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„Affiliation affects social learning in keas (*Nestor notabilis*) and ravens (*Corvus corax*)“

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1 INTRODUCTION

1.1 Social foraging and social learning

Social foraging

Foraging in groups offers a lot of benefits, probably the most important being reliable information about appearance and location of valuable food obtained by watching conspecifics (Gochfeld and Burger 1982). According to the social foraging theory (Giraldeau and Caraco 2000) an individual´s benefits and costs during foraging are interdependent with the behaviour of group members that are foraging together, no matter whether the individuals are attracted towards each other or towards the same food source (Giraldeau and Caraco 2000). However, this can be applicable to other situations beyond the foraging context as well (Giraldeau 1997). According to Coussi-Korbel and Fragaszy (1995) in stable social groups with long-term relationships every aspect of life is influenced by the social context. Hence, it is not only the behaviour of conspecifics that might influence one´s own decisions, but the identity of the group members and their specific relationship. It is therefore very likely that the current social environment has an effect on the likelihood to show social learning for example, and maybe the social context even affects the type of information gained by the individuals creating that specific social context (Coussi-Korbel and Fragaszy 1995).

Social learning

Social learning is involved in a lot of aspects of life and serves crucial functions like predator recognition (Giraldeau 1997), exploiting new food sources (Fisher and Hinde 1949, Mason and Reidinger 1981), learning how to use a food source (Aisner and Terkel 1992), or for naïve individuals to learn about the environment (Coussi-Korbel and Fragaszy 1995), being it the social or ecological environment (Diamond and Bond 1991).

A lot of different behaviours have been subsumed under the term social learning in the literature (Galef 1988). Here, the aim was not to look at the different psychological mechanisms of those processes or to investigate the performance of a socially learned behaviour from a model in terms of whether it is imitation, goal emulation, etc. Social

learning in this study is rather understood on a relatively basic level, namely as a shift in attention and thereby the obtainment of different kinds of information by an observer from a demonstrator.

Hence, when a group of individuals encounters several new objects there are different ways to react towards this situation. Either each individual could engage in object exploration on its own or some kind of social learning mentioned above could drive the decision towards which object to focus one´s own attention. As social learning is a powerful and cheap way of learning crucial aspects of life and gaining valuable information about the social or ecological environment, it is likely to be involved in object exploration as well.

1.2 Social learning mechanisms and influences

1.2.1 Social learning mechanisms

In this study the term social learning means the use of information provided by conspecifics about objects or places. Stimulus enhancement (or object copying, Giraldeau 1997) occurs when an individual directs its behaviour to an object that matches the object a conspecific is attending to. However, local enhancement (or area copying) occurs when an individual adjusts its behaviour towards an area at which conspecifics have currently been seen acting (Giraldeau 1997). A third form of shift in attention and gaining information from a demonstrator thereby would be to go for exactly the object the demonstrator is manipulating at the moment. This is meant when speaking of go for the same object in the following. This form of social learning affords the most valuable information and, if successful, allows for direct access to the item. This kind of social learning mechanism has also been termed tolerated theft (Blurton-Jones 1984) or sharing (von Bayern et al. 2007).

Although information gained by local and stimulus enhancement may be of similar value, stimulus enhancement might provide more secure information than local enhancement, as the observer sees that the demonstrator bird is already manipulating a particular item. Whereas, in case of local enhancement, the outcome is unclear, i.e. whether searching in this area leads to an item of interest (e.g. food). Nevertheless, local enhancement might be particularly relevant for extractive foragers like keas, when they are digging for roots in the ground (Jackson 1960, Huber et al. 2008). Similarly, local enhancement could be important when observing others caching food, like it has been reported for ravens (Bugnyar et al. 2007). In contrast to both forms of enhancement, go for the same object should come with an increased risk of an aggressive encounter. Hence, each of those social learning forms has its pros and cons;

while on the other hand, each of it is advantageous in comparison to not gaining any information at all by watching conspecifics.

That the use of information provided by conspecifics is common among group living animals has been reported in a lot of studies (see following examples). How exactly information is used, though, is still under debate, especially for low-level mechanisms like enhancement (Hoppitt and Laland 2008) Red-winged blackbirds *Agelaius phoeniceus* for example select new food sources according to the choice of their conspecifics (Mason and Reidinger 1981) and florida scrub-jays *Aphelocoma coerulescens* learn to use new food sources when exposed to skilled family members (Midford et al. 2000). Burmese fowl *Gallus gallus* showed both local and stimulus enhancement after being exposed to a conspecific feeding in a specific area or from a certain bowl (McQuoid and Galef 1992). There is anecdotal information that in a play context, juvenile siblings of scrub-jays showed local enhancement, too (Midford et al. 2000). These strategies have been suggested to be influenced by social and non-social factors such as for example affiliations between individuals (Schwab et al. 2008), dominance (Katzir 1983), sex (Stöwe et al. 2006b), age (Diamond and Bond 1991) or behavioural phenotype (Stöwe et al. 2006b).

1.2.2 Parameters influencing social learning

Social relations: affiliation and dominance

Affiliation

In despotic societies the relationships between individuals are characterized by either mainly agonistic interactions or affiliative ones (Coussi-Korbel and Fragaszy 1995). Affiliative relationships offer the benefit of information sharing or support in agonistic interactions (Fraser and Bugnyar 2010). Furthermore affiliated conspecifics are likely to share resources and they are said to react in a predictable way, making the information they provide more reliable. Affiliation moreover affects the likelihood of paying attention towards a conspecific (Coussi-Korbel and Fragaszy 1995 after Chance and Jolly 1970). Variation in the quality of relationships potentially influences a lot more phenomena, such as postconflict behaviour (Aureli et al. 2002), gaze-following (Micheletta and Waller 2012), spatial proximity (Coussi-Korbel and Fragaszy 1995) and novel object exploration (Stöwe et al. 2006). Ravens have been shown to increase attention towards affiliates in comparison to non-affiliated ravens when they watch them handling objects or food (Scheid et al. 2007). Therefore, affiliate relations might lead to directed social learning (Schwab et al. 2008). Moreover, spatial proximity enhances the likelihood of social learning (Coussi-Korbel and Fragaszy 1995), while only affiliated conspecifics seek or are tolerated in proximity. Whether ravens encounter novel objects in a group with siblings, i.e. affiliated group members, or in a group with

familiar but non-sibling (i.e. non-affiliated) birds has an effect on their exploratory behaviour (Stöwe et al. 2006b). In a novel object exploration task, ravens spent more time sitting next to siblings than to non-siblings. Furthermore the mean approach latency was higher in a group of non-sibs than when alone. The birds followed siblings faster to approach the novel object than they followed non-sibs (Stöwe et al. 2006b). Apparently affiliated birds attract each other. In an object choice task ravens handled those objects longer they have seen being manipulated by their siblings, whereas in non-sibling dyads birds did not show such a preference, even when spatial proximity has been controlled for (Schwab et al. 2008). Hence, the relationship between the individual providing and the individual gaining information could well determine the outcome of this situation in terms of social learning. It is likely that affiliation affects social learning.

Dominance

When within a group aggressive interactions end in a certain predictable way and some individuals have priority in access to resources, these relationships are referred to as rank hierarchies (Katzir 1982). Dominance is predicted to affect social learning. In birds social learning is influenced in a positive way, when the demonstrating individual is more dominant in the rank hierarchy in comparison to the observer bird (*Corvus monedula*: Katzir 1983; laying hens, *Gallus gallus domesticus*: Nicol and Pope 1994). On the other hand, Katzir (1982) suggests that high-ranking birds learn more by observing lower ranked birds in exploration, while mid- or low-ranking individuals learn more by their own experience. This makes sense in the light that their access to resources is often restricted by dominant conspecifics forcing them to find alternative resources on their own. Birds low in rank would consequently serve as demonstrators, while individuals high in rank would show high social learning frequencies. Go for the same object is likely shown by high-ranking individuals because they do not have to fear many aggressive interactions directed towards them. The same may hold true for local enhancement. Stimulus enhancement may be the social learning form least affected by dominance.

Individual attributes: sex, age, and behavioural phenotype

Sex

In many species sexes differ in exploratory behaviour (Agren, Zhou and Zhong 1989, Gaulin, Fitzgerald and Wartell 1990) and parental investment patterns, which imposes different costs on individual learning (Choleris and Kavaliers 1999). This facilitates the occurrence of sex differences in several behaviours including social learning. Mice (*Mus musculus*) for example, acquire information differentially from a conspecific, according to their sex (Collins 1988). However, there is no difference in social learning performance between the sexes in common marmosets (*Callithrix jachus*, Bugnyar and

Huber 1997). In keas most foraging groups in the wild are made up of males (Diamond and Bond 1991). When one or more keas start to forage in a certain area, soon other males join them (Diamond and Bond 1991). Hence, the possibility to show social learning here is higher in males than in females. Male ravens were faster to approach novel objects than females, when tested in dyads. Moreover, they spent more time close to and manipulating them. And they joined a conspecific faster in approaching the novel object than females did (Stöwe et al. 2006b). Consequently, the possibility to show any kind of social learning is higher in male than in female ravens, too.

Age

Age is suggested to influence social learning behaviour as the need and quantity of what should be learned differs between subadults and adults. For young, group living individuals that have to learn what to eat, where to forage etc. social learning is of great importance (Nicol 2004). Chicks of domestic fowl (*Gallus gallus domesticus*) for example pay most of their attention towards adults. For them social learning in a foraging context is of greater importance than for adult fowl (Nicol 2004). Some of the keas that took part in the study were still subadult (< 4 years), while the other ones were adult (> 4 years; Tab. 1). Diamond and Bond (1991) have also shown that foraging and social behaviour differs strikingly between subadults and adults. Subadults are, in comparison to fledglings, juveniles, and adults, the age group that approach feeding conspecifics most often (Diamond and Bond 1991) as they seldom find food on their own (Huber et al. 2008). They are therefore dependent on gaining information where to search for food by watching conspecifics. Furthermore they are the age group most often displaced and defended against in a food context and have the least chances to protect resources. Therefore on the other hand subadults show most frequently theft or kleptoparasitism (Diamond and Bond 1991), which would be go for the same object in this study, than any of the other age groups. Hence, in comparison to adults, subadults are more selective in their social interactions as they pay mainly attention to objects that adults control, especially when these objects are very valuable (Diamond and Bond 1991). Social learning seems to be used differentially by different age classes and especially extensively by subadults.

