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Ontogeny of object oriented social play in juvenile ravens (Corvus corax)

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Abstract

Corvids are known for enlarged forebrains and complex cognitive abilities comparable to those of primates. One reason that drives corvid brain evolution may be life in complex social groups. Recent observations show that corvid flocks are individualized societies in which individuals recognizing one another and selectively exchange different behaviours (e.g., preening or third party interventions). It is crucial that such social relationships are formed not only between siblings but also between non-related conspecifics. These social bonds are affected by high rates of affiliative behaviour, low rates of aggression, preening and social play. Young birds and especially corvids are known to play socially and show a wide range of playful behaviour. Further corvids are known for their sophisticated knowledge of others.
It was suggested that social play may be essential for learning about others e.g. predicting a conspecific's behaviour and/or manipulating another for personal benefit. Such abilities might be advantageous for individuals who live in large groups and have to deal with high levels of competition and cooperation.
The aim of this study was to investigate early ontogeny of social and object-oriented behaviour in ravens with emphasis on play. Our questions were when do patterns emerge and how are they affected by social context. I did daily observational protocols with focal individuals and an experiment with a solitary condition and a bystander condition.
Our observational results show that object related behaviour or manipulation occur already in nest. The same goes for sociopositive behaviours like preening. Approach retreat behaviours do not occur from the beginning but dominate the second month. Our experiment shows that the possbility of being observed facilitiates playful object manipulation. The results indicate that object manipulation serves mainly exploratory function in the beginning but later on when social behaviours (sociopositive and socionegative) have developed it may gain a social learning function.

Introduction:

Research focusing on animal play is a quite controversial topic. Although research in animal social behaviour is extraordinarily widespread, research focusing on play is quite rare. Main reason therefore is that it is difficult to define and difficult to elicit under standardized conditions; consequently, it has been little studied. Yet, it is a wide-spread phenomenon with ample consequences on an individual's life and well-being (Oliveira et al, 2010) and has recently received increased attention. Still,the majority of studies focus on few taxa, i.e. mammals such as laboratory rats (Panksepp, 1980), olive baboons (*Papioanubis;* Chalmers, 1980), cats (Bateson & Young, 1981), canids (Biben, 1983), gazelles (Gomendio, 1988), and fur seals (Harcourt, 1991).

Problem of defining play:
Play is difficult to define because of its incrementing nature of the ordinary functional behavioural repertoire of an animal species. The criterions for recognizing play are that i) the performance of the behaviour does not contribute to current survival, ii) it is done spontaneously, voluntary and "done for its own sake", iii) it differs from the serious performance of ethotypic behaviour, iiii) it is performed repeatedly in a similar, but not rigidly stereotyped form, iiiii) the behaviour is initiated when an animal is adequately fed, healthy, and free from stress (e.g., predator threat, harsh microclimate, social instability), or intense competing systems (e.g., mating, predator avoidance). In other words, the animal is in a "relaxed field" (Burghardt 2005). I follow the definition of Burghardt (2005): Play is repeated, incompletely functional behaviour differing from more serious versions structurally, contextually, or ontogenetically, and initiated voluntarily when the animal is in a relaxed or low-stress setting. There is a broad categorization: social play, object play, locomotor play.

Play and Ontogeny:
As described in Burghardt (2005) different kinds of play or play movements may appear and then wane at different time periods, suggesting that play behaviour reflects different behaviour systems in development. To understand the function of a behaviour, it is useful to observe its development through the ontogeny of an individual. Play is typically found in juvenile animals, although in some, including human beings, it can endure throughout life (Bekoff 1997). Therefore most studies of ontogeny have looked at the course of play

throughout the juvenile period: the type, context, frequency, duration, and targets of play (Burghardt, 2005).

Play in birds:

Although social play is broadly distributed among mammals, it is infrequently encountered in other vertebrate taxa (Diamond & Bond, 2003). However it can be found in several groups of birds such as parrots (Diamond & Bond 2002), corvids (Heinrich & Smolker 1998), hornbills (Kemp 2001), (Moreau & Moreau 1944) and Eurasian babblers (Gaston 1977), (Posis 1984; cited in Zahavi 1990).

