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Social Complexity in Corvid Non-breeder Aggregations

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Background

Cognitive skills have evolved in various facets and domains in the animal kingdom with the highest currently known forms being found in mammals and birds (Van Dongen 1998; Roth & Dicke 2005). According to the widest consensus, intelligence is described as livelong behavioural flexibility that evolves due to the need to find solutions to problems which are frequent over the different generations but unpredictable within a generation (Shettleworth 2000). In mammals, some of the most potent problems are generated by living in 'complex' social groups, i.e. large, individualized, semi-permanent aggregations in which individuals have to notice information about others' demeanour, rank, kinship and past history of give-and-take, to use it for appropriate social problem solving (Byrne & Bates 2007a). In birds however, the existence of such complex social systems is debatable (Byrne & Bates 2007b). Accordingly, it remains unclear whether driving factors for brain evolution exist that are valid in birds and mammals. In this thesis, I will first review the current ideas about the evolution of intelligence with a focus on the social domain and an emphasis on possible differences between mammals and birds, and then investigate the social structure and relationships of a large-brained bird species, the common raven, testing assumptions of the social intelligence hypothesis under field conditions. In addition, I will use an operant paradigm on captive corvids (results presented here are only from carrion crows) to examine the birds' ability to individually differentiate conspecifics. Finally, I will discuss our findings on raven social complexity in the light of avian ecology, and give an outlook to future projects and research questions.

Cognition

Species differ in their problem solving abilities and the way they have to interact with their environment (Lefebvre et al. 1997; Reader & Laland 2002; Lefebvre et al. 2004; Sol et al. 2005a). Cognitive skills are thought to develop as an adaptation to challenging environments, and are either restricted to niche-specific problems, enabling the individuals to survive in the specific environment (i.e. foraging techniques), or involve general cognitive abilities like for example planning, causal reasoning or imagination, which can be applied to solve problems in various contexts (Reader & Laland 2002; Emery & Clayton 2004; Lefebvre et al. 2004). It is assumed that outstanding cognitive skills, as seen in human intelligence, are not of different

quality, but rather a combination and improvement of abilities that can also be found in non-human animals (Fuster 2002; Roth & Dicke 2005).

Several demanding environments have been identified as driving factors responsible for the evolution and specialisation on cognition in vertebrates. They either are social ('Social Intelligence Hypothesis': Jolly 1966; Humphrey 1976), or revolve around the physical environment ('Technical Intelligence Hypothesis': Byrne 1997), like difficult to access food ('Extractive Foraging Hypothesis': Parker & Gibson 1977; 'Food Distribution Hypothesis': Milton 1981; 'Kleptoparasitism Hypothesis': Morand-Ferron et al. 2007), or residency in seasonal environments (Winkler et al. 2004; Sol et al. 2005a). Most likely each species combines its own mosaic of challenging environments that drives its cognitive evolution. However, certain factors seem to play a comprehensive role for the development of intelligence in animals (Reader & Laland 2002; Lefebvre et al. 2004).

Social Cognition

One of the most powerful candidates for factors driving brain evolution is the social environment. More specifically, recognizing and appropriately dealing with different types of relationships such as dominance, kin, sexual or alliance partners over time may require enhanced processing capacities. Species (or probably even individuals) that are able to build up larger individual networks possess more brain mass compared to those with smaller networks (primates: Dunbar & Shultz 2007; ungulates, carnivores and primates: Pérez-Barbería et al. 2007; rhesus maqaques: Sallet et al. 2011; humans: Powell et al. 2012). An improved ‘social competence’ is a probable cause of high-end intelligence (Brosnan et al. 2010) with larger brains enabling individuals to behave special in terms of quality of social relationships, network size and structure of social groups (Kudo & Dunbar 2001; Dunbar & Shultz 2007; Sterelny 2007). The reason for this exceptional effect of the social environment on brain evolution is three-fold: firstly, the intentional autonomy of opponents is demanding a life-long need for behavioural and innovative flexibility in interactions with others. The actor is required to remain responsive to the opponents’ interactive scope (Barrett et al. 2007; Shultz & Dunbar 2007), which often is not possible with genetically fixed patterns. Secondly, specialisation and development of certain brain parts are needed to participate in actions of others and perform special pro-active skills like coordination and synchronisation (Gallese & Goldman 1998; Dunbar & Shultz 2007; de

Jaegher et al. 2010). And thirdly the need for computational ability and memory load rises if the number of strong bonded relationships increase (Kudo & Dunbar 2001), or if the perception of a relationship is temporally interrupted by a dispersed society (Barrett et al. 2003).

The boundary conditions for social intelligence to evolve are that individuals of a population have reasons to interact aside of reproduction, like competition and cooperation over limited resources. Individuals further require meeting iteratively in order to be able to learn about others' behaviours and preferences and to form and maintain relationships which can be differentiated by the quality, content and patterning of interactions over time (Hinde 1976). Group composition hence needs to show stable elements or be at least semi-permanently stable over longer time periods (Byrne & Bates 2007a). Finally, members of a society have to depend on each other due to strong learning effects on social behaviour and survival strategies (de Waal & Tyack 2003). The resulting social structure might comprise a relatively complex form of social knowledge, norms and tactics, which can be intuitively described as having an added 'political dimension' (Byrne & Whiten 1988). These preconditions for social complexity are typically found in semi-closed mammal groups with one or more reproductive females. The groups are characterized by female alliance formation for offspring protection and care, and male alliances to gain access to receptive females (primates: Wrangham 1980; lions: Moss & Poole 1983; dolphins: Connor et al. 1999; elephants: Mosser & Parker 2009).

Differences between Birds and Mammals

But what about birds? The forebrain size of birds varies between families comparable to mammals (Iwaniuk & Hurd 2005); however, the requirements for bonding are fundamentally different. Egg incubation and the absence of lactation open the possibility for a division of labour between males and females, leaving social monogamy as a far more common reproductive life history strategy in birds than in mammals (Reichard & Boesch 2003). Accordingly, the attempt to explain the evolution of big brains in some avian taxa like corvids and parrots with sophisticated skills required for pair-bonding ('relationship intelligence': Emery et al. 2007) is debatable. Proposed characteristics for such a sophisticated corvid/parrot pair-relationship, like behavioural synchrony, maintaining spatial proximity and providing social support in conflicts, are also found in smaller brained, long-term monogamous birds like for

example greylag geese *Anser anser* and are not categorically different in big brained birds (Scheiber et al. 2008). Also the social structures of many bird societies are hardly comparable to terrestrial mammalian associations. Birds are far more flexible in movement patterns than mammals. This results in fluid transitions from solitary or pair-wise territorial to social living within seasons or even during each day (Glutz von Blotzheim & Bauer 1993), whereas mammal societies typically stick to one social system for the longest part of their life. If bird societies should turn out to be too fluid to build up relationships other than for reproduction, sophisticated forms of social cognition are not to be expected.

Interestingly, cognitive skills of birds are often well adapted to face physical challenges. Food storage behaviour leads to larger hippocampus sizes (Sherry 1984; Balda & Kamil 1989; Hampton & Shettleworth 1996; Clayton 1998; Pravosudov & Clayton 2001; Garamszegi & Eens 2004), extractive foraging to skills revolving tools and physical coherence (Weir et al. 2002; Huber & Gajdon 2006), and survival in seasonal environments to behavioural flexibility (Greenberg 2003; Sol et al. 2005a; Sol et al. 2005b; Sol et al. 2007). But does this speak against social intelligence as an important factor on bird cognition, or are our measures for social complexity not yet fitting for birds? Examining the quality of bird interactions and relations, for example, may reveal different results concerning sociability than the sheer size of bird aggregations (see also: Bshary et al. 2012).

Study Species and Hypotheses

The aim of this thesis is to investigate social factors as potential driving forces for the evolution of cognitive skills in birds. The underlying working hypothesis is that the ideas of social intelligence are applicable in bird aggregations because first, social structure varies comparably in birds as it does in mammals, and second, birds have, like mammals, developed different cerebrotypes, including brain specialisations on computational capabilities, which are needed for social problem solving (Burish et al. 2004; Iwaniuk & Hurd 2005). Furthermore, in some bird species social challenges are already known to play a role for the use of sophisticated cognitive skills. Corvids, one of the largest brained bird families, heavily compete over food caches. Their ability to remember caches they have seen others make (Bednekoff & Balda 1996a, b; Heinrich & Pepper 1998; Clayton et al. 2001), allows them to efficiently pilfer these caches, which in turn leads storers to display tactics to prevent others from watching, or

confuse others while observing (Bugnyar & Kotrschal 2002; Dally et al. 2006a). They also seem capable of leading others away from cache sites (Bugnyar & Kotrschal 2004) and even of judging the 'knowledge state' of potential competitors, i.e. the likelihood of pilfering particular caches by remembering who was watching which caching event (Bugnyar & Heinrich 2006; Dally et al. 2006b; Bugnyar 2011).

The common raven *Corvus corax* has been praised for its 'intelligence' in folk psychology, popular books and scientific reports (Koehler 1943; Lorenz 1949). This reputation has been corroborated by experimental studies on problem solving and learning, notably in the social domain (Fritz & Kotrschal 1999; Schwab et al. 2007; Heinrich 2011; Bugnyar acc). Here I argue that the raven is also an ideal model species to study forms of social complexity and the possible link between social life and cognition. Ravens not only possess one of the biggest brains of all birds (compared to body size as well as relative forebrain size: Burish et al. 2004), but also face a socio-ecological environment, which makes the need of conspecifics in general, and social allies (bonding partners) in particular, likely for survival. They are long-lived specialised scavengers at carcasses and kills, a food source that is nutritious, but unpredictable in occurrence and abundance and consequently, highly competed for. They depend on conspecifics to learn about food locations (Heinrich & Marzluff 1991; Heinrich et al. 1993; Marzluff et al. 1996) and heterospecific predators to kill prey and open the bodies of carcasses (Harrington 1978; Stahler et al. 2002; Kaczensky et al. 2005). Ravens therefore gather in opportunistically formed non-breeder aggregations in which they either follow knowledgeable conspecifics to a food source (Marzluff & Heinrich 1991; Haffer 1993), or they actively recruit others to food they found themselves (Heinrich & Marzluff 1991; Bugnyar & Kotrschal 2001). The latter is due to the fact that ravens initially fear their food and may need others' company for approaching it (Heinrich 1988). Ravens may spend years or often their entire life in these facultative aggregations. However, so far no patterns could be identified by which these aggregations might be structured. Neither kinship nor affiliative relationships seemingly play a role for grouping decisions (Huber 1991; Heinrich et al. 1993; Heinrich et al. 1994; Parker et al. 1994; Marzluff et al. 1996). Having a closer look at these findings it is possible though, that empirical constraint like huge study areas and a lack of behavioural data have biased the previous data. Hence, the conclusions reached about raven social structure might be premature.

With sexual maturation at 3 – 4 years of age, ravens typically try to defend breeding territories (30 – 40 km^2) with their life-long socially monogamous pair partner (Haffer 1993). However, in satiated populations like in the Austrian Alps, ravens may spend up to 10 – 12 years in non-breeder aggregations, probably waiting for breeding opportunities to become available. Remaining in non-breeder aggregations as sexually mature birds means delaying reproduction; yet, it probably represents the best option for birds 'queuing' for territories (compare to Heg & van Treuren 1998). Some observations even suggest a certain degree of complexity in raven aggregations: individuals show sophisticated social play behaviour (Haffer 1993; Drack 1994), including the sharing and gesture-like showing of objects to others (Pika & Bugnyar 2011). Moreover, captive social groups of immature and mature ravens are characterized by social bonds formed within and between sexes (Lorenz 1931; Gwinner 1964; Heinrich 1999). These affiliative relationships function like the social bonds in primates (Cords & Aureli 2000) as valuable relationships (Fraser & Bugnyar 2010a) and are remembered over years (Boeckle & Bugnyar 2012). Notably, bonded individuals support each other actively in conflicts (Gwinner 1964; Fraser & Bugnyar 2012), reconcile conflicts among themselves (Fraser & Bugnyar 2011) or console one another after severe conflicts with others (Fraser & Bugnyar 2010b).

In this thesis, I examine the social structure of a wild raven non-breeder aggregation in the Northern Austrian Alps, focusing on the level of complexity in respect to social relationships, group stability and fission-fusion dynamics over the day and across seasons and years, respectively. The study population consists of about 200 – 300 wild ravens that regularly forage in the area of the Cumberland Wildpark, a local zoo near Grünau, Upper Austria. About two third of the birds have been trapped and individually marked in the course of this thesis and all birds have been habituated to close distance observation by humans. I have thus been able to track a relatively large number of birds individually across the years.

Depending on the social structure, species differ in their interactive scope from mere co-existing to differentiated relationships in intricate large groups. In chapter 1 we investigate different forms of grouping in ravens and their effects on social behaviour (Braun et al. 2012). Specifically, we are interested in the fluctuation of group membership, and whether ravens show grouping behaviour except for 'external'

reasons like feeding, mobbing and roosting. According to our assumption that the social structure of wild ravens fits the ideas of social intelligence, we expect to find some stable elements in group membership, and forms of sub-group formation characterized by affiliative interactions.

The second chapter attends to the details of the agonistic and affiliate interactions of wild raven non-breeders, with a focus on rank relationships and alliance formation (Braun & Bugnyar 2012). If ravens use non-sexual relationships in a sophisticated way, i.e. politically sensu de Waal (De Waal 1982), we would expect them to actively form and try to maintain social bonds with particular individuals, use these relations for gaining resources and/or status, but prevent others from doing so as well.

Kinship is an important factor for cooperative decisions in human and non-human animals (Hamilton 1964), with corvids being no exception (Baglione et al. 2003). In chapter 3, we conduct a comprehensive analysis of the genetic relatedness of the observed relationships and association levels at our study site (Braun et al. in prep). We expect kinship to play a role when ravens socialize in small sub-groups, which fit a typical clutch size, or when forming affiliated bonds as immature birds. In contrast, kinship should have no effect on pairs formed for reproduction.

Memory for other birds is fundamental for differentiated relationships in a fluctuating group. In chapter 4, we test captive carrion crows (3♀, 3♂), which have the most comparable lifestyle to common ravens in corvids, on computer touch-screens for their ability to discriminate between static visual images of unknown conspecifics (Braun & Bugnyar subm.). Given that birds living in a fluctuating society regularly encounter new individuals, we expect birds to quickly learn to identify and memorize pictures of conspecifics.

In a side-project we followed up our pivotal work on touch-screen use in corvids and tested the crows' performance on computers depending on the presence, identity and activity of bystanders (Rockenbach et al. in prep). Three other projects in which I have been involved are listed in the appendix.

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Socialized sub-groups in a temporary stable raven flock?

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Complex social life serves as one of the main driving forces behind the evolution of higher cognitive abilities in vertebrates. In birds, however, data are primarily derived from captive animals, which strongly contrast with free flying birds in terms of the number of interaction partners as well as available space. In captivity, raven non-breeder groups show strong social bonds and complex tactical manoeuvring, whereas wild non-breeders are thought to resemble anonymous aggregations. Over two years we observed a free flying population of ravens that visits a game park in the northern Alps. We here focus on the daily fission-fusion dynamics, individual spacing, and the influence of spacing on the birds' agonistic and affiliative behaviour. The composition of marked ravens in the local population changed slowly but constantly, although often remaining stable for several weeks. Birds only flocked for feeding, mobbing and roosting, and spent the rest of the day in loose aggregations, characterized by temporary small subgroups of 2 - 5 individuals. Aggression was high during crowd foraging but low outside of a feeding context. Affiliative behaviours, such as sitting within reaching distance, allo-preening and social play, were observed particularly in the small subgroups. These findings suggest that raven aggregations are not as unstructured as previously thought. Birds may spend time and/or interact affilliatively with multiple individuals during the day. This, along with temporary stability in group composition, provides the opportunity for social relationships to develop, and enables the existence of socialized subgroups within free flying raven aggregations.

Introduction

Higher cognitive abilities can be found in many animal species and are especially renowned in some families of birds and mammals. The underlying driving forces behind such abilities are thought to be the same in the different vertebrate taxa. Indeed, the most supported hypothesis for cognitive evolution in mammals, the social brain hypothesis (Byrne & Whiten 1988; Dunbar 1998), has also been successfully applied to a bird family, the corvids (Bond et al 2003, 2007). This hypothesis states that life in complex societies provides special kinds of intellectual problems leading to increased brain size. As such, corvids may use their bigger brains to tactically manoeuvre the social domain: they form alliances and differentiated relationships (Emery et al. 2007; Fraser & Bugnyar 2010a; Fraser & Bugnyar 2012), reconcile conflicts (Fraser & Bugnyar 2011) and console distressed partners (Fraser & Bugnyar 2010b; Seed et al. 2007); moreover, they infer social dominance from observing interactions among others (Paz-y-Mino et al. 2004), employ tactical deception in competition for hidden food (Bugnyar & Kotrschal 2002; Emery et al. 2004) and seemingly attribute knowledge about others' perception and knowledge state when protecting their own food caches (Emery & Clayton 2001; Dally et al 2006) and when pilfering the caches of others (Bugnyar 2011; Bugnyar & Heinrich 2005, 2006).

However, all these results were obtained from captive birds, where group size and interaction patterns are limited by space. In contrast, free living corvid flocks are characterized by a strong fluidity, changing their flock size often within a single day. Flocks of ravens *Corvus corax*, jackdaws *Corvus monedula* and rooks *Corvus frugilegus* vary from large groups of several hundred birds at the night roost to small groups of a handful of individuals during the day. Alternatively, nutcrackers *Nucifraga nucifraga* form large congregations at fruiting trees, but small groups at roosts in the core areas of their home ranges (Haffer 1993; Vander Wall & Balda 1977). Such fluidity is resplendent of some mammalian systems, such as those found in elephants *Loxodonta africana* (McComb et al. 2001), hyenas *Crocuta crocuta* (Holekamp et al. 1997), bottlenose dolphins *Tursiops truncatus* (Connor et al. 1999), spider monkeys *Ateles geoffroyi* (Symington 1990) and chimpanzees *Pan troglodytes* (Smuts et al. 1987). On one hand, a high degree of fission-fusion dynamics may increase the socio-cognitive challenges faced by a species (Aureli et al. 2008; Barrett et al. 2003), and may correlate with the ability to perform certain cognitively demanding skills, such as

inhibition (Amici et al. 2008). On the other hand, the potential for social bonding may be limited under high fission-fusion dynamics and such a society may drift towards anonymity (Byrne & Bates 2007a). To characterize a species as socially complex, we would thus expect (at least) the formation of longitudinally stable sub-groups that enable group members to build up differentiated relationships based on a history of give-and-take interactions (Byrne & Bates 2007a). Furthermore, strong learning effects on social behaviour and survival strategies would necessitate a strong degree of dependence on other group members (de Waal & Tyack 2003). Thus, if the social brain hypothesis does indeed apply to flocks of wild corvids, it needs to be shown that they are not just temporary aggregations resembling an anonymous crowd, but that they represent semi-permanent groups in which such social manoeuvring could be applied (Byrne & Bates 2007b).

Ravens are ideal subjects to illustrate the problem. They typically join non-breeder aggregations in their first three years when they are sexually immature. Birds may also remain in these aggregations as adults, if they are not able to occupy a territory. As territories are large (minimum of 10 km^2) (Rösner & Selva 2005), defended for life (up to 30 years) (Haffer 1993) year round by socially monogamous breeding pairs (Heinrich 1989), and thus are limited in supply, birds may spend several years in non-breeder aggregations, which they mainly use to gather information about, and access to, food locations (Marzluff et al. 1996; Wright et al. 2003). Indeed, ravens can gain a lot by learning from, and cooperating with others: they are specialized scavengers on carcasses of large mammals, a type of food which typically is unpredictable in supply and thus difficult to find. Moreover, carcasses are often defended either by dominant conspecifics or predators such as wolves *Canis lupus* (Stahler et al. 2002). What is yet unclear is to what extent raven aggregations are anonymous or represent groups in which (some) individuals meet regularly over time. Some studies suggest that aggregations of wild ravens lack any form of stability. In one such study, ravens caught from one feeding place, and thus assumed to belong to the same group, dispersed randomly after being marked and released (Heinrich et al. 1994). Additionally, marked non-breeding ravens observed at various feeding places within an area of 10,000 km^2 over two years did not travel in groups or stayed together (Huber 1991). Conversely, other raven populations have shown sub-roost formation (Wright et al. 2003) and environment-dependant stable ‘gang’ foraging (Dall & Wright 2009) where birds that hung out together over the day also slept in closer proximity in

the night roosts. Furthermore, non-breeding ravens are often reported to engage in frequent social play (Drack & Kotrschal 1995; Eklow 1988; Gwinner 1966; Heinrich & Smolker 1998), a behaviour which we would expect from individuals that know each other and maintain close bonds (Diamond & Bond 2003). Are the sophisticated patterns of social manoeuvring that characterise studies of captive ravens therefore the result of unnaturally stable and densely populated conditions in captivity or might studies on free-flying ravens have missed crucial aspects of the social life of raven non-breeder aggregations?

To our knowledge, all previous studies on free-flying ravens were conducted during feeding, either on different garbage dumps (Boarman 2003; Huber 1991) or on deliberately placed carcasses in the wild (Dall & Wright 2009; Heinrich et al 1994; Parker et al 1994; Rösner et al 2005). Aggression rates during crowd foraging are typically very high (Heinrich 1994a), most likely reducing the chances of observing affiliative interactions; under captive situations, affiliative relationships between individuals are best detected in a relaxed context, outside feeding (Drack & Kotrschal 1995), when birds are more likely to approach one another for allo-preening and/or engage in playful interactions. Here, we studied free flying wild ravens within a local zoo in the Austrian Alps, where the birds spend much of the day. Specifically, they use the park for snatching food from the zoo animals and, notably, also for resting, socializing and playing (Drack & Kotrschal 1995). By concentrating our study on this location, we were able to habituate the ravens to close distance observations (down to 25 m) not only at feeding sites but also at areas used for resting and social interactions throughout the day. Our hypothesis was that raven aggregations do not represent an anonymous crowd but contain socialized sub-groups. This should become apparent through the formation of (small) groups during the day, aside from crowd foraging situations, characterized by high levels of affiliative behaviours and low levels of aggression. We therefore investigated the daily fission-fusion dynamics of free-flying non-breeder ravens, the spacing of the individuals during the day, and the dependence of behaviours on individual spacing. We also recorded the change in “flock” composition across the year, whereby the term “flock” infolds all ravens present in the valley on the same day, not a cohesive crowd which moves together. We expected flock composition not to change randomly but to exhibit patterns of stability, so that individual ravens would have the opportunity to build up relationships based on repeated interactions.

