Conclusively, the assumed increase in social object play behaviour in juveniles can be partly accepted, but definitely needs further research.

One potential explanation for the low rates of social interactions might stem from the methodological design. Only behaviours performed within the dedicated playground area were considered in the analyses. Since this area was just a minor part of the aviaries and at least half of the objects were movable, some social interactions could have been missed. Accordingly, another influential factor could relate to vegetational changes in and around the aviaries, leading to respective differences in possible interactions with an individual's environment (e.g., the existence of attractive caching spots further away from the playground). It is also possible that family size – particularly the number of affiliate juveniles in this case – might fundamentally affect social object play and the acquisition of specific cognitive abilities. This assumes that the level of complexity in a species' social

group is considered being positively correlated to brain evolution and development, as well as leading to enhanced cognitive performance with increasing sociality. (Dunbar & Shultz, 2007; see Bugnyar, 2013 for an overview). Inter-family comparisons and extensive longitudinal approaches, investigating the same breeding pairs over several seasons with varying numbers of offspring could provide valuable insights into the potential impact of family size on learning processes.

Referring to previous findings addressing enhanced social learning abilities among kin (Fritz & Kotrschal, 1999; Laland, 2004; Schwab et al., 2008), as well as diverse influences and possible functions of specific social structures on the development of socio-cognitive skills (e.g., to assess the qualities of conspecifics, or to increase one's general fitness through cooperation and bonding; Dunbar, 1998; Braun & Bugnyar, 2012), it could be interesting to study relevant underlying social correlates within the special context of object play. This could make a decisive contribution to a holistic understanding of a young raven's physical, social, and cognitive ontogeny. Accordingly, this study indeed substantiates the idea of specific developmental changes in the social interaction over inedible objects in juvenile common ravens, like an increase in cooperation among siblings, and may encourage further necessary research on this topic.

Conclusion

In sum, the present study revealed strong developmental patterns on explorative and object play behaviour in captive juvenile ravens, as well as significant differences in object-approaching behaviour and object play duration between juveniles and adults when directly compared. This relates in particular to increasing numbers of initial approaches and decreasing approach latencies in juvenile ravens over time. Accordingly, juveniles progressively raised their quantities of (social) object play, while existing or emerged preferences for novelty, respectively, were observed in both age groups. The results nicely fit previous findings on patterns of exploration (e.g., the variable expression of neophobic and neophilic tendencies) and object play (e.g., the general activity increase in juveniles during ontogeny and assumed preferences for novelty). Furthermore, they provide slight insight into the development of crucial socio-cognitive skills associated

with cooperation, competition, and dominance, based upon the influence of object play in juvenile ravens before dispersing. This study may serve as a valuable contribution to the investigation of object play patterns in birds, and might additionally raise further awareness for its general importance in relation to (social) learning processes.