Although many bird species are known to play socially, very few avian taxa exhibit the full range of play behaviours, from play chases to complex reciprocal object play (Fagen, 1981; Ortega & Bekoff, 1987). Parrots and corvids are generally considered to exhibit the most extensive social play of birds (Ficken, 1977; Fagen, 1981; Iwaniuk et al., 2001). Within these taxa, keas, *Nestor notabilis* and ravens, *Corvus corax,* are most frequently cited (Gwinner, 1966; Ficken, 1977; Van Vuren, 1984; Fagen, 1981; Ortega &Bekoff, 1987; Heinrich &Smolker, 1998; Diamond & Bond, 1999).

Corvids can be observed sliding down inclines, pushing and plowing through snow, hanging upside down from branches, riding on boars, play flying, which may involve elaborate aerial play acrobatics by large numbers of young birds (Heinrich &Smolker, 1998).

Corvids play socially wholly or partly in the context of object manipulation (Moreau & Moreau, 1944; Kilham, 1989; Deckert, 1991; Heinrich &Smolker, 1998). Pika & Bugnyar (2011) described showing and offering and interpret it as “play invitation”, note that this pattern has not been described by Heinrich & Smolker (1998), although it is relatively common in the aviary and in the field. Bugnyar et al. (2007) observed the playful caching behaviour of juvenile common ravens. They cache small objects as well as food items which in turn attracts raiders who try to steal the items. The cost of losing an object is considered to be low compared to losing a food item. Bugnyar and co-workers suggest that low-cost play object caching enhances social skills needed for successful raiding. Therefore play was considered to be an essential precursor for predicting a conspecific’s behaviour and/or manipulating another for personal benefit (tactical deception).

Challenges of social life:

Why could it be beneficial for corvids to learn about others in playful context? During their early years they live in non-breeder flocks with high fission fusion-dynamics, characterized

by high levels of cooperation (e.g. food source: to cooperate with others to steal from another species like wolves) and competition (food caches: pilfer from conspecifics; Bugnyar & Heinrich 2006). So judging others may be crucial from early stage on, latest when leaving their parents around two-three months post fledging. However ravens are known to form strong alliances and friendships already in the first months (Loretto et al. 2012) and to differentiate and maintain these relationships during their time in non-breeder groups (Braun & Bugnyar 2012).

As we know from primate-work (Hinde 1976), the social interactions between two animals depend not only on their individual characteristics (e.g., age, sex, dominance rank, temperament) but also on the history of interactions between them, provided that they possess the capacity for individual recognition, have sufficient memory to remember the outcome of social interactions, and repeatedly meet each other (Van Schaik & Aureli 2000).

Playful interactions might have an impact on later alliance formation in a way that alliance partners seal their bond when engaging in harmonic play. Alliance partners are expected to engage in playful behaviours repeatedly and take turns in initiating play. If friendship is strengthened through play, we expect individuals with a more valuable relationship to show more frequent and higher quality play than other dyads.

Questions and Hypotheses:

The aim of this study is to investigate early ontogeny of social and object-oriented behaviour in ravens with emphasis on play. Our questions were twofold: when do patterns emerge and how are they affected by social context.

We used two approaches: i) detailed observations of a group of captive individuals over a 10 week period, starting with 1 week pre-fledging, ii) a behavioural experiment in which we were testing the effect of social context (i.e. the visibility of conspecifics) on playful object manipulation. Based on Heinrich (1995) we expected young ravens to display high interest in objects and to interact with one another already early in life. This could offer opportunity to engage in play shortly after fledging. If playful birds were primarily interested in information about objects, play should go temporally together with object manipulation. Alternatively if birds were interested in information about conspecifics, play should go together with (affiliative) social interactions. In any case play should be negatively affected by the emergence of agonistic behaviours.

In respect to the Experiment: we hypothesized that having visual access to others should positively affect playful object manipulation i.e. increase manipulations when inside view as compared to when view to others is blocked.