Methods

Field site and study animals

The study subjects were derived from a population of free flying wild ravens in the inner Almtal, a small valley in the Northern Austrian Alps. These ravens regularly use parts of the area of the Cumberland Wildpark, a local zoo housing typical Eurasian wild animals. Most of the ravens were usually found in and/or around four large enclosures (przewalsky horse, wolf/bear, wild boar and red/fallow deer; Figure 1) or on an adjacent cliff throughout the day, including the winter months and the breeding season. Hence, they were considered to be non-breeders. The rest of the valley, including the southern and northern part of the game park, is rarely used by non-breeders but is aggressively defended by territorial raven pairs (Drack & Kotrschal 1995). The communal night roost is situated approximately 500 m from the park, on the other side of the cliff; its exact location has changed over the years but it has been consistently used by ravens since the early 1990s (own unpubl. data; compare Wright et al. 2003).

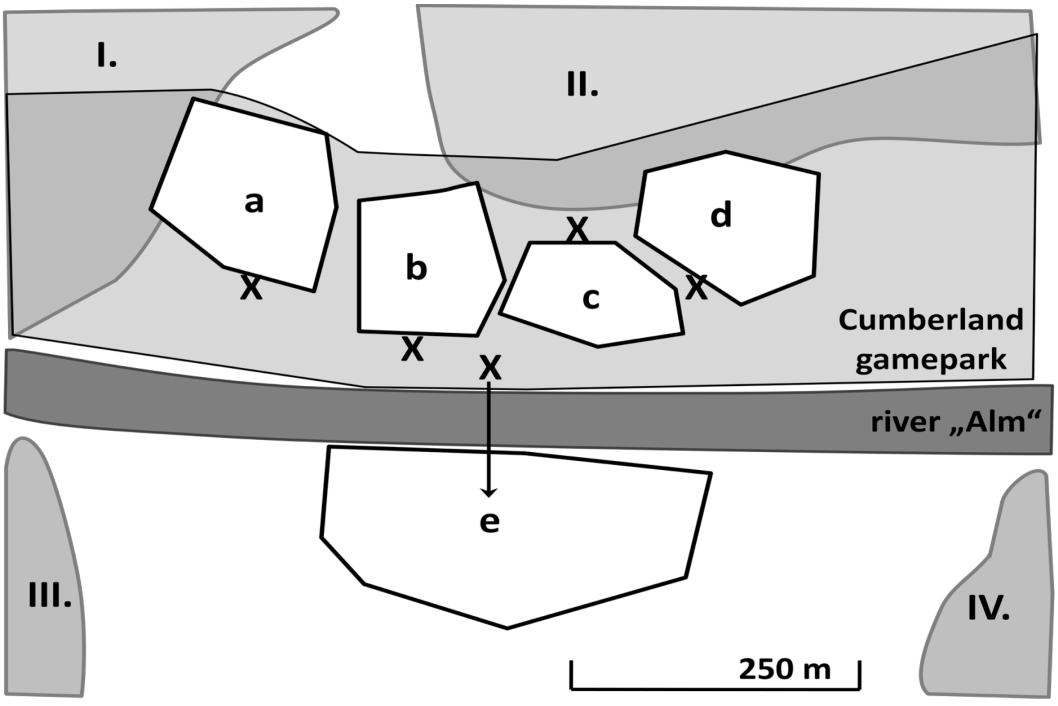

Figure 1: distribution of the wild ravens in the inner Almtal with the areas a-e (a. przewalsky horse *Equus ferus przewalski*, b. wolf/bear *Canis lupus/Ursus arctos*, c. wild boar *Sus scrofa* and d. red/fallow deer *Cervus elaphus/Dama dama*; e. cliff along the park's border) and the surrounding four territories of wild ravens (I. – IV.); the "X" represent the spots from which the areas were observed.

Non-breeders typically arrive at the game park at dawn and leave towards the night roost around sunset. Territorial breeders (all adults and identified as such by defending a territory and/or feeding young) visit the park only occasionally, notably during the morning feeding of the zoo animals (between 7:00 - 10:00). They typically show up in pairs, engage in joint displays and generally dominate the non-breeders, including adult birds (own unpubl. data). During the breeding season, only one of the pair partners shows up at the feedings, carrying off consecutive loads of food towards their territory and nest.

We caught ravens with a drop-in trap (Stiehl 1978) situated in the game park with a mean marking rate of 6 ravens per month (see Table 1 for an overview over the number and sex of the birds trapped), starting in spring 2008. All birds were weighed and marked with individual wing tags (Caffrey 2000) and coloured ring combinations on both legs. Age class was assigned as juvenile (within first year), subadult (second and third year) or adult (older than three years) using mouth and feather colour (Heinrich 1994b); sex was determined from blood samples. To ensure the least possible stress for the birds, they were taken out of the trap, handled and released within the shortest possible time after trapping.

Table 1: list of the number and sex of birds marked over the course of the study, mean number of ravens present in feeding crowds, % of marked birds in feeding crowds and number of days taken records of the individuals present in the valley.

Month	Year	Marked females	Marked males	Total	N°. of birds present	% Ravens marked at feeds	N°. of days recorded flock composition
Jan - Mar	2008	7	2	**9**	19 ± 11	**13.10 ± 13.18**	
Apr - Jun	2008	4	7	**11**	18 ± 11	**23.07 ± 17.01**	
Jul - Sept	2008	18	9	**27**	16 ± 11	**30.21 ± 14.98**	
Oct - Dec	2008	7	11	**18**	24 ± 19	**33.96 ± 16.90**	
Jan - Mar	2009	13	10	**23**	25 ± 16	**43.16 ± 20.43**	
Apr - Jun	2009	2	1	**3**	28 ± 16	**53.54 ± 19.06**	
Jul - Sept	2009	6	6	**12**	27 ± 16	**51.04 ± 20.75**	
Oct - Dec	2009	5	1	**6**	38 ± 22	**44.59 ± 13.83**	**27**
Jan - Mar	2010	-	-	**-**	42 ± 20	**45.26 ± 12.57**	**25**
Apr - Jun	2010	11	13	**24**	36 ± 17	**59.54 ± 18.43**	**62**
Jul - Sept	2010	-	-	**-**	29 ± 11	**58.58 ± 13.35**	**11**

Data collection

Flock size and composition

After a habituation phase of three months in autumn 2007, we started data collection at the five different observation areas in and around the gamepark (Figure 1). Data for the present study were not taken before summer 2008, so the ravens were already fully habituated and did not change their behaviour due to the observer's presence. Overall flock size estimates and identities of marked ravens present were taken each morning while the bears/wolves and wild boars were being fed (7:30 until 9:00 am), as all marked ravens recorded during the day participated in the morning feeds. Only one marked raven was not present at any of the feeds despite being observed twice in the gamepark during the day. All data were collected with binoculars and a tape recorder.

To check for variation in flock composition, we analyzed data on the presence of marked ravens over one year. For these analyses we used data from October 2009 until the end of September 2010, because during that time we had 100 marked ravens and sufficient recordings of the flock composition during the morning feeds to run our analyses. We recorded the flock composition on 125 days distributed over eight months within that year. Within these eight months we investigated the variation in the presence of the 100 birds. Depending on how often they were in the valley, we assigned all birds to one of four 'presence categories' for each of the months. If a marked subject was present on more than two thirds of the days within a month, they were labelled 'stable'. Birds which were present between one third and two thirds of the sampling days were categorized as 'changing', because 86% of them either arrived within that month for a longer stay, or left within that month after a longer period of presence, and were thus changing to or from residency. If birds were present for less than one third of observations per month, they were labelled 'visitors', and finally, those that were not present at all were counted as 'absent'.

Individual spacing and behaviour

In addition to data collected during the scheduled feeding times of the gamepark animals, we conducted 33 observation rounds between June 2008 and March 2009 either between 9:00 and 11:30 ('morning' observation), between 12:00 and 14:30 ('midday' observation), or between 15:00 and 17:30 ('evening' observation). To control

for the influence of the time of day on the patterns of spacing and behaviour, we distributed the number of rounds evenly over the three times of day. Each observation round was started at the horse enclosure, followed by the wolf/bear enclosure, the cliff, wild boars and finally the fallow deer enclosure. At each location, scan samples were conducted every 90 seconds to systematically record all ravens present. Typically 10 such scans were done before switching to the next location, however, time constraints resulted in a maximum of only 6 scans per location for some rounds. In total, 23 full rounds were sampled (with 10 scans per location), 8 in the morning and at midday, and 7 in the evening. Ten shorter rounds (with 6 scans per location) were conducted, 3 in the morning, 3 at mid-day, and 4 in the evening. During each scan, the identities (if possible) of all ravens within the enclosure/on the cliff were recorded along with the distances to their two nearest neighbours and their behaviour (see Table 2 for behavioural definitions). Within one meter of another raven, individual spacing was estimated in 25 cm steps, from 1 m onwards we preceded in 50 cm steps until 3 m, from 3 to 50 m we estimated distances in 5 m steps, starting with 5 m, and from 50 m on we used 10 m steps. To facilitate estimates of close distances between the birds (within 3 m), the body size of the ravens (approx. 50 cm body length from head to tag, and 10 cm body width) was taken as a reference. For longer distances, we took enclosure structures with 3 m and 10 m lengths as references. If a raven was alone in the enclosure, we used 300 m as a standard nearest neighbour distance as this was doubling the maximal distance that we observed between two ravens during all observational rounds. Ravens were recorded as being in a group if the intergroup distance (the spacing from the edge of the group to the next raven) was at least 10 times as long as the intragroup distance (mean distance from each group member to its two nearest neighbours within the group). All other ravens were labelled “solitary”. As ravens have typical calls and displays that result in conspecifics either approaching (food calls for unspecific receivers, courtship displays for a specific receiver) or staying at distance (territory calls for unspecific receivers, vocal show-off for a specific receiver) from the signaller (Gwinner 1964; Heinrich 1989), ravens may signal their social intentions even when solitary.

Aggression

To have a closer look at the effect of number of birds present and food context on aggression rates, over 46 days from February to May 2010, T.W. recorded data on aggressive conflicts at either one or two (N = 17) morning feedings (bear/wolf and wild boars) for 30 min each, and took additional 30 min samples outside feeding times, once (N = 5), twice (N = 28) or thrice (N = 13) a day. Data on aggression were only collected at the wolf/bear, wild boar and deer enclosures and comprised 43 h of observation time during morning feeds and 50 h during the rest of the day (non-feeding context).

Table 2: behavioural categories for solitary individuals and groups

Category	**Behaviours**	
	Solitary individuals	**Groups**
Agonistic	Territory calls	Approach retreat
	Vocal show off	Forced retreat
		Fight
		Chase flight
Neutral	Locomotion and sitting	Locomotion and sitting
Affiliative	Food calls	Social play
	Courtship displays	Sitting close
		Allopreening
		Invite preening
		Courtship displays
Comfort behaviour	Preening/shaking	Preening/shaking
+ foraging	Resting/sleeping	Resting/sleeping
	Singing	Singing
	Individual play	Individual play
	Foraging	Foraging
Others	Departing	Departing
	Undefined vocalisations	Undefined vocalisations

Data analyses

Statistical analyses were conducted using SPSS 19.0 (SPSS Inc., Chicago, IL, U.S.A). We used multinomial generalized linear mixed models to determine the effects of age and sex on the presence patterns of the birds. The presence-category served as the dependent variable, age and sex as fixed factors and subject identity and month as random factors. To account for possible seasonal effects on sociality we also checked whether the distribution of presence categories changed over the months. We therefore ran a separate model with month as a fixed factor and subject identity as random factor. Wilcoxon signed-ranks tests were used for comparisons between the morning feedings and observation rounds on the same day, either for the number of ravens present (N = 31 days), or the aggression rates during morning feeds and non-feeding situations (N = 46 days). A Mann-Whitney-U test assessed differences in the number of birds present in groups or remaining solitary. We ran separate linear mixed models on each behavioural category to see whether being in a group or solitary had an effect on the extent to which a particular behavioural category was expressed. We therefore took the mean number of birds per observation round that were solitary or in groups, and calculated the proportion of grouped and solitary birds engaged in the different behavioural categories. The five behavioural categories served as dependent variables and whether the subject was solitary or in a group was taken as a fixed factor. The mean number of grouped and solitary individuals and the recording date were entered as random factors. All tests performed were two-tailed and α was set to 0.05.

Results

Flock size and composition

We recorded a mean number of 38 ± 17 birds (mean ± SD) present at the morning feeds (N = 442 days of data collection). Over the particular year in which the threshold of 100 marked birds was reached, only 60 of the 100 birds were seen (29 female, 10 adult, 13 subadult, 6 juvenile; 31 male, 11 adult, 15 subadult, 5 juvenile). When comparing the distribution of presence of the marked ravens over the year, more birds were either ‘stable’ or ‘absent’ than ‘changing’ or ‘visiting’ (Figure 2). Neither sex ($F_{3.468}$ = 0.630, P = 0.596), nor age ($F_{6.468}$ = 1.781, P = 0.101) had an effect on the presence patterns. There was a change in the distribution of presence categories over

the year ($F_{21.456}$ = 2.663, P < 0.001), which was mainly due to a constant increase of absent birds and a constant decrease of stable present birds. When dropping those two from the data, the percentage of visiting birds and changing birds did not differ within the year ($F_{7.101}$ = 2.663, P = 0.286). All birds switched their presence category in at least one month with the exception of six birds whose presence was stable over the whole period of observation.

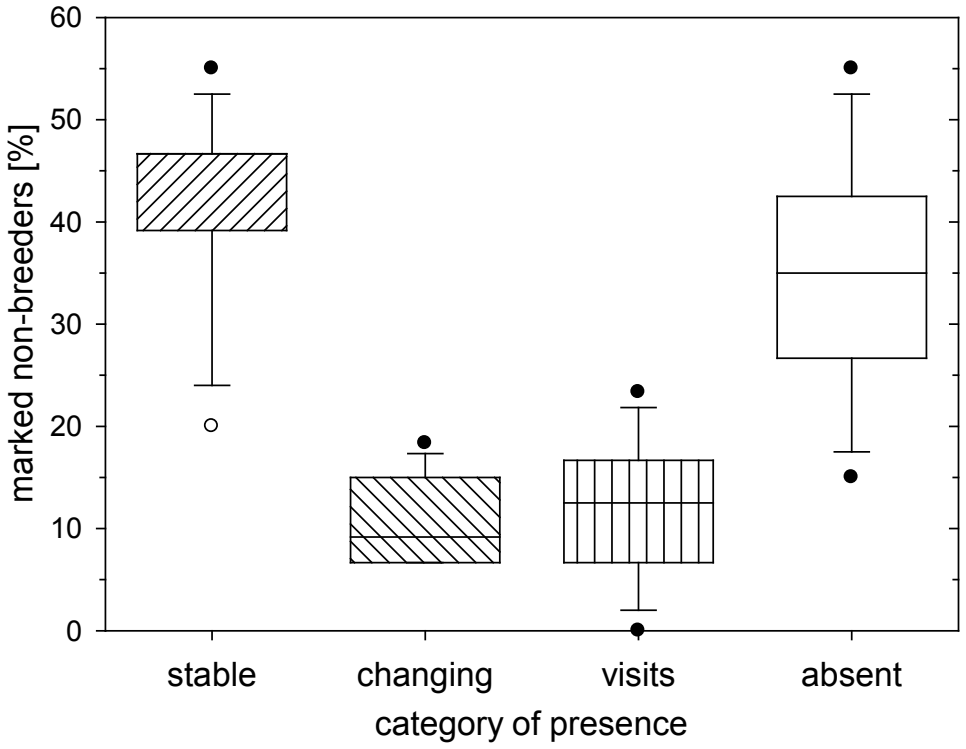

Figure 2: median number of marked nonbreeders whose presence was stable, who were changing it, just visited the Almtal, or were absent.

Individual spacing and behaviour

The maximum number of birds seen during the morning feeds did not differ from the total number of birds seen the same day during the later observation round (Z_{31} = -0.284, P = 0.776. This indicates that we were able to find most of the ravens during the rounds, although we cannot confirm this for unmarked birds.

During non-feeding conditions, there was no difference in the number of birds which were solitary and those in small groups (U_{33} = -0.475, P = 0.636) with a mean of 15 ± 7 solitary birds and 16 ± 11 ravens in groups per observation round. Solitary birds

kept a mean distance of approximately 70 ± 69 m from their neighbours, whereas mean nearest neighbour distances in groups (intragroup distance) was 2.54 m ± 2.20 m, and intergroup distances (between groups and surrounding individuals) was 65 m ± 80 m (the large standard deviations result from the adopted 300 m distance if the group, or the individual was alone in the observation area). Mean group size was 3.5 ± 1.2 ravens (N = 192 groups).

Birds differed in the behavioural categories expressed if in groups or solitary. Some behaviours were never observed in groups such as singing (total N = 5), whereas others were confined to groups, like social interactions. Nevertheless, solitary ravens were also able to express their social intentions through their vocalizations (see methods). Linear mixed models revealed that grouping ravens engaged in only slightly more agonistic behaviours than solitary ones (grouping birds 6.10 ± 1.59 % (mean ± SE) and solitary birds 1.72 ± 1.73 %, $F_{1.70} = 3.474$, $P = 0.067$), however, they differed strongly with regards to affiliative interactions (grouping birds 14.19 ± 2.05 % and solitary birds 2.19 ± 2.23 %, $F_{1.33} = 16.753$, $P < 0.001$). Solitary ravens in contrast performed more neutral behaviours like sitting and locomotion than grouping birds (grouping birds 50.37 ± 3.77 % and solitary birds 63.13 ± 4.09 %, $F_{1.70} = 5.265$, $P = 0.025$). No effect of individual spacing was apparent on the frequency of comfort behaviours expressed (grouping birds 15.36 ± 2.62 % and solitary birds 14.84 ± 2.73 %, $F_{1.33} = 0.059$, $P = 0.810$) or on the final category, the undefined vocalizations and departures (grouping birds 13.98 ± 3.47 % and solitary birds 18.61 ± 3.78 %, $F_{1.29} = 0.864$, $P = 0.360$).

Aggression

Aggression rates were significantly higher during feeds than in non-feeding situations with a mean conflict rate of 0.60 ± 0.31 conflicts per individual during one hour of feeding compared to 0.07 ± 0.15 conflicts per individual during one hour of the rest of the day ($Z_{46} = -5.650$, $P < 0.001$). No significant difference was found between the aggression rates per individual between the wolf/bear feeds and wild boar feeds ($Z_{17} = -1.633$, $P = 0.102$), nor between the three different non-feeding time slots per day ($\chi^2_{13} = 1.130$, $P = 0.568$), or if only two enclosures were visited ($Z_{28} = -1.495$, $P = 0.135$).

Discussion

Our study reveals that raven groups are not as unstructured in their aggregation patterns as previously thought. The dichotomy between anonymous aggregations in the wild and socialized sub-groups with differentiated relationships in captivity cannot be fully resolved with this study; however, we can show that the foundation for socialized sub-groups is present in a free-flying raven population.

According the assumption that ravens form anonymous aggregations, groupings should only be found in response to external factors like increasing foraging efficiency, antipredator defence or reducing thermoregulatory demands (Beauchamp 1999; Shoemaker & Phillips 2011). During our observation periods, ravens gathered in one area for foraging. In addition, they assembled at their communal roost every evening and flocked for mobbing (personal observation). The formation of large aggregations therefore has a strong external component in those ravens, which conforms to the findings in most literature (Marzluff et al. 1996; Wright et al. 2003) and our expectations for temporary and anonymous aggregations.

Aside from these gatherings, however, ravens could be found either alone or in small sub-groups over the day. As predation pressure is relatively weak in these large birds (Haffer 1993), the necessity to remain in groups could, in an anonymous set up, be explained by increased foraging efficiency (Beauchamp 2010; Dall & Wright 2009). During our observations, no pronounced differences were found in foraging rates between ravens in groups and solitary birds. Rather, ravens seemed to selectively join other individuals to engage in affiliative behaviours. In an anonymous setting, affilliative behaviours should be limited to pair partners or those that are in the process of pair formation. In our data set, ravens were found in subgroups of a mean of 3.5 individuals, exchanging affiliative behaviours with more than one partner. This makes it unlikely that pair formation would be the only explanation for grouping in ravens.

Small sub-groups characterized by affiliative interactions might consist of close kin, due to direct or inclusive fitness benefits (Carlisle & Zahavi 1986, Canestrari et al. 2005). The mean group size of 3.5 individuals is well within the range of typical clutch sizes of ravens (Haffer 1993), so this scenario might be possible. However, so far hardly any effects of kinship have been reported in wild ravens (Parker et al.1994, but see Webb et al. 2009). Future research is needed to disentangle whether or not small groups of ravens may form around siblings in wild ravens.

Irrespective of kinship, it is worth to point out that, aside of crowd-foraging, group formation in ravens does correlate with affiliative behaviours. This supports the idea, that ravens form and maintain bonds within the aggregation of non-breeders (Hinde 1976); something that has so far only been shown in captive ravens (Fraser & Bugnyar 2010a). The stability in flock composition over several months would also provide the opportunity for repeated interactions within dyads to occur, a fundamental requirement for differentiated relationships to form (Byrne & Bates 2007b).

Such valuable relationships could be used by non-breeder ravens to cope with the scramble competition that characterizes crowd foraging (Heinrich 1988). Individuals may support each other during and/or after conflicts (Fraser & Bugnyar 2010a, b, Fraser & Bugnyar 2012). Social embedding may also enable ravens to better access food (Huber 1991) and minimise distress during food competition (Fraser & Bugnyar 2010a). Indeed, aggression rates in small groups were virtually absent in comparison to the situation in the foraging crowd. We have to bear in mind that our study site is characterized by a relatively stable environment with a predictable food supply, possibly affecting aggression rates as well as the time needed for foraging; notably, it might allow individuals to allocate extra time for socializing. Still, ravens have a long history with humans, from joining hunter-gatherers to feeding on the dead bodies at battle fields and, more recently, at garbage dumps. Hence, it remains speculative how socially ‘artificial’ the situation at our study site actually is and underlines the importance of taking into account the huge flexibility of the species.