References

- Asakawa-Haas, K., Schiestl, M., Bugnyar, T. & Massen, J. J. M. (2016). Partner choice in raven (*Corvus corax*) cooperation. PLoS One 11:e0156962.
- Auersperg, A. M. I. (2015). Exploration technique and technical innovations in corvids and parrots. In: Animal Creativity and Innovation. Kaufman, A. B. & Kaufman, J. C. (eds.), pp. 45–72. Elsevier Academic Press.
- Bateson, P. (2014). Play, Playfulness, Creativity and Innovation. Animal Behavior and Cognition 2:99–112.
- Bekoff, M. & Byers, J. A. (1981). A critical reanalysis of the ontogeny of mammalian social and locomotor play: An ethological hornet's nest. In: Behavioral Development: The Bielefeld Interdisciplinary Project. Immelmann, K., Barlow, G. W., Petrinovich, L. & Main, M. (eds.). Cambridge University Press, New York.
- Bekoff, M. (1984). Social play behavior. Bioscience 34:228–233.
- Bekoff, M. (2001). Social play behaviour: cooperation, fairness, trust, and the evolution of morality. Journal of Consciousness Studies 8:81–90.
- Bjorklund, D. F. & Gardiner, A. K. (2010). Object play and tool use: developmental and evolutionary perspectives. In: The Oxford Handbook of the Development of Play. Pellegrini, A. D. (ed.), pp. 153–171. Oxford University Press.
- Boucherie, P. H., Loretto, M. C., Massen, J. J. M. & Bugnyar, T. (2019) What constitutes "social complexity" and "social intelligence" in birds? Lessons from ravens. Behavioral Ecology and Sociobiology 73:1–14.
- Boucherie, P. H., Gallego-Abenza, M., Massen, J. J. M. & Bugnyar T. (2022). Dominance in a socially dynamic setting: hierarchical structure and conflict dynamics in ravens' foraging groups. Philosophical Transactions of the Royal Society B (In Press).
- Boyd, R. & Richerson, P. J. (1988). An evolutionary model of social learning: The effect of spatial and temporal variation. In: Social learning: Psychological and biological perspectives. Zentall, T. R. & Galef Jr., B. G. (Eds.), pp. 29–48. Hillsdale, NJ: Erlbaum.
- Braun, A. & Bugnyar, T. (2012). Social bonds and rank acquisition in raven nonbreeder aggregations. Animal Behaviour 84:1507–1515.
- Bugnyar, T., Schwab, C., Schloegl, C., Kotrschal, K. & Heinrich, B. (2007a). Ravens Judge Competitors through Experience with Play Caching. Current Biology 17:1804–1808.
- Bugnyar, T., Stöwe, M. & Heinrich, B. (2007b). The ontogeny of caching in ravens, *Corvus corax*. Animal Behaviour 74:757–767.
- Bugnyar, T. (2013). Social cognition in ravens. Comparative Cognition & Behavior Reviews 8:1–12.
- Burghardt, G. M. (1998). Play. In: Comparative Psychology: A Handbook. Greenberg, G. & Haraway, M. M. (eds.), pp. 725–735. Garland Publishing Co.

- Burghardt, G. M. (2005). The genesis of animal play: Testing the limits. MIT Press, Cambridge, MA.
- Clayton, N. S. (1993). Storage of stones by jays *Garrulus glandarius*. *Ibis* 136:331–334.
- Clayton, N. S. (1994). The role of age and experience in the behavioural development of food-storing and retrieval in marsh tits, *Parus palustris*. *Animal Behaviour* 47:1435–1444.
- Coleman, S. L. & Mellgren, R. L. (1994). Neophobia when feeding alone or in flocks of zebra finches, *Taeniopygia guttata*. *Animal Behavior* 48:903–907.
- Coussi-Korbel, S. & Frigaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour* 50:1441–1453.
- Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology* 6:178–190.
- Dunbar, R. I. M. & Shultz, S. (2007). Evolution in the social brain. *Science* 317:3144–3147.
- Emery, N. J. & Clayton, N. S. (2015). Do birds have the capacity for fun? *Current Biology* 25:R16–R20.
- Fagen, R. (1981). *Animal Play Behavior*. Oxford University Press, New York.
- Ficken, M. S. (1977). Avian play. *The Auk* 94:10.
- Fraser, O. N. & Bugnyar, T. (2010). The quality of social relationships in ravens. *Animal Behaviour* 79:927–933.
- Fritz, J. & Kotrschal, K. (1999). Social learning in common ravens, *Corvus corax*. *Animal Behaviour* 57:785–793.
- Goodwin, D. (1986). *Crows of the World*. 2nd Edition. University of Washington Press, Seattle.
- Greenberg, R. S. (1990a). Ecological plasticity, neophobia, and resource use in birds. *Studies in Avian Biology* 13:431–437.
- Greenberg, R. S. (1990b). Feeding neophobia and ecological plasticity: a test of the hypothesis with captive sparrows. *Animal Behaviour* 39:375–379.
- 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.
- Heinrich, B. (1988). Why do ravens fear their food? *Condor* 90:950–952.
- Heinrich, B. (1989). *Ravens in Winter*. New York: Simon & Schuster.
- Heinrich, B. (1995). Neophilia and exploration in juvenile common ravens, *Corvus corax*. *Animal Behaviour* 50:695–704.
- Heinrich, B. & Smolker, R. (1998). Play in common ravens (*Corvus corax*). In: *Animal Play*. Bekoff, M. & Byers, J. A. (eds.), pp. 27–44. Cambridge University Press.
- Heinrich, B. (2011). Conflict, cooperation, and cognition in the common raven. *Advances in the Study of Behavior* 43:189–237.

