



Relationship quality and gestural communication in Common Raven (*Corvus corax*) pairs

by

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"As species go, corvids will continue to evolve – mentally and physically – and amaze and challenge us well into the future." John Marzluff*

* in Marzluff, & Angell 2013

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Abstract

The quality of social relationships has already been assessed in various animal species, for example in primates, non-primate mammals and also in birds. These studies showed variations in relationship quality within and between animal groups which influenced the pattern, distribution and functions of many behaviours. However, they focused on relationships between members of social groups, while the quality of bonds in pair-living species has not been investigated. The present study aimed to add to this debate by investigating relationship quality in members of the corvid family, ravens (Corvus corax), which form long lasting pair bonds. The first research question concerned whether raven pairs differ in pair bond quality. Furthermore, ravens have been found to use highly sophisticated gestures which have been suggested as useful tools to test and/or strengthen an already existing bond. The second research question thus concerned whether relationship quality influences communicative exchange. Referring to the first question, differences in the frequencies and durations of specific social interactions allowed to group raven pairs into harmonic or inharmonic couples. These two groups were subsequently compared in their use of communicative signals. Nevertheless, this study was not able to reveal any significant effect of relationship quality on communicative exchange within raven pairs, except for two of 24 signal types where a significant effect was found on the duration per occurrence and on communicative success respectively. As the use of gestural signals in ravens has never been studied in much detail before, the present study is the first to provide systematic information about the relationship of strength of bond and gestural communication.

Die Qualität sozialer Beziehungen wurde bereits in verschiedenen Tierarten untersucht, so zum Beispiel in Primaten, anderen Säugetieren und in Vögeln. Diese Studien zeigten Variationen in der Qualität dieser Beziehungen auf, welche das Muster, die Verbreitung und die Funktionen verschiedener Verhaltensweisen beeinflussten. Dies traf sowohl auf Beziehungen innerhalb, wie auch zwischen Tiergruppen zu. Jedoch legten diese Studien den Fokus auf Beziehungen zwischen Mitgliedern sozialer Gruppen, während die Qualität der Bindungen von in Paaren lebenden Arten nicht untersucht wurde. Die vorliegende Studie soll diese Wissenslücke schließen, indem die Qualität der Paarbindung in einer dauerhaft monogam lebenden Rabenvogelart, dem Kolkraben (Corvus corax), untersucht wird. Darüber hinaus wurde festgestellt, dass Kolkraben in ihrer Kommunikation Gesten benutzen, die möglicherweise dazu dienen, eine bereits bestehende Paarbindung zu testen und/oder zu stärken. Auf diesem Fund basierend befasste sich die zweite Forschungsfrage damit, ob die Qualität der Paarbindung den kommunikativen Austausch innerhalb von Rabenpaaren beeinflusst. In Bezug auf die erste Forschungsfrage ermöglichten Unterschiede in den Frequenzen und Dauern spezifischer sozialer Interaktionen die Einteilung der Rabenpaare in harmonische oder unharmonische Einheiten. Diese zwei Gruppen wurden daraufhin in Bezug auf die Nutzung kommunikativer Signale verglichen. Nichtsdestotrotz konnte in der vorliegenden Studie kein signifikanter Effekt von der Qualität der Paarbindung auf den kommunikativen Austausch festgestellt werden. Eine Ausnahme stellten zwei von 24 untersuchten Signaltypen dar, wo ein signifikanter Effekt der Parabindungsqualität auf die Dauer pro Auftreten eines Signals bzw. auf den kommunikativen Erfolg gefunden wurde. Da die Nutzung von Gesten bei Raben noch nie zuvor im Detail untersucht worden ist, liefert die vorliegende Studie als erste systematische Informationen zur Beziehung zwischen der Stärke der Paarbindung und der gestischen Kommunikation.

1. Introduction

Animal social relationships

Various animal species live in social groups as group life brings about certain advantages to group members: Sociality increases food-finding ability as well as predator detection and enables communal activities such as mobbing dangers, learning from others and subdividing labor (Marzluff & Angell 2013). Social groups feature a social structure based on a network of relationships among the group members (Hinde 1984). According to Hinde, to describe this structure, the properties of the component relationships as well as their patterning have to be characterized. Such patterning can be for example linear or involving ramifying networks of varying density and extent. A relationship between two individuals ranges over an extended period of time and is based on a succession of interactions between those individuals. These interactions, in turn, are influenced by the history of past interactions (Hinde 1984). Hence, not only the content and quality of the component interactions are important for the characterization of a single relationship, but also their patterning in time, i.e. their absolute and relative frequencies, when they occur with respect to each other and how they affect each other (Hinde 1976; 1984). As relationships exist "between enemies as well as between friends, between those who are forced into each other's company as well as between those who seek it" (Hinde 1984, p.14), variation in relationship quality has been found to occur within and between diverse animal groups and has been suggested to account for the pattern, distribution and functions of many behaviours (Fraser & Bugnyar 2010). For example, Goodall (1967) identified the quality of relationships between individuals to influence spontaneous social behaviour in free-ranging chimpanzees (Pan troglodytes). Kutsukake (2006) observed vigilance level to increase in both male and female chimpanzees when a lessassociated group member was nearby. In the common raven (Corvus corax) Stöwe and colleagues (2006) discovered relationship quality to have an impact on novel object exploration as, for example, individuals joined siblings faster to approach novel objects than non-siblings. Numerous other studies have revealed further effects of relationship quality on the likelihood of aggressive conflict (in chimpanzees: Wittig & Boesch 2003), postconflict behaviour (in longtail macaques, Macaca fascicularis: Cords & Thurnheer 1993; in lemurs, Lemur catta and Eulemur fulvus rufus: Kappeler 1993), mother-infant interactions (in Japanese macaques, Macaca fuscata: Schino, D'Amato & Troisi 1995; in brown capuchin monkeys, Cebus apella: Weaver & de Waal 2002), reciprocity (in chimpanzees: Watts 2002; in coatis, Nasua nasua: Romero & Aureli 2008), tolerance to inequity (in chimpanzees: Brosnan, Schiff & de Waal 2005) and social learning (in guppies, *Poecilia reticulata*: Chapman, Ward & Krause 2008; in dogs, *Canis familiaris*: Pongrácz et al. 2008; in the common raven: Schwab et al. 2008). According to Cords and Aureli (2000), there are three particular qualities of social relationships: value, compatibility and security. Relationship value refers to the direct benefits gained as a result of the relationship, such as agonistic support or food sharing. Compatibility measures the level of tolerance and affiliation between the individuals and reflects the ease with which partners can interact, which is influenced by the temperament of the partner and the individuals' shared history of social exchanges. Security, however, indicates the perceived probability for a change in the relationship with the partner, which depends on the predictability and consistency of the partner's behaviour over time. All three qualities have already been confirmed by Fraser, Schino and Aureli (2008) in chimpanzee and by Fraser and Bugnyar (2010) in common raven social relationships.