Taken together, our study confirms that raven life as a non-breeder is characterized by competition and yet also by the need to cooperate (Heinrich 2011). This may drive the need for increased social complexity and differentiated relationships of the type previously described for captive ravens. Our data provides the first suggestive evidence that such socialized sub-groups exist in free-flying raven flocks.

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Social Bonds and Rank Acquisition in Raven Non-Breeder Aggregations

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Complex social life has been characterized as cognitively challenging and recently, social relationships such as long-term social bonds and alliances have been identified as key elements for brain evolution. Whereas good evidence is available to support the link between social relations and cognition in mammals, it remains unsatisfying for birds. Here we investigated the role of avian social bonds in a non-breeder aggregation of ravens, *Corvus corax* in the Austrian Alps. We individually marked 138 wild ravens, representing approximately half of a population that uses the area of a local zoo for foraging. For two years, we observed the dynamics of group composition and the birds' agonistic and affiliate interactions. We identified two levels of organisation, the formation of an unrelated local group and the individuals' engagement in social bonds of different length and reciprocity pattern. Whereas belonging to the local group had no significant effect on conflicts won during foraging, the individual bonding type did. Birds which engaged in affiliate relationships were more successful when competing for food than those without such bonds. Interestingly, bonded birds did suffer from aggression by other bonded birds and, probably as a consequence, most of the ravens' social relations were not stable over time. These results support the idea that social bonding and selective cooperation and competition are prominent features in non-breeding ravens. Proximately, bonding may qualify as a social manoeuvre that facilitates access to resources; ultimately it might function to assess the quality of a partner in these long-term monogamous birds.

Introduction

Social living has evolved manifold in the animal kingdom and reached all imaginable forms from huge anonymous aggregations to small cohesive groups structured by differentiated relationships. Differences in social structure emerge from ultimate and proximate factors like the underlying ecological pressures and physiological properties such as morphology and hormonal constitution (Whitehead 1997; Goodson et al. 2012). The social structure sets the platform upon which the members of a population meet, and hence determines the degree upon which they need to interact and communicate. It has a strong potential to drive the evolution of socio-cognitive skills (Byrne & Whiten 1988; Dunbar 1998) and more complex forms of sociality should be accompanied by sophisticated social cognition. This is well documented in mammals (Dunbar & Bever 1998; Connor et al. 1999; Kudo & Dunbar 2001; McComb et al. 2001; Byrne & Corp 2004), but leaves many open questions in birds (Beauchamp & Fernandez-Juiric 2004; Iwaniuk & Arnold 2004; Emery et al. 2007).

A critical point concerns the indices which are used to measure social complexity. Mammal social complexity initially was based on group size: primates living in larger social groups have larger brains, supposedly because they have to deal with an increased number of dyadic relationships compared to species living in smaller groups (Dunbar 1992; Barton 1996; Dunbar 1998). In birds and some other mammals, group size does not consistently correlate with social complexity: aggregations might be large without any social relevance for the individual like in anonymous herds (Pérez-Barbería et al. 2007), or conversely, affiliate interactions may extend to members of other groups with overlapping ranges like in dispersed societies (Smuts et al. 1987; Byrne & Bates 2007; Randic et al. 2012). Other indices for social complexity seem to be rather primatocentric and incompatible for a lot of other taxa, like for example frequency of tool use and tactical deception (Reader & Laland 2002; Byrne & Corp 2004), or grooming clique size (Kudo & Dunbar 2001). Individual network size of strong bonded relationships, in contrast, turns out to be for many species a good proxy for social complexity (Kudo & Dunbar 2001; Dunbar & Shultz 2007); as a consequence, the ability to build up social bonds is in the process of becoming a key concept for social complexity. In vertebrates pair-bonding probably initiated a qualitative shift from loose aggregations of individuals to complex negotiated

relationships which are generalised to all social partners in only a few taxa, for example in anthropoid primates (Shultz & Dunbar 2007).

Detailed knowledge of a species' social structure is needed in order to classify them correctly according to their social complexity. So far, however, we are lacking data on the relevance and gradation of social relationships in many taxa, particularly in birds. The high mobility of birds and seasonal variability of social structure in a lot of them complicate an otherwise easy comparison to the mammalian systems (Seed et al. 2009). Social monogamy, which is a rare bonding pattern in mammals (Broad et al. 2006), is, due to egg incubation and the lack of lactation, a very common social strategy in birds, raising the possibility of totally different bonding patterns in birds and mammals. Relative brain size (measured by a regression of brain volume against body weight), however, shows a correlation with social structure in birds, with those aggregating in well-arranged groups of 5-30 individuals and those with a long-term social monogamous or cooperative mating system having the largest brains (Emery et al. 2007). Brain structures evolved in convergence to mammals indicating specialisations on social problem solving in some bird families (Burish et al. 2004). Furthermore corvids, one of the biggest brained bird families, display bonding patterns which have no immediate reproductive relevance, but rather social ones: rooks, *Corvus frugilegus* (Emery et al. 2007), jackdaws, *Corvus monedula* (de Kort et al. 2006), and ravens (Lorenz 1931; Gwinner 1964; Heinrich 1999; Fraser & Bugnyar 2010a) form strong bonds with group members of the same and different sex while still sexually immature. Ravens remember those bonds for years, even after becoming territorial breeders (Boeckle & Bugnyar 2012). Similar to primates (Fraser et al. 2008), raven bonds can be characterized as valuable relationships, whereby male-male and male-female relations tend to be more compatible and secure than female-female relations (Fraser & Bugnyar 2010a). Bonded birds are likely to reconcile conflicts (Fraser & Bugnyar 2011), actively support one another in conflicts with others (Gwinner 1964; Fraser & Bugnyar 2012) and console one another after severe conflicts with others (Fraser & Bugnyar 2010b). Social bonds thus seem to be critical in achieving and maintaining (high) dominance rank (Gwinner 1964).

All these studies, however, have been conducted on captive ravens, whereas in the wild, they are thought to assemble in anonymous aggregations in which they have no affiliations until they are sexually mature and mate for life. From then on they defend large areas (>>10 km^2) year round (Heinrich 1989; Rösner & Selva 2005) and,

due to their long life span of up to 30 years, often for decades (Haffer 1993). Independent offspring are not tolerated in the parental territory and join non-breeder aggregations for foraging and roosting. Ravens are holarctically distributed scavengers that compete with potentially dangerous predators for their prey (Heinrich 1989; Stahler et al. 2002). They need to cooperate with con-specifics to overcome the power of predators or even the dominance of a pair of territorial breeders (Marzluff & Heinrich 1991). Yet, to date, there is hardly any evidence for social bonding within non-breeder groups of wild ravens. Marked birds disperse randomly (Huber 1991; Heinrich et al. 1994; Marzluff et al. 1996) and genetic relatedness within foraging groups is not higher than between them (Parker et al. 1994), which would be expected if siblings would join the non-breeders together.

Here we made a new attempt at investigating social bonds in wild ravens. Unlike other studies (Huber 1991; Heinrich et al. 1994), we focused on one study site at which non-breeders assemble on a daily basis; in addition, we significantly increased the percentage of marked birds (50% of the ravens were marked in our study, compared to 10-20% in previous studies) as well as observational effort. We examined the social dynamics of raven groups, notably when social bonds were formed, how long they did last and what they were used for. Assuming that the birds' sophisticated socio-cognitive patterns shown in captivity are of relevance under field conditions, we hypothesized that (i) social bonds should play a role in the birds' acquisition and maintenance of dominance rank, (ii) social bonds should form independent of immediate reproductive reasons in several age classes, but (iii) higher ranking ravens could intervene in the formation of bonds and complicate its maintenance. In contrast, if social bonding follows reproductive reasons in an anonymous setting, then (i) they should gradually change with maturation and (ii) once formed, adult bonds should hold until a territory becomes available.

Material and Methods

Field site and study animals

The study was conducted on a wild population of common ravens roaming in the Northern Austrian Alps and regularly using the Cumberland Wildpark, a small local zoo in the inner valley of the river Alm, 6km near the village Grünau. Groups of ravens visit the park year round, mainly for foraging, but also for playing and socializing (Drack

& Kotrschal 1995). They consist mostly of non-breeders (i.e. sexually immature birds and sexually mature but not reproductively active birds) that communally roost in a side valley adjacent to the Wildpark. Over the day, non-breeding ravens disperse over a relatively restricted area of the valley, which contains four enclosures in the park (przewalsky horse *Equus ferus przewalski,* wolf/bear *Canis lupus/Ursus arctos*, wild boar *Sus scrofa* and red/fallow deer *Cervus elaphus/Dama dama*) and a cliff right outside the park's border (but observable from within the park; Figure 1). The rest of the inner part of the valley (approximately 100 km^2, including ½ of the park) is occupied by seven territorial breeding pairs, which aggressively defend their territories from being used by non-breeders but frequently join the groups in the park for foraging (Drack 1994). All ravens are well habituated to the presence of human observers. In general, they can be studied from a close distance (< 25 m) with the help of binoculars and video cameras. For the present study, the main observer (A.B.) invested three months to ensure that the ravens were fully habituated to her person, allowing her to walk around and move between enclosures and observation sites without causing any disturbance or flight responses.

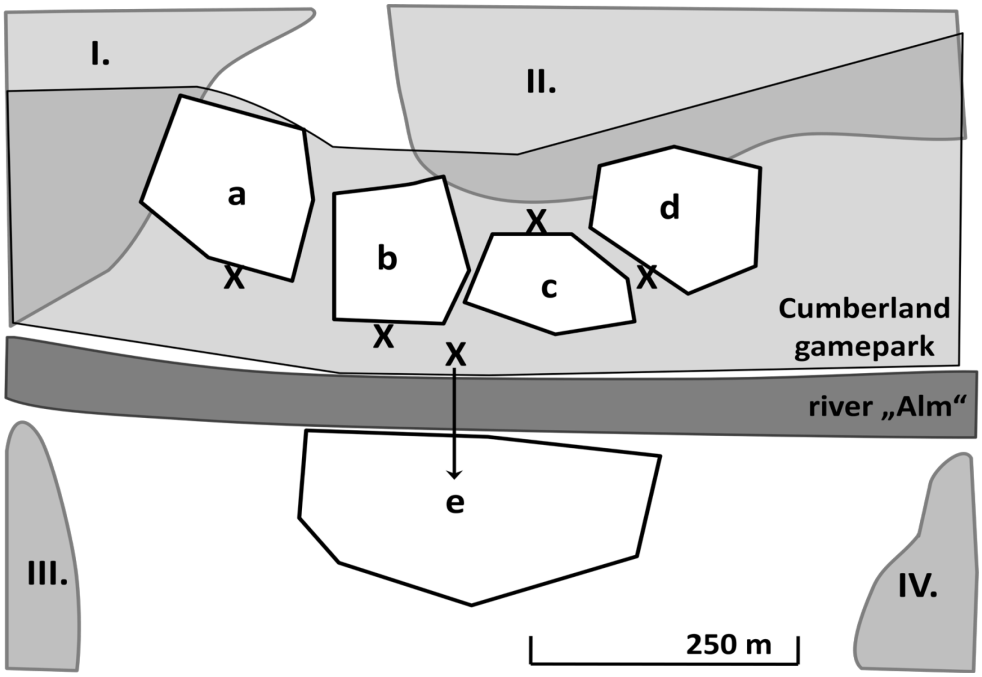

Figure 1: Sketch of study site in the inner valley of the river Alm, Austrian Alps. White areas a-d represent our observation sites in the Cumberland Wildpark (a. przewalsky horse, b. wolf/bear, c. wild boar, d. red/fallow deer) and area e represents the cliff along the park's border; "X" marks the exact observation point in each of the areas. Grey areas with Latin numbers (I. – IV.) symbolize the breeding territories surrounding the study site. Dark grey area symbolizes the river Alm as natural border of the Wildpark.

Trapping and marking

During the study period we caught a total of 120 wild ravens with drop-in traps (Stiehl 1978) with a mean rate of 6 ± 6 ravens per month. Traps (3 x 3 x 3m) were located in the Wildpark; they were equipped with perches and positioned in shady areas next to the enclosures the ravens use for foraging. Traps were regularly checked during the day so that the time ravens spent in captivity was reduced to a minimum (< 2 hours). Trapped birds were photographed, weighed and measured. Age class was determined by mouth and feather colour and assigned to juvenile (within their first year) if the mouth linings were pink and the plumage colour brown, subadult (second and third year), if the mouth linings were pink with black spots and plumage was black, and adult (from third year on), if mouth linings were black and plumage too (Heinrich & Marzluff 1994). To analyse sex and genetic relatedness we took 50 to 200 µl of blood from the alar vein. Birds were marked with a patagial wing-tag (Caffrey 2000) and an individual combination of colour rings and a numbered metal ring from the Vogelwarte Radolfzell on the legs. Additionally, we released 15 captive-bred but raven-raised juvenile birds (7 f, 8 m; marked in the same way as the wild-caught birds) during the course of the study period. The release of captive-bred birds followed the procedure of re-introduction programs for ravens in Germany (Koch et al. 1986) and always resulted in the integration of the released birds into the non-breeder flock within a month. Three wild birds were already marked with colour rings from a former study, in which the scrounging tactics and movement coordination of wild ravens were observed (Bugnyar & Kotrschal 2001, 2002b). Altogether 138 ravens (73 f, 65 m) could be individually identified over the course of the study.

Data collection

Within two years, from August 2008 to July 2010, the ravens were observed on a total of 392 days during the morning feedings of the wild boars and the bears/wolves. Presence at feedings served as a reference for flock composition; only in two cases a marked bird was observed in the valley without being present in the morning feeds. Feedings took place between 7:00 and 9:00, comprising 30 min data collection at the wild boar enclosure and 15 min at the bear/wolf enclosure. These observations in the morning were supplemented by 183 observation rounds that occurred during the day, which were conducted either between 9:00 and 11:00 (morning), 11:00 and 13:00 (mid-day) or between 16:00 and 18:00 (evening); a round consisted of five 15 min

protocols taken from fixed positions that provided a good overview of the five enclosures regularly used by the ravens (Figure 1). In all protocols, we used a combination of scan and behavioural sampling (Martin & Bateson 1986). The number of ravens present and the identity of marked birds were recorded every five minutes. Additionally, all agonistic and affiliative interactions (Table 1) involving a marked bird were recorded on an *ad libitum* basis, which means that all interactions were recorded unless more than two were occurring at once (in those rare cases, the focus was on those interactions occurring first). Affiliative interactions were counted only once per day to avoid pseudoreplication.

Table 1. Definition of behavioural parameters.

Behavioural category	Behaviour	Description
Agonistic interactions	Approach-retreat	approached bird retreats without contact
	Forced retreat	approached bird retreats after being threatened
	Fight	contact aggression involving both individuals hitting each other
	Chase flight	one individual flies in pursuit of another trying to grab him; no playful vocalisations
	Show off	Acoustic and visual display of dominance, without contact
	Subordination	Defensive acoustic and visual display without contact
Affiliate interactions	Contact sitting	sitting within one body's length of a partner
	Allo-preening	preening the plumage of a partner
	Inviting preening	bowing towards partner, with fluffed head feathers and/or twinkling inner eyelids
	Food/Object offering/sharing	approaching with an object held towards the partner and passing it over or manipulating object jointly
	Displaying	female and male courtship displays and joint show-off against others

A total of 37 marked ravens (28 % of the total number of marked birds) were observed in more than two thirds of the days sampled (all data corrected for the time span the birds were marked), indicating that these birds were using the valley on a regular basis; these birds will be called locals hereafter (Table 2). 20 ravens (15 % of the total number of marked birds) were present in approximately half of the days sampled and called frequent visitors hereafter. Finally, 75 ravens (57 % of the total number of marked birds) were present in less than one third of the days sampled and called infrequent visitors hereafter. In Table 2 we listed the number of individuals

contributing to the data sets of either affiliative or agonistic interactions, separated according to their presence in the valley.

Observations were carried out using binoculars and a digital voice recorder. To ensure that the observations were not affected by differences in habituation of the birds, it was regularly checked that marked birds that were observed feeding in the morning could be found during the day as well.

Table 2: Number of individuals contributing to the data for the total of birds present over the time of data collection, the observed affiliations or the conflicts. The data is divided according to the residency of the birds.

	Birds present		**Affiliative interactions**		**Agonistic interactions**	
	males	**females**	**males**	**females**	**males**	**females**
Local ravens	22	15	20	15	17	13
Frequent visitors	9	13	8	8	8	9
Infrequent visitors	30	43	7	8	14	10
Total number	**61**	**71**	**35**	**31**	**39**	**32**

Data processing and statistical analysis

To account for possible seasonal differences (Gwinner 2003), we divided a year into three phases, each lasting four months: Phase 1 (from July to October) reflects the summer time when juvenile ravens leave their families and integrate into the non-breeder groups; Phase 2 (from November to February) reflects the winter time with high group densities and high levels of recruitment to ephemeral food such as carcasses; Phase 3 (from March to June) reflects the breeding season, with territorial ravens exerting pressure on non-breeders by strongly defending food sources and displaying their superiority in resource holding potential.

Each bird was aligned to one of four bonding classes for each phase: **Un-bonded**: the bird was never seen in any affiliate interaction with another bird. **Casually bonded:** the bird was observed in affiliate interactions with others; however, interactions were not directed towards the same individuals for longer than one month, or if lasting longer, were always initiated by the same individual. **Closely bonded**: the

bird was observed in friendly interactions with a specific partner over more than one month, and interactions were initiated by both partners. **Territorial**: the bird was paired, defending a territory and was not observed in the game-park except at feeding times.

We used a generalised linear mixed model (GLMM) to test which factors influenced the outcome of agonistic encounters, with the outcome of an encounter (won/lost) as response variable, identity of the opponents as random factors and the age and bonding class for the specific phase, the sex and residency of the birds as fixed factors. Furthermore, we performed two linear mixed models (LMM) to test (1) the effect of age and sex on the propensity of individuals to switch bonding classes or partners, using number of switches as response variable, sex and age class as fixed factors and identity of subject as random factor; (2) to reveal the effects of bonding classes and sex on the likelihood to win within-sex agonistic interactions, using percentage won interactions as response variable, bonding class and sex of the individuals as fixed factors, and identity of the individual as random factor. For all mixed models, we used a step-up strategy whereby fixed factors were added to the model sequentially. Akaike's Information Criteria (AIC) values were used to assess all possible candidate models and if the difference in AIC values between models was less than two, we averaged the best models (Pinheiro & Bates 2000; Burnham & Anderson 2004). Only the effects of fixed factors in the best models are presented.

Mann-Whitney-U tests were applied to compare the percentage of marked ravens within the flock at the beginning and the end of the study and the distribution of bonding classes within the group of local birds with the distribution found within the group of visitors. For the latter, we normalized the data by converting them into percents. A Spearman-Rho correlation was used to test for a relationship between the length of time an individual was marked and the length of time that individual was recorded present in the valley. The distribution of bonding classes over the phases was compared using a Kruskal-Wallis test, and the competitive ability of individuals when changing bonding status was compared with a paired T-test. All analyses were conducted in SPSS v.19. Data conformed to normality whenever parametric tests were used. All tests were performed two-tailed and α was set to 0.05.

Results

Residency and feeding flock composition

A mean (± SD) number of 40 ± 18 ravens were present in the valley per day. Out of those, 20 ± 9 ravens were individually marked, whereby the percentage of tagged birds slightly increased during the study period, from 42 ± 17% in the first half year to 59 ± 19 % in the last half year of the study (U = -6.03, N = 73, P < 0.01). Thus, from the total number of 138 marked birds, only a small proportion could be observed in the valley per day. The majority of birds showed up in the valley rather infrequently (see Table 2). There was no correlation between the time a bird was marked and the time it was present in the valley (r_s = -0.14, $N1$ = 133, $N2$ = 135, P = 0.11).

Foraging groups of ravens were composed of all age classes (Figure 2). As expected, sexually immature birds were in the majority (marked juveniles within their first year of life: 25 ± 2% = 4 ± 3 individuals; subadults in their second and third year: 54 ± 7% = 8 ± 4 individuals); however, also 21 ± 5 % = 5 ± 3 sexually mature birds were present, out of which 3 ± 2 % = 1 ± 1 birds could be classified as local territory holding breeders. Groups were not cohesive units, i.e. birds were coming and going during the feedings of the zoo animals, which lasted between 10 - 40 minutes/enclosure. On average, marked ravens were recorded as ‘present’ at a feeding site in 59 ± 17 % of the five-minute scans taken during that feeding. The rest of the time, birds were scattered over the surrounding area, carrying off food loads to cache or eat them in private.

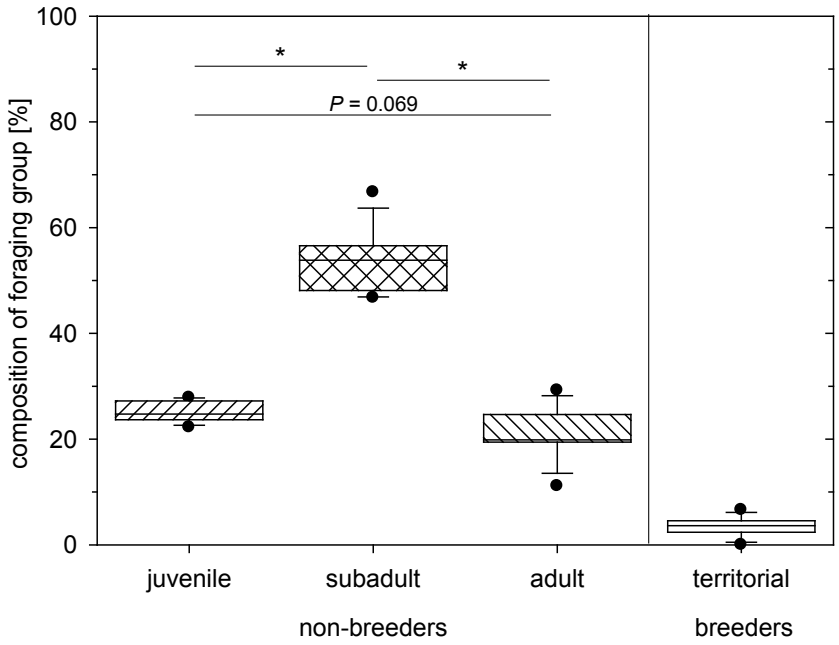

Figure 2: Composition of raven foraging groups according to age class and breeding status. Boxplots represent median, 25%- and 75% quartile, whiskers indicate 10%- and 90%-range, and circles represent outliers.