Behavioural phenotype

A lot of animal studies have shown that individuals differ in their way to master everyday challenges (Koolhaas et al 1999). Individuals can be differentiated according to sets of behavioural and physiological stress responses to show a proactive / bold or reactive / shy coping style (Koolhaas et al 1999). Animals with different behavioural phenotypes might react differently to the same treatment (Groothuis and Carere 2005), it is therefore important to take individual behavioural phenotypes into consideration. It was shown that exploration behaviour correlates with certain behavioural phenotypes

such as boldness for example, which are consistent over contexts and development for each individual (Koolhaas et al. 1999, Groothuis and Carere 2005, Stöwe et al. 2006). Individual ravens differ in the amount of time manipulating novel objects and in the amount of time spent sitting close to those objects (Stöwe et al. 2006b). This is suggested to be due to differences in behavioural phenotype.
Proactive pigs are less inhibited in approaching novel objects, but spend simultaneously less time exploring them in comparison to reactive conspecifics (Hessing 1994 after Koolhaas et al. 1999). In dairy calves it was observed as well, that the more reactive the individual, the more time it needs to approach a novel object (van Reenen, unpublished observation after Koolhaas et al. 1999). Therefore, I would argue that proactive individuals are more likely to function as demonstrators because they encounter the objects first and consequently reactive birds would show more social learning as they can gain information by watching conspecifics.
Birds that are very fast to explore a new environment, being characterized as proactive, also more quickly form behavioural routines (Groothuis and Carere 2005). They furthermore spend less time near conspecifics, which both suggests them to be less attentive to others´ behaviour and therefore show less social learning than reactive individuals.

1.3 Why study keas and ravens?

Sol et al. (2005) have shown that large brained birds such as parrots and corvids where more innovative when introduced to a novel environment in comparison to smaller brained birds and are therefore suitable for testing explorative behaviour. Both keas and ravens show a vast variety of similarities, such as high sociality (Jackson 1960, Clarke 1970 and Huber et al. 2008 for keas and Bugnyar and Heinrich 2006 and Bugnyar et al. 2007 for ravens), extended association with their parents (Jackson 1960, Clarke 1970 and Huber et al. 2008 for keas and Ratcliffe 1997 for ravens), formation of non-breeder groups when subadult (Jackson 1960 for keas and Ratcliffe 1997 for ravens), long potential life span, and opportunistic foraging or omnivory (Clarke 1970, Diamond and Bond 1991 for keas and Ratcliffe 1997 for ravens). Moreover, keas are known for their exploratory behaviour and curiosity (Huber et al. 2008). Ravens are said to be very exploratory birds, too, when neophobia has not yet developed and/or is controlled for (Heinrich 1995) and are thus suitable for testing in an exploratory context.
In keas social dynamics have not been studied extensively yet, although they are known for their complex social behaviour (Diamond and Bond 1991). Keas seem to show quantitatively less social interactions in general in comparison to ravens (own observation) but have shown to manipulate conspecifics to cooperate (Tebbich et al. 1996) and use them as social tools (Range et al 2009). Like in ravens, theft of food from group members is an important foraging strategy, especially for subadults (Huber et al.

2008). Paying attention to conspecifics handling objects is consequently shown already early in life (Diamond and Bond 1991).
Ravens are well known for their manipulative use of conspecifics to meet their own goals and for their social competences. They have been reported to use bystander affiliation (Fraser and Bugnyar 2010b), alliances (Marzluff and Heinrich 1991, Fraser and Bugnyar 2012) and 'tactical' deception (Bugnyar and Kotrschal 2002, 2004). Furthermore they are very attentive to others manipulating items (Scheid et al. 2007) and raiding caches made by conspecifics is a standard foraging technique (Bugnyar and Kotrschal 2002, Bugnyar and Kotrschal 2002b). This is even applied to non-edible objects (Bugnyar et al. 2007, 2007b). Notably, the finding and raiding of caches is depending on observing others when caching, i.e. social learning about the exact location through delayed local enhancement (Bugnyar and Kotrschal 2002).
Both species use social learning as a common strategy to gain information (Huber et al. 2001, Bugnyar and Kotrschal 2002, Stöwe et al. 2006, Huber et al. 2008). The many similarities both species share and their social competences make them perfect candidates for testing the influence of social relations on social learning in a comparative study.

1.4 Aim and predictions

Following Coussi-Korbel and Fragaszy (1995), I am interested in whether the frequency or form of social learning shown by the birds is exhibited differentially as a function of the identity of the bird that provides the information. Therefore I tested, whether being in a group of affiliated or non-affiliated conspecifics or the whole group of conspecifics influences the frequency or form of social learning. Specifically, I addressed the following questions: (i) whether the social environment influences object exploration, (ii) how birds are influenced in their exploration behaviour (i.e. what form of social learning is shown), and (iii) whether social relations (affiliation, dominance) and individual attributes (sex, age, behavioural phenotype) influence social learning.

As keas are highly neophilic and known for their extreme manipulation of objects, I expected them to be more explorative and to show more pronounced manipulation of the objects than ravens. Similarly, due to their neophobia, ravens are expected to show less manipulation.
Since social learning is a strategy used by keas and ravens (Huber et al. 2001, Stöwe et al. 2006), I predicted that the birds will choose the objects or area to attend to according to the behaviour of their group members, i.e. show social learning in this experimental set-up. Similarly, due to differences in manipulation behaviour, I expect to find differences in social learning as well, with keas showing more social learning than ravens.

Stimulus enhancement offers the certainty about gaining a valuable item (as a group member is manipulating it) without the cost of a possibly aggressive interaction. If such costs and benefits influence social learning and if perhaps additional properties of the objects play a role, I would predict stimulus enhancement to be shown most often.
Increased attention towards, and closer proximity between affiliates are predicted to increase social learning probabilities. If affiliation affects social learning, I would predict social learning frequencies to be higher in affiliated than in non-affiliated bird groups.
Birds positioned high in the rank hierarchy are likely to show more local enhancement and go for the same object than low-ranking individuals, because they do not need to fear high costs of aggressive encounters. If the position in the rank hierarchy has an influence on social learning, I would, in line with Katzir (1982), predict that high-ranking individuals show more social learning than low-ranking ones. Males are more prone to approach and join conspecifics. Thus, if sex has an effect on social learning, I would predict males to show more social learning than females. Subadults are dependent to find food by watching conspecifics. If age influences social learning, I would predict subadults to show more social learning than adults; especially more go for the same object. Proactive individuals approach novel objects faster than reactive ones and they attend less to the behaviour of conspecifcs. If behavioural phenotype affects social learning, I would predict reactive individuals to show more social learning than proactive ones. In exact, reactive birds are expected to avoid possible aggressive interactions and therefore might show stimulus enhancement rather than local enhancement or go for the same object.

2 METHODS

2.1 Subjects and housing

Both species, keas and ravens, are housed at Haidlhof Research Station near Bad Vöslau, Austria. All birds are marked with coloured leg bands for individual identification. The group of keas consisted of 19 individuals, 11 males ranging from 12 to 1 year in age and 8 females ranging from 11 to 1 year in age. For the current study, 11 subjects were chosen to match the number of tested ravens (see Tab. 1). Outside experiments, all keas were housed as a social group in a 52,0m x 10,0m x 5,40m big aviary with several branches, nest boxes, artificial ponds, stones, and flower beds. The floor is made of fine-grained sand. The aviary can be divided into several subcompartments one of which can be visually separated (Fig. 1). The flock of ravens consisted of two groups. The focal group of this study held 6 male and 5 female birds, which were all at the end of their first year (see Tab. 1). They were housed in a 15,0m x 15,0m x 5,00m big aviary with several branches, tree trunks, artificial ponds, stones, trees, and flower beds (Fig. 1). A second group of 3 female ravens was housed adjacent

in a 10,0m x 18,0m x 5,0m big aviary. Subjects of this group were used for a preference test. The whole aviary complex is made up of several compartments that are connected by runways and can be opened and closed for experiments. Birds of both species received their normal diet throughout the experiments. Keas were fed three times per day with fruits, seeds, vegetables, dairy products, and other protein sources. Ravens were fed once a day with meat, dairy products, eggs, fruits and vegetables. Water was available *ad libitum*.

Tab. 1: Subjects participating in the experiments

	Keas			***Ravens***	
Name	***Sex***	***Age***	***Name***	***Sex***	***Age***
Coco	female	4 years	**Anton**	male	1 year
Frowin	male	7 years	**Elen**	female	1 year
Hope	female	4 years	**Heidi**	female	1 year
Kermit	male	7 years	**Jakob**	male	1 year
Linus	male	7 years	**Jonas**	male	1 year
Lilly	female	4 years	**Klara**	female	1 year
Pick	male	7 years	**Lasse**	male	1 year
Plume	female	4 years	**Lena**	female	1 year
Sunny	female	4 years	**Sophie**	female	1 year
Tammy	male	4 years	**Sven**	male	1 year
Willy	female	4 years	**Willi**	male	1 year

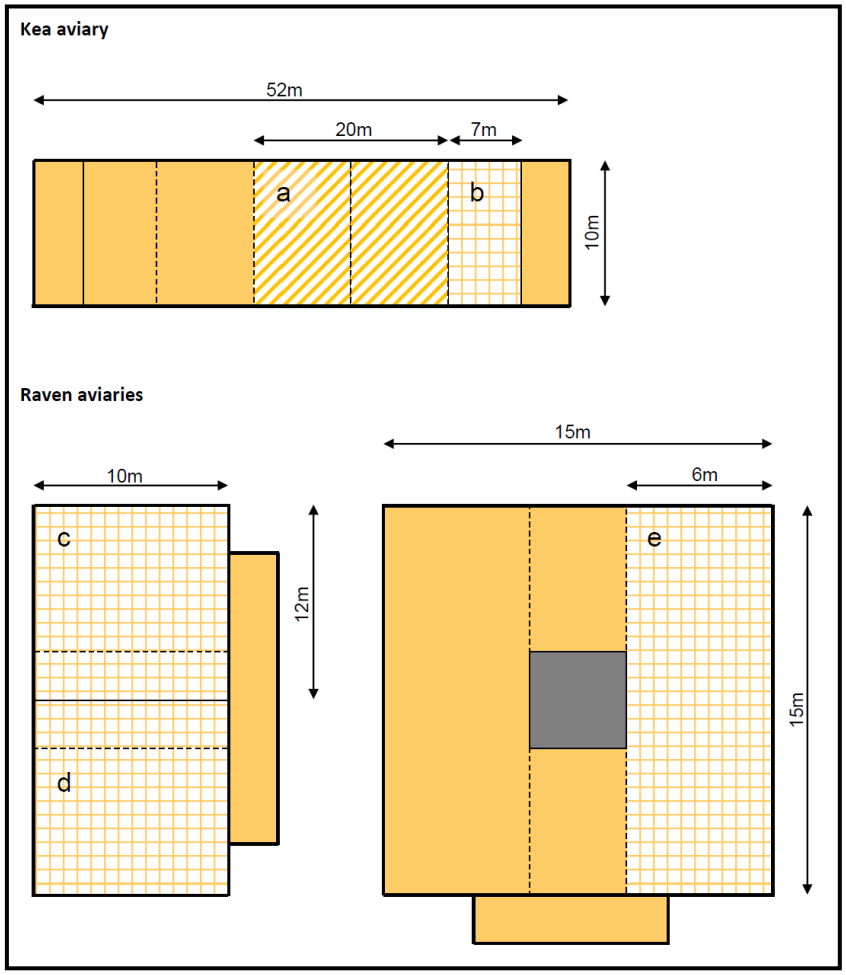

Fig. 1: Simplified scheme of the aviary complex of keas and ravens (note that the aviary for the handraised ravens is not depicted here) with patterned testing compartments

2.2 Observational data and experimental procedure

Social relationships and dominance hierarchy in the groups of keas and ravens were determined by assessing frequencies and durations of socio-positive and socio-negative behaviours outside the experiments. With the help of these protocols, a baseline activity of social interactions and object manipulation activities was also determined. In the keas, group protocols were conducted twice a week, each lasting about 25min and containing scan samples of each bird and behavioural samples of the whole group (Martin and Bateson 2008). Behavioural samples during feedings were conducted about five times per week. In addition, social protocols were conducted once a week for 5min each bird using focal sampling method (Martin and Bateson 2008). As keas show social interactions less frequently than ravens, group protocols and behavioural samples during feeding were chosen for analysing affiliations and dominance. Social protocols of ravens were conducted one to two times per week for 5min per bird. Those focal

samples were done either after or before having provided them with food. For ravens social protocols were used to analyse affiliations and dominance. Social protocols for both species were videotaped and coded with Solomon coder.