Complex social systems and advanced cognition

The existence of variations in relationship quality inside large, stable social groups poses a challenge for all group members: Individuals have to recognize social partners and continuously track their position, social behaviour and foraging success. Beyond that, they have to classify them by age, sex, genetic relationship, reproductive status and dominance rank, and update this information as circumstances change (Cheney & Seyfarth 1990; Emery 2004). These intellectual demands are reflected in the large brains of primate species, an order being characterized by social system complexity (Whiten & Byrne 1988; Byrne & Whiten 1988). Dunbar (1998) integrated this observation in his "social brain hypothesis" which states that precisely the special kinds of intellectual problems provided by life in complex societies are responsible for an increased brain size in social species. Moreover, it implies that constraints on group size arise from the information-processing capacity of the primate brain, e.g. to remember who has a relationship with whom and to manipulate information about a set of relationships. The "social brain hypothesis" complements the "social intelligence hypothesis" by Humphrey (1976) which asserts that intelligence did not evolve to solve physical problems, but instead to process and use social information which could then be used for deception (Byrne & Whiten 1988). Humphrey's hypothesis has overtaken all the main alternative hypotheses (Emery 2004), such as the older "physical intelligence hypothesis" which supposes that intelligence, particularly human intelligence, is the result of intense selection for the use of tools and other manipulations of the environment (Fitch, Huber & Bugnyar 2010). Seed, Clayton and Emery (2008; p.1425) describe a complex social system as a "biological marketplace" of potentially cooperative and competitive relationships which affords advanced cognitive skills "in order to cooperate efficiently and in way that optimizes personal gain, namely only when necessary, and only with effective partners that will share the profits of cooperative action, and/or reciprocate cooperative assistance". Thus, to persist successfully in a complex social system, where the social environment is ever changing and largely unpredictable, a scope of mental defenses is needed, such as the capacity to recognize, remember, anticipate, analyze, and think strategically (Savage 2005). This is why social complexity is often considered a critical driving force in the evolution of high levels of social intelligence (Jolly 1966; Humphrey 1976; Byrne & Whiten 1988; Emery et al. 2007).

Convergent evolution in distant related species

In mammals, an expanded prefrontal cortex has been suggested to be special to the primates and the origin of their advanced cognitive abilities (Emery 2004). Birds do not have a neocortex, but certain areas of the forebrain have been suggested to represent functionally equivalent structures: the nidopallium and mesopallium (Emery 2004; Emery & Clayton 2004). Particularly these areas have been found to be significantly larger in corvids than in other birds (with the exception of some parrots; Rehkamper, Frahm & Zilles 1991; Reiner et al. 2004; Emery & Clayton 2004). The corvids, a family of passerine birds, include over 120 species of crows, ravens, rooks and jackdaws, as well as jays, magpies and nutcrackers (Clayton & Emery 2005). When standardized for their body size, they have the largest brains of any bird, the crow brain even being the same relative size as the chimpanzee brain (Emery & Clayton 2004). Moreover, when comparing the forebrain to brainstem ratio of corvids (Corvidae) and parrots (Psittaciformes) to other avian species, the pattern of difference closely resembles the difference of neocortex to brainstem ratio between the great apes and other primates and insectivores (Emery 2004; Emery & Clayton 2004).

Furthermore, in spite of being phylogenetically distant from the primates, the corvids show striking similarities in many aspects of their behaviour and cognition (Fraser & Bugnyar 2010). Indeed, they have been found to be capable of a whole host of cognitively demanding tasks which were previously considered to be the exclusive domain of apes and other primates. Some examples are cooperative problem solving (Seed, Clayton & Emery 2008), insight (Heinrich 1995), episodic-like memory (Clayton & Dickinson 1998), tactical deception (Heinrich 1999; Bugnyar & Kotrschal 2002) and tool-use (Jones & Kamil 1973; Hunt 1996). These comparable mental abilities are believed to have evolved through a process of divergent brain evolution with convergent mental evolution (Emery 2004; Emery &

Clayton 2004; Clayton & Emery 2005). Convergent evolution occurs when distantly related organisms respond to similar evolutionary pressures by the development of similar traits (Keeton & Gould 1986). In other words, birds and mammals evolved large and interconnected forebrains from different basic parts of our common reptilian ancestor's brain but similar selective pressures in their environment led to the evolution of comparable cognitive abilities. In fact, both primates and corvids face the same socioecological challenges, such as locating perishable food distributed in time and space or understanding the relationships between different individuals within large social groups (Emery 2004). An example for a corvid species facing such socioecological challenges is the common raven (Corvus corax), the largest member of the corvid family and the ecologically and geographically most widely distributed bird on the planet (Heinrich 2011). Common ravens live in a complex social system which consists of gregarious non-breeding individuals associating in flocks on the one and monogamous breeding pairs living in established territories on the other side (Heinrich et al. 1994). Sub-adult ravens typically join the non-breeder flock in their first three years when they are sexually immature and remain in these aggregations as adults, if they are not able to occupy a territory (Braun et al. 2012). Flock members form social relationships as well as pair bonds while they roost communally, share information and exploit food resources together (Heinrich 2011; Selva et al. 2011). Emery (2004) suggests that, to solve the environmental problems within large social groups, four cognitive tools are needed which have driven the evolution of complex cognition in both corvids and apes: causal reasoning, flexibility, imagination and prospection. In summary, living in a complex social and physical environment provides both challenges and opportunities which may have selected for large brains and complex cognition in both primates and corvids (Seed, Emery & Clayton 2009). According to Pika and Bugnyar (2011; p. 4), "examples of convergent evolution in distantrelated species will provide crucial clues to the types of problems that particular morphological or behavioural mechanisms were 'designed' to solve". In this regard, examples of convergent evolution may also be useful when it comes to unraveling the origin of language.