Affiliation patterns and structure of social bonds

During the course of the study, a total of 472 affiliative interactions involving marked birds (*N* = 68, of which 62 were non-breeders and 6 were territorials) were recorded. These were comprised of the following behaviours: 'contact sitting' (28 % of the cases), 'allo-preening' (27 % of the cases), 'inviting allo-preening' (23 % of the cases), 'joint object play' (8 % of the cases) and 'pair displays' (14 % of the cases). Affiliate interactions could occur between the same individuals over an extended time period (58 % of the cases, involving *N* = 32 marked ravens) or involve several individuals over shorter time periods (42 % of the cases, involving *N* = 60 marked ravens). The resulting relationships were characterized as closely bonded (same individuals, extended period) and casually bonded (short periods, see Methods). Significantly more birds were either un-bonded or closely bonded than casually bonded (H_2 = 7.64, *P* = 0.02; Figure 3). The distribution of bonding classes is similar in the subgroup of local birds ($N_{\text{un-bonded}}$ = 9, $N_{\text{casually bonded}}$ = 10, $N_{\text{closely bonded}}$ = 14, $N_{\text{territorial}}$ = 3) and in the subgroup of regularly visiting ravens ($N_{\text{un-bonded}}$ = 7, $N_{\text{casually bonded}}$ = 4, $N_{\text{closely bonded}}$ = 7, $N_{\text{territorial}}$ = 1) (*U* = -0.29, *N* = 4, *P* = 0.77). Infrequent visitors showed up in the valley too rarely to determine their bonding status.

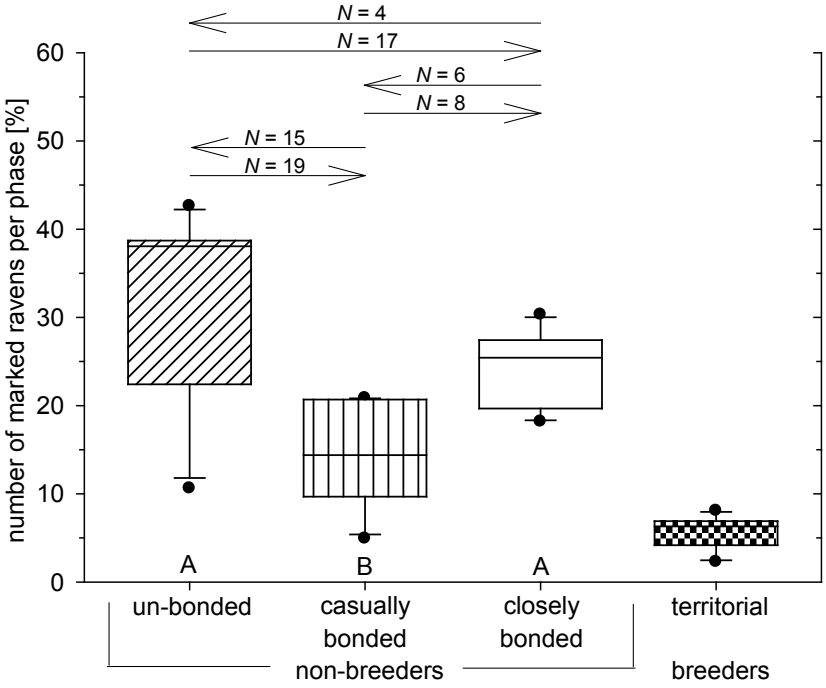

Figure 3: Mean number of marked birds belonging to the four bonding classes. Boxplots represent median, 25%- and 75% quartile, whiskers indicate 10%- and 90%- range, and circles represent outliers. Significantly more individuals per phase are either un-bonded or closely bonded than in casual affiliations (Letters at the bottom indicate statistical difference, $H_2 = 7.64$, $P = 0.02$). Territorial ravens were not included in the statistics as they do not belong to the non-breeders. Arrows and sample sizes refer to total number of switches that occurred between the classes.

Interestingly, with the exception of territorial breeders (which were considered a special case of closely bonded birds), most ravens did not maintain a given affiliation constellation over the entire study period. In fact, 48 marked ravens (71 % of ravens in affiliations) switched partners in the course of the study and/or shifted between bonding classes between the three phases of a year and/or between years (see Figure 3 for visualization). There was no effect of sex on the propensity to switch either partners ($F_{33.36} > 0.01$, $P = 0.96$) or bonding class ($F_{34.69} > 0.01$, $P = 0.94$). However, there was an age effect: subadult ravens switched partners significantly more often (mean ± SE: 1 ± 0.17 switches) than both juveniles (0.03 ± 0.21 switches) ($df = 42.78$, $P < 0.01$) and adults (0.35 ± 0.25 switches) ($df = 65.37$, $P = 0.09$; all post-hoc tests Bonferroni corrected). This also holds if we only compare yearling ravens (within their second year; 0.99 ± 0.21 switches) with juveniles (within their first year; 0.03 ± 0.21 switches; $df = 32.87$, $P = 0.01$) to control for the longer time ravens are classified as subadults as compared to juveniles. The propensity to switch bonding classes showed similar age effects with yearling ravens switching classes significantly more often (1.27

± 0.20 switches) than juveniles (0.40 ± 0.20 switches) (*df* = 33.33, *P* = 0.01), and no difference among the other age classes, either subadult (1.17 ± 0.17 switches) and adult ravens (0.71 ± 0.24 switches) (*df* = 65.15, *P* = 0.35), or juveniles (0.38 ± 0.20 switches) and adults (*df* = 65.94, *P* = 0.89). On average, non-breeding ravens of all age classes (*N* = 62) interacted with at least 3 ± 2 affiliation partners in the course of the two-year period. This number is relatively conservative since unmarked ravens involved in affiliate interactions with marked birds were counted as one bird.

We had individual information for both partners for 60 affiliation constellations. Interestingly, most of these constellations (78 %) were asymmetric in age with one partner being older than the other (66 % older females, 34 % older males). 92 % of the affiliation constellations were of opposite sex; 8 % concerned male-male combinations. All male-male combinations (*N* = 5) were seen only once, and affiliate interactions between females were never observed.

Agonistic interaction patterns and structure of dominance hierarchy

At the feeding sites, a total of 1,513 conflicts between marked competitors (*N* = 103) were recorded. Out of those, 19 % were directly about food; however, the majority of 81 % were not food related and involved approach-retreat interactions of low and high intensity (17 % retreats; 37 % forced retreats), subordination displays (10 %) or dominance displays (5 %), fights (4 %) and unresolved conflicts (8 %). The outcome of an agonistic encounter was significantly influenced by the relative sex (F_4 = 8.71, $P < 0.01$), age (F_4 = 11.03, $P < 0.01$) and bonding class (F_{14} = 2.47, $P < 0.01$), but not the residency of both combatants (F_3 = 0.15, *P* = 0.93). In general, males dominated females, older birds dominated younger ones, and birds with affiliation partners dominated singletons.

Stable individualised dominance hierarchies are characterised by dyadic resolved relations, in which the same individual from a dyad keeps winning the conflicts (unidirectional dyad). Only 35 of the marked dyads had more than the 6 agonistic interactions, which are necessary to calculate the dyadic asymmetry. With less interactions and a binomial probability of *P* = 0.5 it is not possible to reject the null hypothesis, which is that the dyad is symmetric. All 35 dyads were unidirectional, with conflicts being won in 97 ± 6 % of the cases by the same individual. Of the three dyads for which age, sex and bonding class were matched (as these affect the outcome of an

encounter, see above), all were fully unidirectional (i.e. conflicts were always won by the same individual).

Benefits and limitations to bonding

Combining information on the ravens' affiliation constellation and behaviour in conflicts allows us to structure foraging groups hierarchically and separately for each of the sexes (Figure 4). A LMM reveals significant effects of bonding class ($F_{3.428}$ = 21.57, P < 0.01) and the interaction between sex and bonding class ($F_{3.428}$ = 7.64, P < 0.01) on the percentage of within-sex agonistic interactions won. Splitting the data according to the sex still gives significant effects of the bonding classes on the competitive ability of the individuals in both: females ($F_{3.102}$ = 8.00, P < 0.01), and males ($F_{3.340}$ = 28.08, P < 0.01).

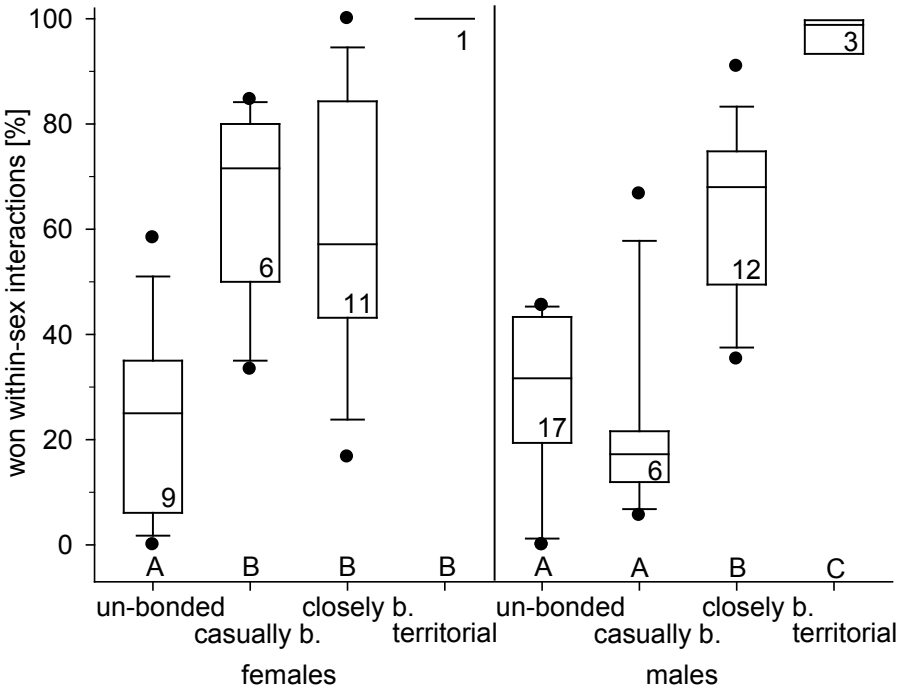

Figure 4: Percentage of won interactions for different bonding classes plotted separately for females and males (including only within-sex agonistic interactions). Number in the bars indicates the number of individuals per category; only individuals with at least six observed interactions were included. Letters on the x-axis represent statistical differences (LMM results described in the text). Boxplots represent median, 25%- and 75% quartile, whiskers indicate 10%- and 90%- range, and circles represent outliers.

In females, un-bonded birds have lower competitive ability compared to the other bonding classes [un-bonded (N = 9) -casually bonded (N = 6): 29 ± 7 % vs

62 ± 8 % won conflicts, P = 0.02; un-bonded - closely bonded (N = 11): 29 ± 7 % vs 58 ± 6 % won conflicts, P = 0.02; un-bonded – territorial birds (N = 1): 29 ± 7 % vs 100 ± 0 %, P = 0.05], whereas all other bonding classes have the same competitive ability (all P > 0.05). In males, on the other hand, un-bonded birds (N = 17) do not differ from casually bonded (N = 6) birds (31 ± 4 % vs 15 ± 6 % won conflicts, P = 0.24), but have significantly lower competitive ability than closely bonded or territorial birds [unbonded-closely bonded (N = 12): 31 ± 4 % vs 63 ± 4 %; P < 0.01; unbonded-territorial (N = 3): 31 ± 4 % vs 97 ± 9 %; P < 0.01; casually bonded–closely bonded: P < 0.01, casually-bonded-territorial: P < 0.01, closely bonded-territorial: P = 0.01; all Bonferroni corrected]. Thus, females appear to benefit in conflicts from any type of affiliation, whereas males only benefit when they are closely bonded. It is worth mentioning that the affiliation partners did not actively help, or were not in close spatial distance to the target of aggression (< 2 m) in most of these conflicts. It is thus likely that the mere presence of affiliated/bonded individuals at the foraging site is enough for the effect observed. In those cases, in which the bonding status of birds changed from closely to casually bonded or unbonded, respectively (N = 17), the competitive ability dropped significantly (T_{16} = 2.92, P = 0.01). Hence, the observed differences in competitiveness are mainly caused by bonding status and not so much by physical properties of the birds.

Interestingly, third-party separating interventions could be regularly observed during affiliation bouts, i.e. two birds that were sitting in contact and/or engaged in allo-preening were separated by a third bird that was previously not involved in the interaction. Out of the total of 472 affiliative interactions, 34 were interrupted by a third party this way, resulting in the displacement of one or both affiliation partners. Individuals acting as interveners were always affiliated themselves, mostly exclusively (85 % of interventions by $N_{\text{closely bonded birds}}$ = 8 and $N_{\text{territorial breeders}}$ = 4) and sometimes casually (15 % of cases by $N_{\text{casually bonded birds}}$ = 3). Un-bonded birds were never observed to intervene in others' affiliate behaviours. Targets of interventions could be identified in 23 cases: some interventions were directed at birds that were engaged in an affiliate interaction with the bonding partner of the intervener (13 % of the cases, $N_{\text{constellations}}$ = 3), but in most of the cases (87 %, $N_{\text{constellations}}$ = 20), both targets had no obvious relationship to the intervener, but were in a casual or closely bonded relationship themselves.

Discussion

This is, to our knowledge, the first study that demonstrates different structural levels within raven non-breeder aggregations: firstly, a loose organisation composed of local birds, regular visitors, and infrequent visitors and secondly, the individuals' engagement in consecutive social bonds. In all age classes, birds tried to bond with other individuals (often older ones and of opposing sex) by offering and exchanging affiliate behaviours. When bonded, they won more conflicts in feeding situations; yet, birds rarely maintained the same bonding status over the study period of two years. Ravens, which live in long-term monogamy as adult breeders thus showed considerable flexibility in forming and using affiliate relationships as non-breeders.

Local group formation in ravens could have been expected, as studies on raven roosting behaviour regularly describe troops of 5 to 30 birds arriving and departing together (Marzluff et al. 1996; Wright et al. 2003), or even sub-roost formation (Dall & Wright 2009). However, the group of local non-breeders in our field site is not characterized as a discrete, cohesive group. It is a quite loose organisational pattern that becomes apparent through longer observation periods and probably resembles a geographical distribution, for example, dialect regions in humans, rather than independent social units. It is however, the main pool of individuals from which our marked members chose their bonding partners and we cannot exclude the possibility that the group forms among individuals that prefer each other's company. Analysis of the kinship pattern will be an important next step.

Results from winter-flock formation in other song birds show that individuals with prior residency, i.e. those birds which were earlier in a flock, have an advantage in agonistic encounters (magpie *Pica pica*: Eden 1987) that even outweighs the effects of body size and age (great tit *Parus major*: Sandell & Smith 1991; willow tit *Poecile montanus*: Koivula et al. 1993) and enhances the individuals' chances of survival through its first winter (marsh tit *Poecile palustris*: Nilsson & Smith 1988). The group of locals within our non-breeders would thus be expected to have prior residency advantages over visiting ravens, but this was not the case. Local birds did not win more agonistic conflicts at the foraging sites than birds that were using the valley only infrequently. It therefore seems that the effects of age and bonding status are stronger predictors for status than prior residency in ravens.

The conditions at our study site may be considered as artificial in respect to the predictability of food availability, causing a proportion of ravens (our 'local' birds) to give up their vagrant life. One might also argue that this man-made stability in food supply could have triggered increased competition at feeding sites and thus changed the settings for social bonding. Consequently, our findings may appear to be less applicable to other raven populations. However, as in our game park setting, ravens living in relatively undisturbed environments tend to forage together with large predators like wolves and bears (Stahler et al. 2002). In central Europe, they have recently started to exploit these species held in captivity. In fact, the foraging conditions encountered by ravens in our study now represent a typical scenario for the Alpine area (Koch et al. 1986; Huber 1991). Note that ravens generally display high flexibility in adapting to human-shaped environments, using human-made resources for hundreds to thousands of years, from scavenging on carcasses at battle fields to feeding on human remains (Heinrich 1999). Furthermore, stable raven roosts are known from all over the holarctis, with numbers regularly exceeding our records by many individuals (>2000 ravens: Engel et al. 1992; up to 5000: Wright et al. 2003; >350 ravens: Blázquez et al. 2009). Similarly, our mean number of ravens at feeding locations ranges well within the typical number reported for non-breeder flocks from naturalistic settings (Bialowieza National Park, Rösner et al. 2005). Finally, non-breeders are typically found together with territorial breeders at food sources (Marzluff & Heinrich 1991; Heinrich 1994). Likewise, the mixed structure of all age classes in foraging groups is known already from previous studies (Huber 1991). So the agonistic and affiliate interaction patterns observed in this study are presumably unaffected by the relatively constant foraging conditions.

In aviary situations, corvids typically form linear dominance hierarchies (Heinrich 1994; Izawa & Watanabe 2008; Scheid et al. 2008). If groups are large and open, however, linear dominance hierarchies are thought to be rare in the animal kingdom (Drews 1993), because the mechanism to form them cannot rely solely on intrinsic factors (e.g. body size, age, sex, or confidence) but has to build on the memory of consecutive encounters within the specific dyad (Barnard & Burk 1979). In accordance with this, linear dominance hierarchies in wild corvids are only reported from species which form small, cohesive groups like the cooperative breeding carrion crows *Corvus corone* (Chiarati et al. 2010) and Florida scrub jays *Aphelocoma coerulescens* (Woolfenden & Fitzpatrick 1977). In ravens the picture is ambivalent: on one hand,

non-breeder aggregations are large, open groups with unstable group composition, making linear dominance hierarchies unlikely. On the other hand, ravens are spending years as non-breeders, and aggregations may, according to our current data, comprise a number of long-term core members. This would support the formation of linear dominance hierarchies, at least in certain sub-groups. Our sample size of agonistic encounters between marked ravens is too small to draw conclusions for the whole study group of non-breeders. Yet, in all dyads that provided enough data for statistical analysis, we found stable dominance relationships with unidirectional dyads. Data from studies under similar conditions (Huber 1991) support this trend: if dyads have repeated conflicts, the same individual will be dominant over the other for a long time period (over one month in the study by Huber, up to two years in this study). Note that in those analyses the individuals' sex, age and bonding status needs to be considered since all these factors determine the outcome of an encounter. Older birds, which are dominant over younger ones, males that dominate females and affiliated/mated individuals that are dominant over singles, describe a structure of dominance hierarchy which is typical for birds (Gauthreaux 1978; Lamprecht 1986; Piper & Have Wiley 1989; Moore et al. 2003).

What characterizes raven aggregations, however, is the structure and plasticity of the social bonds birds possess before sexual maturation and the beginning of breeding, respectively. Similar to primates (e.g. de Waal & van Roosmalen 1979; Noë & Hammerstein 1995; Henzi & Barrett 1999), these bonds are formed through investment by one or both individuals and differ in terms of duration and degree of reciprocity between the dyads. Individuals who have a bonding partner clearly benefit while foraging, whereby females already profit from unidirectional, casual relations. Presumably, the ability to assert oneself is dependent on the bonding status (and stronger in females than in males), since most of the conflicts are initiated by bonded birds. Notably, the effect of winning conflicts is lost again if a pair breaks up. These results do not fit the alternative explanation of bonded ravens reflecting a particular phenotype, which combines both competitive ability and attractiveness (i.e. high quality individuals being bonded and therefore winning conflicts). Instead, older partners of the opposite sex are preferred by both sexes, indicating the attractiveness of status and/or resource holding power, because age correlates with rank. In contrast to primates (e.g. Kummer et al. 1974; Cheney et al. 1986), ravens do not seem to establish and maintain a social network of several affiliates but focus on one bonding partner at a

time. However, birds do switch bonding partners and, presumably as a consequence, their affiliation status regularly changes across seasons and years. All these components support the idea that the bonds of non-breeding ravens serve as a social manoeuvre, which is decoupled from direct reproductive goals. The findings fit to those obtained from captive groups of ravens, where birds also form valuable relationships with a few individuals only (Fraser & Bugnyar 2010a) and selectively use them in aggressive encounters (Fraser & Bugnyar 2010b, 2011).

Finally, the question remains why this bonding tactic is not adopted by all non-breeders since bonded individuals gain easier access to resources. There are a couple of possible, mutually not exclusive, explanations: firstly, subordinate ravens have the possibility to gain access to food by means other than interference competition, i.e. the selective pilfering of food caches (Heinrich & Pepper 1998; Bugnyar & Kotrschal 2002a). Ravens are capable of observational spatial memory, remembering the location of food caches they see others make (Bednekoff & Balda 1996; Heinrich & Pepper 1998). Given that they can also learn to withhold their intention and judge the appropriate timing of pilfering (Bugnyar & Heinrich 2005, 2006), they may rely on cognitive skills rather than resource holding potential which would be enhanced by bonding. Secondly, the age asymmetry seen in most of the bonding attempts suggests that preferred partners are higher-ranked than the selecting individual. However, as most pairings were of opposite sex, the hierarchical distance between the partners is not a direct one. Females may have a difficult time achieving acceptance by older males, which could easily displace them; interestingly, attempts of young males were often also ignored by older females. Obviously, being attracted to older opposite sex partners limits the opportunities as the older partner would have to choose against his/her preferences. Thirdly, and probably most interestingly, bonded ravens are regularly facing harassment by other bonded ravens, including territorial breeders. This might be the case because strongly bonded birds are relatively dominant at feeding sites and territorial pairs tend to attack the most dominant of the non-breeders first (Marzluff & Heinrich 1991). However, during the formation of bonds, which generally occurs outside of feeding, others may already intervene regularly and severely. For instance, the most enduring chase flights, lasting in full speed for up to 10 minutes, were observed between territorial females chasing other bonded females (A. Braun, unpubl. data). If the extra costs of this harassment by others outweigh the benefits of a given bond, we would expect it to cease. A critical point may be whether or not the new

bonding partner joins the conflict and actively helps or, at least, provides post-conflict affiliation, as demonstrated under aviary conditions (Fraser & Bugnyar 2010b).