Immelmann, K. & Beer, C. (1989). A Dictionary of Ethology. Harvard University Press, Cambridge, MA.

Jacobs, I. F., Osvath, M., Osvath, H., Mioduszevska, B., von Bayern, A. M. P. & Kacelnik, A. (2014). Object caching in corvids: Incidence and significance. *Behavioural Processes* 102:25–32.

Kahlenberg, S. M. & Wrangham, R. W. (2010). Sex differences in chimpanzees' use of sticks as play objects resemble those of children. *Current Biology* 20:1067–1068.

Kendal, R. L., Coe, R. L. & Laland, K. N. (2005). Age differences in neophilia, exploration, and innovation in family groups of callitrichid monkeys. *American Journal of Primatology* 66:167–188.

Kenward, B., Schloegl, C., Rutz, C., Weir, A. A. S., Bugnyar, T. & Kacelnik, A. (2011). On the evolutionary and ontogenetic origins of tool-oriented behavior in New Caledonian crows (*Corvus moneduloides*). *Biological Journal of the Linnean Society* 102:870–877.

Kuczaj, S. A., Makecha, R., Trone, M., Paulos, R. D. & Ramos, J. A. A. (2006). Role of peers in cultural innovation and cultural transmission: Evidence from the play of dolphin calves. *International Journal of Comparative Psychology* 19:223–240.

Laland, K. N. (2004). Social learning strategies. *Learning and Behavior* 32:4–14.

Mainwaring, M. C., Beal, J. L. & Hartley, I. R. (2011). Zebra finches are bolder in an asocial, rather than social, context. *Behavioural Processes* 87:171–175.

Mettke-Hofmann, C., Winkler, H. & Leisler, B. (2002). The significance of ecological factors for exploration and neophobia in parrots. *Ethology* 108:249–272.

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* 69:1209–1220.

Miller, R., Lambert, M. L., Frohnwieser, A., Brecht, K. F., Bugnyar, T., Crampton, I., Garcia-Pelegrin, E., Gould, K., Greggor, A. L., Izawa, E., Kelly, D. M., Li, Z., Luo, Y., Luong, L. B., Massen, J. J. M., Nieder, A., Reber, S. A., Schiestl, M., Seguchi, A., Sepehri, P., Stevens, J. R., Taylor, A. H., Wang, L., Wolff, L. M., Zhang, Y. & Clayton, N. S. (2021). Socio-ecological correlates of neophobia in corvids. *Current Biology* 32:1–12.

O'Hara, M. & Auersperg, A. M. I. (2017). Object play in parrots and corvids. *Current Opinion in Behavioral Sciences* 16:119–125.

Ortega, J. & Bekoff, M. (1987). Avian play: comparative evolutionary and developmental trends. *The Auk* 104:338–341.

Osvath, M. & Sima, M. (2014). Sub-adult Ravens Synchronize their Play: A Case of Emotional Contagion? *Animal Behavior and Cognition* 1(2):197–205.

Pellis, S. M. (1981). Exploration and play in the behavioural development of the Australian Magpie *Gymnorhina tibicen*. *Bird Behavior* 3:37–49.

Pellis, S. M. & Burghardt, G. M. (2017). Play and exploration. In: *APA Handbook of Comparative Psychology: Vol. 1: Basic Concepts Methods, Neural Substrate, and Behaviour*. Call, J., Burghardt,

G. M., Pepperberg, I. M., Snowdon, C. T. & Zentall, T. (eds.), pp. 699–722. Washington DC: American Psychological Association.