The mystery of language evolution

Social cognition is closely linked to the evolution of language as advanced mental abilities are needed in the course of language acquisition (Fitch 2000). On the one hand, this refers to the capacity for imitation for the signaling component and, on the other hand, to theory of mind, i.e. the ability to attribute mental states to oneself and to others (ToM; Corballis 2002;

Bradbury & Vehrencamp 2011). The latter is needed to deduce word meanings and communicate pragmatically (Clark 1987; Macnamara 1972). Human language can be defined as a bidirectional system which permits the expression of arbitrary thoughts as signals and the reverse interpretation of those signals as thoughts (Fitch, Huber & Bugnyar 2010). It is a system for representing and communicating complex conceptual structures, irrespective of modality (Fitch 2000) and, because of its complexity and creativity, a unique feature to our species (Corballis 2002). While all other forms of animal communication appear to be limited to a relatively small number of signals, restricted to limited contexts, human language seems to have no limit to the amount and sort of information it can convey (Corballis 2002). As there are no antecedents of language to be found elsewhere in the animal kingdom, the question arises how such a complex form of communication happened to evolve in the Homo sapiens. An answer to this question was already proposed in the eighteenth century by the philosopher Condillac who suggested that human language evolved from gestures (Condillac 2001). Gestures are a subset of communicative signals and can be defined as movements of the limbs or head and body that are directed towards a recipient, are goal-directed, mechanically ineffective and receive a voluntary response (Pika 2008). Support for Condillac's "gestural theory" derives from the reconstructions of vocal tracts of fossil remains which revealed that our primate ancestors lacked the anatomical structures needed for modern speech (Fitch 2000; Corballis 2002). Nevertheless, effective hunting of large mammals is thought to have been almost impossible for cooperative big-game hunters without the exchange of environmental information in order to coordinate hunting activities and teach these skills to the young (Hewes 1973). Thus, early hominids are suggested to have communicated using manual and facial gestures, possibly supported by grunts and cries which may later have developed into autonomous vocal language, embellished by gesture but not dependent on it (Corballis 2002). This suggestion is supported by human children using gestures for communication before their first spoken words (Arbib, Liebal & Pika 2008) and adult speakers accompanying all their speech with expressive manual gestures (cospeech gestures; McNeill 1992; 2005). The gestural theory of language evolution is opposed by theories which state that human speech evolved directly from nonhuman primate vocalizations (Fitch, Huber & Bugnyar 2010). In other words, the human line is supposed to have begun to produce and to imitate complex patterns of sound before there was any appearance of either gestural or vocal language (Andrew 1962; 1963). An example which is often cited in this context, are the alarm calls used by vervet monkeys. Both Diana monkeys (Cercopithecus diana) and Campbell's monkeys (Cercopithecus campbelli) utter distinct alarm calls in association with different predators which lead to different escape responses in receivers (Cheney & Seyfarth 1990; Zuberbühler 1999; 2001). As these signals have a distinct acoustic structure, are produced in response to a particular external object or event and elicit a response in nearby listeners similar to that which the external object or event normally elicits, they qualify as referential signals (Zuberbühler 2000). This, in turn, is a requirement of language (Corballis 2002). However, there is currently no evidence that any species of ape uses such specific alarm calls or any other vocalizations that appear to be referential (Cheney & Wrangham 1987). Thus, it is highly unlikely that vervet monkey alarm calls could be the direct precursor of human language (Pika et al. 2005). Furthermore, it is often claimed that transmission of tool-making and tool-using techniques would have had to be based on speech (Hewes 1973). Hewes objects this view by pointing out that the handling down of tool traditions might also have depended not on speech but on visual observation, i.e. gestural imitation. Nevertheless, he adds that full development of spoken language might have facilitated the learning and diffusion of new techniques. Corballis (2002) admits that vocalization must have played a prominent role in language for otherwise the biological adaptations necessary to produce articulate sound would scarcely have evolved. Hence, the topic is still under debate. To finally solve the mystery of language evolution, scientists have focused on comparative research, by studying similarities and differences to human mechanisms in our closest living relatives, the great apes.

Communication in nonhuman primates

The use of vocalizations as well as gestures for communicative purposes is common across primate species, both in captivity and in the wild (Arbib, Liebal & Pika 2008; Goodall 1986; Tomasello et al. 1994; 1997). However, there are several crucial differences between gestural and vocal signaling in primates. First of all, primate vocalizations are largely emotional and usually triggered by internal or external stimuli (Hewes 1973). As opposed to gestures, they do not seem to underlie close voluntary control or inhibition (Hewes 1973; Corballis 2002) and are usually broadcast instead of being directed to a specific recipient (Hewes 1973). Furthermore, primates cannot learn to produce new sounds outside their ordinary species-specific repertoire and pair them with meanings, as is the case in humans (Snowdon 1990; Janik & Slater 1997). This, in turn, does not apply to primate gestures: primate gestural repertoires are open to incorporation of new gestures at both an individual and a population level (Arbib, Liebel & Pika 2008). Apes were found to create new gestures routinely (Pika et al. 2005) as well as to learn new gestures, pair them dependably with meanings and use them

communicatively (Fitch 2000; Arbib, Liebal & Pika 2008). Moreover, gestural repertoires of primates, especially those of great apes, are characterized by a high degree of individual variability, not only regarding age classes - as might also be the case for vocalizations - but also between groups or populations (Pika et al. 2005). Beyond that, primates have been found to use gestures flexibly for multiple communicative ends and in multiple contexts - typically those with a clear social component - with the use depending on the behaviour of the recipient (Pika et al. 2005; Arbib, Liebal & Pika 2008). In contrast, primate vocalizations are usually expressed in evolutionarily urgent situations (e.g. avoiding predators, defending against aggressors, traveling as a group, discovering food) which is suggested by Pika and colleagues (2005) as the reason for their low flexibility of use. Interestingly, primate gestures have been found to be used mainly for imperative purposes in dyadic (Pika et al. 2005; Pika 2008) but seldom in triadic interactions (Corballis 2002; Pika et al. 2005). Dyadic interactions involve two individuals and the gesture is applied to attract the attention of "the other" to oneself, usually in a way that invites reciprocation (Pika 2008). Two examples for chimpanzee dyadic gestures are "slapping the ground" in front of the recipient to attract the recipient's attention and "poking" at the desired partner in order to initiate play (Tomasello, Gust & Frost 1989). Triadic gestures, in turn, involve a third object and are used to attract the attention of others to this entity (Pika 2008). They are therefore referential (Corballis 2002, Pika 2008) and require advanced cognitive capacities, as the recipient must deduce the signaler's intended meaning (Pika 2008). There are few data on the use of referential gestures in primates and most of the existing literature concerns "pointing" gestures of captive chimpanzees when interacting with humans (Leavens, Hopkins & Thomas 2004). The almost invariable use of gestures in dyadic contexts as well as their almost exclusive use for imperative purposes are considered by Pika and colleagues (2005) as making primate gestures crucially different from human gestures. Contrarily to humans, primates do not use their gestures symbolically, i.e. in intersubjective acts of reference, which would be functionally very similar to language (Pika et al. 2005). To sum up, "neither the vocalizations nor the gestures of nonhuman primates show any clear evidence of an incipient path of evolutionary modification which may have turned these signals into language" (comment by D. Maestripieri in Arbib, Liebal & Pika 2008, p. 1066). Maybe, as stated by Lovejoy (2009), to reconstruct the evolution of human language the likely adaptations of early hominins have to be viewed generally, rather than with specific reference to living chimpanzees only. This statement is supported by Bond, Kamil and Balda (2003) who stress that some of the factors leading to the evolution of human intelligence must be general, having effects on the cognitive abilities and organization of other vertebrate species, too. This is the point where the common raven enters into the picture.