Overall, we can show that a large-brained bird species, which has the time, through delayed maturation, and the need, through strong competition, to operate socially, does so. The evolutionary function of non-reproductive bonding in ravens is most likely to assess the quality of a partner before deciding on a life-long monogamy. Away from that, however, non-reproductive bonding in ravens may qualify as a social manoeuvre facilitating access to resources and increasing status.

Acknowledgments

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Kinship and Association Patterns of Wild Non-Breeder Ravens

Manuskript in preparation

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The need to compete and cooperate over long time periods drives the development of differentiated relationships in many animal species. Most commonly the problem of unknown reciprocation of costly favours is solved through kin favouritism. In corvids, a bird family characterized for surviving in harsh environments, nepotism is a common trait. Although the common raven maintains differentiated relationships, and invests actively into valuable relationships with siblings in captivity, surprisingly little is known about nepotism in the wild. Over three years we recorded the association patterns of individually marked ravens in a valley in the Austrian Alps at three different scales: 1) birds that were simultaneously present, 2) birds which were found in visual distance to each other during daily activities, and 3) birds that physically interacted with each other. We analysed the blood samples of 134 ravens (64 males, 70 females) regarding their relatedness, using 12 polymorphic microsatellite loci. Birds which were simultaneously present in the valley or socialising during the day were less related to each other than to birds not present in the valley or at the socialising site. Kinship had no significant effect on the number of conflicts won and the birds' social status within the non-breeders, respectively. However, kinship had a strong effect on same age dyadic affiliative interactions, especially on rare male-male affiliations. These findings corroborate results from captive non-breeder groups and indicate that, also in the wild, raven siblings may have a high tolerance to each other, and possibly even help each other to manoeuvre the social field or to buffer social stress.

Introduction

The ability to cooperate with other individuals has far reaching consequences for animal social life (for a summary see: Donaldson & Young 2008). Teaming up with others can be beneficial in avoiding predators or accessing food sources (Axelrod & Hamilton 1981). Within groups, conflicts of interest can lead to some individuals cooperating to monopolise resources (Seyfarth & Cheney 2012), avoid infanticide (Silk et al. 2003; Cameron et al. 2009) and buffer stress (Engh et al. 2006).

A crucial aspect of cooperation is that partners have to invest in others, without knowing whether favours will be returned in future (Axelrod & Hamilton 1981). This dilemma often is avoided by choosing close kin as cooperation partners (Sachs et al. 2004), and thereby benefiting individuals who share genes (Hamilton 1964). If an individual helps a relative to reproduce, he passes its genes to the next generation and increases its Darwinian fitness (West et al. 2002). Cooperation with kin can be achieved due to recognition systems for relatedness and direction of cooperative acts to kin (Queller 2000), or due to spatial association with kin and a general tendency for cooperative behaviour (Eshel & Cavalli-Sforza 1982). Other mechanisms for the evolution of cooperative systems are by-product cooperation, in which individuals benefit from the automatic consequences of another's self-interested actions (West-Eberhard 1975), or directed reciprocation, in which each side takes turn in reciprocating the benefit to their partner (Trivers 1971).

Social bonds refer to a special type of cooperative relationships out of a pool of differentiated relationships that characterise most social systems of higher vertebrates (Cheney 2011), and can be distinguished due to the content, quality and distribution of interactions over time (Hinde 1976). Mechanisms of bonding are thought to derive from mother infant bonding in mammals, in contrast to pair bonding in birds (Broad et al. 2006; Lim & Young 2006). Accordingly, network size and preferred bonding partners differ between those taxa (Emery et al. 2007; Dunbar & Shultz 2010). Patterns of partner choice and high investment in bond formation and maintenance (Sapolsky et al. 1997; Silk 2007), however, are remarkably similar in birds and mammals (Seed et al. 2009; Fraser & Bugnyar 2010). In both taxa, special neuro-anatomical adaptations can be found (Güntürkün 2005), helping an individual to co-act with its partners of interest (Pacherie & Dokic 2006), or even have empathy for their concerns (Engen & Singer 2013; Ostojic et al. 2013).

In birds, corvids, a big brained bird family, are of particular interest due to their social capabilities (Bond et al. 2010; Heinrich 2011; Pika & Bugnyar 2011). They are colonising the most demanding environments of the world (Haffer 1993), from deserts to inner cities, and show many cognitive adaptations to their specific ecological demands (memory load: Vander Wall & Balda 1981; tool use: Hunt 1996; social understanding: Bugnyar & Heinrich 2005). In birds, cooperation partners typically are socially monogamous pair partners (Emery et al. 2007), or the retained offspring from previous years, if territory quality allows for it and parents are tolerant enough (Komdeur 1992; Emlen 1995; Baglione et al. 2002; Ekman & Griesser 2002). Cooperative breeding is quite common in corvids (Cockburn 1996), and close kin often cooperates to raise the offspring of successive years (McGowan & Woolfenden 1989; Baglione et al. 2003; Griesser 2003; Griesser & Ekman 2004, 2005; Griesser et al. 2006), however, the typical cooperative partner in corvids is the socially monogamous pair partner (Emery et al. 2007; Seed et al. 2009).

It is known that during sexual immaturity, corvids may form alliances with their nest-mates, which later are replaced by a strong bonded relationship to their pair partner (Seed et al. 2007; Scheid et al. 2008; Loretto et al. 2012). Partners support each other in conflicts (Emery 2006; Fraser & Bugnyar 2012), and invest quite a lot in these relationships which can be classified as valuable relationships (Fraser & Bugnyar 2010). Corvids typically form linear dominance hierarchies (Tamm 1977; Izawa & Watanabe 2008; Scheid et al. 2008; Chiarati et al. 2010), and probably are able to assess their own rank in relation to others by observing their interactions (Pinyon jays: Paz-y-Mino et al. 2004). Quite a number of corvids opportunistically join so called non-breeder aggregations to gain access to food, avoid predators, and for thermoregulatory reasons (Röell 1978; Delestrade 1994; Marzluff et al. 1996; Shoemaker & Phillips 2011). They remain in these aggregations either between breeding seasons, or year round until sexual maturity or territory availability. As indicated in the name, birds in non-breeder aggregations forego reproduction, and it is yet only marginally investigated, how such aggregations are structured.

Work on raven non-breeders showed that non-breeder aggregations are structured by local sub-groups (Dall & Wright 2009; Braun et al. 2012), and age, sex and bonding status (Huber 1991; Heinrich 1994; Braun & Bugnyar 2012). Ravens are, as adults, defending huge territories (~25km^2) year-round, with their life-long socially

monogamous pair partner, and are highly intolerant towards offspring after independence (Heinrich 1989; Boarman & Heinrich 1999). Offspring therefore roams around as floaters, and, after reaching sexual maturation with three years of life, try to find an unoccupied territory together with their pair partner (Haffer 1993). As scavengers, ravens actively recruit conspecifics to food sources, which they can't access themselves (Marzluff et al. 1996; Bugnyar et al. 2001). Recruitment doesn't favour kin (Parker et al. 1994), but opportunistically attracts all ravens in the nearer surrounding (Heinrich & Marzluff 1991; Bugnyar & Kotrschal 2001). Ravens subsequently engage in heavy scramble competition for the food (Heinrich 1989). Resource holding potential is not correlated with size or fighting ability, but resides with the individuals having an appropriate status (Braun & Bugnyar 2012). Aside from feeding competition, ravens regularly socialise in groups of a mean of four birds (Braun et al. 2012), which perfectly fits the mean number of a typical clutch size in ravens (Haffer 1993).

So although nepotism seems unlikely to explain the composition of groups travelling together (Parker et al. 1994), it still might well be possible that local sub-groups or socialising groups are based on nepotism. Over three years, we investigated the relatedness of non-breeder ravens associating with each other at three different scales: 1) birds that were simultaneously present in a valley in the Austrian Alps, 2) birds which were found in visual distance to each other during daily activities, and 3) birds that physically interacted with each other. Two scenarios might apply for raven non-breeder aggregations.

1- "nepotistic support": ravens remain as close as possible to related birds, and gain rank benefits due to passive or active social support. Relatedness among special groups is expected to be high; either among birds which are frequently in the valley, and therefore try to stay close to their natal territory or among birds found in visual distance to each other and socialising during the day. Ravens with close relatives present should win more conflicts.

2- "queuing for territories": ravens choose places where kinship is low to wait for territories and avoid inbreeding. Relatedness is expected to be very low among birds, and especially low among those which typically roam around the valley. Relationships should be mainly mated pairs.

Methods

Field site and study animals

In the inner Almtal, a 10 km long valley in the Northern Alps, Upper Austria, floating non-breeder ravens use a Gamepark, which houses typical Austrian wild animals, to scrounge food from the zoo animals. During the day, ravens can be found in a dense area of the valley, the northern half of the park, and an adjacent cliff (Figure 1). The rest of the valley is occupied by territorial breeding pairs which rigorously keep the non-breeders out of their territory. Only if a rich food source is present which attracts many non-breeders, they overcome the defence of territory holders and remain in the territory until the food source is depleted. Each evening non-breeder ravens gather and depart for a roosting place in the forest one kilometre apart from the Gamepark.

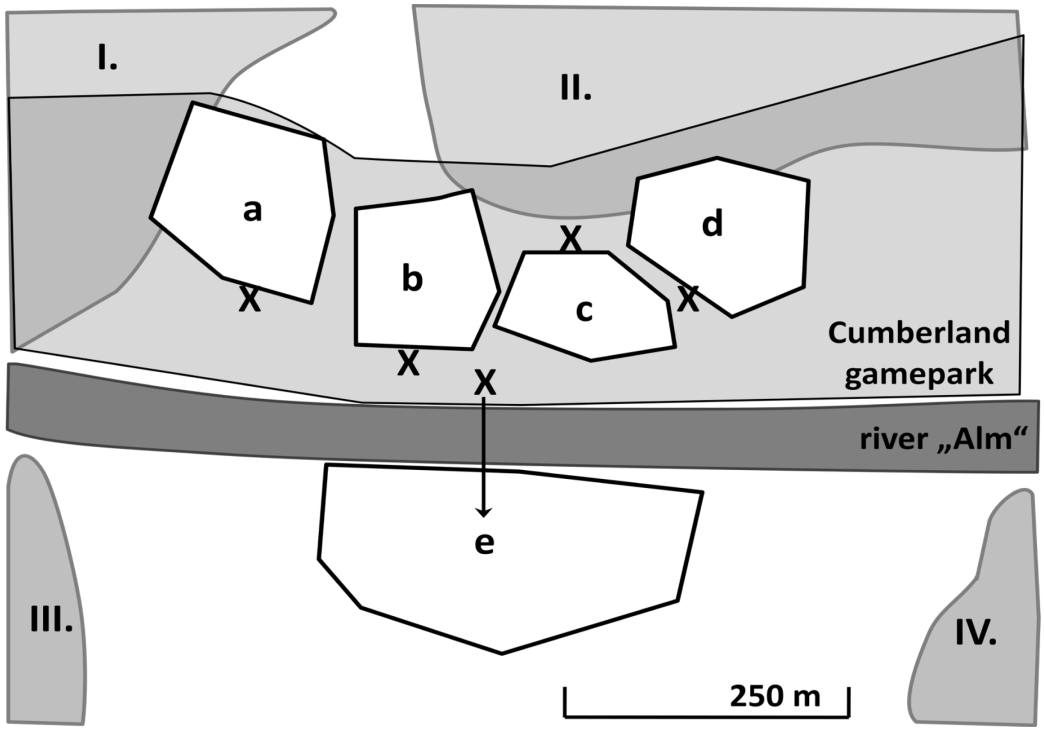

Figure 1: distribution of the wild ravens in the inner Almtal with the areas a-e (a. przewalsky horse *Equus ferus przewalski,* b. wolf/bear *Canis lupus/Ursus arctos*, c. wild boar *Sus scrofa* and d. red/fallow deer *Cervus elaphus/Dama dama*; e. cliff along the park's border) and the surrounding four territories of wild ravens (I. – IV.); the "X" represent the spots from which the areas were observed.

We caught birds with a drop-in trap situated in the Gamepark, and marked nestlings at cliff-nests if the access was possible. From spring 2008 to winter 2011 we marked a total of 134 ravens. From each bird we collected 50 – 200 µl of blood from the alar vein and stored it in pure alcohol. The birds were measured and weighed, and marked with an individual soft plastic wing-tag piercing through the patagium, and an individual colour ring combination on both legs. Age was assigned as juvenile (0 – 1 year), sub-adult (2 – 3 year) and adult (from 3-4 years on) using mouth linings and feather colour (Heinrich & Marzluff 1994).

Collecting behavioural data

Data was collected on a daily basis during morning feedings of the zoo animals and during standardized rounds through the Gamepark over the day. Birds were well habituated to close human presence, and observable from a distance up to 5 m. All the non-breeders typically gather at the morning feedings of the brown bears and wolves, and about half an hour later, at the feedings of the wild boars (see Figure 1). Each day we identified all marked ravens present in the valley, and counted the total number of ravens present. At least once a week we confirmed the total number of ravens counted at the feeds with those counted at evening gatherings when departing for the night roost. The standardized rounds were taken from June `08 to March `09 and started at the horse enclosure followed by the wolf/bear enclosure, the cliff, the wild-boars, and ended at the fallow deer enclosure. At each enclosure we scanned the number of ravens present, their identity and spacing, and recorded the behaviour they were engaged in (see Braun et al. 2012 for details). We ad libitum collected all dyadic interactions that involved at least one marked raven. The frequency and duration of all behaviours of a dyad was recorded for five minutes using binoculars and a voice recorder. A specific dyad was sampled only once a day.

Kinship analyses

DNA was extracted using a salt-based method described in Richardson et al. (2001). We tested 24 published Primer sets for amplification and polymorphism on eight raven samples. Nine loci were originally developed for corvus species, eight for the mariana crow, *Corvus kubaryi:* Ck.1B5D, Ck.1B6G, Ck.2A5 A, Ck.4A3G, Ck.4B6D, Ck.5A4B, Ck.5A4D, Ck.5A5F (Tarr & Fleischer 1998), and one for the Mexican Jay, *Aphelocoma ultramarina*: Mjg1 (Li et al. 1997). The remaining 15 loci

Table 1: Loci mixed in the three different panels A - C and deviating adjustments in number of cycles and annealing temperature (Ta) from the general PCR program (see methods). Furthermore we listed the range of allele sizes found in the population, the fluorescence label used for the loci, and the Primer amount used for PCR amplification. Samples sizes are given as the number of gene-copies that successfully amplified and number of alleles reflects those found in the population for all twelve loci. The expected heterozygosity is estimated according to Nei (1978), and probability for heterozygote deficiency is calculated with ML-relate, using a Hardy Weinberg test for excess homozygotes (Rousset & Raymond 1995) with 100,000 randomizations (Guo & Thompson 1992). The Bonferroni corrected p-values indicate those microsatellite loci with a high probability for null-alleles (bold values).

	Locus	n° cycles in PCR	Ta of PCR	Allele sizes	Primer Label	Primer amount	Sample size	Number of alleles	Expected heterozygosity	P-value for heterozygote deficiency
Panel A	Ck.1B5D	40	55°C	86 – 94 bp	FAM	0.50 µM	268	5	0.71	0.049
	Ck.5A4B	35	60°C	115 – 138 bp	NED	0.25 µM	268	8	0.73	0.564
	Ck.5A4D	40	55°C	88 – 94 bp	HEX	0.50 µM	268	4	0.68	0.131
	Ck.5A5F	35	55°C	140 – 158 bp	FAM	0.25 µM	268	7	0.51	**>0.001**
Panel B	Ck.1B6G	35	55°C	112 – 126 bp	HEX	0.25 µM	268	5	0.68	0.659
	Ck.2A5A	35	55°C	149 – 158 bp	NED	0.25 µM	268	5	0.73	0.855
	Ck.4A3G	35	55°C	74 – 83 bp	FAM	0.50 µM	266	4	0.37	**0.004**
	Ck.4B6D	35	55°C	155 – 176 bp	FAM	0.25 µM	268	8	0.77	0.039
Panel C	Mjg1	35	55°C	174 – 258 bp	NED	0.25 µM	260	27	0.94	0.414
	Ase9	30	55°C	108 – 112 bp	NED	0.25 µM	268	3	0.57	0.587
	Pdo5	35	55°C	217 – 238 bp	FAM	0.25 µM	268	8	0.61	0.055
	Esc6	35	55°C	108 – 112 bp	FAM	0.25 µM	268	3	0.45	0.857

were originally developed for other passerine species: Mcy4 (Double et al. 1997), Mme12 (Jeffrey et al. 2001), Fhu2 (Ellegren 1992), Pocc1, Pocc6, Pocc8 (Bensch et al. 1996), Ase9, Ase10, Ase18 (Richardson et al. 2000), Pdo5 (Griffith et al. 1999), Esc2, Esc6 (Hanotte et al. 1994), Pca7, Pca8 and Pca9 (Dawson et al. 2000). From these loci, twelve were polymorphic in our raven population (see Table 1) and, hence, used for genotyping.

PCR reactions were carried out in 10 µl volumes containing 20 - 50 ng DNA, 0.2 mM of each dNTP, 0.25 or 0.50 µM of forward and reverse primer, 10 mMTris-HCl, 50 mMKCl, 1.5 mM $MgCl_2$ and 0.15 U Taq DNA polymerase (Roche Diagnostics GmbH, Mannheim, Germany). The PCR program was as follows: 1 min. 94°C, 30 - 40 cycles of 94°C for 30s, Ta for 45s and 72°C for 45s, followed by 72°C for 2 min (see Table 1 for locus specifics). Before separation on an AB3730 DNA analyzer, fluorescently labelled PCR products of all microsatellites were mixed into three panels of four loci each, according to product size and label colour (Table 1). Allele lengths were determined using the Genemapper 4.0 software (Applied Biosystems Inc.).

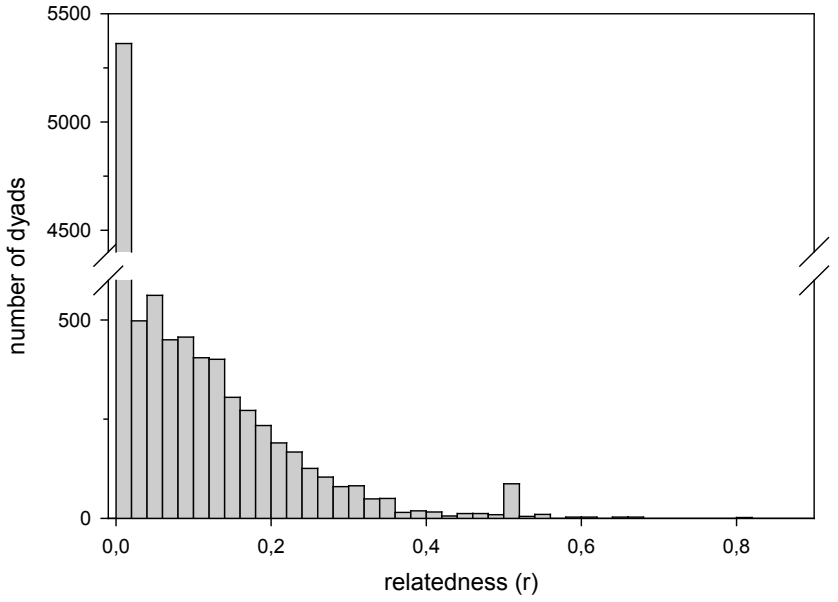

Figure 2: frequency distribution of relatedness (r) in the population, estimated with ML-relate (Kalinowski et al. 2006)

To estimate allele frequencies and pair wise genetic relatedness (r), we used the ML-relate computer program (Kalinowski et al. 2006), which accommodates for null alleles during relatedness estimations (see Table 1), and can handle missing loci. We had a total of five missing loci. The frequency distribution of relatedness estimators

(Figure 2) shows a high number of unrelated dyads and some closely related dyads in our sample.

Statistical analyses

After estimating pair wise genetic relatedness for all possible dyads, we compared the average relatedness of different groups with each other using linear mixed models (LMM) with the relatedness estimator r as response variable, individual identity as random variable, and group membership as fixed variable. In a first LMM we hence compared average relatedness of birds belonging to different residency groups, and in another LMM we compared dyads which interacted friendly with those that interacted aggressively with each other. A final LMM was conducted using age and sex as fixed factor, individual identity of both dyad members as random factor, and again, relatedness as response variable. Post-hoc tests were pair wise comparisons with LSD. A oneway Anova helped us to compare the average relatedness of birds found in visual distance (same enclosure), and those interacting with each other, with the average relatedness of all the dyads present on the same day. The same was done using maximum relatedness of birds found in visual distance, or interacting with each other, to compare it with the maximum relatedness of birds simultaneously present in the valley.

Results

Association patterns over the day and residency patterns over months

In the morning, a mean (± SEM) of 40 ± 18 birds participated at the daily feedings of the zoo animals. During the day, a mean (± SEM) of 14 ± 1 ravens could be found in visual distance to each other, i.e. in and around of enclosures, whereby the mean (± SEM) group size was 3.5 ± 1.2 ravens. About half of the ravens observed during the daily monitoring sessions were banded and could be individually identified. Conflict rates were high during competition for food at the morning feeds, and decreased to one tenth of the conflicts when ravens dispersed over the area of the game-park during the rest of the day (Braun et al. 2012). Affiliative encounters, in contrast, could be observed over the whole day.

Over the months, marked ravens differed in their degree of residency in the valley. 37 birds (28 %) were seen in more than two-thirds of the monitoring events and were thus labelled ‘locals’; 22 ravens (17 %) were observed about half of the time and were thus labelled ‘frequent visitors’ and 73 ravens (55 %) which were almost never present were called ‘infrequent visitors’ (Braun & Bugnyar 2012).