Testing took place in three different conditions: (i) in the whole group, (ii) in subgroups of affiliated birds, and (iii) in subgroups of non-affiliated birds. Experiments for the whole group were conducted before and after each separation into the subgroups (see Tab. 2 for detailed time schedule). In the whole group condition, 11 birds were tested in one social group. In the affiliated birds and non-affiliated birds condition, the birds were separated into two subgroups of four birds and one subgroup of three birds. In keas, experiments for subgroups took place in a visually shielded testing compartment (7,0m x 10,0m x 5,40m; Fig. 1, compartment b). Experiments involving the whole group took place in a larger not-shielded compartment of their aviary (20,00m x 10,0m x 5,40m; Fig. 1, compartment a). Ravens separated in subgroups were housed and tested in a 10,0m x 12,0m x 4,90m aviary for two of the three groups (Fig. 1, compartments c and d) and a 6,00m x 15,0m x 5,00m big aviary for the third group (Fig. 1, compartment e). In the affiliated birds condition, the subgroups consisted of two female and two male affiliates; in the non-affiliated birds condition, subgroups consisted of two non-affiliated females and two non-affiliated males. For the keas separating individual birds in subgroups is no problem, as they are used to this procedure and could be called by name or carried by hand into the testing compartment. Hence, subgroup formation took place right before the experiments started. In the ravens, however, subgroup formation was more difficult as the birds generally feared human experimenters; hence, they were individually caught, placed into the respective compartments and remained in their subgroups for the entire separation time of about two weeks. Separation into groups of affiliated birds took place from April 25th to May 9th. Separation into groups of non-affiliated birds was from May 30th to June 13th.

Tab. 2: Time schedule and grouping in the experiments

Condition	**Frequency of sessions**	**Grouping of birds**
Whole group	2 sessions	1 x 11 birds
Affiliated birds	2 sessions	2 x 4 birds 1 x 3 birds
Whole group	2 sessions	1 x 11 birds
Non-affiliated birds	2 sessions	2 x 4 birds 1 x 3 birds
Whole group	2 sessions	1 x 11 birds

Three pairs of objects with varying complexity were presented to the birds. Purple and mint green wooden squares, pink and cupreous angled metal tubes and sheep and rabbit figures made of a kind of clay (Fig. 2). Complexity was supposed to increase from squares to figures.

Fig. 2: Object pairs used in the experiments (squares, tubes, figures)

One experimental session consisted of three trials right after each other. Per trial, four pairs of objects of the same kind, but varying in colour or shape within the pair, were presented (Fig. 3). The order of presentation of objects of different kinds was counter-balanced. The objects were positioned in a way that four object pairs were positioned in a square with an approximate distance of 2 meters between the object pairs and about 20cm between the single objects of a pair (see Fig. 3). The objects were positioned in the birds' sight. In case of the keas, birds had to be prevented from approaching the objects during baiting by a wire mesh partition. After giving them access to the objects, birds were allowed to manipulate the objects for 20 minutes; then they were removed by the experimenter and replaced by the next four pairs of objects.

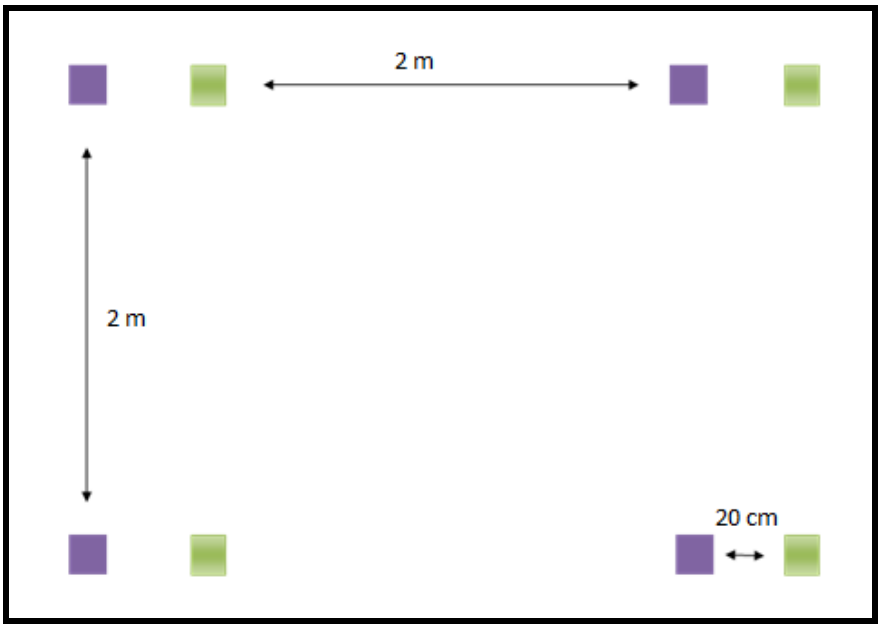

Fig. 3: Arrangement of the objects (here squares) during testing

The experiments were video recorded using two video cameras at a time (Sony Handycam DCR HC24E and Canon Legria HF S10 or Panasonic HDC-SD40). Videos were coded with the Solomon Coder. Frequencies and durations were coded of what bird manipulated which objects for how long and at which place, what bird joined whom, so which form of social learning was shown by which bird and a few other behaviours.

Preference tests were conducted with 3 keas and 3 ravens (separately housed group) that did not participate in the study to test whether objects of the same kind but varying in colour or shape, were similarly attractive to the birds. Indeed, these tests revealed that there was no preference for one object over the other when presented in a pair (i.e. purple and green square; pink and cupreous tube; sheep and rabbit figure).

2.3 Tonic immobility and novel room exploration

Individual keas were carried by hand if possible or caught with a net, transferred into a novel room and subjected to a tonic immobility test, i.e. they were laid on the back, while being held by the human experimenter with one hand on the neck and one hand on the legs. The experimenter at once released the bird and went away, closing the doors of the room afterwards. The time the birds needed to right themselves was measured. After 5min a door leading to their home aviary was opened and the bird could leave the novel room. The time to leave was measured. If the bird did not leave the room within 15min, it was gently guided outside by a human experimenter. The

whole procedure was videotaped from outside the room. Individual ravens were caught with a net and put in a transport box. They were then transferred into a novel room, taken off the boxes and subjected to the same procedure as the keas. Birds were classified into proactive / bold and reactive / shy individuals according to the time they needed after tonic immobility handling to get up again and according to their explorative behaviour in the novel room. Individuals that needed long to right themselves and those that spent only short times on the ground and showed a lot of stress behaviour were classified as reactive / shy individuals. Those birds that right up fast and showed less stress behaviour were categorized as proactive / bold. Keas, that explored the novel room extensively on the ground, and ravens that dared to land on the ground or on low branches were categorized as proactive / bold, too.

2.4 Statistical analysis

We operationally defined three social learning categories: stimulus enhancement referred to those instances when an individual directed its behaviour towards an object that matched the object a conspecific had manipulated less than 5 seconds ago; if a bird for example had manipulated a purple square and another bird went within 5 seconds to either one of the other 3 purple squares. Local enhancement referred to those instances when an individual went to the location at which a conspecific had manipulated an object not longer than 5 seconds ago (or still was manipulating the object). Here, the bird started manipulating the other object of that pair or simply investigated the location: e.g. a bird manipulated the green square in the upper left corner (Fig. 3) and a conspecific started manipulating the purple square in that corner. Go for the same object referred to those instances when an individual went to the object a conspecific had been manipulating not longer than 5 seconds ago or was still manipulating. The time frame of 5 seconds was chosen, because it revealed to include over 90% of all social learning events in comparison to a 10 seconds time frame. Data were analysed using the statistic software PASW Statistics 20 by SPSS Inc. and the handbook by Janssen and Laatz (2010). All test results are two-tailed and significance level was set at 0,05. All variables were tested for normal distribution.

(i) effects of the social environment on object exploration (social learning)

To analyse total species differences in the effects of the social environment on object manipulation, I used t-tests to compare frequencies and durations of object manipulation between the two species. Similarly, I compared total social learning frequencies between the species in sum and separately for each social learning form using t-tests.

For analysing relative species differences in the effects of the social environment on object exploration in relation to manipulation frequencies, I first calculated how often birds handled an object or went to an area as a consequence of the behaviour of a conspecific (i.e. sum of stimulus enhancement, local enhancement and go for the same object) relative to the frequency of object manipulations. I then compared this index of social learning in relation to manipulation between the two species using a t-test.

To test for preferences of a particular object type (squares, tubes, figures) or the influence of complexity or any other trait of the objects on manipulation, I applied ANOVAs or GLMs if the assumption of equality of variances has been violated.

(ii) kind of influence on exploration behaviour (what form of social learning is shown)

To analyse within and between species differences in what form of social learning birds show, I compared the relative proportion of social learning forms using a GLM. To test for random attraction to the objects and areas, I compared frequencies of stimulus enhancement, local enhancement and go for the same object to chance levels per species, using paired t-tests.

(iii) effects of social relations (affiliation, dominance) and individual attributes (sex, age, and behavioural phenotype) on social learning

To analyse effects of affiliation on social learning, I first of all calculated mean frequencies and durations of manipulations per condition (affiliated birds, non-affiliated birds, and whole group), as manipulation is a prerequisite to show social learning. Differences between the conditions were then tested using repeated measures GLMs and Bonferroni post-hoc tests. Secondly, mean social learning frequencies per condition were compared using repeated measures GLMs and Bonferroni post-hoc tests.

To test for effects of dominance rank (ravens), sex (keas and ravens), and age (keas) on social learning, I applied appropriate correlations according to the scales of measurement. It was not possible to test for age effects in the ravens, as the birds did not vary in age. Moreover, the effect of the position in the rank hierarchy in the kea

could not be tested as some of the birds had a circular rank-hierarchy, which is common for keas (Huber et al. 2008).

Behaviour in the experiments compared to daily life

To compare the birds' object manipulations in the experiment with their manipulations of small objects shown outside the experiment in daily life, I used paired t-tests for both durations and frequencies of manipulations. Furthermore frequencies and durations of social interactions during social protocols were correlated with mean frequencies of social learning events during the experiments with Pearson correlations.