General Methods

Subjects and Housing

I used a group of 7 juvenile ravens. Two ravens were taken from the wild and two were from captive breeders with about 34-37 days prior to fledging and hand raised at the Konrad Lorenz Research Station (KLF). I kept them according to their provenance separated in two nests during raising. They fledged in May 2008. They were fed every 2 – 2 ½ hours. Water was available ad libitum. The other three ravens were raised by their ravens parents in a zoo in Wels, Upper Austria. They joined the group in their fourth week post fledging, they were two weeks older than the hand-raised birds and were kept in one social group together with the other juveniles. All birds were individually banded with coloured leg-rings.

After fledging I moved the 4 ravens into an outdoor aviary in the Cumberland Gamepark in Grünau im Almtal, Upper Austria. (See Fig. 1.) The aviary (ca. 240m2; Fig. 1) consists of three sections, each made of one to three compartments, which allows separation of individuals during experiments. (Coloured part of Fig.1.) In the left part of the aviary a breeding pair was housed and they were always spatial separated from the young ravens. The big sections of the aviary had natural vegetation, rocks, water basins, perches, trees and bushes as well as rain protected platforms and shades.

Unfortunately the 3 raven-raised individuals developed symptoms for a brain disease. And all of them sooner or later started to separate from the group and consequently used to be excluded from the analysis.

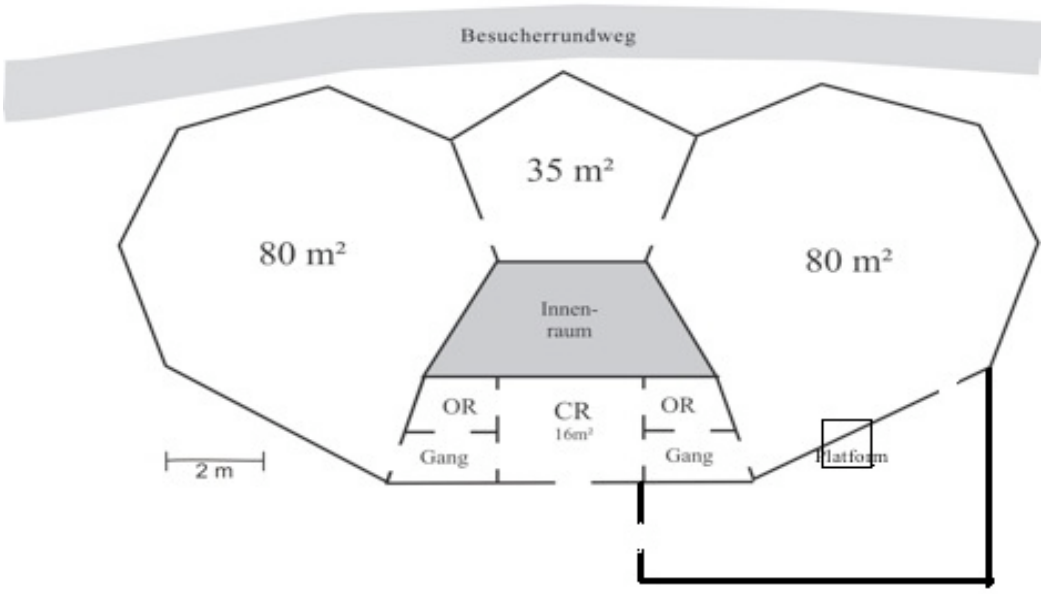

Figure 1. Sketch of the aviary at KLF

Data collection and Analysis:

Observations in the group:

Individuals were observed twice a day (morning and afternoon). I used focal observations focusing on affiliative, aggressive (social structure development of the group) and mainly object manipulation (either solitary and social) behaviours twice a day. See Table 1 for definitions. Each bird was observed in a pseudo-randomized order (I controlled for not having one individual two times in a row) for 5min. before feeding, 5min during feeding and 10min. after feeding during each sampling period.

All protocols were videotaped.