Common raven communication

The common raven is described by Heinrich (1999) as being very expressive: Raven individuals communicate by a combination of voice, patterns of feather erection and body posture. Concerning raven vocalizations, little is known as the vocal repertoire is very large and complex (Gwinner 1964). Besides, raven calls are highly variable and specific call types can be replaced by imitated environmental sounds (Gwinner 1964; Heinrich 1999). Another difficulty in studying raven calls concerns the flexibility of their use: although most calls are assigned to specific situations, they can also be used in other contexts (Gwinner 1964). According to Heinrich (1999), raven calls have one basic message, which is to draw attention to the calling individual. Beyond that, they indicate functions with increasing specificity coming from context. As these characteristics do not fulfill the criteria for referential signals (see Zuberbühler 2000), raven calls seem not to be used as language. However, Bugnyar, Kijne and Kotrschal (2001) found a possible exception in the common raven vocal repertoire: They observed ravens to respond to the sight of food with one type of long yell, the so-called "haa" call which varied with the type but not with the amount of food and decreased during feeding. In general, "haa" calls were reliably associated with the discovery of food and thus may be used as functionally referential signals, transmitting information on the occurrence of food that is difficult to reach. Furthermore, referential vocalizations may be applied in raven recruiting behaviour (Fitch, Huber & Bugnyar 2010). Common ravens are not only foraging generalists but also carcass specialists, carcasses being a rich and highly ephemeral food source (Heinrich 2011). However, they are difficult to locate and often defended by predators or dominant conspecifics (Fitch, Huber & Bugnyar 2010). Thus, it pays a vagrant, nonbreeding individual to team up with other solitary conspecifics in order to overcome this defense (Heinrich 1988; Marzluff & Heinrich 1991). Such teaming up in ravens is called recruitment and can either occur by using nocturnal roosts as information centers (Marzluff, Heinrich & Marzluff 1996; Wright, Stone & Brown 2003) or attracting others to the carcass via food calls (Heinrich & Marzluff 1991; Bugnyar, Kijne & Kotrschal 2001). The timing and location of food calling appears to provide functionally referential information to receivers (Fitch, Huber & Bugnyar 2010). Bickerton (2010) suggests that it may actually be the scavenging lifestyle which encourages the evolution of referential communication.

Considering the similar lifestyle of human ancestors, who might also have depended on information transfer about large carcasses in order to exploit them cooperatively, he suggests ravens to represent a convergent case, where recruitment selected for socio-cognitive and communicative abilities. However, Bickerton's hypothesis has yet to be tested scientifically (Fitch, Huber & Bugnar 2010).

Apart from vocalizations, body language is described by Heinrich (1999) as being also extremely important to ravens. In his book "Mind of the raven" he depicts several postures of dominant and subordinant birds. A detailed description of raven non-vocal communication is given by Gwinner (1964) who stresses the plasticity and flexibility of raven gestures and compares them with gestural signals in other bird species. However, only few studies concerned with non-vocal communication in birds and even fewer studies dealt with nonvocal signaling in ravens, so that virtually nothing is known about gestures in birds (Pika & Bugnyar 2011). Quite recently Pika and Bugnyar (2011) found the use of declarative gestures not to be restricted to the primate lineage when they observed wild ravens to use dyadic and even triadic gestural signals for communicative purposes. In fact, this is another aspect which adds to the growing evidence that ravens are in many cognitive domains comparable to primates and offers a different starting point to the study of language origins (Bugnyar & Kotrschal 2004). Raven triadic gestures are distinct object-oriented behaviours, showing and offering, which are directed mainly to already attending recipients of the opposite sex (Pika & Bugnyar 2011). Pika and Bugnyar suggest that these gestures function as "test signals" to evaluate the interest of a potential partner and/or to test and strengthen an already existing bond. As a monogamous bird, the common raven forms long-term partnerships which typically last a life-time (Heinrich 1999). Thus, ravens invest relatively long time periods to find and choose the right partner (Gwinner 1964; Heinrich 1999). In the course of pair formation, both individuals demonstrate their willingness to cooperate by allo-preening and offering food as well as support during agonistic encounters to their chosen partner (de Kort, Emery & Clayton 2003; 2006; von Bayern et al. 2005; Emery et al. 2007). This is important, as ravens, like humans, rely heavily on cooperation between pair-partners which is advantageous in capturing food and/or taking it from powerful opponents (Heinrich 1999), coordinating reproduction and nestling care as well as in defending the territory against conspecifics (Bradbury & Vehrencamp 2011; Selva et al. 2011). Such cooperation requires successful communication between the partners and learned responsiveness to partner signals (Bradbury & Vehrencamp 2011). This leads to the question if the use of such specific gestures and gestures in general depends on the strength of the pair bond or rather the quality of the

relationship between pair partners. According to Pika and Bugnyar (2011), it may have been the motives to form and maintain affiliative relationships which have been crucial in boosting not only the cognitive but also the vocal and non-vocal communicative abilities in ravens.

Aims and hypotheses

As already mentioned in the first section, Fraser & Bugnyar (2010) found raven social relationships to vary in value. These variations manifested themselves in differences in the frequency of affiliative and agonistic social interactions between the individuals. However, this study focused on relationships within non-breeder groups of ravens while the quality of bond in monogamous pairs was not investigated. Interestingly, both Heinrich (1999) and Lorenz (1935) observed raven pairs to form partnerships "of convenience" which were quickly dissolved when a better matching partner was found. Moreover, extra-pair copulations in wild ravens have been reported (Heinrich 1999). These observations permit the assumption that raven pair bonds differ in their quality, too.