3 RESULTS

(i) effects of the social environment on object exploration (social learning)

Total differences in duration and frequency of object manipulations between the species were compared using t-tests. Those revealed that both frequencies and durations of manipulations of the objects differ between keas and ravens (*frequencies: T= 2,181, df= 18, α= 0,043; durations: T= 2,891, df= 18, α= 0,010*). As expected, keas manipulated the objects longer and more frequently than ravens. Similarly, t-tests were done to compare total numbers of social learning events between the species. Those revealed that there is a difference in the frequency of social learning events between the species with keas showing more social learning than ravens (*T= -2,251, df= 14,508, α= 0,040*). In detail, frequencies of stimulus enhancement differ between the species with keas showing again more stimulus enhancement than ravens (*T= -3,342, df= 13,93, α= 0,005*). However, the frequencies of go for the same object do not differ between the species (T= *0,048, df= 20, α= 0,962*) and after a sequential Bonferroni correction after Holm (Rice 1989) the frequencies of local enhancement do not differ any more, too (*T= -2,089, df= 20, α> 0,050*).

For analysing relative species differences in the effects of the social environment on object exploration relative to manipulation, an index of social learning frequency in relation to manipulation was calculated. This index was compared using a t-test, which revealed that there is no difference between keas and ravens in the frequency of social learning if frequencies of manipulations are taken into consideration (*T= 0,692, df= 18, α= 0,498*). Hence, both species are equally affected in their exploration behaviour by their social environment.

To test for preferences of a particular object type or the influence of complexity or any other trait of the objects on manipulation, frequencies and durations of manipulations of the different object pairs were compared with an ANOVA. In keas the difference of

the objects has no influence, neither on frequency nor duration of manipulation (*frequency:* $F_{2,27} = 0,084$, $\alpha = 0,919$; *duration:* $F_{2,27} = 0,299$, $\alpha = 0,744$). In case of the ravens, frequencies of manipulations do not differ between the object pairs, either ($F_{2,27} = 0,714$, $\alpha = 0,499$). However, if we look at the duration of manipulation of the object pairs, complexity or any other trait of the objects has an influence on the duration of manipulation ($F_{2,27} = 5,366$, $\alpha = 0,011$, Fig. 4). A Tamhane post-hoc test specified that the duration of manipulation of the figures tends to differ from the tubes ($\alpha = 0,053$; note that Tamhane post hoc tests can be non-significant, although a GLM reveals significant differences as it has less power than a GLM), with tubes being manipulated the longest. The duration of manipulation between squares and figures does not differ ($\alpha = 0,466$), nor does the duration of manipulation differ between squares and tubes ($\alpha = 0,197$).

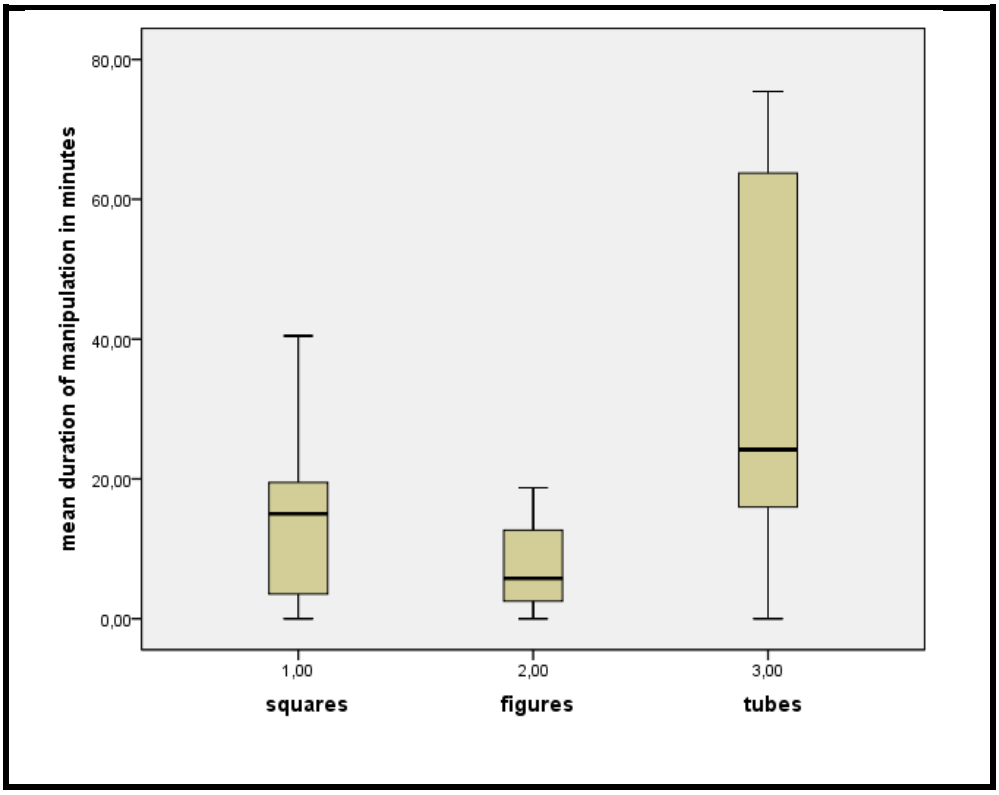

Fig. 4: Mean durations of manipulations per bird per object type in ravens

(ii) kind of influence on exploration behaviour (what form of social learning is shown)

A GLM was done to analyse whether keas or ravens used any of the social learning forms preferably and whether the single forms differ in their proportion between the species. This revealed that there is a significant difference between the proportions of the social learning forms ($F_5 = 30,228$, $\alpha < 0,000$, see Fig. 5). A Tamhane post-hoc test specified that there are no differences in the single social learning forms between the

species, but within (Tab. 3). Hence, the pattern of which form of social learning is used in what proportion is very similar in keas and ravens. In both species stimulus enhancement is the form shown most frequently, followed by go for the same object and local enhancement has been shown least often (Fig. 5). Within keas the proportions of go for the same object and stimulus enhancement differ (*α< 0,000*) and local and stimulus enhancement differ (*α< 0,000*). The proportions of go for the same object and local enhancement do not differ (*α= 1,* see Tab. 3). Within ravens the proportions of go for the same object and stimulus enhancement differ (*α= 0,031*) and local and stimulus enhancement differ as well (*α< 0,000*). Moreover, the proportions of go for the same object and local enhancement differ in the ravens (*α= 0,001,* Tab. 3).

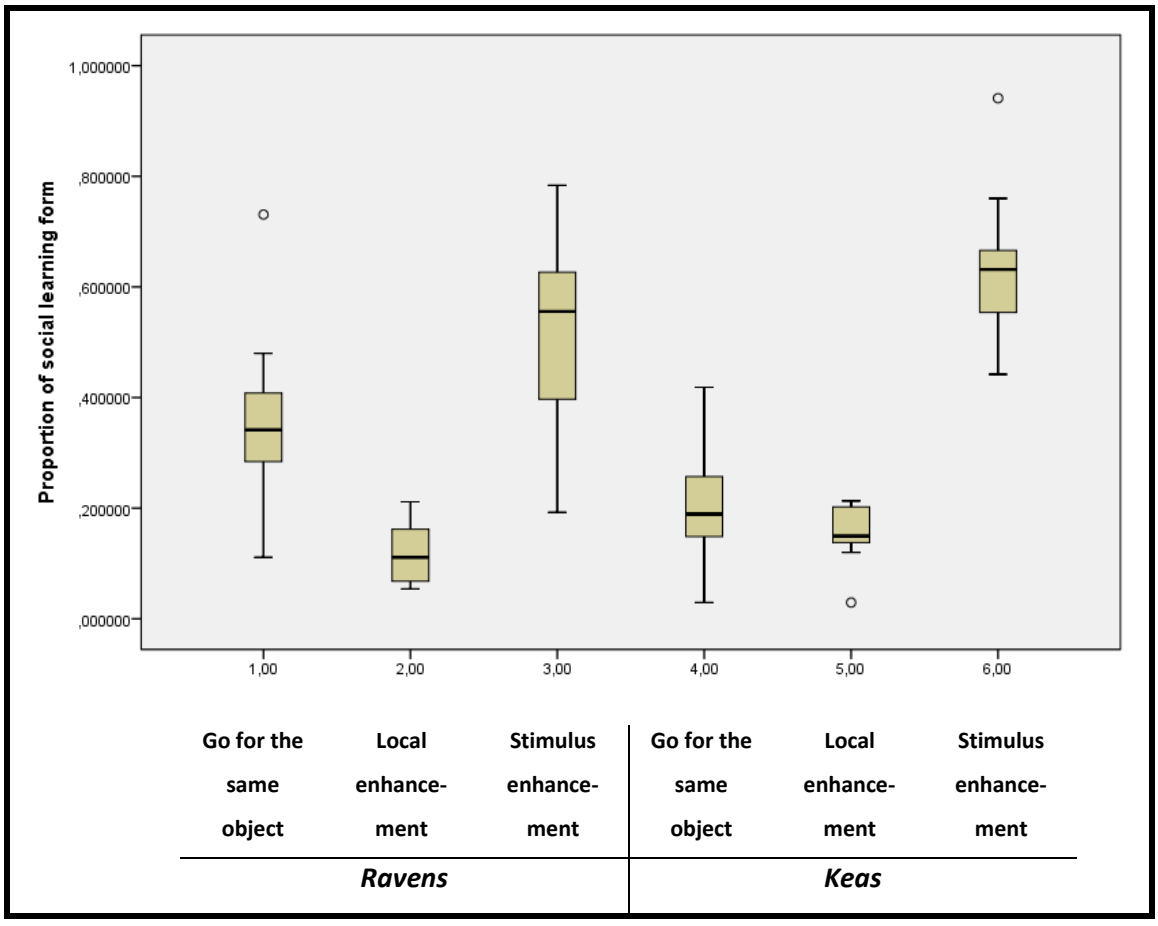

Fig. 5: Difference between the proportion of stimulus enhancement, local enhancement, and go for the same object between and within the species

Tab. 3: Results of a Tamhane post-hoc test after having tested for differences in the proportion of stimulus enhancement, local enhancement, and go for the same object between and within the species with a GLM

Social learning form and species	relation	Social learning form and species	p-value
go for the same object kea	>	local enhancement kea	α= 0,741
go for the same object kea	<	stimulus enhancement kea	α< 0,000
local enhancement kea	<	stimulus enhancement kea	α< 0,000
local enhancement raven	<	stimulus enhancement raven	α< 0,000
local enhancement raven	<	local enhancement kea	α= 1,000
stimulus enhancement raven	<	stimulus enhancement kea	α= 0,971
go for the same object raven	>	local enhancement raven	α= 0,001
go for the same object raven	<	stimulus enhancement raven	α= 0,031
go for the same object raven	>	go for the same object kea	α= 0,148

Frequencies of each form of social learning were compared with expected frequencies if each form of social learning was shown by chance. The form go for the same object is shown more frequently both by keas and ravens than expected by chance (*keas: T= 2,784, df= 10, α= 0,019; ravens: T= 4,376, df= 13, α= 0,001*). However, local enhancement is shown less frequently than expected by chance (*keas: T= -5,807, df= 10, α< 0,000; ravens: T= -7,315, df= 13, α< 0,000*). In case of stimulus enhancement keas show more of this form of social learning than chance level would explain (*T= 4,348, df= 10, α= 0,001*), while the frequency with which ravens show stimulus enhancement does not differ from expected frequencies by chance (*T= 0,122, df= 13, α= 0,905*).