All data were analysed with SPSS 19.0 and PASWStatistics 18.0. I first conducted a Principal component analysis (PCA) to reduce the set of variables. PCA is a statistical technique that can be used to identify underlying factors, or principal components, that explain the pattern of correlations within sets of variables (Tabachnick&Fidell 2007).

I also did cross correlations in PASWStatistics 18.0. Cross correlations show the correlation between two series at the same time. The Cross correlation function (CCF) between two series shows the lag at which they are most highly correlated. The plots display correlations at both negative and positive lags. A negative lag indicates that the first series, *play*, follows the second series (*object related, cache related, socio positve, approach retreat*).

A positive lag indicates that the first series, *play*, leads the second series.

Behavioural Experiment:

The Experiment was conducted over a period of 10 weeks, starting from the first week post fledging. All birds were fully habituated to be separated from the group at the beginning of the experiment. The tests were conducted in the experimental compartments of the aviary and birds were observed across the experimental conditions with only the test birds having visual access to the test area: 1) in private condition in which they were tested individually; 2) a social condition in which they were in front of their conspecifics (labelled as bystander). I looked at i) what were they doing with the objects and ii) what they were doing with the objects in front of others.

I presented a set of two different portable objects, i.e. a small coloured plastic item and a bigger plastic item, for example a tiny cup so they could also stick something smaller into the tiny cup. I defined the duration of a bout from the moment when the bird first touched the object until the time the object was abandoned/unused more than 5 min. I recorded various types of interaction among object holder(s) and other individual(s) (bystander). I also recorded how each participant behaved towards others (bystanders) including approaching and leaving. I divided the behavioural variables into patterns which are performed solitary and patterns which are performed socially. Then I compared them over the two conditions: alone or when there is a bystander.

All experiments were video-taped for analysis. I conducted paired t-tests for the solitary performed behaviours using SPSS 19.0. For the socially performed variables the sample size did not allow statistical testing.

Results

i) Observations: Which patterns and when do they emerge?

From the 14 observed behavioural variables, five components were extracted by the PCA. Components 1, 2, 3, 4, and 5 explain 37,5%, 17,3%, 8,9%, 8,1%, 6,1% of overall variance, totalling 73,9%. See table 1 for loadings for each of the behavioural variables on each extracted components.

The first extracted component included high loadings from the behavioural variables approach-request, play invitation, chaseflight, touch/touch back. All of these behaviours show a playful character so I labelled this variable „play related“. The second component had high loadings of load, transport, stick to/in and cover, which I labelled „cache related“. The third extracted component was characterised by high loadings of object handling and therefore

represented „object related“ behaviour. The fourth component included behavioural variables approach-retreat and forced retreat that's why I labelled it „approach retreat“. And the fifth and last component extracted was only one behavioural variable such as groom and I labelled it „socio positive“.

Table 1.
Values represent coefficients of correlation between each variable and each component. Values of>0.5 or<_0.5 (marked in bold) were considered high loadings.

Table 1
Varimaxrotatedcomponentmatrix

	Variable	Component				
		1	2	3	4	5
Play related behaviours	Approach-request	**0.817**	0.226	0.393	−0.021	0.100
	playinvitation	**0.803**	0.111	0.192	0.175	−0.050
	chaseflight	**0.902**	0.104	0.052	0.063	−0.155
	touch/touch back	**0.775**	−0.067	0.311	0.135	0.240
Cache related behaviours	loading	0.108	**0.836**	0.279	0.057	0.127
	transport	0.243	**0.812**	0.192	0.265	0.056
	stick to/in	−0.007	**0.895**	0.147	0.253	0.093
	cover	0.007	**0.797**	−0.280	0.248	−0.002
Object related behaviours	pilfer	0.279	0.021	**0.711**	0.024	−0.211
	manipulatingtogether	0.107	0.140	**0.812**	0.120	0.010
	manipulate	0.249	0.000	**0.837**	−0.060	−0.081
Approach retreat behaviours	approach-retreat	0.122	0.295	−0.156	**0.813**	−0.045
	forcedretreat	0.298	0.079	−0.033	**0.689**	0.098
Sociopositiv behaviours	grooming	−0.013	−0.142	0.142	−0.078	**−0.909**

The development of object-related behaviours (object manipulation) occur already in the nest, peak in 4th week post fledging and then decline to levels lower than in nestling phase. Cache-related behaviour does not occur before week 2 post fledging, increases till week 5 and then occurs approximately at a same rate as object manipulation (see Fig. 2.).