Average relatedness, residency and association patterns

Average relatedness among marked birds is very low with (r = 0.07 ± 0.001) but significantly differs between categories of residency (Figure 3: $F_{2.106}$ = 14.616, P < 0.001). Local birds are on average less related to each other (mean relatedness among local birds: r = 0.061 ± 0.002) than the frequent or infrequent visitors (mean relatedness among frequent visitors: r = 0.077 ± 0.006, F = 218.885, P = 0.011 and among infrequent visitors r = 0.080 ± 0.003, F = 65.169, P < 0.001). Frequent and infrequent visitors do not differ from each other in mean relatedness (F = 217.610, P = 0.674).

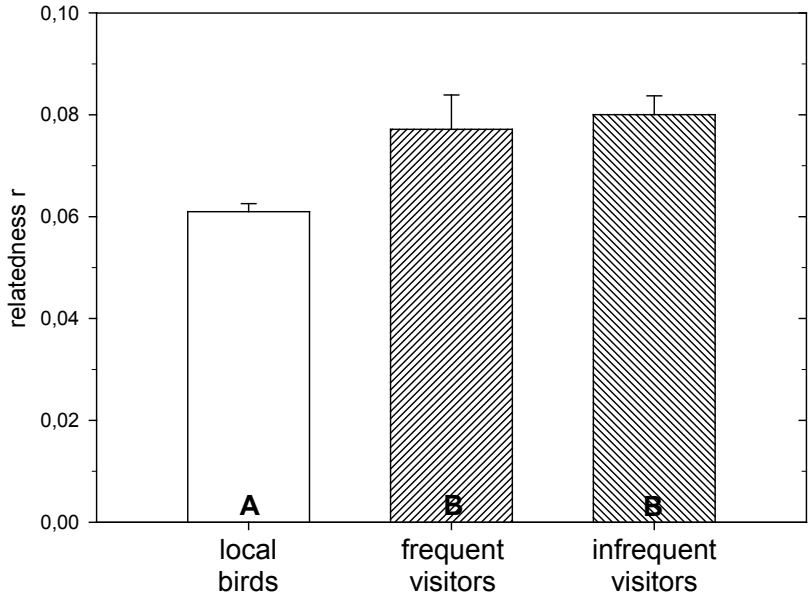

Figure 3: relatedness among the three categories of residency. Birds which are most commonly present with each other in the valley are significantly less related to each other than birds which are less often present in the valley.

Birds that are found in visual distance to each other during the day (15 ± 2 marked dyads per enclosure), are not closer related to each other than the average relatedness of ravens present in the whole valley on the same day, with a mean r = 0.078 ± 0.121 per bird (F_2 = 0.131, P = 0.877). However, around 5 % of the days dyads are closely related with an r > 0.3 from which again 44 % have an r = 0.5.

Maximum relatedness and association patterns

The maximum relatedness of the birds simultaneously present in the valley is relatively high with a daily mean ± SEM per bird of r = 0.384 ± 0.017, N = 7226 dyads. Birds found in visual distance to each other over the day share a significantly but only marginally lower maximum relatedness to each other (r = 0.239 ± 0.126, N = 221), than to other birds present the same day (F_2 = 107.823, P < 0.001). Birds involved in affiliate interactions have a significant but only slightly higher maximum relatedness to other birds present in the valley that day than birds which interact agonistically (r = 0.382 ± 0.011, $N_{affiliate}$= 519, r = 0.366 ± 0.010, $N_{agonistic}$ = 1119, $F_{1.1634}$ = 4.538, P = 0.033).

Most affiliate dyads are non-kin (mean $r_{affiliate\ dyads}$ = 0.09 ± 0.02, N = 59). However, sex and age class are significant factors on the degree of relatedness of a dyad (see Figure 4: age: $F_{1.49}$ = 10.912, P = 0.002, sex: $F_{1.50}$ = 18.767, P < 0.001), with same age dyads sharing more alleles than different age dyads ($r_{same\ age}$= 0.19 ± 0.06, N = 14, $r_{different\ age}$= 0.07 ± 0.02, N = 45), and same sex dyads sharing more alleles than opposite sex ones ($r_{same\ sex}$= 0.30 ± 0.11, N = 6, $r_{different\ sex}$= 0.07 ± 0.02, N = 53).

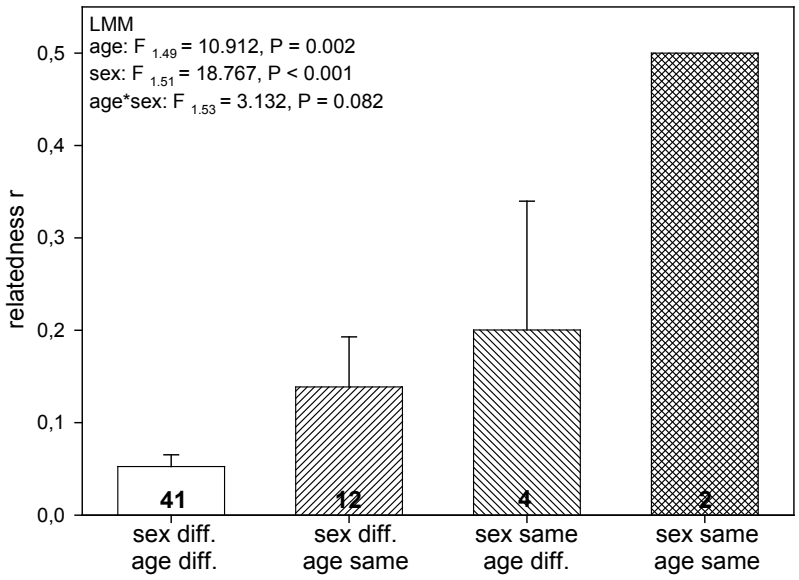

Figure 4: shared alleles among affiliated pairs. Most affiliations are between opposite sex and different age. Same age affiliations or same sex affiliations are associated with close relatedness.

Discussion

We found effects of relatedness on all three association levels observed. Relatedness differed depending on residency in the valley, association patterns over the day, as well as affiliative and agonistic dyadic interactions. Effects, however, strongly differed in intensity, and depended on the type of analysis, i.e. average or maximum relatedness.

The average relatedness in our raven population is very low (but perfectly fit to average scores reported from other corvid studies: Baglione et al. 2003), and even lower in the group of local birds when compared to those ravens who only visit occasionally. Also, birds that spend the day in close distance are not particularly related to each other, and most observed affiliations occur between pair-like partners, i.e. opposite sex and unrelated. This supports the hypothesis that ravens use their time as non-breeders to queue for territories, and similar to Parker (1994), not to roam around with relatives to specifically cooperate with close kin.

Maximum relatedness, on the other hand, is relatively high in our sample. Again comparable to Parker et al. (1994), we found a non-negligible number of closely related dyads in our sample, which indicates that the patterns observed at our study site reflects a general pattern of raven non-breeder groups, largely irrespective of environmental conditions. Birds of Parker et al. were observed in Maine, where ravens are highly vagrant (Heinrich et al. 1994), form non-stable roosts, and recruit conspecifics over long distances (Heinrich 1988; Marzluff et al. 1996). This drastically differs from our study site in the Alps, where some ravens use the valley quite stable over several months to feed (Braun et al. 2012), the area for the night roost can be found year-round in the same forest (Drack 1994), and the birds typically recruit each other to food sources from short distance (Bugnyar et al. 2001; Bugnyar & Kotrschal 2001).

Within groups of non-breeders, hence, some close relatives can be found, although interactions between them are rare. Specifically in same age and same sex affiliate dyads, kin plays an important role. This supports findings from captive ravens, in which siblings have valuable relationships (Fraser & Bugnyar 2010a). In captive peer-groups, dyads form functional alliances, which are characterized by mutual tolerance around food, active and passive social support in agonistic encounters (Fraser & Bugnyar 2011, 2012), and post conflict consolation (Fraser & Bugnyar

2010b). These alliances tend to be of same sex, and are usually formed by male nest mates (Fraser & Bugnyar 2010a). Interestingly, we couldn't find evidence for affiliative parent-offspring contact after dispersal, as there were no different-age-class-contacts with relatedness around 0.5.

Taken together, we found strong support for the queuing hypothesis, and some support for the nepotism hypothesis, however, effect of the latter remains relatively weak. The fact that we do find sibling affiliate interactions together with the knowledge about the intensity in which sibling alliances can be maintained and used by captive ravens, opens the possibility for long-term valuable relationships in raven siblings also in the wild. As pair-like relationships seem to be the preferred option to invest in, sibling alliances might serve as a back-up plan for social support in case that no pair-like partner is available. It remains to be investigated, whether close kin relationships have an effect on survival or stress management in wild non-breeder ravens at all.

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Do Carrion Crows learn to discriminate Pictures of unknown Conspecifics on an individual Basis?

Manuskript submitted to *Animal Cognition*

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The ability to discriminate between conspecifics is an important prerequisite to build up differentiated relationships. Many corvid species build up relationships in groups formed for foraging and roosting, whereby the degree of social dynamics and structure of these gatherings is little understood. Responses in behavioural and playback experiments suggest good individual recognition abilities in several species. However, results from studies in the visual domain are less clear: rooks *Corvus frugilegus* seem to be able to discriminate conspecifics in video clips but not in static pictures. We here investigated the ability of carrion crows *Corvus corone corone* to differentiate between conspecifics depicted on a touch-screen computer. We trained six carrion crows (3f, 3m) in a two-choice task for discriminating several pictures of unknown individuals. Subsequently, we tested the crows for generalization of their learned discrimination to novel pictures of the same individuals. Four birds (2f, 2m) solved the discrimination task and all of them transferred to novel pictures in the first cycle of probe trials. However, two birds (both males) strongly responded to the non-reinforced structure of the probe trials and temporarily dropped to random or even significant incorrect choices. We conclude that carrion crows are able to discriminate between 2D representations of unknown conspecifics. The fact that they got the first probe trials with new pictures correct suggests that their discrimination was based on individual recognition rather than rote learning. The non-stabile performance of some birds makes firm conclusions difficult and calls for methodological adjustments of the test procedure.

Introduction

The recognition of interaction partners is useful in various contexts of social life like mate guarding, investment in offspring, territorial defence and/or inbreeding avoidance. The mechanisms and cognitive processes involved, however, differ dramatically between contexts and species (see Mateo 2004). The most precise form of recognition is individual recognition (Beecher 1989), in which opponents are uniquely identified according to their distinctive characteristics and memorized through iterated interactions (Dale et al. 2001). Individual recognition needs detailed recognition and memory systems on the side of the receiver (Dennis et al. 1973) and distinct individualised cues and/or signals from the sender (Tibbetts and Dale 2007; Sheehan and Tibbetts 2010). These traits should evolve in species whose social system favours individual recognition over easier forms of recognition.

In the last decade, complex social systems have been described in a variety of distantly related species (de Waal and Tyack 2003). At the core of all these societies are individualised relationship networks (Dunbar and Shultz 2007) which are impossible without individual recognition. Individuals build up distinct relationships that differ between dyads in respect to content, quality and temporal patterning of interactions (Hinde 1976), and help them to reduce the costs of social life like competition (Aureli et al. 2002) and social stress (Silk 2007). Similar patterns may be also found in long-term monogamous birds (Dunbar and Shultz 2007; Emery et al. 2007). Notably, members of the family Corvidae have been suggested to provide an example of convergent evolution between mammals and birds in respect to cognitive skills (Emery and Clayton 2004), and some corvid species seem to be particular suited for testing the idea of sociality being one of the driving forces of the evolution of intelligence (Emery and Clayton 2005; Bugnyar acc). Corvid brains are among the biggest known from birds (Burish et al. 2004), and indeed corvids show sophisticated skills in the social domain like transitive inference (Paz-y-Mino et al. 2004), tactical deception (Bugnyar and Kotrschal 2002, 2004), social learning (Bednekoff and Balda 1996; Fritz and Kotrschal 1999), forms of perspective taking and possibly even knowledge attribution (Bugnyar and Heinrich 2005; Dally et al. 2005, 2006; Emery and Clayton 2001). Hence, corvids are an exemplary bird family in which we would expect the individuals to distinctly recognize each other. True individual recognition is however not always easy to show, as the perceiver of a given unique phenotypic cue has to

alter his behaviour to make the recognition visible to us (Mateo 2004; Tibbetts and Dale 2007). The context has to be relevant for the tested subject like juvenile screams for vervet monkeys (Cheney and Seyfarth 1982) or fighting scream sequences in baboons (Cheney and Seyfarth 1999; Bergman et al. 2003).

Belonging to the song-birds, corvids have been shown to contain individual call characteristics (Berger and Ligon 1977; Allenbacher et al. 1995; Yorzinski et al. 2006; Baker 2009) and that receivers can perceive these calls as originating from different individuals (Marzluff 1987; Hopp et al. 2001; Roskraft and Espmark 1984; Kondo et al. 2010; Boeckle and Bugnyar 2012). In the visual domain, several studies indicate that corvids are attentive to behaviours of specific individuals, like dominants, kin and affiliates (e.g. Scheid et al. 2007; Schwab et al. 2007). In the context of food caching, some species even take into account whether given competitors have been present or absent during the making of particular caches, and adjust their cache protection and pilfering tactics accordingly (Bugnyar 2011; Bugnyar and Heinrich 2005, 2006). These tactics seem impossible without visual identification of conspecifics. Still, only few studies have explicitly tested for individual discrimination by confronting birds with images of conspecifics while controlling for any auditory cues. Interestingly, rooks preferred to observe their pair partners in video clips but not in static images (Bird and Emery 2008), suggesting that discrimination of individuals requires movements. We here followed up the birds' apparent problems with static images using an operant set-up, which allowed the test subject to interact with the stimuli. We thus tested crows for discriminating 2D pictures of unknown conspecifics using a computer screen and a forced two-choice procedure.

The colour vision of birds is rather different from that of mammals, including humans (Bowmaker 1998). Notably their sensitivity in the UV part of the spectrum may cause problems in correctly identifying 2-D images of naturalistic stimuli such as conspecifics on computer screens in RGB-mode (red-green-blue). Corvids' colour vision is biased towards violet than towards ultraviolet (Ödeen and Hastad 2003), indicating that the general problem of inadequate UV presentation with images in RGB-mode on computer screens does not apply as intensely for corvids as for other songbirds with peaks in UV. Moreover, results from recent work on pigeons, a bird family which naturally relies on UV-information for partner choice, imply that these birds can learn to discriminate pictures of conspecifics presented on computer screens

but their performance depends on the general test set-up, stimulus quality and content as well as the subjects' pre-experience with 2-D stimuli (Candland 1969; Jitsumori and Makino 2004; Nakamura et al. 2003; Ryan 1982; Ryan and Lea 1994; Wilkinson et al. 2010; Bradshaw and Dawkins 1993).

We here applied a well approved setup for pigeons (Wilkinson et al. 2010; Nakamura et al. 2003) on carrion crows: first the birds had to learn to discriminate multiple views of unknown conspecifics that were arbitrary classified to belong to the positive or negative category; in a subsequent transfer test, the crows were asked to assign novel views of the learned individuals to the two contingencies. We were interested if crows were able to learn the discrimination, how long it would take them to do so and whether the discrimination was based on rote learning or individual recognition. In case of the latter, crows should be able to generalize to novel pictures and views of the trained individuals in the transfer task.

Methods

Animals and housing

We used three female and three male carrion crows (Table 1). The birds were kept in pairs in three adjacent outdoor aviaries at the Konrad Lorenz Forschungsstelle in Grünau, Austria. Two aviaries were connected with a test compartment (4 x 4 m), which could be accessed by the birds through two separate doors. The third aviary had its own test compartment with comparable dimensions. The touch-screen was fitted into a wall of the test compartments with the food dispenser right underneath. The orientation of the touch-screen ensured that birds in the outdoor aviaries could not see what was displayed at the screen, although they could actually see and hear the working bird if they chose to. All crows voluntarily participated in the study and entered the test compartment after being called by name. We did not keep them at a reduced weight, but conducted the experiment before the daily feedings in the morning and afternoon to ensure their motivation to participate. The reward consisted of highly preferred dog food pieces that are usually not part of their daily diet.

Table1: Overview of the crows used in the experiment, showing sex (m = male, f = female), age (in years), housing status (pair 1-3) and reinforcement contingency (S+ for A or B)

subject	age	sex	housed	S+
Klaus (K)	1	m	pair 1	A
Franz (F)	3	m	pair 2	A
Bärchen (B)	2	m	pair 3	B
Töffel (T)	2	f	pair 1	A
Gabi (G)	3	f	pair 2	A
Petra (P)	4	f	pair 3	B

Four of the crows were trained on the touch screen computers during the course of this study. The two oldest females (3 and 4 years) had already been trained in the year before and had successfully participated in a discrimination study (compare Aust et al. 2008). However, they had no experience with pictures of conspecifics on computer screens.

Stimuli

We used colour photographs of wild crows as stimuli. Pictures were taken in three public parks in Vienna, where crows are very tame because they regularly are fed by humans. Also, the distance of about 250 km to Grünau makes it unlikely that any of the depicted crows has been in contact with the tested crows of our captive colony before. Vienna lies in the hybrid zone of carrion crows *Corvus corone corone* and hooded crows *Corvus corone cornix* (Glutz von Blotzheim and Bauer 1993). Typically, crow aggregations contain both species (in a ratio of 1:3 carrion to hooded crows) and their hybrids (which may range from a more carrion-like habitus to a more hooded-like habitus). To correct for potential recognition problems or facilitations due to the more coloured plumage of hooded crows and hybrids, we chose the same number of stimulus birds with carrion crow and hooded crow habitus. To correct for brightness (Humphrey 1972), we took the pictures on one sunny day between 9 o'clock in the morning and 16 0'clock in the afternoon. All pictures were taken with a Canon - EOS 450D camera equipped with a 200 mm fix-lens with 1:2.8 apertures. We avoided photographing the same crow multiple times (because all crows were unmarked) by focusing on one crow until all pictures were shot before switching to the next one. Furthermore we only took pictures of two carrion crows and two

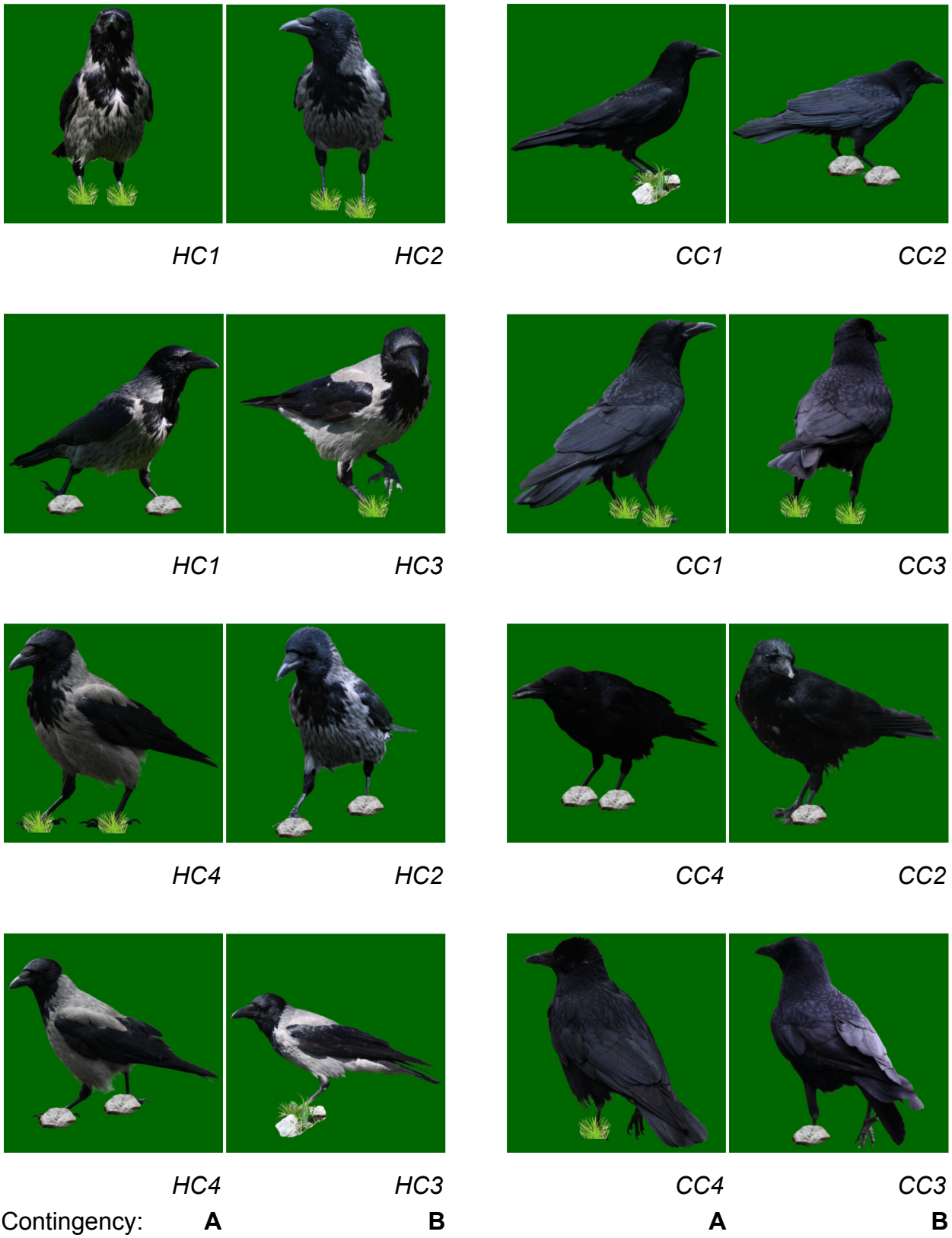

Figure 1: Example of eight possible stimulus bird combinations from different views. HC1+2 = hooded crows with hybrid appearance, HC3+4 = hooded crows, CC1-4 = carrion crows. Stimulus class A contained HC 1+4 and CC 1+4, whereas class B contained HC and CC 2+3

hooded crows per flock and park, taking one sub-species after the other. Only birds which approached to 10 m or less were pictured. To decrease the amount of covered body parts, we shot pictures only on gravelled walkways or short-cut meadows. Per bird, we used 12 pictures from at least 8 orientations (front, back, both sides and the four intermediates; for examples see Fig. 1).