(iii) effects of social relations (affiliation, dominance) and individual attributes (sex, age, and behavioural phenotype) on social learning

Social relations: affiliation and dominance

Affiliation

Repeated measures GLMs were done to analyse the effect of affiliation on the duration or frequency of manipulations of the objects. This GLM revealed that both durations and frequencies of manipulations differ between the conditions in the keas (*duration: $F_{1,121}$ = 7,520, α= 0,017; frequency: F_2 = 17,487, α< 0,000*). A Bonferroni post-hoc test specified that the duration differs between the whole group and the affiliated birds group (*α= 0,051*), with manipulation being longest in presence of affiliates. Durations in

the whole group condition and the non-affiliated birds condition differ by trend (*α= 0,060*). Note that Bonferroni post hoc tests can show non-significant differences, although a GLM revealed significant differences, as a Bonferroni test has less power than a GLM. Duration of manipulation does not differ between the two conditions in the subgroups (*α= 1*). The frequencies of manipulations differ between the whole group and the affiliated birds group according to a Bonferroni post-hoc test (*α< 0,000*) and between the whole group and the non-affiliated birds group as well (*α= 0,037*). Highest frequencies have been shown in the affiliated and non-affiliated birds condition. The frequencies of manipulations in the two conditions with subgroups do not differ (*α= 0,174*). For the ravens the GLMs revealed that durations of manipulation of the objects differ only by trend between the conditions (F_2 *= 3,163, α= 0,064*) while the conditions differ if we look at the frequency (F_2 *= 13,205, α< 0,000*). A Bonferroni post-hoc test specified that the whole group differs from the affiliated birds group (*α= 0,002*) and from the non-affiliated birds group (*α= 0,036*). Highest frequencies of manipulations have been shown in the affiliated birds condition and lowest when being in the whole group. Again, the frequencies of manipulations in the two conditions with the subgroups do not differ from each other (*α= 0,111*).

If we visualize the development of frequencies of object manipulations across sessions (Fig. 6), it can be seen that the birds manipulated a lot more frequently when being in the subgroups. The group size therefore has an effect on the frequency of manipulations with smaller groups having higher frequencies and longer durations of object manipulations than bigger groups, as affiliated and non-affiliated birds condition do not differ (see above).

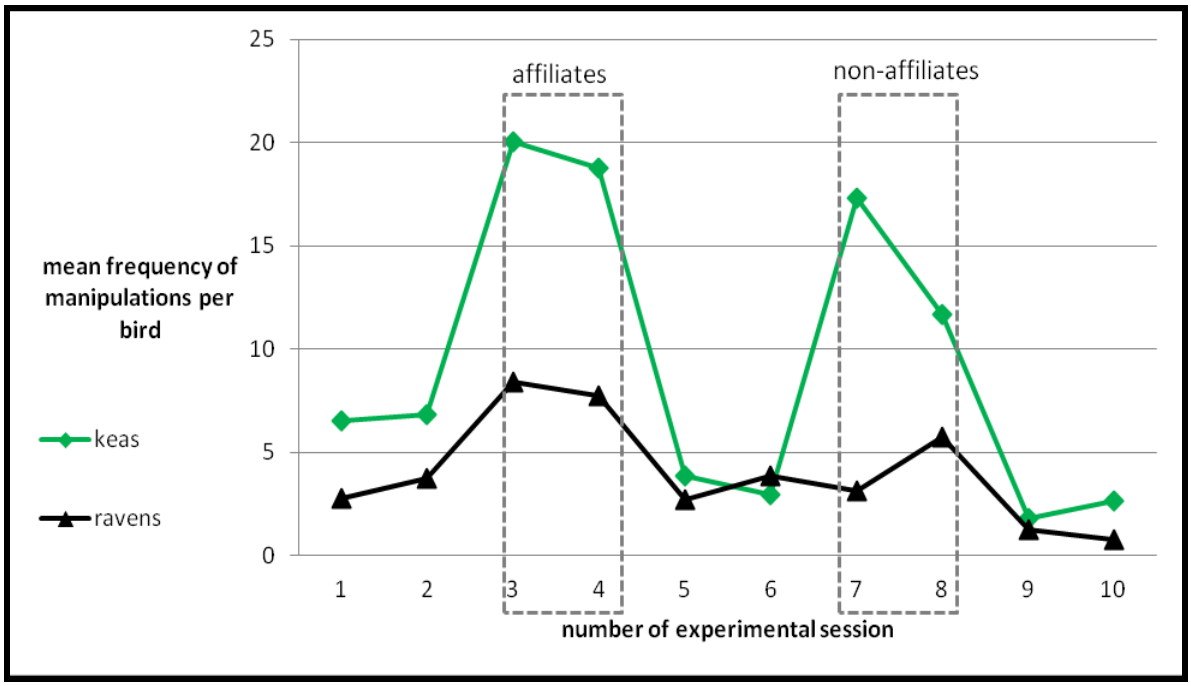

Fig. 6: Mean frequency of manipulations per bird across sessions (sessions 3 and 4 are the affiliated birds condition, sessions 7 and 8 are the non-affiliated birds condition)

To analyse the effects of affiliation on social learning repeated measures GLMs and Bonferroni post-hoc tests and sequential Bonferroni corrections after Holm (Rice 1989) were calculated for each species. Those revealed that both keas and ravens differ in the frequency of social learning events depending in which social condition they are (i.e. whole group, affiliated and non-affiliated birds group; *keas:* $F_{1,157} = 13,93$, $\alpha < 0,017$; *ravens:* $F_2 = 10,179$, $\alpha < 0,017$). A Bonferroni post-hoc test for the keas specified that the whole group condition differs from the affiliated birds condition ($\alpha = 0,020$) and the whole group condition differs from the non-affiliated birds condition ($\alpha = 0,046$), with highest social learning frequencies in the affiliated birds condition and lowest in the non-affiliated birds condition (Fig. 7). Furthermore, the affiliated birds condition and the non-affiliated birds condition differ ($\alpha = 0,007$).

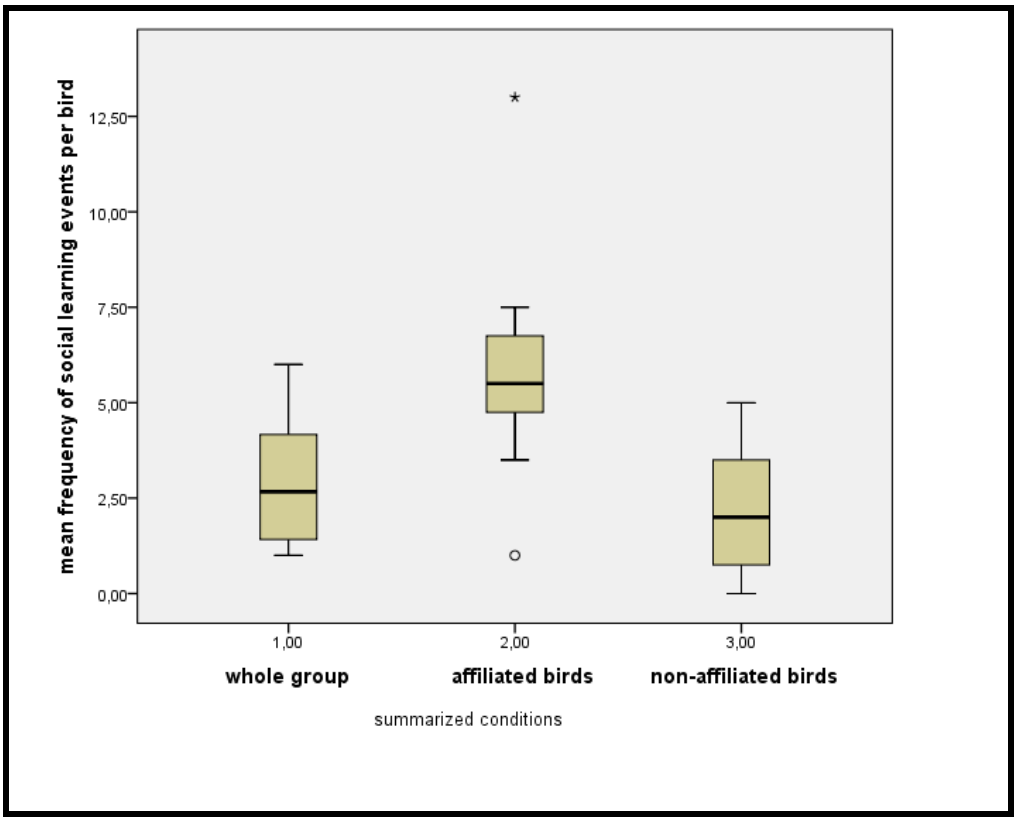

Fig. 7: Difference in mean frequencies of social learning events between the conditions whole group, affiliated birds, and non-affiliated birds in keas

For the ravens a Bonferroni post-hoc test revealed that the whole group condition and the affiliated birds condition differ significantly ($\alpha = 0,045$) and the affiliated bird condition differs from the non-affiliated birds condition ($\alpha = 0,011$; Fig. 8). As in case of the keas social learning frequencies in the ravens are highest in the affiliated birds condition.