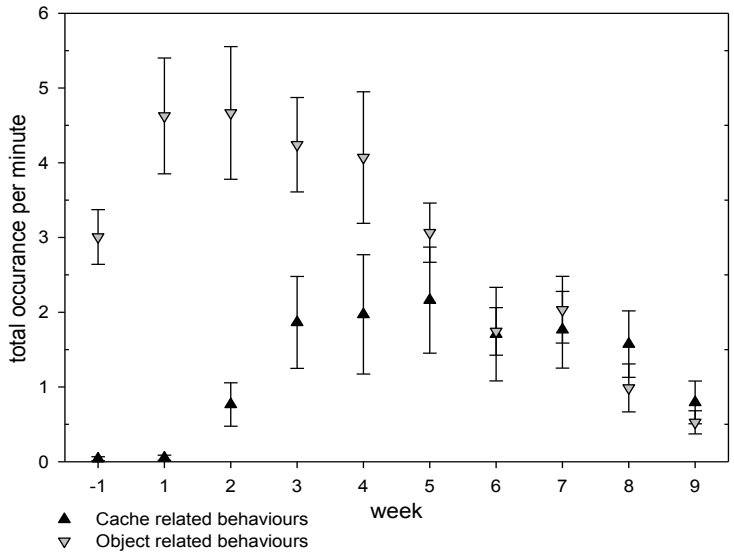

Figure 2. Object Manipulation. Occurence of cache related behaviours and object related behaviours from week -1 to week 9 postfledging.

The development of components describing playful and social interactions show that the first few play-related interactions occur already in nest, increase within first month and peak in week 4 postfledging. Afterwards they decline to levels comparable with nestling stage. Sociopositive behaviours are also present already in the nestling stage and they remain low over the entire period. Socionegative behaviours, in contrast, are not existing until end of the first month postfledging, but dominate in the second month (see Fig. 3.).

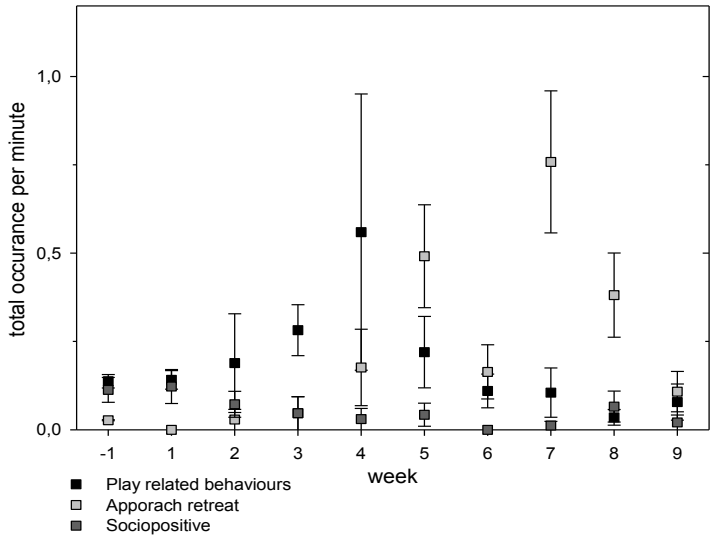

Figure 3. Social Interactions. Occurence of play related behaviours, approach-retreat behaviours and socio positive behaviour over 10 weeks.

Play related behaviours and object related behaviours reveal a positive correlation at lag 0 indicating that these two patterns change at the same time (see Fig. 4.).