Pika, S. & Bugnyar, T. (2011). The use of referential gestures in ravens (*Corvus corax*) in the wild. *Nature Communications* 2:560.

Pollok, B., Prior, H. & Güntürkün, O. (2000). Development of object permanence in food-storing magpies (*Pica pica*). *Journal of Comparative Psychology* 112:13–25.

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

Reader, S. M. & Laland, K. N. (2003). Animal innovation: an introduction. In *Animal innovation*. Reader, S. M. & Laland, K. N. (eds), pp. 3–35. Oxford University Press, Oxford.

Renner, M. J. (1988). Learning during exploration: The role of behavioural topography during exploration in determining subsequent adaptive behaviour. *International Journal of Comparative Psychology* 2:43–56.

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

Smith, P. K. (2010). *Children and play*. Wiley-Blackwell, Chichester, UK.

Stettner, L. J. (1974). The neural basis of avian discrimination and reversal learning. In: *Birds, brain and behavior*. Goodman, I. J. & Schein, M. W. (eds.), pp. 165–201. Academic Press, New York.

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* 73:68–75.

Thorpe, W. H. (1956). *Learning and Instincts in Animals*. Methuen and Co., London.

Torigoe, T. (1985). Comparison of object manipulation among 74 species of non-human primates. *Primates* 26:182–194.

von Bayern, A. M. P., de Kort, S. R., Clayton, N. S. & Emery, N. J. (2007). The role of food- and object-sharing in the development of social bonds in juvenile jackdaws (*Corvus monedula*). *Behaviour* 144:711–733.

Wenig, K., Boucherie, P. H. & Bugnyar, T. (2021). Early evidence for emotional play contagion in juvenile ravens. *Animal Cognition* 24:717–729.

Winkler, H. & Leisler, B. (1999). Exploration and curiosity in birds: functions and mechanisms. In: *Proceedings of the 22nd International Ornithology Congress*. Adams, N. & Slotow, R. (eds), pp. 915–932. University of Natal, Durban.

Appendix

Abstract

Exploratory behaviour is assumed to expand the knowledge about an individual's environment, which forms the basis for the acquisition of relevant adaptive skills. Since playful behaviour builds upon the principles of exploration, and furthermore, enhances its accompanied learning processes and modulates acquired abilities, the general importance of play is evident. This is argued being particularly true for animals inhabiting broad and diverse habitats as feeding generalist, like common ravens (*Corvus corax*). Therefore, this study was conducted on six captive raven families, composed of 12 adults and 14 juveniles, to investigate object play behaviour in relation to its ontogeny. This incorporated adequate measurement of its quantitative development including an individual's approaching behaviour, observation of changes in social interactions during play, and the analysis of prevailing preferences for specific objects within a seven-week time frame. Object play behaviour was experimentally induced by providing the birds with familiar and novel inedible objects. Juvenile ravens showed increasing mean object play durations, as well as the development of strong neophilic tendencies, resulting in higher numbers of initial object approaches, along with decreasing latencies. Accordingly, both age groups tended to preferably interact with novel objects. In terms of sociality, juveniles raised their numbers of social interactions during play, depicting developmental changes in cooperative behaviour. In sum, this work supports previous findings on exploratory and play behaviour, while additionally providing valuable insight into the underlying ontogeny of (social) object play in captive juvenile ravens, within a formative period characterized by pronounced learning abilities.