In total, four carrion crows and four hooded crows were chosen as stimulus birds. They were separated in two stimulus classes (A and B) by assigning similar birds to different classes (see Fig. 1). Thus both classes A and B contained two carrion crows and two hooded crows; one with strong grey-black contrast in the plumage and one with more hybrid appearance. The background of stimulus pictures was erased and replaced with a uniform green (cf. Wilkinson et al. 2010; Nakamura et al. 2003). As the feet of the stimulus birds often were partially hidden by grass, we intentionally covered the feet in all stimuli with either sketched grass patches or stone images. We controlled for a similar distribution of foot coverage per stimulus bird (compare Wilkinson et al. 2010). Pictures were displayed on the screen in a size of 3.8 cm x 3.8 cm.

Apparatus

We used a 15-inch TFT computer screen interconnected with an infrared touch-frame in the front. The food reward was presented on a plate 5 cm below the touch-screen. The whole setup was controlled using 'embedded-C-Lab' computer hardware and the 'CognitionLab' software package (both developed by M. Steurer, Department of Cognitive Biology, University of Vienna, Austria).

Procedure

Computer training and forced two-choice procedure

After habituating the birds to the computer set-up, we conducted several training steps to get the birds (1) motivated to persistently interact with the computer and (2) experienced to work with still digitised pictures, as studies have shown that picture recognition in humans and non-human animals is facilitated by prior exposure to pictures (Bovet and Vauclair 2000). The first step was a simple train-to-peck procedure involving 40 different pictures of different colours and shapes but matched in size (3 x 3 cm) appearing consecutively at random places on a white screen triggering the food delivery when touched. As soon as the crows regularly completed 20 trials, they went

on to the next step, involving a simple discrimination training to learn about forced two choice procedures first with simple geometrical stimuli (circle vs. triangle) then with complex natural stimuli (fish vs. flower). In both tasks, pecking the correct stimulus elicited food delivery and an auditory signal while the screen turned blank for a second. Choosing the incorrect stimulus led to another auditory signal and a red screen for one second, followed by the same stimulus-pair presentation again (correction trial). Criterion was 80 % correct over 5 sessions and mastered by the birds on average after 11 ± 6 sessions (142 ± 50 trials) in the triangle-circle discrimination and 19 ± 5 sessions (258 ± 71 trials) in the fish-flower discrimination.

Discriminating pictures of conspecifics: Training step 1

The six crows were assigned to contingency A or B, with positive stimulus birds from contingency A being negative in contingency B and the other way round. Four crows were trained in contingency A, and two were rewarded for the stimuli of contingency B (see Table 1). The procedure was similar to the one described above: we presented the crows with 10 pictures of each of the stimulus birds, whereby pictures of the four positive and the four negative stimulus birds were randomly paired with each other. All stimuli were presented within one session comprising 40 trials, with the first repetition of the same pairing occurring after four sessions. In total there hence were 160 combinations of the stimuli. Birds completed one session per day, split into 20 trials in the morning and 20 trials in the afternoon. Inter-trial-intervals and correction-inter-trial-intervals were set at 2 seconds. To prevent overtraining, we set criterion to the smallest significant deviation from random performance, which is a mean performance of 68 % over 6 sessions without dropping below 60 % performance in one of them. To insure stable working, the birds had to work at least 20 sessions, but if birds did not reach criterion within 100 sessions, we excluded them from further testing.

Discriminating pictures of conspecifics: Training step 2

Because previous work with crows and ravens on touch screen computers showed that they could be highly sensitive to slight changes in the setup (i.e. no reward/feedback in the probe trials; Aust et al. unpubl. data), we introduced a second training step to confront the crows with the lack of reinforcement of later test trials. We therefore interspersed non-reinforced trials into the discrimination training procedure

described above. Within every 10 trials, one trial was lacking the feedback for either the correct choice (no food reward), or the negative one (no red screen, no correction trial). Criterion for training step two and thus criterion to proceed to the transfer test was a performance above 75 % in four out of five sessions or a mean of 75% performance over five sessions.

Transfer test to novel pictures

Test sessions comprised 22 trials, with 20 trials with known pictures from discrimination training and a non-reinforced test trial interspersed within each 10 trainings trials. Two previously unknown views of each stimulus bird served as test pictures. The totals of eight positive and negative test pictures (2 pictures per bird, 4 birds per contingency) were displayed over the course of four test sessions. Four test sessions represent one cycle of test stimulus presentation and will be called test cycle in the further text. We conducted three test cycles in which no test-picture pairing appeared twice.

Data analysis

To test for the effect of the different contingencies on performance in the discrimination training, we conducted an ANOVA using the percentage of correct first choice in the training sessions as response variable, subjects as random variable, and contingency as fixed variable. Two tailed binomial tests were applied to see whether performance of birds was deviating from random, and a Kruskal-Wallis test compared the performance of the different birds with each other. Performance differences within a bird, either within different stimuli-types or between test trials and training trials, were compared using paired t-tests.

Results

Discrimination training one and two

Two birds (female G, male K) stopped participating after 33 and 35 sessions, respectively; their mean performance over the last six sessions did not deviate from chance (female: 50 ± 5 % correct first choices; male: 57 ± 7 % correct first choices; Binomial test both $P > 0.05$). The remaining four crows reached the criterion for the first training step after a mean of 67 ± 17 sessions (Fig. 2). There was no effect of the different contingencies A and B on the performance of the birds, $F_{1.60} = 0.79$, $P = 0.38$.

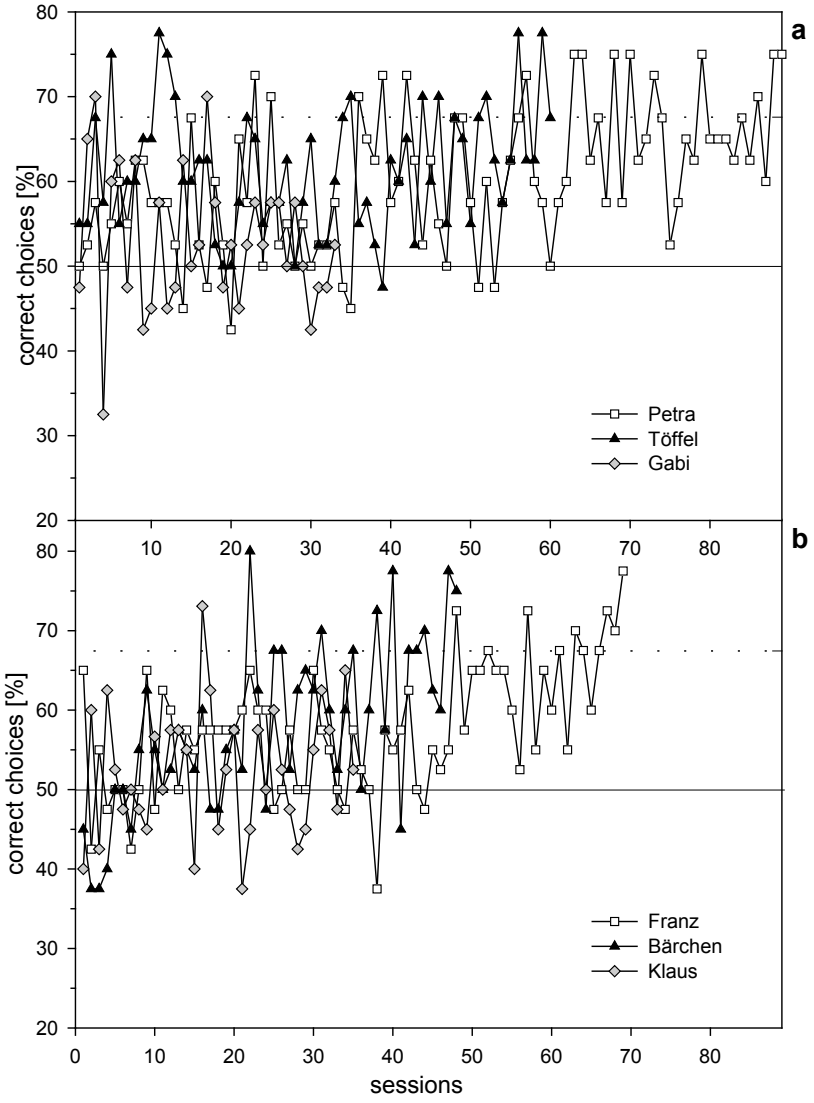

Figure 2: Learning curve in the first training step for the three females (a) and the three males (b); dashed lines indicate level of significance; straight lines represent random choice

In the second training step, in which every 10 training trials contained one trial that was unreinforced the crows' performance differed strongly. Two birds (female P, male F) were only slightly affected by this change and reached the second criterion after nine sessions. One male (B) strongly responded to the changed setup and needed 44 sessions to reach the criterion again. The remaining female (T) did not reach the criterion in this task at all. This female was the quickest of all crows to learn the discrimination, scoring four times in a row above 70 % correct within the first 20 session. However, with time she became more and more variable in her performance,

scoring from 55 % to 78 % correct per session. We tried to stabilize her performance by increasing the costs following wrong choices, i.e. prolonging the time the screen turned red. We did so three times: from 1 to 2 seconds, from 2 to 3 seconds, and from 3 to 5 seconds. Indeed, she reached the level of correct first choices required for the criterion in each session following an increase in time-out delay, Binomial Test: $P = 0.017$, but then dropped to 58 % in the following sessions again, Binomial Test: $P = 0.268$. We therefore were tempted to conclude that she seems able to do the discrimination, however lacks the motivation to show it consistently. Due to our small sample size, we included her in the transfer test despite she did not reach criterion. She did not differ from the others in the test, $H_3 = 0.246$, $P = 0.970$.

Table 2: Performance of the crows [% correct first choice] in the three cycles of test stimulus presentation

subject	cycle 1	cycle 2	cycle 3	cycle mean
Franz (F)	75	25	75	58.33
Bärchen (B)	87.5	50	75	70.83
Töffel (T)	62.5	62.5	87.5	70.83
Petra (P)	62.5	87.5	62.5	70.83
total mean	71.88	56.25	75	

Transfer test

Overall, the birds responded to novel views of depicted crows with a mean of 67.71 ± 6.25 % correct first choice, which is significantly above chance, Binomial test: $P < 0.05$. Importantly, they perfectly discriminated the novel pictures to the trained individuals at their first presentation (first cycle of probe trials, Table 2). Interestingly, the two males reversed their choice in the second presentation cycle but chose correctly in the third cycle again; the two females, in contrast, performed relatively constant in all three cycles.

Performance during the training trials in the test did not differ from those during the training, $T_3 = 0.291$, $P = 0.790$, nor did the performance differ for either hooded crow or carrion crow stimuli (last five trainings sessions: hooded crow stimuli 67.50 % ± 9.47 % vs carrion crow stimuli 77.00 % ± 2.00 % correct first choices, $T_3 = -2.006$, $P = 0.138$; test session: hooded crow test stimuli 58.33 % ± 11.79 % vs carrion crow stimuli 77.09 % ± 17.18 % correct first choices, $T_3 = -1.406$, $P = 0.254$).

Discussion

Our study shows that carrion crows can learn to discriminate static pictures of unfamiliar crows displayed on a computer screen in RGB-mode. However, there were big individual differences in the number of sessions needed to reach criterion, if it was reached at all. This suggests that some crows had difficulties with the task whereas others were highly sensitive to any changes in the set-up and reward structure. Nevertheless, the crows' performance in the first cycle of transfer test suggest that they were able to instantly discriminate new pictures and views of the trained stimulus birds, indicating that they might have learned to individually recognize the depicted birds.

Songbirds are known for their ability to discriminate conspecifics acoustically (Baker 2009; Berger and Ligon 1977; Allenbacher et al. 1995; Yorzinski et al. 2006; Marzluff 1987; Hopp et al. 2001; Roskraft and Espmark 1984; Kondo et al. 2010), and some species can visually identify conspecifics based on plumage variation alone (Lank and Dale 2001; Whitfield 1986). However, to our knowledge this is the first study providing evidence that a bird species wit h a rather inconspicuous plumage variation can discriminate unknown conspecifics via static visual information alone.

Our pictures comprised carrion crows as well as hooded crows, which clearly differ in their appearance. The hooded crow stimuli showed an individual variation in plumage patches and black-grey contrast whereas the carrion crow stimuli were pitch-black. Accordingly, hooded crows might have been easier to identify than carrion crows. In contrast, carrion crow pictures might have been preferred over those of hooded crows by our (carrion crow) test subjects because the former have a more familiar appearance to them (Candland 1969; Kendrick et al. 1996; Ryan 1982; Wilkinson et al. 2010) and/or the hooded crow pictures were perceived as another species (cf. Saino and Scatizzi 1991; Saino and Villa 1992; Rolando 1993). Interestingly, our crows did not show any preference for pictures of either species. This indicates that either the different appearance of carrion crows and hooded crows is more strongly perceived by us humans than by the carrion crows (Rolando 1993), or that the ability to discriminate hooded as well as carrion crows is resting on a more general visual discrimination ability of carrion crows. Pigeons, for example, are not only able to discriminate between photographs of individual pigeons (Nakamura et al.

2003), but also those of humans (Jitsumori and Makino 2004; Troje et al. 1999). Firm conclusions are difficult because of the small sample size of tested birds.

Although carrion crows were able to correctly align novel views to learned contingencies, this does not mean that these pictures were perceived as representations of real objects (Weisman and Spetch 2010; Aust and Huber 2006; Watanabe 1993, 1997) or even representations of 3-D objects (Jitsumori 2010). It might be that the crows learned the training stimuli by heart and were able to deduce any features from the stimuli like e.g. contrast, acuity, or brightness, to correctly choose the test stimuli. The instant discrimination of the novel pictures is difficult to explain by rote learning but it is in line with the assumption that crows could recognize certain parts of the depicted individuals or, possibly, the identity of the depicted birds. This also would fit to recent findings from pigeons, which treated the computer stimuli as representations of real entities when distinguishing social partners from strangers (Wilkinson et al. 2010).

Unfortunately, our results from the transfer task are hampered by the fact that two of the four birds (the two males) chose randomly or even significantly incorrect in the second presentation cycle. This either suggests that they remembered the novel stimuli after a single presentation and tried the alternative option because of the missing positive reinforcement, or that the novel pictures confused the birds in the second cycle of stimulus presentation. That crows are highly sensitive to reward structure was already evident from training, in which the male B took 44 sessions (5 times as many as the others) to reach criterion again after the introduction of unrewarded trials. Also the female T, which temporarily responded to every increase in time-out after wrong choices, provides support for the fact that crows are very sensitive to changes in the set-up. Future studies need to consider these motivational issues in their set-up.

What may be the real life advantage for carrion crows to visually differentiate between unknown conspecifics even without interacting with them? The social system of carrion crows ranges from vagrant non-breeder aggregations with socially monogamous territorial breeders (Richner 1990) to cooperative breeders defending a territory in small groups (Baglione et al. 2002a, b), and even communal breeding (Abshagen 1963; Loman 1985). In all these systems, crows may meet various conspecifics repeatedly over time. Quickly learning about the other's identity could give

them an edge in any kind of interaction, from managing conflicts and judging dominance status to competition for food (compare also Paz-y-Mino et al. 2004; Chiarati et al. 2010; Fraser and Bugnyar 2012).

Taken together, carrion crows were able to discriminate between complex visual stimuli, like for example unknown conspecifics, on a computer touch-screen, and to correctly align novel views of theses conspecifics to the right contingency. This discrimination might well be based on individual recognition rather than rote learning, because the birds' first response to novel views of learned individuals was correct. How much crows can deduce from observation alone, however, remains to be investigated in future studies.

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Discussion

Sociality has evolved as a strategy for animals to cope with their environments, and, in turn, provides an environment that needs to be coped with (Alexander 1974; Dunbar & Shultz 2007). The dependence on sociality and its levels of complexity promotes brain specialisations and behavioural characteristics in mammals, but lacks fundamental data and a firm theoretical basis in birds. Existing comparative work focuses on large-brained species and takes the fact, that higher forms of cognition has evolved in distantly related mammalian and avian species, as an argument for convergent evolution on the basis of comparable socio-ecological problems (Marino 2002; Emery & Clayton 2004; Seed et al. 2009; van Horik et al. 2012), however, a deeper examination of the comparability of mammalian and avian socio-ecology are missing (Bshary et al. 2012). With the present thesis, I try to shed light on the degree of complexity found in the social structure of wild common ravens. In the following, I will discuss our results and suggest a framework on avian social complexity that allows us to compare the current results with those of mammals.

The socio-ecology of the investigated raven population confirmed characteristics described in other studies, and further revealed new structural details. The tendency of raven non-breeders to form groups for foraging is well documented: individuals clearly profit from joining others in respect to finding and accessing food that is defended by predators or dominant conspecifics (Marzluff et al. 1996; Wright et al. 2003). In such situations, ravens actively recruit others, either from nearby with food-calls, or from distant night-roosts (Heinrich 1988; Heinrich & Marzluff 1991; Bugnyar & Kotrschal 2001). Ravens also regularly form groups when confronted with new or unusual situations involving food; a seeming carcass could be a sleeping or sick yet dangerous animal (Heinrich 1988). Human persecution might have exaggerated this innate neophobia of ravens, and probably indirectly selected for increased sociality. However, the main problem commonly faced by non-breeders is the food defence of dominant territorial pairs. It typically takes more than seven ravens to be able to eat in the presence of territory holders (Heinrich 1994; Wright et al. 2003).

This tendency of non-breeding ravens forming groups is supported by the current studies. In our valley, the ravens came each morning from the adjacent night roost to an area in and around the Cumberland Wildpark (roughly 2 km^2) for foraging.

Most food was available during the morning feedings of zoo animals (i.e. wolves, bears, wild boars), at which the majority of birds participated on a daily basis. In these aggregations, conflicts were common and provoked appeasement calls by subordinates almost every few seconds. Interestingly, most conflicts were not directly about food but simply about access to a particular position (like a post of the fence) or without any obvious reason and thus presumably about status. After foraging, most ravens remained in loose aggregations and formed small sub-groups in which they frequently engaged in friendly interactions. This type of group formation has been known only from anecdotes and could be demonstrated here for the first time. Raven non-breeder groups thus show relatively strong dynamics over the day, with groups fusing during foraging and fissioning into subgroups for socializing. While the former goes together with an increase in conflicts, the latter is characterized by a drop in conflicts (Braun et al. 2012).

So what are the signs for social complexity in our raven scenario if we take social complexity as a 'political' dimension that is added to social life (De Waal 1982; Byrne & Whiten 1988)? Firstly, group composition and membership fluctuation was more complex as reported in other studies (Huber 1991; Heinrich et al. 1994; Parker et al. 1994), with a core unit of birds being present over long time periods, and others passing by in irregular intervals (Braun et al. 2012). Most birds therefore had a high likelihood to meet iteratively over months or sometimes years, raising the possibility that they might come to recognize each other individually. Judged by the reaction of 'local' ravens to a bird that came back to the valley after a long period of absence, they seemed to instantly categorize the newcomer, probably because they remembered who it was. This interpretation is in accordance with recent findings from ravens in captivity that were able to differentiate former group members from non-group members and even former 'friends' from 'foes' up to three years after they had been in contact with these birds (Boeckle & Bugnyar 2012).

Secondly, the ravens socialised in small groups characterized by affiliative behaviours. Thus ravens actively tried to build up affiliate relationships or social bonds, possibly because being bonded benefited them in daily competition for food. Attractive bonding partners were of opposite sex and older age; as rank correlates with age in ravens, this hints towards an attractiveness of "power" (Braun & Bugnyar 2012). A similar phenomenon was described by Seyfarth (1977) as rank attractiveness model

for female monkeys, and latter confirmed for spotted hyenas (Smith et al. 2007), and female primates (Schino 2001). The idea behind it is that, when social partners vary in their relative value, individuals should initiate partnerships with those of the highest value (Seyfarth 1977; Noë & Hammerstein 1995). Social status contributed highly to relative dominance rank in wild ravens, and was determined not so much by body size or aggression, but by the ability of having bonding partners. Social bonds in non-breeding ravens may therefore function as alliances for gaining and maintaining status.

Thirdly, ravens that were forming a bond tended to face aggression by other bonded birds. Specifically, older ravens intervened in affiliative behaviours of others, suggesting that these third-party interventions function to prevent others from forming stable bonds. Indeed, most bonds of non-breeders were flexible in duration, and only few of them lasted longer than several months (Braun & Bugnyar 2012).

Although involving sexually immature ravens, most bonds were formed between unrelated males and females and thus resembled mated pairs. Nonetheless, bonds among close kin, notably between same sexes, could also be observed, indicating that ravens may actively work on their social relationships, possibly as a tactic to manoeuvre the social field and/or to buffer social stress (Braun et al. in prep). Interestingly, non-sexual bonding was not accompanied by active giving of food, but by other commodities like allo-preening and playful offering of non-edible objects (compare also: Pika & Bugnyar 2011), which contrasts reports from relationship formation in rooks (Emery et al. 2007) and jackdaws (de Kort et al. 2003, 2006), which, unlike ravens, breed in colonies.

Taken together, raven non-breeder groups show features of an individualized society, with non-reproductive social bonds playing an important role; a fact that characterises social complexity in mammals, but so far was not known for birds. But how comparable are mammalian and avian societies regarding their structure and complexity? Birds and mammals differ in respect to locomotion and reproduction, which results in tremendous differences for social structure. Raven non-breeder aggregations reveal three main discrepancies to typical mammalian social structure: (1) resource type competed for, (2) number of bonding partners, and (3) group stability. As they all play a crucial role for the applicability of the social intelligence hypothesis (Barrett et al. 2007; Byrne & Bates 2007a, b), I will discuss these three aspects in further detail.

(1) In mammals, high ranking males commonly gain prior access to receptive females, whereas high ranking females gain protection for their offspring (Wrangham 1980; Moss & Poole 1983; Connor et al. 1999; Mosser & Parker 2009; Seyfarth & Cheney 2012). Both are aspects which have high selective potential as they affect an individuals' reproductive success, and strongly invested, long-term grown relationships are beneficial (Silk 2007a, b). The resource type that high ranking non-breeding ravens achieve prior access to essentially is food. As high quality food can be gained by several means in corvids, long-term social bonds may be of advantage but not a necessity. Ravens that lack the support of a partner could for example specialise on pilfering of food caches. Their ability for observational spatial memory allows ravens to remember and pilfer the caches of dominant conspecifics (Heinrich & Pepper 1998).