Play related and cache related behaviours show positive correlations at lag 0 and lag +6 indicating that the beahviours change at the same time and that cache related behaviours preceeds play related behaviours (see Fig. 5.).

Play related and sociopositive behaviours correlate at lag -6 indicating that play follows sociopositive behaviour (see Fig. 6.).

Play related and approach retreat behaviours did not correlate significantly at any time (see Fig. 7.). For Fig. 4. – Fig. 7. x-Achsis show lag number. y-Achsis show cross correlation function. Horizontal lines indicate significance levels ($p < 0,05$).

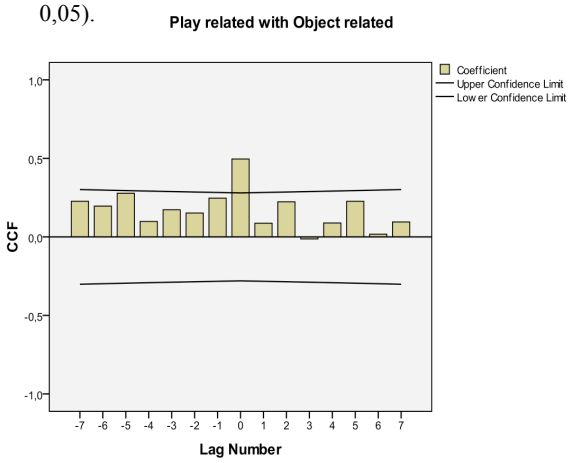

Figure 4. Cross correlation between play related behaviours and object related behaviours.

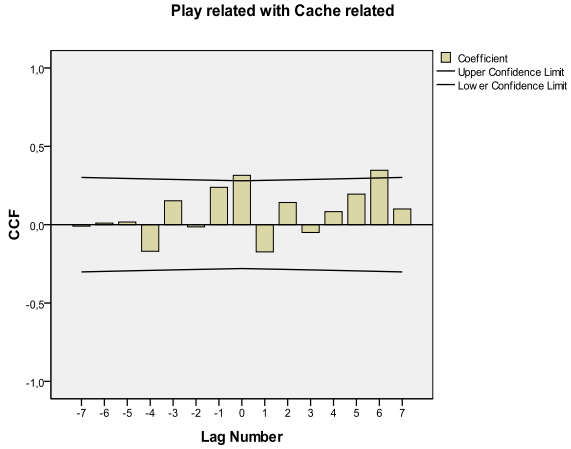

Figure 5. Cross correlation between play related behaviours and cache related behaviours.

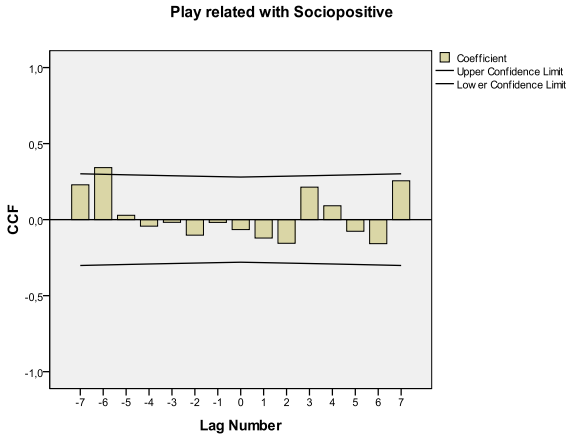

Figure 6. Cross correlation between play related behaviours and sociopositive behaviours.

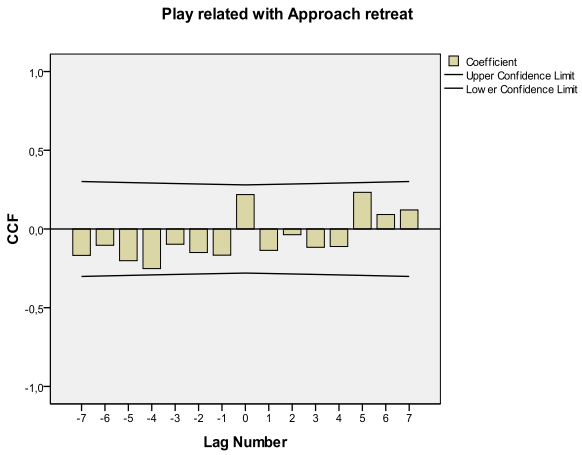

Figure 7. Cross correlation between play related behaviours and approach retreat behaviours.

ii) Experiment: Effects of visibility of conspecifics on playful object manipulation?