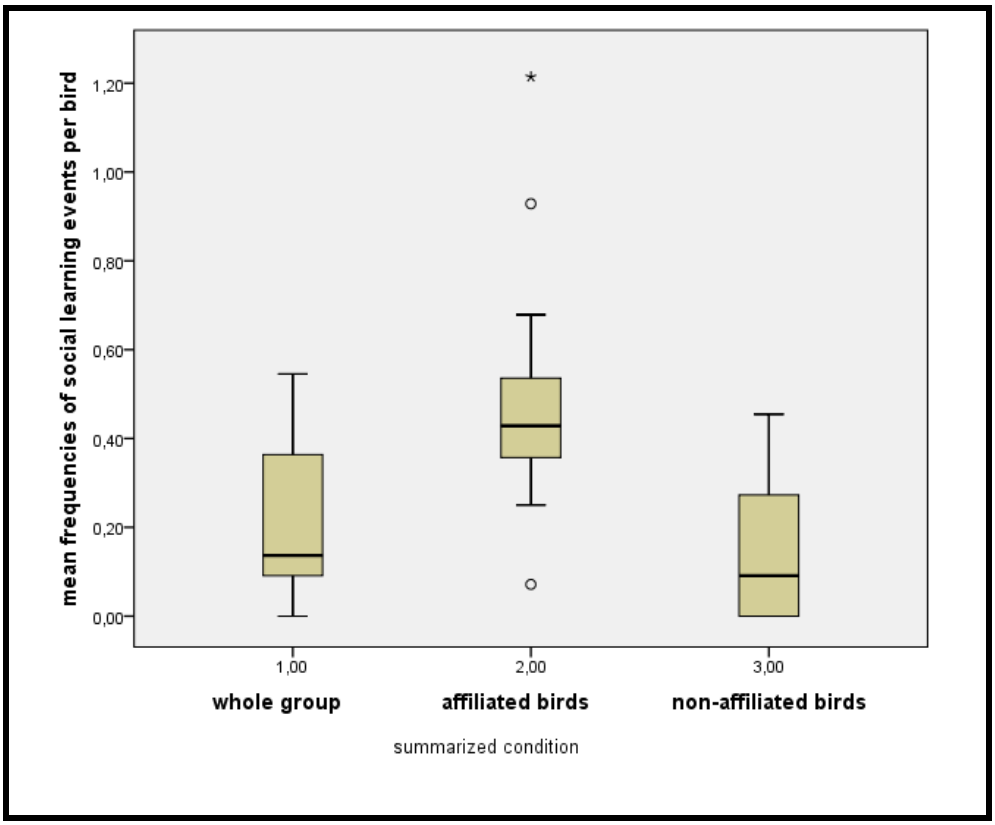

Fig. 8: Difference in frequency of social learning events between the conditions whole group, affiliated birds, and non-affiliated birds in ravens

Dominance

The influence of the position in the rank hierarchy on the frequency of social learning in general, or on any of the three forms of social learning specifically, was tested with Spearman rank-order correlations. Those revealed that overall higher-ranking birds show more social learning than lower-ranking birds (r_s*= -0,797, N= 11, α= 0,003*). In detail and after a sequential Bonferroni correction after Holm (Rice 1989), individuals´ frequencies of stimulus enhancement and local enhancement were influenced by the birds´ position in the rank hierarchy (*stimulus enhancement:* r_s*= 0,682 N= 11, α< 0,050,* see Fig. 9a*; local enhancement:* r_s*= -0,688, N= 11, α< 0,050,* see Fig. 9b). Higher-ranking individuals were the ones showing more local enhancement and simultaneously less stimulus enhancement than their lower-ranking group members. The frequency of go for the same object is marginally influenced by the position in the rank hierarchy (r_s*= -0,545, N= 11, α= 0,083,* see Fig. 9c).

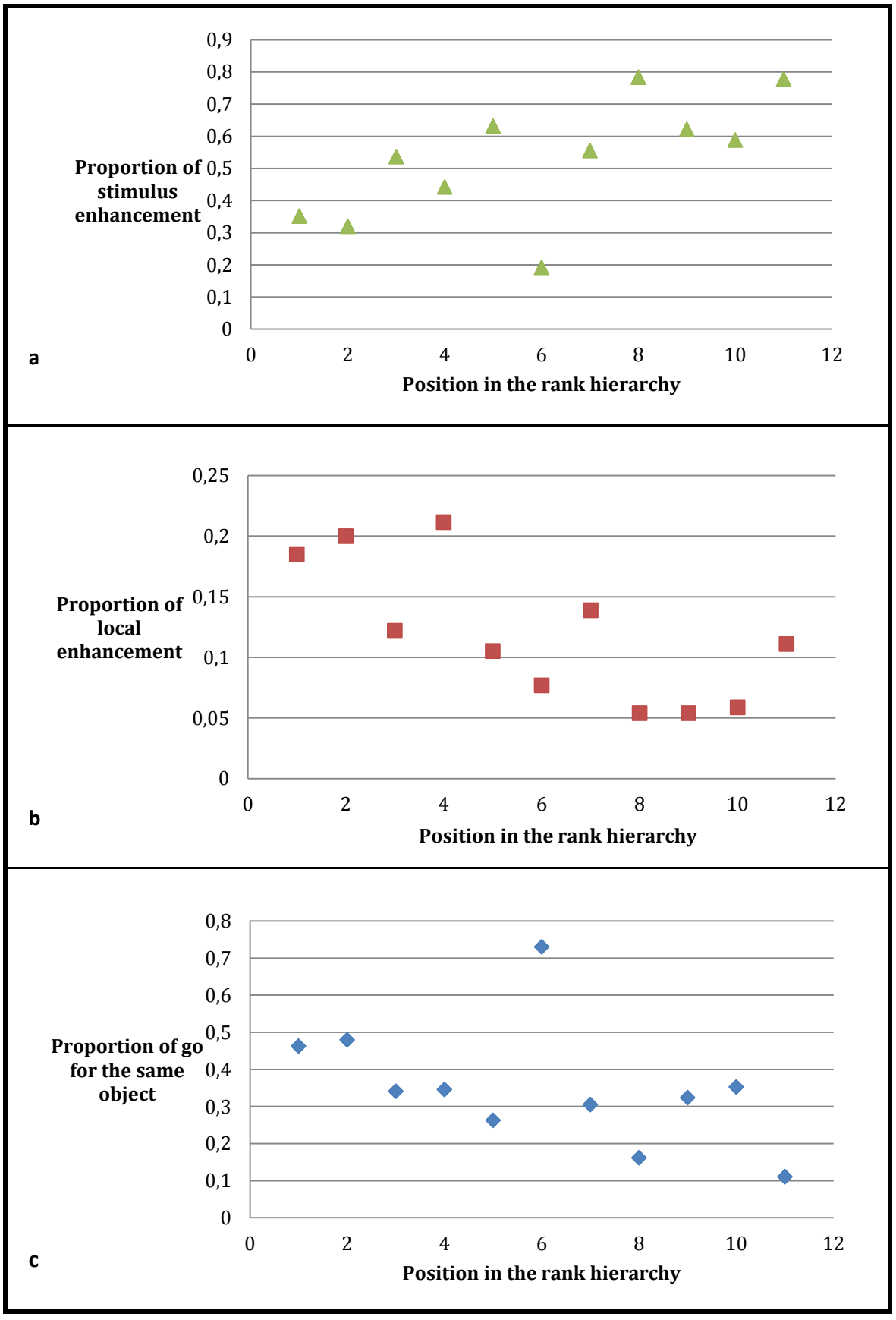

Fig. 9: Relation between the position in the rank hierarchy and the proportion of a) stimulus enhancement, b) local enhancement and c) go for the same object used by the ravens

Individual attributes: sex, age, and behavioural phenotype

Sex

The correlation done to test whether sex has an influence on the frequency or type of social learning shown, revealed that sex does neither influence the frequency of social learning shown in general, nor any of the social learning types go for the same object, stimulus or local enhancement specifically (*keas: social learning: Cramer´s V= 1, N= 11, α= 0,358; go for the same object: Cramer´s V= 0,904, N= 11, α= 0,439; local enhancement: Cramer´s V= 1, N= 11, α= 0,276; stimulus enhancement: Cramer´s V= 1, N= 11, α= 0,358; ravens: social learning: Cramer´s V= 1, N= 11, α= 0,276; go for the same object: Cramer´s V= 1, N= 11, α= 0,439; local enhancement: Cramer´s V= 0,671, N=11, α= 0,292; stimulus enhancement: Cramer´s V= 0,904, N=11, α= 0,439*).

Age

The correlation that was done to test the influence of the age of the keas (subadult or adult) on the frequency or form of social learning shown, revealed that neither social learning in general, nor go for the same object, local or stimulus enhancement specifically are influenced by the age (*social learning: Cramer´s V= 1, N= 11, α= 0,358; go for the same object: Cramer´s V= 0,896, N= 11, α= 0,452; local enhancement: Cramer´s V= 0,896, N= 11, α= 0,452; stimulus enhancement: Cramer´s V= 1, N= 11, α= 0,358*).

Behavioural phenotype

Correlations between behavioural phenotype and frequency of social learning events were done to test whether the behavioural phenotype of a bird has an influence on the type or frequency of social learning events shown by the bird. This is neither the case for keas (*Cramer´s V= 1, N= 11, α= 0,358),* nor for ravens *(Cramer´s V= 1, α= 0,276*). Frequencies of stimulus enhancement, local enhancement, and go for the same object have been correlated separately with social learning, too. Again the behavioural phenotype of the bird does not affect its social learning performance (*Keas: go for the same object: Cramer´s V= 1, N= 11, α= 0,265; local enhancement: Cramer´s V= 0,873, N= 11, α= 0,472; stimulus enhancement: Cramer´s V= 1, N= 11, α= 0,350; Raven: go for the same object: Cramer´s V= 1, N= 11, α= 0,276; local enhancement: Cramer´s V= 0,654, N= 11, α= 0,320; stimulus enhancement: Cramer´s V= 0,878, N= 11, α= 0,487*).

Behaviour in the experiments compared to daily life

Frequencies and durations of manipulations of small objects during social protocols were compared with frequencies and durations of manipulations of the objects used in the experiments with the help of paired t-tests. Those revealed that keas manipulated the objects in the experiments longer than in the social protocols (*T= -4,297, df= 10,467, α= 0,001*). However, they manipulated small objects in the social protocols more frequently than in the experiments (*T= 7,562, df= 13,296; α< 0,000*). In case of the ravens, both frequencies and durations of manipulations were higher during social protocols in comparison to experiments (*duration: T= 3,791, df= 10, α= 0,004; frequency: T= 4,234, df= 10, α= 0,002*). For ravens only the data of social protocols done after having fed the birds are used because frequencies and durations of different behaviours differ between the two conditions before feeding and after feeding (*frequencies: Z= -7,052, N= 429, α< 0,000*, *durations: Z= -5,049, N= 429, α< 0,000*) and there is more data available in the after feeding condition.

The correlation of frequencies and durations of social interactions (friendly and agonistic) per minute during the social protocols with frequencies of social learning events per minute during the experiments revealed that the frequency of social interactions is negatively correlated with the frequency of social learning events in keas (*Pearson´s r= -0,314, N= 11, α= 0,042*). The more social interactions a kea showed during social protocols, the less frequently it showed social learning in the experiments. Moreover, neither durations of social interactions and social learning events in keas and in ravens, nor the frequency of social interactions and social learning events in ravens are correlated (*duration keas: Pearson´s r= -0,314, N= 11, α= 0,348; duration ravens: Pearson´s r= 0,094, N= 11, α= 0,783; frequency ravens: Pearson´s r= 0,099, N= 11, α= 0,772*).

4 DISCUSSION

(i) effects of the social environment on object exploration (social learning)

Although keas show higher frequencies of manipulations of the objects and higher social learning frequencies than ravens, there is no difference between the species in the use of social learning if we look at social learning frequencies in relation to manipulation. Keas are well known for their extreme manipulations of objects. It is therefore not surprising and in line with the predictions that keas show higher manipulation frequencies and consequently higher absolute social learning frequencies. Keas and ravens differ in one very obvious trait, namely the reaction towards new objects or known objects at new places. Keas are extremely neophilic birds, while ravens even fear their food (Heinrich 1988) if it is positioned at an unusual place, being

the exact opposite with their neophobia. This may explain well the difference in total numbers of manipulations of the objects and subsequently absolute social learning frequencies between the species. However, both species' exploration behaviour is equally affected by the social environment. They choose the objects and area to attend to according to the behaviour of their group members. This is in line with the predictions and the assumption that in stable social groups every aspect of life is influenced by the social environment (Coussi-Korbel and Fragaszy 1995).
The frequencies of manipulations of the different objects did neither differ in the keas nor the ravens. However, the ravens manipulated the tubes the longest in comparison to other object types. The attractiveness might have been that they could easily carry the tubes around in their throat pouch, like they do with food or small objects they find. Furthermore, the tubes could be cached most easily due to their small and slim shape and were cached, recached, and pilfered frequently.