(2) The underlying physiological constitution for the formation of relationships differs in mammals and birds. Whereas mammalian relationships origin in mother-infant bonding (Kummer 1971; Broad et al. 2006), bird relationships are derived from pair bonding (Emery et al. 2007; Seed et al. 2009). Birds typically defend a territory together with their long-term pair partner, and sometimes build up families by allowing their offspring to remain within the territory (Ekman & Griesser 2002). This physiological and socio-ecological background leads us to expect long-term bonding partners to be reduced to very few, usually one, at a time. Even though ravens in our population eventually broke up relations and serially bonded with different partners over time (i.e. years), their affiliative social networks seems relatively small compared to those from mammals. Likewise were the majority of affiliations not affected by kin. Long-term bonds can be seen as a test run of pairs for later social monogamy while queuing for territories. The few affiliations which did not fit this pattern were those of close kin. The option to form strong alliances with their siblings therefore exists in wild ravens. Unfortunately, our data do not allow us drawing a conclusion about a possible bias for kinship in early raven networks, or about the role of siblings for older ravens. Further studies are needed to see whether or not kinship has an influence on the social embedding in wild raven non-breeders at all.

(3) Bird aggregations contradict the establishment of social complexity with its membership fluidity. Individual recognition is hard to imagine in a society in which many conspecifics are met on a daily basis but their identity is changing frequently. Different mechanisms might act to solve this problem. First, individuals might learn to

recognize only those that are met regularly. In our local raven population this would mean dealing with a number of about 30 to 40 birds, whereas in regions with larger raven aggregations, this might be facilitated by sub-roost formation (Wright et al. 2003), and a preference to hang out with those that are familiar (Dall & Wright 2009). It nonetheless requires quick learning and good memory abilities. Our current study on carrion crows' discriminative abilities of unknown conspecifics via pictures (Braun & Bugnyar subm.) provides an indication in this direction. A second possibility is to categorize others based on observable cues like body size, condition, affiliation status etc. This kind of scenario is strongly supported by our results, as raven aggregations prove to be structured by age, sex (compare also: Huber 1991; Heinrich 1994) and bonding status (Braun & Bugnyar 2012). Rank strongly depended on age (with older birds being dominant over younger ones) sex (with males being dominant over females) and bonding status (with birds having a strong bond dominating those with weaker or no bonds). Remarkably, also third party interventions in others' alliance formation of others differed, depending on social status, age and sex. Refined class level recognition would thus be sufficient to respond appropriately to almost all of the encounters in our raven population, and most interestingly, to those encounters that resemble the lynchpin of social complexity in ravens.

Conclusion

Despite of these pronounced differences between avian and mammalian socio-ecology, it is striking, how similar the patterns of formation, maintenance and usage of bonds are in both taxa. Core features are i) the exchange of affiliative behaviours, close spatial proximity, active and passive social support in conflicts, ii) selectivity in partner choice, and iii) role of kinship (see also: Baglione et al. 2003; Griesser et al. 2006; Emery et al. 2007; Fraser & Bugnyar 2010). The frequent use of third-party interventions, not only in conflicts, but in affiliate interactions, that could be observed in ravens, raise the possibility of a sophisticated game of power which would put ravens on a level comparable to cognitively sophisticated mammals like higher primates, dolphins and social carnivores.

To classify the level of social complexity in raven non-breeders according to mammalian social complexity, we need to consider results from other corvids as well. The class level structure of rank relations and third-party interventions are typical for

bird social systems (Gauthreaux 1978; Lamprecht 1986; Piper & Have Wiley 1989; Moore et al. 2003), and therefore expected to be the general case in corvids. Relationships decoupled from direct reproduction, as seen in raven non-breeders, however, are probably rare in most corvids, as they often pair up early for life. Ravens therefore may be exceptional in their flexibility of choosing and using bonding partners during their aggregative and non-reproductive part of live. Having a closer look into partner choice and bonding patterns outside the breeding season and/or in situations when socialising, in ravens and in other corvids, might help to get a more differentiated view on the whole picture.

A possible explanation for the flexible bonding patterns of ravens can be found in their feeding ecology. They are classified as one of the most versatile bird species (Boarman & Heinrich 1999), surviving in harsh environments by being a food generalist with specialisation on difficult to access food. Accessibility is granted due to social agents like cooperative conspecifics and food producing heterospecifics. In general, corvid intelligence is based on its feeding ecology, which is intertwined with a demanding social ecology (Kamil 2004; Bond et al. 2007), leading to a sophisticated handling of the social realm as well (Bugnyar & Kotrschal 2002; Paz-y-Mino et al. 2004; Heinrich 2011; Braun & Bugnyar 2012). This goes in line with recent reflections on mammalian intelligence, in which the interaction of both, physical and social problem solving, seem to mingle for the evolution of sophisticated intelligence (Byrne & Bates 2010). Probably, each animal branch has reached its own kind of intelligence on the basis of its own mosaic of physiological, ecological and social characteristics (Barton & Harvey 2000; Reader & Laland 2002; Lefebvre et al. 2004; Sol et al. 2007), and social characteristics are definitely one to reckon within birds as well.

Finally, the question remains, whether association patterns in our population were artificially stabilised due to the predictable food situation, and friendly interactions exaggerated in this stress reduced surrounding (Martin 1982; Barrett et al. 1992). I therefore will try to compare these data with ravens living in environments with predictable food sources but changing food locations. This is ideally realised in ravens following wolf packs, like for example in the Yellowstone National Park, where the wolves have been re-introduced in 1996, and ravens follow them ever since (Stahler et al. 2002). If food predictability leads to stable association patterns, we would expect some raven non-breeders to specialise on a pack for feeding and others to fluctuate.

The question is, whether they show as frequent play and socialising behaviours, whether they gain high resource holding potential through bonding (or rather by knowing the wolves?), and whether older pairs also attempt to regulate relationship formation of others.

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Intelligence, i.e. the ability for lifelong flexible problem solving, has evolved several times within the vertebrates and is likely driven by similar environmental demands. While social complexity is widely accepted as one of these demands in mammals, it has yet not been adequately investigated in birds. Moreover, for those studies that exist, there seems to be a mismatch between social demands and cognitive skills. The common raven, for example, is one of the biggest brained bird species, performing excellent in socio-cognitive tasks under experimental conditions; yet it is renowned for a very simple opportunistic and anonymous social live in the wild. In the course of my PhD, I investigated the social complexity of a wild raven population, which regularly uses a game park in the Northern Alps, Upper Austria, for foraging. In a first study, we assessed the consistency of group composition (i.e. ravens present at foraging and socializing sites per day) and the behavioural patterns expressed in groups were compared to those shown by solitary individuals. The second study examined the political dimension of raven non-breeders, e.g. the benefits and limitations of affiliative relationships of wild ravens, and focused on dyadic and triadic interactions involving marked individuals. In the third study, we checked for the effect of kinship involved in association and interaction patterns of wild non-breeders. In a fourth study, we tested captive corvids (carrion crows) on computer touch-screens for their ability to learn about unfamiliar individuals, like for example new-comers in non-breeder groups, from static pictures only. Overall, the work revealed that raven non-breeder ‘aggregations’ reflect a social system with different levels of complexity. The composition of marked wild ravens changed constantly, though only slowly over the months, providing the possibility of individuals to meet iteratively over time. Aside from the aggregations for mobbing, feeding and roosting, ravens regularly gathered in small subgroups of 2-5 individuals. These subgroups were characterized by high rates of affiliative behaviours. Bonding patterns were mainly derived from pair bonding and followed Seyfarth’s rank attractiveness model, with all age classes trying to bond with older individuals of opposite sex. Raven social bonds were vulnerable for harassment by other bonded ravens, especially territorial ones, but benefited each partner in respect to resource holding potential. Birds engaged in serial bonds over the years, but tended to stick to one partner at a time. Nepotism played only a minor role in wild raven bonding and most bonds had a pair-bond like structure with partners being of distant relatedness and opposite sex. Occasionally, however, same age dyads, and

even same sex affiliative dyads of close kin could be observed, raising the possibility that under certain conditions or development stages, ravens might use siblings as alliance partners. The conducted operant study showed that corvids can learn to identify unknown conspecifics from static visual pictures and are able to transfer the learned discrimination to novel views of the same conspecifics. Altogether, our findings show that corvid non-breeder aggregations are characterized by complex social interactions which require differentiated knowledge about conspecifics. Nevertheless, these aggregations are ephemeral in character and fundamentally differing from stable terrestrial mammalian societies. Bearing the differences between mammalian and avian socio-ecology in mind, the outcome of its societies are remarkably similar and comparable. Further research should investigate, whether semi-closed groups exist, e.g. in the form of ravens associating with wolf packs, and how group stability affects the social complexity found in raven non-breeders.

Intelligenz, i.e. die Fähigkeit für lebenslanges flexibles Problemlöseverhalten, hat sich konvergent in mehreren Vertebratentaxa aufgrund von gleich wirkenden Umwelteinflüssen entwickelt. Während bei Säugern der größte Evolutionsdruck im sozialen Bereich zu finden ist, und sich die größten Hirne entwickelten wenn soziale Kompetenz gefragt war, fehlen vergleichbare Untersuchungen bei Vögeln. Tatsächlich zeigen die wenigen existierenden Studien bei Vögeln Unstimmigkeiten zwischen kognitiven Fähigkeiten und sozialen Anforderungen. Der Kolkrabe zum Beispiel hat eines der größten Vogelhirne, und zeigt in Experimenten erstaunliche soziale Fertigkeiten, soll jedoch in freier Wildbahn ein eher einfaches, anonymes und opportunistisches Sozialleben führen. Im Rahmen meiner Doktorarbeit untersuchte ich die soziale Komplexität einer wilden Kolkrabenpopulation in einem Wildpark in den nördlichen Alpen in Oberösterreich, der ihnen als Nahrungsquelle dient. In einer ersten Studie wurde die Konstanz der Gruppenzusammensetzung an Futter- und Sozialisierungsplätzen ermittelt und die Verhaltensmuster von Raben in Kleingruppen gegenüber Einzeltieren verglichen. Die zweite Arbeit diente dazu, Einblicke in die politische Dimension der Rabengesellschaften zu bekommen, also die Vor- und Nachteile von Beziehungen der wilden Raben untereinander, und richtete ein spezielles Augenmerk auf die dyadischen und triadischen Interaktionen. Eine dritte Analyse kümmerte sich um den Einfluss von Verwandtschaft auf Assoziationen und Interaktionsstrukturen. Schließlich prüften wir, ob Korviden (Rabenkrähen) unbekannte Individuen, z.B. Neuankömmlinge in Nichtbrütergruppen, allein anhand statischer Bilder an Computern unterscheiden lernen können. Die Ergebnisse zeigen, dass Rabenverbände die Bedingungen für die Anwendung von sozialer Intelligenz in sich bergen, und dass sie als komplexe soziale Systeme charakterisiert werden können. Die Zusammensetzung an markierten wilden Raben veränderte sich zwar konstant über die Monate, jedoch nur langsam, womit die Möglichkeit gegeben war, dass sich Individuen wiederholt trafen. Abgesehen von den bereits bekannten Raufgemeinschaften beim Fressen, dem gemeinsamen Mobben, und den Schlafplatzgemeinschaften, konnten die Raben regelmäßig in Kleingruppen von 2-5 Individuen angetroffen werden, welche sich durch hohe Raten an freundlichen Verhaltensweisen auszeichneten. Beziehungen hatten die Gestalt von Paarbindungen, und folgten Seyfarth’s Rang-Attraktivitäts-Model, indem Raben allen Alters Kontakt suchten zu älteren andersgeschlechtlichen Artgenossen, selbst wenn beide noch nicht

geschlechtsreif waren. Rabenbeziehungen waren anfällig für Angriffe von anderen verpaarten Raben, insbesondere von territorialen Paaren, aber boten jedem Paarpartner ein gesteigertes Potenzial Ressourcen zu gewinnen und zu halten. Die Vögel konnten über die Jahre seriell mit unterschiedlichen Partnern angetroffen werden, hatten jedoch zu einem Zeitpunkt immer nur einen Bindungspartner. Nepotismus spielt nur eine untergeordnete Rolle bei Rabenbeziehungen im Freien, und die meisten Paare hatten die Struktur von Paarbindungen, mit entfernt verwandten Partnern unterschiedlichen Geschlechts. Gelegentlich konnten jedoch gleichaltrige Dyaden, teilweise gleichengeschlechtlich mit hohem Verwandtschaftsgrad, in affiliativen Interaktionen beobachtet werden, was bedeutet, dass Raben ihre Geschwister als Allianzpartner nutzen können. Das Ergebnis der Computerarbeit zeigt, dass Korviden fähig sind, unbekannte Artgenossen anhand von statischen Bildern unterscheiden lernen zu können, und anschließend neue Ansichten der gelernten Artgenossen richtig zuzuordnen. Alles in allem sprechen unsere Daten dafür, dass Nichtbrüter-verbände bei Korviden von komplexen sozialen Interaktionen und Beziehungen geprägt sind, welche ein fundamentales Wissen über die Artgenossen voraussetzt. Der Charakter dieser Verbände zeigt sich im Vergleich zu Verbänden terrestrischer Säuger als sehr dynamisch, und weißt auch weitere beträchtliche Unterschiede auf. Die sozio-ökologischen Unterschiede zwischen Vögeln und Säugern im Hintergrund haltend, ähneln sich die Gesellschaften beider Taxa jedoch erstaunlich stark. Zukünftige Forschungsprojekte sollen herausfinden, ob bei wilden Nichtbrüter-raben auch geschlossene Gesellschaften existieren, z.B. in Form von Rabengruppen, die mit Wolfsrudeln assoziieren, und wie sich Gruppenstabilität auf die soziale Komplexität von Rabengruppen auswirkt.

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Corvids can decide if a Future Exchange is worth waiting for

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Evidence for time-dependent calculations about future rewards is scarce in non-human animals. In non-human primates, only great apes are comparable with humans. Still, some species wait for several minutes to obtain a better reward in delayed exchange tasks. Corvids have been shown to match with non-human primates in some time-related tasks. Here, we investigate a delay of gratification in two corvid species, the carrion crow (*Corvus corone*) and the common raven (*Corvus corax*), in an exchange task. Results show that corvids success decreases quickly as delay increases, with a maximal delay of up to 320 s (more than 5 min). The decision to wait rests both on the quality of the prospective reward and the time required to obtain it. Corvids also apply tactics (placing the reward on the ground or caching it) that probably alleviate costs of waiting and distract their attention during waiting. These findings contrast previous results on delayed gratification in birds and indicate that some species may perform comparably to primates.

Heart Rate Responses to induced Challenge Situations in Greylag Geese (*Anser anser*)

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Adequate short-term responses to stressors are of great importance for the health and well-being of individuals and factors modulating the physiological stress response (e.g., controllability, suddenness, familiarity) of a stimulus are well described under laboratory conditions. In the present study we aimed at investigating the stress response in greylag geese (*Anser anser*) in the field, confronting individuals with naturally occurring stressors. We measured beat-to-beat heart rate (HR) via fully implanted transmitters during three different experimental challenges: (1) catching and holding, (2) confrontation with a model predator, and (3) approach by different humans. We compared this to a control period and HR during agonistic encounters, a naturally occurring stressor. All three experimental situations evoked a HR increase. Highest HR responses were elicited by catching and holding the animals. In the third experiment, HR responses were greatest when the geese were approached by a human stranger (i.e., somebody the geese have never seen before). Hence, geese discriminated between different kinds of stressors and adjusted their physiological response depending on the type of stressor. Our results show that geese were able to discriminate between individual humans. In line with a number of lab studies, we suggest that particularly the controllability of certain situation determines the intensity of the HR response, also in a natural setting in the field.

Testing Cache Protection Tactics in Common Ravens, *Corvus corax*

Manuskript submitted

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Most food storing corvids possess observational spatial memory (OSM), allowing them to remember caches they have seen others make. This ability is part of a cognitive arms race between cachers and pilferers. Cachers reduce the transmission of visual information when making a cache or try to divide the attention of observers to several potential cache sites. However, the effectiveness of these tactics has never been tested. We investigated common ravens' reliance on OSM when pilfering caches of others during group foraging (study 1), and when pilfering caches made by a human experimenter. To distract the birds, we manipulated the number of caches (study 2) and the number and type of re-cachings (study 3). Our results indicate that the majority of pilfering in ravens was based on OSM. Increasing the number of caches did not affect their pilfer efficiency, and multiple re-caching and fake caching had only minor effects. This suggests that these tactics may be of limited importance for ravens under natural conditions. In contrast, caching out of view of others reliably resulted in efficient cache protection, supporting the idea that OSM exerts selection pressure on ravens' cognitive skills like for example perspective taking.

Influence of Conspecifics on the Performance of Carrion Crows in Operant Tasks

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Severe stress has detrimental effects on cognitive performance, whereas mild stress results in an even increased performance in cognitive tasks. Social stress is known as one of the most intense forms of stress. We tested carrion crows, an intelligent and social bird species, for the effect of the presence of conspecifics on their motivation and ability to concentrate when working on operant tasks. In a first experimental series, we were interested in their accuracy to peck a dot randomly appearing on a screen, depending on the social attitude towards a conspecific performing the same task in an adjacent cage. Tolerant dyads had good accuracy, whereas competitive dyads were strongly affected by the social presence, and sometimes even refused to participate. In a second series, we tested affiliate dyads in adjacent cages with a serial learning task and manipulated the start time of the participants. There was no evidence for a motivational effect of prior start, or the use of social learning when having the opportunity to observe. Crows were, however, significantly faster in learning the discrimination in a social situation compared to a solitary one. In total, our results suggest a strong influence of the presence and identity of conspecifics on cognitive performance of carrion crows, with a motivational effect of affiliative partners, and a discouraging one of competitive dyads.

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Braun, A., Bugnyar, T. & Kotrschal, K.: Observational spatial memory in cache pilfering by common ravens (*Corvus corax*); **poster**

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EG – Meeting

Braun, A., Kotrschal, K. & Bugnyar, T.: Ravens differentiate between edible and non-edible items when pilfering; **talk**

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ASAB Easter Meeting 2008

Braun, A., Kotrschal, K. & Bugnyar, T.: object caching in ravens; a by-product or a means of social play?; **talk**

18. – 20. July 2008, Dijon, France

4th European Conference on Behavioural Biology

Braun, A., Kotrschal, K. &. Bugnyar, T.: What is more attractive for ravens: to pilfer food or object caches?; **talk**

30. August – 6. September 2008, Obernai, France

The Tect-Incore summer school: "tools of the trade in cooperation research"

Braun, A, Wascher, C., Dufour, V. & Bugnyar, T.: Ravens performance in an exchange task; **talk**

19. – 24. August 2009, Rennes, France

31st International Ethological Conference

Braun, A & Bugnyar, T.: How to cope with others? Social dynamics in wild ravens, **poster**

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Behavioural Ecology and Self-organization group

Braun, A & Bugnyar, T.: Social dynamics in common ravens' non-breeder groups; **talk**

22. – 28. August 2010, Campos do Jordao, Brazil
25th International Ornithological Congress
Braun, A & Bugnyar, T.: Social complexity vs open group structure in wild ravens; **talk**

17. – 18. September 2010, Budapest, Hungary
Incore Conference "Cooperation: an Interdisciplinary Dialogue"
Braun A. & Bugnyar T.: Third-party interventions in wild ravens (*Corvus corax*); **poster**

25.11.2010, Vogelwarte Sempach, Switzerland
Braun, A., Bugnyar, T.: Sozialstruktur eines Nichtbrütertrupps von Kolkraben; **invited talk**

16.02. 2011, University of Neuchatel, Switzerland
Department of Eco-Ethology
Braun, A. Bugnyar, T.: Social bonding and rank acquisition in raven non-breeder flocks; **invited talk**

17. – 19. February 2011, Zürich, Switzerland
Ethoges Meeting "Cooperation and Conflict"
Braun, A. Bugnyar, T.: Rank acquisition through social bonds in ravens (*Corvus corax*); **talk**

09.05.2011, University of Vienna, Austria
Department of Cognitive Biology
Braun, A., Bugnyar, T.: Social dynamics in wild ravens; **talk**

29.01.2012, University of Groningen, Netherlands
Behavioural Ecology and Self-organization group
Braun, A., Bugnyar, T.: Social structure of a wild raven non-breeder aggregation; **talk**

Publications

Braun, A. (2008): Observational spatial memory in ravens (*Corvus corax*). *Ehto-News,* **59**; S. 36

Wascher, C.A.F., Scheiber, I.B.R., Braun, A. & Kotrschal, K. (2011): Heart rate responses to induced challenge situations in greylag geese (*Anser anser*). *Journal of Comparative Psychology,* **125**, 1, S. 116-119

Dufour, V., Wascher, C.A.F., Braun, A., Miller, R. & Bugnyar, T. (2011): Corvids can decide if a future exchange is worth waiting for. *Biology Letters*, **8**, 2, S. 201-204, doi: 10.1098/rsbl.2011.0726

Braun, A., Walsdorff, T., Fraser, O.N. & Bugnyar, T. (2012): Socialized sub-groups in a temporary stable raven flock? *Journal of Ornithology*, **153**, 1, S. 97-104, doi: 10.1007/s10336-011-0810-2

Braun, A. & Bugnyar, T. (2012): Social bonds and rank acquisition in raven nonbreeder aggregations. *Animal Behaviour*, **84**, 6, S. 1507-1515, doi: 10.1016/j.anbehav.2012.09.024

Braun, A. & Bugnyar, T. (submitted): Do carrion crows learn to discriminate pictures of unknown conspecifics on an individual basis? *Animal Cognition*

Braun, A., Kotrschal, K. & Bugnyar T. (submitted): Testing cache protection tactics in common ravens, *Corvus corax. Plos ONE*

Braun, A., Komdeur, J., van der Felde, M., Kingma, S. A. & Bugnyar, T. (in preparation): Kinship and association patterns of wild non-breeder ravens.

Rockenbach, C., Braun, A., Kotrschal, K. & Bugnyar, T. (in preparation): Influence of conspecifics on the performance of carrion crows in operant tasks.

Wong, S., Braun, A., Bugnyar, T. (in preparation): Ontogeny of play in common ravens, *Corvus corax*.

Braun, A., Kotrschal, K. & Bugnyar, T. (in preparation): Ravens remember the content of caches they observed during making.