A valuable relationship was classified by van Schaik and Aureli (2000) as one where the individuals spend more time in close proximity and show more affiliative behaviour (e.g. grooming/allo-preening) towards each other. Moreover, lower rates of agonistic conflict should be observed (e.g. aggression and submission) but more agonistic support against a third party. Following this classification, the aim of this study will be

- to use the most common affiliative and agonistic interactions between pair-partners as well as proximity patterns for assessment of relationship quality in raven pairs and
- (2) to analyze the influence of relationship quality on communicative exchange between pair-partners with a special focus on gestural communication.

In this context, I will test the hypothesis that raven pairs differ in pair bond quality according to their social interactions. This hypothesis derives from the prediction that differences in social behaviour between pairs, i.e. varying frequencies of communicative signals used in affiliative (allo-preening, contact sitting etc.) and agonistic (fighting, pecking etc.) context will lead to the extraction of specific relationship quality components. These, in turn, will allow to group raven pairs in two different categories: harmonic pairs with a high quality relationship and inharmonic pairs with a low quality relationship.

The second hypothesis is that pair bond quality has a significant influence on communicative exchange in raven pairs. If this hypothesis is true, then I predict the frequencies of

communicative signals in general or at least those of specific communicative signals to differ between harmonic and inharmonic raven pairs.

Concerning differences in the general use of gestures, harmonic pairs may use on average a larger diversity of gestural signals as well as a larger number of gestural signals in different signal categories than inharmonic pairs. Furthermore, they may show a higher flexibility in gesture use by adjusting their gestures to the attentional state of the recipient as well as higher communicative success than inharmonic pairs. Therefore, inharmonic pairs may show a higher escalation level concerning gestures used in an agonistic context than harmonic pairs.

Referring to the specific use of gestures, specific signal types may be used more often by harmonic than by inharmonic pairs or vice versa. This may apply to the signal's general use and/or to its use in different contexts. In addition, harmonic pairs may be more successful in attaining a signal type's communicative goal than inharmonic pairs.

Because of the lack of studies investigating the use of gestures in birds, both hypotheses will be tested using methods established in primate research.

This study will be the first to provide systematic information about the relationship of pair bond quality and exchange of social interactions in raven pairs. Possible differences in relationship quality shall be exposed by using a wide range of behaviours, an approach which has already been suggested by Fraser and Bugnyar (2010) for future studies on this topic. These differences may help to explain behavioural data in general as, according to Fraser and Bugnyar (2010; p. 927), "understanding the nature and variability in social relationships is a critical factor in our understanding of how animals behave." Last but not least, the results gathered in this study shall add to the "little knowledge we have of raven relationships" (Fraser & Bugnyar 2010: p. 927).

2. Materials and Methods

2.1. Study Subjects and Housing

Social interactions were observed in nine common raven (*Corvus corax*) pairs in captivity. Seven pairs were kept in zoological gardens at various locations in Germany and Austria while two pairs were housed at the Max-Planck-Institute for Ornithology in Seewiesen (Bavaria). All individuals except two females were adult birds. Ten individuals were raised by raven couples in captivity, while four individuals were handreared. Another individual was of wild origin and in three cases no information could be obtained concerning the rearing. A detailed list of all the subjects studied including some life-history parameters (e.g. reproductive success, relationship tenure, etc.) is supplied in the annex (Annex: Table 1). Those seven raven pairs that were kept in zoological gardens were well habituated to people. For the other two pairs a few days of habituation to the observer were added to the observation schedule, to enable the collection of their natural behaviour.

All raven pairs were kept in aviaries containing trees, branches, stones, tree trunks and shallow pools for bathing. As ravens are omnivorous birds (Seed, Emery & Clayton 2009), all individuals were fed once a day with a mixed diet of meat, vegetables, fruits, vitamins, eggs, carbohydrates (e.g. rice or noodles) and milk products. They could obtain water from the bathing pools which were filled with fresh water every day.

Most birds were marked with coloured leg-rings for individual identification. Because males are usually larger than their female counterparts (Gwinner 1964; Engisst-Dueblin & Pfister 2002), body size was consulted in distinguishing the sexes when there were no leg-rings (Haag, Munich). However, as this is not a reliable distinctive feature (Gwinner 1964), the shape of the beak was used as an additional criterion: females have a finer beak than males (Enggist-Dueblin & Pfister 2002). Furthermore, females feature shorter crest feathers with a less metallic glaze as well as shorter head and flank feathers (Gwinner 1964).

2.2. Data Collection

Data were collected from the end of June 2013 to the end of October 2013, with each raven pair being observed for seven to nine consecutive days, depending on the weather conditions. On rainy days observational sessions were postponed to avoid a bias in the data set, as rain is known to reduce raven activity (Haffer et al. 1993). For the observation of each raven pair two different sampling techniques following Martin and Bateson (2007) were adopted:

2.2.1. Focal Animal Sampling

This sampling form was applied to obtain frequencies as well as durations for all social interactions between the pair partners. It was used in six sessions per day, each with a duration of 3 x 5 min, seven days in row, with continuous sampling as recording rule (see Martin & Bateson 2007). In these sessions the individuals were filmed with a HD-camera (Canon Legeria HFM40 HD-Camcorder) from outside the aviary, the focus changing from session to session between male and female.

Four sampling sessions were spaced around feeding time in the morning while two sessions were carried out in the afternoon without a feeding background. Referring to the morning sessions, at least one session was recorded one hour before feeding time. Another session took place just after the zookeeper left the aviary after cleaning and providing food for the raven pair. A third session was recorded one hour after feeding time. The last morning session was either placed two hours before feeding time or two hours after feeding time, depending on the feeding schedule at each sampling location. It was taken care that the last morning session was recorded not later than 12 a.m. to avoid a bias through reduced activity resulting from summer heat in the midday hours. The afternoon sessions always took place at 4 and 5 p.m. Unfortunately it was not possible to get feeding time recordings for all raven pairs as not all institutions fed their ravens before noon. Thus, to avoid a bias, all feeding time recordings were finally excluded from the data set.

During each session, all occurrences of social interactions between the pair partners were recorded. If the focus animal became out of sight, the respective time span was subtracted from the total recording time which was then elongated for the period the out-of-sight-situation prevailed. This was also the case if the non-focal individual became out of sight in a distance of 0 - 1 m to the focal animal, thus making it impossible to determine its behaviour in close proximity to the focal animal.

2.2.2. Scan Sampling

In order to obtain proximity patterns for each raven pair, additional scan samplings were carried out directly before and after the focal sampling sessions, a total of 12 scans per day. Each scan had a duration of 5 min and the distance between the pair partners was determined with instantaneous sampling as recording rule, i.e. it was estimated at every full minute, using the proximity parameters described in 2.4.2.