(ii) kind of influence on exploration behaviour (what form of social learning is shown)

Why stimulus enhancement is the form of social learning shown most frequently (as predicted) might be due to that it is the social learning form that offers the certainty about gaining a valuable item (because a group member is manipulating it) without the cost of a possibly aggressive interaction. Moreover, in case of the ravens, when showing stimulus enhancement, the birds reduce the risk of the objects being dangerous in comparison to local enhancement. If birds see a group member manipulating a green square for example, they can be relatively sure that green squares apparently are safe to manipulate. Again while considering that go for the same object being the most secure object to aim at, bares high costs of aggressive interactions. The costs of a possible aggressive interaction with a conspecific might be consequently the reason, why go for the same object is not shown more frequently. That keas show so low frequencies of local enhancement was not expected. Keas are extractive foragers and probably gain a lot of information where to dig for roots by watching conspecifics.
The pattern of which form of social learning is used in what proportion does not differ between keas and ravens. Thus, despite differences in total amounts, the pattern of how strong and in what kind keas are influenced by the behaviour of conspecifics is the same in comparison to ravens. Moreover, that the frequencies of each form of social learning differ from values expected by chance (except for stimulus enhancement in ravens) suggests an active, socially influenced decision by the birds what to attend to and where to go, rather than a random attraction to the area, the object and the bird manipulating an object.

(iii) effects of social relations (affiliation, dominance) and individual attributes (sex, age, and behavioural phenotype) on social learning

The predictions have been that in groups of affiliated birds social learning frequencies will be higher than in non-affiliated bird groups. The results found in this study support this prediction, both keas and ravens are influenced in their frequency to show social learning by the presence of certain individuals namely affiliated group members. Affiliative relationships are characterised by low levels of aggression, reducing the costs (i.e. a potential fight) contingently arising from an attempt to go for the same object. Furthermore, as affiliative group members spent a lot of time in proximity and are more attending to each other, the reliability of affiliates concerning information provided by them might be higher than in non-affiliates. The use of information provided by affiliates might be therefore shown more frequent than the use of information provided by group members with whom the relationship is characterised by higher levels of aggression. It seems to be that the behaviour of affiliated group members is more contagious than that of non-affiliated and that affiliated birds attract each other (see also Stöwe et al. 2006, Stöwe et al. 2006b).

Frequencies and durations of manipulations in case of the keas and frequencies in case of the ravens differed between subgroups and the whole group, being higher in the subgroups. Additionally, the frequency of manipulations of the objects did not differ between the subgroups. Apparently for the decision to manipulate objects, it does not matter who is around, but how many individuals are around. As both keas and ravens are very curious birds (Heinrich 1995, Huber et al. 2008) the reason for higher levels of manipulations in small groups could be due to not having to keep track of social interactions between the members of the group and changes in the social network (Cheney and Seyfarth 1990), but to simply engage in curiosity satisfaction or object play (especially in case of the keas). Moreover in smaller groups the objects per bird relation is higher than in bigger groups meaning the probability to go for an object that was lying around without having to steal it from another bird is higher in smaller groups than in bigger ones. However, in the whole group condition it was seldom the case that all objects have been manipulated simultaneously. Furthermore for low-ranking individuals the probability to be displaced from any objects is lower in smaller groups, having less group members present that are higher-ranking than in the whole group condition. However, if this reason alone accounted for the difference one would expect a difference between the two conditions, because non-affiliate relations are accompanied by higher levels of aggression.

In the ravens, a strong correlation has been found between position in the rank hierarchy and the frequency of social learning in general, and the frequency of stimulus and local enhancement specifically. It has been predicted that high rank goes in line with high social learning frequencies, especially local enhancement and go for the same object. That high-ranking ravens show more local enhancement than lower ranking ones hints towards how strong the decision what form of social learning to show, is

connected with the costs of a probable escalation when coming in the vicinity of the demonstrating bird. This is necessary when showing local enhancement and go for the same object. For high ranking birds those costs are lower than for low-ranking ones, which possibly accounts for the differences. Statistical analysis revealed that the frequency of go for the same object is only marginally influenced by the position in the rank hierarchy, although the relation between high rank and extensive usage of this form is the same as in local enhancement. The lack of a significant correlation might be due to one outlier (Fig. 9c), that showed the highest proportion in usage of this social learning form in the whole group, while positioned in the middle of the hierarchy. For showing stimulus enhancement it is not necessary to come closer than about 2m (the distance between the object pairs positioned in a square), which is far enough to not elicit possible aggressions between the group members. This might be the reason why it is shown mainly by low ranking individuals.

In respect to age in the kea it was predicted that subadults show more go for the same object than adults and more stimulus enhancement than local enhancement. In general it was predicted that subadults show more social learning than adults. However, the age has no effect on the frequency or form of social learning shown by the keas. Predictions have been deduced from foraging contexts, though, and may be not applicable in a non-foraging context. Moreover, Range et al. (2009) have shown that attention, which is a prerequisite for social learning, paid by non-adult keas towards adults or juveniles did not differ. Furthermore, the birds categorized as subadults are in their fourth summer after hatching standing at the border to adulthood. To categorize them as subadults and subsequently compare their behaviour with the behaviour of adults is therefore a question of a few months. If the study would have been conducted in autumn or winter they would have been categorized as adults. I would expect to find greater differences between juveniles and adults, as juveniles still have to learn a lot more about daily life in comparison to subadults being nearly adult and mature. Furthermore, it was predicted, that males show more social learning than females, which could not be approved by the results of this study. This is in line with the findings of Bugnyar and Huber (1997). Here the explanations are the same as in respect to the age: the predictions have been deduced from a foraging context and therefore could have been rather not applicable in a non-foraging context than being deniable in general. The behavioural phenotype does not correlate with the frequency of social learning shown by each bird. This might be due to too simple categorization of the behavioural phenotype in this study. Seven parameters might be to less to characterize a birds´ personality and to deduce its behaviour hereby.

Keas manipulated the objects in the experiments longer than small objects during social protocols, but more frequently during the social protocols in comparison to the experiments. The reason might be that the objects used in the experiments were new for the keas and therefore interesting over a longer period of time, while small objects manipulated during social protocols have been simple items like twigs or stones lying around in their aviary all day. However those natural items are found in high quantity in

their aviary and were therefore encountered and manipulated more frequently than the objects offered to the birds in low quantity and rarely during the experiments. Why the ravens manipulated small objects more frequently and for longer times during social protocols than during the experiments is surprising at first glance. However the birds´ neophobia might be an explanation for this. Some birds showed 'jumping jack' displays, a display shown when dangerousness of objects is estimated while approaching it (Heinrich 1988), even in their 8th encounter of the objects. At this time the objects have been inside their aviary for about 3 hours and 20 minutes in total and have been manipulated several times before. It might be that this fear hindered the birds from manipulating the objects more frequently and for longer times. The objects manipulated during the social protocols however were, as well as in case of the keas, simple items belonging to the equipment of the aviary.
The more social interactions a kea showed during the social protocols, the less frequently it showed social learning in the experiments. This is quite an unexpected result. My expectations have been that high frequencies of social interactions in daily life are in line with high frequencies of social learning in the experiments. So that individuals differ in their 'social competences' with some individuals showing frequent interactions and attending very attentively to their social environment and others showing less interest in social issues. It seems to be more the case that every individual invests a certain time or effort in social issues though, being high either in the social protocols or in the experiments, irrespective of individual differences. It could moreover be that birds having only rarely social interactions actively try to seek social contact during play with objects in the experiments. Keas show social object play (Diamond and Bond 2004), which might offer the possibility to build up social contact without fearing to induce too hard aggressions.

The difference in the consequence of providing the same information to different individuals with varying relationships results in differentiations of behaviour within groups and enhanced transmission of valuable information between pair-mates, parent-offspring dyads (Coussi-Korbel and Fragaszy 1995) and affiliates. This adds to the efficiency, variability and flexibility of a group to react towards changes in the environment (Coussi-Korbel and Fragaszy 1995). Those advantages of affiliative relationships may, next to direct fitness consequences of enhanced offspring survival (Silk et al. 2009) and reproductive success (Schülke et al. 2010), add to explain the evolution of friendships.

Advantages of comparative studies are the possibility to directly compare the results of each species with each other and not having to consider that differences in the performance could be due to differences in methodology, housing or anything else. Even better, it is easier to find explanations for the differences in the results, because they must be beyond the similarities between the species. For this study this is obviously the difference in the reaction towards novel objects, the keas´ extreme

neophilia and the ravens´ neophobia. Despite these differences both species are similarly influenced in their exploration behaviour by the social environment in general and by affiliated group members specifically. Hence, the results of the study highlight the importance of the specific social setting for all studies investigating sociocognitive abilities.

5 REFERENCES

Agren, G., Zhou, Q. and Zhong, W. (1989). Ecology and social behavior of Mongolian gerbils (*Meriones unguiculatus*) at Xilinhot, Inner Mongolia, China. Animal Behaviour 37:11-27.

Aisner, R. and Terkel, J. (1992). Ontogeny of pine cone opening behaviour in the black rat, Rattus rattus. Animal Behaviour 44:327-336.

Aureli, F., Cords, M. and van Schaik, C.P. (2002). Conflict resolution following aggression in gregarious animals: a predictive framework. Animal Behaviour 64:325-343.

Blurton-Jones, N.G. (1984). A selfish origin for human food sharing: Tolerated theft. Ethology and Sociobiology 5:1-3.

Bugnyar, T. and Huber, L. (1997). Push or pull: An experimental study on imitation in marmosets. Animal Behaviour 54:817-831.

Bugnyar, T. and Kotrschal, K. (2002). Observational learning and the raiding of food caches in ravens, Corvus corax: is it 'tactical' deception? Animal Behaviour 64:185-195.

Bugnyar, T. and Kotrschal, K. (2002b). Scrounging Tactics in Free-Ranging Ravens, *Corvus corax*. Ethology 108:993-1009.

Bugnyar, T. and Kotrschal, K. (2004). Leading a conspecific away from food in ravens (*Corvus corax*)? Animal Cognition 7:69-76.

Bugnyar, T. and Heinrich, B. (2006). Pilfering ravens, *Corvus corax*, adjust their behavior to social context and identity of competitors. Animal Cognition 9:369–376.

Bugnyar, T., Schwab, C., Schloegl, C., Kotrschal, K. and Heinrich, B. (2007). Ravens Judge Competitors through Experience with Play Caching. Current Biology 17:1804-1808.

Bugnyar, T., Stöwe, M. and Heinrich, B. (2007b). The ontogeny of caching in ravens, *Corvus corax*. Animal Behaviour 74:757-767.

Chance, M.R.A. and Jolly, C. (1970). Social Groups of Monkeys, Apes and Men. Jonathan Cape, London.