From the 12 solitary performed behaviour patterns the number of loading, caching and sitting differs between the two conditions. The number of loadings is significantly higher when in the bystander condition, sitting and caching show just a trend. That means the test birds load and cache more when they are in the bystander condition and sit less (see Fig. 8.).

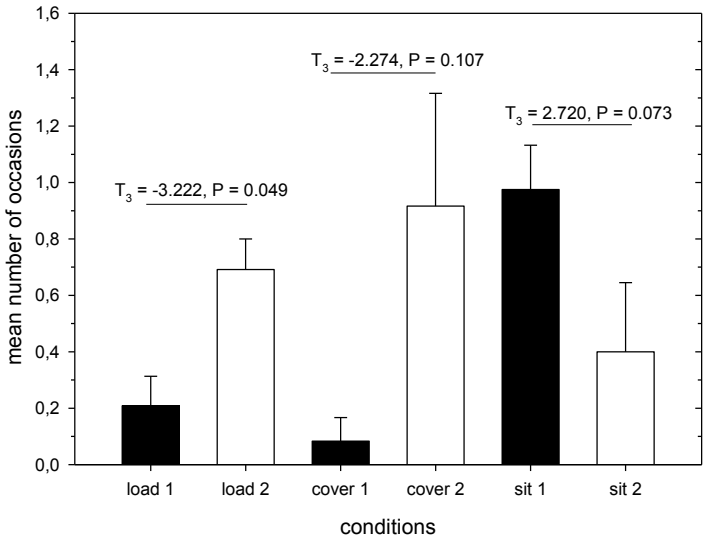

Figure 8. Solitary performed behaviours. Number of loading, caching, sitting per testsession in two conditions. Black bars solitary condition. White bars condition with a possible bystander.

Discussion

My observations reveal two kinds of object-oriented behaviours which are manipulation and caching. There are different developmental trajectories: manipulation precedes caching by roughly a month. The latter may go together with the development of cognitive skills, specifically the birds' acquisition of Piagetian Stages of object permanence (Piaget 1937/1954). This corresponds to a previous study showing that the skills for making caches are affected by the memory capacities for temporary unvisible items (Bugnyar et al. 2007). Object permanence is considered as a fundamental cognitive skill that may serve as basis for more complex cognitive mechanisms (Ujfalussy et al. 2013).

We know that corvids who play socially often do so in the context of object manipulation, so our results fit to those of Moreau & Moreau (1944), Kilham (1989), Deckert (1991), Heinrich & Smolker (1998). Juvenile ravens spent much time in object manipulation and their drive to manipulate all kinds of objects (edible or inedible) has been described as „neophilia" (Heinrich 1995). A similiar phenomenon has been termed „play" in Australien magpies, *Gymnorhina tibicen* (Pellis 1981a,b). Object manipulation and play related behaviour correlate positively in time, which points towards attraction to conspecifics that manipulate objects rather than just being attracted to objects per se.

The sociopositive behaviours are present from beginning but remain at low rates. The socionegative behaviours are not present from the beginning but develop at the end of the first month. Although not significant socionegative behaviours seem to cross-correlate negatively with object manipulation and play (see Fig. 8.). This raises the possibility that the decline in object oriented behaviour and play may be caused by agonistic behaviour. The expression of patterns may thus be constrained by developing dominance relations, which fits to findings in Loretto et al. (2012).