2.3. Data Processing

Focal sampling resulted in over 90 hours of observational samples which were then used to prepare a behavioural protocol for each raven pair using Microsoft® Office Excel© 2007. For this purpose a coding scheme was applied, which assigned individual code numbers to each defined behaviour and had been designed based on a coding scheme for gestures used in primate research. When viewing the samples, all occurrences of social interactions between the pair partners were listed in an Excel worksheet, these data set entries being complemented by date, recording time and feeding condition (either before feeding, at feeding time or after feeding) as well as code numbers for the following variables:

- signaler + recipient
- start time
- end time (only for states)
- duration (only for states)
- communicative bout
- attentional state of both signaler and recipient
- mechanical ineffectiveness
- response voluntariness

- category of signal
- type of vocalization (if applicable)
- body posture of both signaler and recipient
- feather posture of both signaler and recipient
- response behaviour of recipient
- context
- escalation level (if applicable)

For detailed variable definitions see 2.4.2.

Following the classification by Martin & Bateson (2007), two fundamental types of behaviour pattern were distinguished: events and states. Events are defined as behaviour patterns of relatively short duration (here: less than one second), such as discrete body movements or vocalizations. States, however, are behaviour patterns of relatively long duration, such as prolonged activities, body postures or proximity patterns. In the case of events, the behaviour per hour, in each raven pair. States were recorded as sequences of action, i.e. an action was counted as one state even if it was interrupted by short breaks, unless these breaks were shorter than 5 ± 1 sec. Only when there was a time lapse of more than 6 seconds or a different behaviour occurred in between, a new state was registered. For states, the frequency per hour as well as the duration per occurrence (in seconds) were calculated.

Scan sampling records were transferred to another Excel-file where the proportion of time spent in specific distances to each other (see 2.4.2.: partner proximity) was calculated for each studied pair.

Before subjecting the frequencies per hour and durations per occurrence to statistical analysis in order to test for differences in the use of specific communicative signals between harmonic and inharmonic pairs, their values were used to calculate the mean and standard deviation for each signal type in each group. This was done for the frequency per hour and duration per occurrence in an affiliative and agonistic context separately as well as for both contexts together (total frequency per hour and total duration per occurrence). A specific communicative signal was only analyzed if it occurred at least three times in at least one harmonic and one inharmonic pair.

Additionally, response behaviour was investigated to define a communicative goal for each signal which could then be used to compare communicative success between the two groups. For this purpose, behavioural responses towards a certain signal were calculated into percentages of all responses. If a specific response behaviour accounted for at least 30% of all responses, this particular response was defined as the signal's communicative goal. Consequently, communicative exchanges yielding this response were defined as communicatively successful interactions. To compare communicative success between harmonic and inharmonic raven pairs for a certain signal, the percentages of communicatively successful interactions were tested between the two groups using non-parametric tests. When the total of a specific signal scored around 100 observations, response behaviour was analyzed in the two context categories separately, too.

Communicatively successful interactions were additionally used to assess the overall communicative success in raven pairs. This was done for each raven pair by calculating the average number of gestures used within a communicative bout before a signal type's communicative goal was achieved. This analysis included all signal types where a communicative goal had been determined before.

Furthermore, display behaviour (bowing display, head up display, shrug display, bent up display and rattle beak) was tested for differences in responses concerning the occurrence of the same display, another display form, another behavioural response, no obvious response or the occurrence of an arbitrary display (equals same display + another display form as response). This was done to assess if harmonic pairs perform display behaviour more often conjointly than inharmonic pairs. For this purpose, the frequencies of responses in these four categories were tested for differences between the two groups using non-parametric tests.

2.4. Definitions

2.4.1. Raven Social Interactions

Definitions for social interactions are based upon those of Gwinner (1964). However, as not all observed behaviours were included in Gwinner's work, the ethogram was complemented by own descriptions of raven behaviour.

Allopreening: Individual touches another individual's feathers with its beak for more than 2 seconds or handles another individual's feathers in its beak (state).

> Figure 1: Allopreening (Haffer et al. 1993).

Approach:Individual approximates another individual, resulting in both
individuals residing in reaching distance to each other (event).

Begging: Individual crouches and flaps the wings while its beak is opened widely towards another individual, often uttering begging calls (state).

Bent up display: Individual leans into almost horizontal body posture and back again, moving its head slowly upwards when moving up, simultaneously vocalizing.

Billing:Subtle beak contact between individuals which may be
accompanied by food transfer from beak to beak (state).

Bowing display: Individual bends into almost horizontal body posture while the wing bows are strut apart and the tail is fanned. In most cases short vocalizations are uttered, accompanied by choking movements of the head. Individual then bends upwards again and may repeat this behaviour several times (state). Alternatively to bending the whole body, only the head may be moved downwards and/or the intertarsal joints may be bent. **Figure 2:** Bowing display (Haffer et al. 1993).

Chase away: Individual approaches another individual and forces it to leave (event).

Chase flight: Individual pursues another individual in flight (state).

Contact sit: Individuals reside in close distance to each other with the possibility to enable body contact (state).

Crude billing: Similar to billing, but individual contacts another individual's beak roughly in this case (state).

Displacement: Individual approaches another individual and the latter retreats within 3 seconds (event).

Feeding: Individual approaches another individual with feeding sounds, often accompanied by wing twitching, and passes food into the recipient's open throat. The recipient 'gauzes', whimpers and takes the food with the beak turned 90° in the axis against the other individual's beak (event).



Following: Individual flies/goes in the same direction as another individual, max. 3 seconds after the latter has left with both birds successively arriving in the same area (= within a distance of 1 to 2 m; event).

Grab: Individual seizes another individual's body part in its beak for less than 2 seconds (event).

Head up display: Individual holds up its head while stretching its neck, with fluffed head and/or lanceolate throat feathers, strutting apart the wing bows

and uttering various kinds of vocalizations (state). Additionally the tail may be fanned.

- Hold: Individual lays its foot on another individual's body part, in most cases its foot or back (event).
- Hold beak: Individual takes another individual's beak into its own beak or pushes its beak into another individual's beak. Both individuals stay motionless with their beaks locked for at least 2 seconds (state).
- Kick: Individual contacts another individual's body with its foot (tactile version) or lifts its foot in another individual's direction (visual version; event).
- Open beak: Individual faces another individual with its beak unclosed, possibly with snap intention (state).
- Open up beak: Individual tries to push its beak into another individual's closed beak or tries to unfasten another individual's beak with its own beak (event).