Cheney, D.L. and Seyfarth, R.L. (1990). How Monkeys See the World. University of Chicago Press, Chicago.

Choleris, E. and Kavaliers, M. (1999). Social Learning in Animals: Sex Differences and Neurobiological Analysis. Pharmacology Biochemistry and Behavior 64:767-776.

Clarke, C.M.H. (1970). Observation on population, movements and food of the kea (*Nestor notabilis*). Notornis 17:105-114.

Collins, R.J. (1988). Observational learning of a left-right behavioral asymmetry in mice (*Mus musculus*). Journal of Comparative Psychology 102:222-224.

Coussi-Korbel, S. and Fragaszy, D.M. (1995). On the relation between social dynamics and social learning. Animal Behaviour 50:1441-1453.

Diamond, J. and Bond, A.B. (1991). Social Behavior and the Ontogeny of Foraging in the Kea (Nestor notabilis). Ethology 88:128-144.

Diamond, J. and Bond, A.B. (2004). Social play in kaka (*Nestor meridionalis*) with comparison to kea (*Nestor notabilis*). Behaviour 141:777-798.

Fisher, J. and Hinde, R. A. (1949). The opening of milk bottles by birds. British Birds 42:347-357.

Fraser, O.N and Bugnyar, T. (2010). The quality of social relationships in ravens. Animal Behaviour 79:927-933.

Fraser, O.N. and Bugnyar, T. (2010b). Do Ravens show Consolation? Responses to Distressed Others. Public Library of Science ONE 5:e10605.

Fraser, O.N. and Bugnyar, T. (2012). Reciprocity of agonistic support in ravens. Animal Behaviour 83:171-177.

Fritz, J. and Kotrschal, K. (1999). Social learning in common ravens, *Corvus corax*. Animal Behaviour 57:785-793.

Galef, B.G. Jr. (1988). Imitation in animals: History, Definition and Interpretation of Data from the Psychological Library. In: Social learning: Psychological and biological perspectives. Zentall, T.R. and Galef, B.G. Jr. (eds.), pp. 3-28. Lawrence Erlbaum Associates, Hillsdale.

Gaulin, S.J.C., Fitzgerald, R.W. and Wartell, M.S. (1990). Sex differences in spatial ability and activity in two vole species (*Microtus orchrogaster and M. pennsylvanicus*). Journal of Comparative Psychology 104:88-93.

Giraldeau, L.A. (1997). The ecology of information use. In: Behavioural Ecology: an Evolutionary Approach. 4th edition by Krebs, J.R. and Davies, N.B. (eds.), pp. 42-68. Blackwell Science, Oxford.

Giraldeau, L.A. and Caraco, T. (2000). Social Foraging Theory: (Monographs in Behavior and Ecology). Princeton University Press, Princeton.

Gochfeld, M. and Burger, J. (1982). Feeding enhancement by social attraction in the Sandwich tern. Behavioral Ecology and Sociobiology 10:15-17.

Groothuis, T.G.G. and Carere, C. (2005). Avian personalities: characterization and epigenesis. Neuroscience and Biobehavioural Reviews 29:137-150.

Heinrich, B. (1995). An Experimental Investigation of Insight in Common Ravens (Corvus corax). The Auk 112:994-1003.

Heinrich, B. (1988). Why Do Ravens Fear their Food. The Condor 90:950-952.

Hessing, M. (1994). Individual behavioural characteristics in pigs and their consequences for pig husbandry. PhD Thesis, Agricultural University, Wageningen.

Hoppitt, W. and Laland, K.N. (2008). Social Processes Influencing Learning in Animals: A Review of the Evidence. Advances in the Study of Behavior 38:105-165.

Huber, L., Rechberger, S. and Taborsky, M. (2001). Social learning affects object exploration and manipulation in keas, *Nestor notabilis*. Animal Behaviour 62:945-954.

Huber, L., Gajdon, G.K., Federspiel, I. and Werdenich, D. (2008). Cooperation in Keas: Social and Cognitive Factors. In: Origins of the Social Mind by Itakura, S. and Fujita, K. (eds.), pp. 99-119. Springer, Japan.

Jackson, J.R. (1960). Keas at the Arthur´s Pass. Notornis 9:39-58.

Janssen, J. and Laatz, W. (2010). Statistische Datenanalyse mit SPSS. 7. Auflage, Springer Verlag, Berlin, Heidelberg.

Katzir, G. (1982). Relationships between social structure and response to novelty in captive jackdaws, *Corvus monedula* L., I. Response to novel space. Behaviour 81:231-263.

Katzir, G. (1983). Relationships between social structure and response to novelty in captive jackdaws, Corvus monedula L., II. Response to novel palatable food? Behaviour 86:183-208.

Koolhaas, J.M., Korte, S.M., de Boer, S.F., van der Vegt, B.J., van Reenen, C.G., Hopster, H., de Jong, I.C., Ruis, M.A.W. and Blokhuis, J.H. (1999). Coping styles in animals: current status in behavior and stress-physiology. Neuroscience and Biobehavioural Reviews 23:925-935.

Martin, P. and Bateson, P. (2008). Measuring Behaviour: An Introductory Guide, pp. 48-68. Cambridge University Press, Cambridge.

Marzluff, J.M., and Heinrich, B. (1991). Foraging by common ravens in the presence and absence of territory holders: An experimental analysis of social foraging. Animal Behaviour 42:755-770.

Mason, J.R. and Reidinger Jr., R.F. (1981). Effects of social facilitation and observational learning on feeding behavior of the red-winged blackbird (*Agelaius phoeniceus*). The Auk 98:778-784.

Mc Quoid, L.M. and Galef Jr., B.G. (1992). Social Influences on Feeding Site Selection by Burmese Fowl (*Gallus gallus*). Journal of Comparative Psychology 106:137-141.

Micheletta, J. and Waller, B. M. (2012). Friendship affects gaze following in a tolerant species of macaque, *Macaca nigra*. Animal Behaviour 83:459-467.

Midford, P.E., Hailman, J.P. and Woolfenden, G.E. (2000). Social learning of a novel foraging patch in families of free-living Florida scrub-jays. Animal Behaviour 59:1199-1207.

Nicol, C.J. and Pope, S.J. (1994). Social learning in small flocks of laying hens. Animal Behaviour 47:1289-1296.

Nicol, C.J. (2004). Development, direction, and damage limitation: Social learning in domestic fowl. Learning & Behavior 32:72-81.

Range, F., Horn, L., Bugnyar, T., Gajdon, G.K. and Huber, L. (2009). Social attention in keas, dogs, and human children. Animal Cognition 12:181-192.

Ratcliffe, D. (1997). The Raven. Academic Press, San Diego.

Rice, W.R. (1989). Analyzing tables of statistical tests. Evolution 43:223-225.

Scheid, C., Range, F. and Bugnyar, T. (2007). When, What and Whom to Watch? Quantifying Attention in Ravens (Corvus corax) and Jackdaws (Corvus monedula). Journal of Comparative Psychology 121:380-386.

Schülke, O., Bhagavatula, J., Vigilant, L. and Ostner, J. (2010). Social Bonds Enhance Reproductive Success in Male Macaques. Current Biology 20:2207-2210.

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

Silk, J., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M. and Cheney, D.L. (2009).The benefits of social capital: close social bonds among female baboons enhance offspring survival. Proceedings of the Royal Society B 276:3099-3104.

Sol, D., Duncan, R., Blackburn, T. M., Cassey, P. and Lefebvre, L. (2005). Big brains, enhanced cognition, and response of birds to novel environments. Proceedings of the National Academy of Sciences 102:5460-5465.

Stöwe, M., Bugnyar, T., Heinrich, B. and Kotrschal, K. (2006). Effects of Group Size on Approach to Novel Objects in Ravens (*Corvus corax*). Ethology 112:1079-1088.

Stöwe, M., Bugnyar, T., Loretto, M.-C., Schloegl, C., Range, F. and Kotrschal, K. (2006b). Novel object exploration in ravens (*Corvus corax*): Effects of social relationships. Behavioural Processes, doi:10.1016/j.beproc.2006.03.015.

Tebbich, S., Taborsky, M. and Winkler, H. (1996). Social manipulation causes cooperation in keas. Animal Behaviour 52:1-10.

Von Bayern, A.M.P, de Kort, S.R., Clayton, N.S. and 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.

6 APPENDIX

6.1 Summary

The study aimed at investigating the influence of the social context (i.e. affiliation or non-affiliation between group members) on social learning in an object exploration task in keas (*Nestor notabilis*) and ravens (*Corvus corax*). The term social learning in this study is used when stimulus and local enhancement or go for the same object a conspecific is manipulating are shown, concentrating not at the psychological processes but the type of information that can be obtained. The comparative study has shown that keas show higher frequencies of social learning as a consequence of higher frequencies of manipulation than ravens. However, if an index of social learning and manipulation is computed there is no species difference any more. The exploration behaviour of both species is equally influenced by the social environment. Even the pattern of the usage of all three forms of social learning is the same with stimulus enhancement being used most frequently and local enhancement least. The social context strongly affected social learning with frequencies being highest between affiliated group members. The results of the study highlight the importance of the social setting for every study aiming at investigating sociocognitive abilities.

6.2 Zusammenfassung

Das Ziel dieser Studie war es, den Einfluss des sozialen Kontextes (freundschaftliche oder nicht-freundschaftliche Beziehung zwischen Gruppenmitgliedern) auf das soziale Lernen im Objektexplorationskontext bei Keas (*Nestor notabilis*) und Raben (*Corvus corax*) zu untersuchen. Der Begriff soziales Lernen wird in dieser Studie verwendet, wenn von der Verstärkung eines Stimulus oder Ortes die Rede ist, oder vom Versuch das gleiche Objekt zu bekommen, welches ein Gruppenmitglied zurzeit manipuliert. Hierbei beziehe ich mich nicht auf die psychologischen Prozesse, sondern vielmehr auf die Art der Information, die gewonnen werden kann. Die vergleichende Studie konnte zeigen, dass Keas als Konsequenz häufigerer Manipulationen häufiger soziales Lernen zeigen als Raben. Nach Berechnung eines Index aus sozialem Lernen und Häufigkeit von Objektmanipulation zeigte sich jedoch, dass es keinen Unterschied zwischen den Arten gibt, in wieweit sie sich von der sozialen Umgebung bei der Manipulation von Objekten beeinflussen lassen. Auch das Muster der Häufigkeit des Gebrauchs der drei sozialen Lernformen ist bei beiden Arten gleich, wobei die Verstärkung eines Stimulus am häufigsten und die Verstärkung des Ortes am wenigsten gezeigt wurde. Der soziale Kontext hatte großen Einfluss auf die Häufigkeit, mit der soziales Lernen gezeigt wurde, wobei in den Gruppen mit freundschaftlichen Beziehungen zwischen den Gruppenmitgliedern am meisten soziales Lernen stattfand. Die Ergebnisse dieser Studie verdeutlichen die Wichtigkeit des sozialen Milieus für die Untersuchung von soziokognitiven Fähigkeiten in weiteren Studien.

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