Zusammenfassung

Es wird angenommen, dass Explorationsverhalten der Wissenserweiterung eines Individuums bezüglich seiner Umgebung dient, was die Grundlage für die Aneignung relevanter adaptiver Kompetenzen bildet. Da Spielverhalten auf den Prinzipien von Exploration aufbaut, darüber hinaus die damit assoziierten Lernprozesse verstärkt und die erworbenen Fähigkeiten moduliert, ist dessen Wichtigkeit evident. Dies scheint insbesondere auf Tiere zuzutreffen, welche große und abwechslungsreiche Habitate als Nahrungsgeneralisten bewohnen, wie beispielsweise Kolkraben (*Corvus corax*). Aus diesem Grunde wurde die vorliegende Studie an sechs Kolkrabenfamilien durchgeführt, welche sich aus 12 adulten und 14 Jungtieren zusammensetzten, um die Ontogenese von Objektspielverhalten zu untersuchen. Dies beinhaltete die Messung dessen quantitativer Entwicklung unter Miteinbeziehung des individuellen Annäherungsverhaltens, der Beobachtung von Veränderungen in sozialen Interaktionen während des Spiels und die Analyse von vorherrschenden Präferenzen für spezifische Objekte, während eines 7-wöchigen Untersuchungszeitraumes. Etwaiges Objektmanipulationsverhalten wurde mithilfe der Darbietung von vertrauten und unbekannten nicht-essbaren Objekten induziert. Die Jungraben zeigten sowohl einen Anstieg in der mittleren Objektspieldauer, als auch eine Entwicklung von stark neophilen Neigungen, welche sich in einer gesteigerten Anzahl an Erstkontakten zu den Objekten, bei gleichzeitiger Verringerung der jeweiligen Latenzzeiten, niederschlugen. Dazu passend, tendierten beide Altersgruppen dazu, bevorzugt mit den unbekannten Objekten zu interagieren. In Bezug auf das Sozialverhalten, zeigten die Jungvögel einen Anstieg in der Anzahl sozialer Interaktionen während des Spiels, was entwicklungsbedingte Änderungen im Kooperationsverhalten aufzeigt. Schlussfolgernd befürwortet diese Arbeit bereits postulierte Erkenntnisse zu Explorations- und Spielverhalten, bietet jedoch darüber hinaus einen wertvollen Einblick in die zugrundeliegende Ontogenese des (sozialen) Objektspiels von gefangenen Jungraben, während eines, durch ausgeprägtes Lernvermögen gekennzeichneten, wesentlichen Lebensabschnittes.

Addition to Behaviour Analyses

Table 3. Detailed description of investigated behaviours in addition to information given in the methods part.

Behaviour	Description
Initial Playground Approaches & Approach Latencies	An initial playground approach was fulfilled, as soon as the overall first contact of an individual with the provided material took place during a test trial. Therefore, only one initial approach was possible per experimental conduction. The designation stands in relation to the very first bird interacting with the objects proactively initializing (social) object play behaviour and, consequently, eliciting a specific group response. Approach latencies were defined as the time between the onset of the experimental trial and the first contact of the respective individual with the test material. In contrast to initial playground approaches, latencies were collected for every playground approaching individual once per trial.
Object Play Duration – Familiar vs. Novel Objects	In this study, object play behaviour was broadly diversified and could be referred to as object manipulation in a playful context in a general sense. These behaviours were performed in various ways by manipulating the provided objects either with the subject's beak or feet. In conclusion, object play was specified as target-oriented physical manipulation of the test material, which comprised the provided objects as well as the associated boards. Since ravens' physical manipulations are usually performed in series of short behavioural outputs – so called behaviour-specific bouts –, a two-seconds rule was introduced to separate series of behaviours properly. If interruptions between single manipulations lasted longer than two seconds, the previous bout ended with the last contact to the object, and a new series of manipulations started with the subsequent manipulation of the test material. This way, biases in the coding of object play durations were excluded effectively. Manipulation times of familiar and novel objects were considered and, therefore, coded separately for each individual, to investigate potential preferences in relation to the objects' qualities.
Proximities & Social Object Play (SOP)	Social object play was based on the requirements for defined object play behaviour, but with the addition that manipulations were performed in proximity to at least one other conspecific. Individual's positioning was considered as in proximity, if two or more ravens were in direct reaching-distance to one another (70 cm or closer). Passive and active behaviours, like watching others play, or co-manipulating, transferring, and stealing objects are therefore summarized and equally represented within the concept of SOP. In relation to hypotheses testing, numbers and durations of social object play were determined on an individual level.