Peck: Individual strikes another individual with its beak (event).

- Poke: Individual pushes its beak in another individual's plumage for less than 2 seconds (event).
- Present: Individual exposes body part to another individual, often accompanied by pulling the nicitans slowly over the eyes (state).
- Pull: Individual draws a body part of another individual in its own direction (event).

Push: Individual uses its beak or head to move a body part of another individual in the desired direction (event).

Raise beak: Individual heaves its beak, resulting in an angle of 90 - 135° between head and neck, depending on intensity (event).

Figure 4: Raise beak (Haffer et al. 1993).



- Rattle beak: Individual stands erect and clatters beak slowly, non-rhythmically, while the crest feathers are fluffed. The wings might be braced and variable forms of snapping may occur (state).
- Scrounging: Individual pinches/steals an object which is in possession of another individual (event).
- Sharing: Individuals feed/manipulate simultaneously on the same object (event).
- Shrug display:Individual moves its head slightly down and its wing bows slightly
up simultaneously, while uttering short vocalizations (state).

Small thin posture: Individual attaches its plumage very tightly to the body, pulls its head in between the shoulders and bends the intertarsal joints (state).



Figure 5: Small thin posture (Haffer et al. 1993).

Snap:	Individual claps its beak fast towards another individual (event).
Ctore docum	
Stare down:	Individual lowers its head, often jerkily, and stays for more than two
	seconds with its beak pointed towards the ground (state).
Thick head:	Individual fluffs its head and throat feathers maximally (state).





Tilt head:Individual resides next to another individual and bends its head
sideways (state).Touch:Individual contacts another individual's body with its beak for less
than 2 seconds (event).

Transfer: Individual passes an item to another individual or lets another individual take it (event).

2.4.2. Variable Definitions

The following variables were used to describe occurrences of social interactions between pairpartners in detail when a behavioural protocol was prepared for each raven pair.

Attentional state:Depending on the partner's position within the visual field, three
attentional states were distinguished: (1) "attending", i.e. oriented
directly towards the partner (partner at an angle of 0° within the
visual field), (2) "sideways", i.e. partner within an angle of 160°
towards either of the two body sides within the visual field, and (3)
"not attending", i.e. partner within an angle of more than 160°
towards either body side within the visual field. A behaviour was
directed to the other individual if the signaler was either attending or
sideways to the recipient.



Body posture: It was chosen between seven body postures for each individual: "normal" (sitting or standing in horizontal posture, wing bows tight), "relaxed" (sitting or standing in horizontal posture, wing bows lowered slightly), "agitated" (standing in horizontal posture, with elongated throat, eyes wide open, rapid movements), "straightened up" (sitting or standing in horizontal posture, head held up, throat stretched), "bend forward" (head held low while tail directed upwards), "u-posture" (tail directed upwards; neck, back and tail form a U-shaped curve) and "crouching" (sitting with head drawn in between the shoulders).

- Category of signal: Four signal categories were defined, depending on the perceptual system to receive them: (1) tactile signals included physical contact with the recipient, (2) visual signals generated a mainly visual component with no physical contact, (3) tactile and auditory signals where physical contact was combined with a vocalization and (4) visual and auditory signals where the visual component was accompanied by a vocalization.
- Communicative bout: One communicative bout equals a communicative exchange between two individuals with no more than 5 ± 1 sec. separating the consecutive signals. Motor activity as approaching or following are not counted as parts of a communicative bout.
- Context: A context category was assigned to each communicative bout, choosing between an affiliative and an agonistic context. A communicative bout was defined as having an agonistic context if the recipient showed an agitated body posture as response towards a signal and/or if it immediately retreated or if the interaction involved chasing and/or physical hitting by at least one individual. If none of these behaviours was observed, the context was determined as affiliative. Moreover, only for agonistic contexts the assignment of an escalation level was possible, as it depended on the behaviours described above. If a communicative bout could neither be defined as affiliative, nor as agonistic, it was registered as undecided.
- Escalation level: An escalation level was assigned to agonistic interactions only and depended mainly on the recipient's response: if the recipient retreated immediately, the escalation level was defined as low, if it showed an agonistic visual response it was defined as moderate and if the sequence involved agonistic physical body contact between the individuals, it was defined as high.

Feather posture: Feather posture was classified either as feathers tight, loosely, partly fluffed or full fluffed. If feathers were partly fluffed, it was added which parts were concerned, for example head and throat feathers or throat and leg feathers.

MechanicalA signal was defined as mechanically ineffective if it was notineffectiveness:performed to act as direct physical agent but the recipient carried outmore than 50% of an action towards the signaler's intended goal.

- Partner proximity: The distance between the pair partners was assessed according to four categories: "close proximity", i.e. less than 0.5 m apart (= contact sitting), "close to moderate proximity", i.e. 0.5 1 m apart, "moderate to low proximity", i.e. 1 m 3 m apart or "low proximity", i.e. the individuals more than 3 m apart from each other.
- Response behaviour: For every social interaction the immediate reaction of the recipient was determined. A behavioural response was registered if the recipient either began an action, stopped an action, continued a previous behaviour or avoided the signaler i.e. backed away. For a beginning, stopped or continued behaviour, the exact action was defined, too. If there was no behavioural response, an attentional state change from orientated toward to orientated away and vice versa as well as a vocal response could be determined as further responses. When neither a behavioural, nor an attentional nor a vocal response occurred, "no obvious response" was assigned to the interaction.

ResponseThe recipient has the choice of reacting or not reacting towards thevoluntariness:signaler's action.

The entries for the attentional state of the signaler as well as for mechanical ineffectiveness and response voluntariness served to discern gestural from non-gestural signals.

Vocalization types, body postures and feather postures were used to distinguish different display behaviours within and between raven pairs. Moreover, body as well as feather postures were eventually consulted when the definition of contexts proved difficult.

2.5. Statistical Analysis

Before being subjected to further analysis, all behavioural variables were plotted in Microsoft® Office Excel© and the mean values as well as standard deviations were calculated in order to get an overview of the data set. Moreover, all variables were tested for normal distribution by using the Kolomogorov-Smirnov-Test. An alpha level of 0.05 was adopted for all tests. All analyses were carried out in IBM® SPSS® Statistics version 21.0.0.0.