As expected the development of caching goes together with play. Possibly these behaviours rely on similar cognitive and/or motoric prerequisits. Moreover learning about conspecifics may take place during playful object caching in a social setting (Bugnyar et al. 2007). Importantly, our observational findings receive support by our experiment: social context per se does not hinder play, on the contrary, the possbility of being observed facilitiates playful object manipulation. Having conspecifics around thus leads to a higher likelihood of playful object manipulations and, under daily life conditions, interactions over these objects. Such interactions may contribute to the acquisition of sophisticated social knowledge, i.e. how others are behaving in various situations, including the formation of social relationships like alliances and/or friendships (Fraser & Bugnyar 2010). Such relationships may be of affiliative character – in this case the playful interaction remains – or, more often, become socio-negative – in that case the play is interupted or stoped. This could explain why overall rates decline.

It is noteworthy that young corvids have an extensive developmental period before they become independent from their parents (Clayton & Emery 2005). Ravens live in a wide range of geographical and ecological diversity and experience a great deal of seasonal diversity

(Heinrich 1999). Their food sources and dangers are not static that's why object play and manipulation may serve to familiarize young ravens with potential food items that may be unique to their ecological circumstances (Heinrich 1995). Learning about what is good to eat or not, and what is dangerous and what is not in a „play" context without pressure may be critical for later success. It thus seems likely that play occurs for the development of certain adult skills.

Taken together, very young ravens already show a variety of playful activities, most of which are linked with object manipulation and, in a later stage, with caching. Sociopositive behaviours seem to support playful interactions, whereas socionegative behaviours may hinder them. Overall, play is facilitated by a social setting.

For detailed insight it would be useful to conduct a study over a longer period of time. We suggest that it may be interesting to collect data over the first six months post fledging or even longer when the juveniles become independent from their parents and join the non-breeder groups. Also increasing the sample size could provide crucial clues concerning the comparison between sex and kinship.

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Zusammenfassung

Corviden sind bekannt für ihren vergrößerten präfrontalen Cortex und ihre komplexen kognitiven Leistungen, die vergleichbar sind mit denen von Primaten. Ein Grund für diese Entwicklung des Gehirns könnte das Leben in sozial komplexen Gruppen sein. Neueste Beobachtungen zeigen dass es in Corvidengesellschaften wichtig ist sich individuell zu erkennen und ganz selektiv gewisse Verhaltensweisen miteinander auszutauschen. Die individuellen sozialen Beziehungen gibt es nicht nur unter Verwandten wie zBsp. Geschwistern sondern auch zwischen nicht verwandten Artgenossen. Diese sozialen Bindungen sind charakterisiert durch viel soziopositives Verhalten und wenig Aggression, gegenseitige Gefiederpflege und soziales Spielverhalten.
Man weiß von jungen Vögeln, vor allem in der Familie der Rabenvögel, dass sie ein hohes Maß an Sozialspiel und eine Bandbreite an Spielverhalten zeigen.
Man vermutet dass das Spielen mit Anderen ein Schlüssel sein kann um seine Artgenossen kennen und einschätzen zu lernen. Um beispielsweise das Verhalten eines Anderen voraussagen zu können und/oder andere Individuen zu manipulieren für den eigenen Vorteil. Diese Fähigkeiten könnten von Vorteil sein wenn man in großen sozialen Gruppen lebt und konfrontiert ist mit einem hohen Level an Konkurrenz und Kooperation.
Das Ziel dieser Arbeit war die Untersuchung der frühen Entwicklung von sozialem und objektorientiertem Verhalten mit dem besonderen Fokus auf Spielverhalten.
Unsere Fragen waren wann entwickeln sich die einzelnen unterschiedlichen Verhaltensweisen und wie werden sie beeinflusst von sozialem Kontext.
Ich habe tägliche Sozialprotokolle genommen und außerdem ein Experiment mit zwei Konditionen gemacht.
Die Beobachtungsergebnisse werden unterstützt durch die Ergebnisse aus dem Experiment. Soziopositive Verhaltensweisen scheinen Spielverhalten zu steigern, und sozionegative Verhaltensweisen können Spielverhalten hemmen. Alles in allem wird Spielverhalten durch ein soziales Gefüge gesteigert.

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