2.5.1. Principal Component Analysis (PCA)

A principal component analysis (PCA) was used in order to obtain composite measured of relationship quality, following the approaches by Fraser, Schino and Aureli (2008) in chimpanzee as well as Fraser and Bugnyar (2010) in common raven groups. The PCA is a statistical technique used to identify underlying factors which explain the pattern of correlations within sets of variables (Tabachnik & Fidell 2007). In other words, it identifies the combinations of variables which explain the greatest amount of variation in a multivariate data set. It is especially useful for large data sets as it reduces the large number of independent variables to a few behavioural dimensions which account for a large proportion of the variance and covariance of the original variables (Fraser, Schino & Aureli 2008; Martin & Bateson 2007). These behavioural dimensions, or principal components (PC), are linear combinations of the original variables. The first PC explains the largest amount of information, the second PC explains the second largest, while being as different as possible from the first PC, and so on (Martin & Bateson 2007). The aim is to find as few components as possible which explain as much variance in the data set as possible (Fraser, Schino & Aureli 2008). The behavioural variables chosen for the PCA analysis were the frequencies per hour and durations per occurrence of the most common non-gestural social interactions as well as the scan sampling proximity measures (see 2.4.2.). Furthermore, only those social interaction were used which occurred at least three times in at least three different raven pairs (Table 1). Data were analyzed at the dyadic level, i.e. the variables comprised the total values for both male and female.

The PCA provides coefficients of correlation between each behavioural variable and each extracted component and relative scores for each dyad for each component. A minimum eigenvalue of 1.0 was used to determine the number of components extracted from the PCA. Moreover, a varimax rotation was applied to simplify the interpretation of the components which is an orthogonal rotation method minimizing the number of variables that have high

loadings on each component (Tabachnik & Fidell 2007). Coefficients of correlation greater than 0.5 or less than -0.5 were considered to be such high loadings.

Variable name	Variable description
Allo-preening	Frequency per hour observation time + average duration per occurrence
Approach	Frequency per hour observation time
Billing	Frequency per hour observation time + average duration per occurrence
Contact sit	Frequency per hour observation time + average duration per occurrence
Following	Frequency per hour observation time
Affiliative Behaviours	Frequency per hour observation time
Chasing away	Frequency per hour observation time
Displacement	Frequency per hour observation time
Agonistic Behaviours	Frequency per hour observation time
Close proximity	Percentage of observation time
Close to moderate proximity	Percentage of observation time
Moderate to low proximity	Percentage of observation time
Low proximity	Percentage of observation time

Table 1: Variables entered into the PCA.

According to Fraser, Schino and Aureli (2008), application of the PCA method allows to investigate relationship quality in more detail rather than focusing on relationships as a whole, by using individual behavioural variables or relying on broad demographic categories (e.g. age, sex combination). Being based on multiple behavioural variables, it allows the full degree of variation in relationship quality to be quantified. Furthermore, components of relationship quality are identified in a non-subjective manner, reflecting more closely the animal's perspective and the complex patterning of their multiple social interactions (Fraser, Schino & Aureli 2008). As outlined by Fraser, Schino and Aureli (2008; p. 839), "by providing composite, quantitative measures for each component, this method [the PCA] represents a significant improvement for the study of adult–adult social relationships".

2.5.2. Multivariate Analysis of Variance (MANOVA)

The extracted principal components were subsequently tested for influences of life-history traits (e.g. relationship tenure, age difference) on relationship quality using a multivariate analysis of variance (MANOVA). This is an extension of the univariate analysis of variance (ANOVA) which performs an analysis of variance on more than one dependent variable and explicitly takes into account the correlations between the dependent variables (Gray & Kinnear 2012). The multivariate test helps to decide whether a difference between groups is caused by different relationships among the dependent variables, or just one underlying factor (Martin & Bateson 2007). For each life-history trait a separate MANOVA was conducted, the

trait representing the independent variable while the scores obtained for each dyad for each of the components extracted from the PCA served as dependent variables.

2.5.3. Two-factor Mixed Factorial ANOVA and Non-parametric Tests

In order to test for differences between the two groups, harmonic and inharmonic, in a first step the overall group effect on a behavioural variable was analyzed, using a two-factor mixed factorial ANOVA. This method exposes within-subject effects of a specific variable (e.g. context, category of signal) as well as between-subject effects of a grouping variable (here: harmonic vs. inharmonic) on the data set (Gray & Kinnear 2012). As only differences between groups were important for this study, the between-subject effect results were considered only.

In a second step, non-parametric tests (here: Mann-Whitney-U-Tests) were applied for posthoc comparisons. These tests consider weather particular scores are higher or lower than other scores and are better suited to working with small data sets (n < 10) than parametric tests (Martin & Bateson 2007).

Exact F-, U- and p-values are given in the text and added in the diagrams when significant. In tables, significant values are highlighted using bold font. P-values being smaller than 0.001 are listed as < 0.001.

3. Results

3.1. Relationship Quality Components

To investigate whether ravens can be grouped into harmonic and inharmonic pairs according to their use of specific affiliative and agonistic interactions, a principal component analysis was carried out. Application of this method led to the extraction of five principal components. While Component 1 explained 42.21% of the overall variance, components 2, 3 and 4 explained 19.7%, 13.7% and 11.47%, respectively. Finally, component 5 explained 6.81% of the overall variance, resulting in a total of 93.89% overall variance explained. Loadings for each of the behavioural variables on each extracted component are presented in Table 2 in the annex. The first component was characterized by high loadings of affiliative behaviours in general, contact sit, approaching, billing, billing duration and close proximity (individuals 0 m -0.5 m apart). Component 2 showed high loadings of agonistic behaviours in general, displacement, chasing away and moderate to low proximity (individuals 1 m - 3 m apart) as well as a negative high loading from allo-preening. The latter showed a high loading on the third extracted component, too, together with contact sit duration, billing duration and again close proximity. Only two behavioural variables showed high positive loadings on each of the remaining two components, namely allo-preening duration and following on component 4 and contact sit duration as well as close to moderate proximity (individuals 0.5 m - 1 m apart) on component 5. Component 5 additionally showed a high negative loading of low proximity (individuals more than 3 m apart). Note that feeding, sharing, transfer, peck and scrounging had to be excluded as distinct variables from the PCA analysis as they occurred either in less than three different pairs or less than three times in at least three different pairs. However, they remained included in the "all affiliative" and "all agonistic" variables, respectively. As the first three components already explained 75.65 % of the overall variance, they solely were consulted regarding the classification of raven pairs into a harmonic and an inharmonic group. This is a common practice as the other components do not really contribute to explaining the overall variance anymore (Fraser, Schino & Aureli 2008; Fraser & Bugnyar 2010). The classification into groups was achieved using a threshold value, calculated from the loading values for each component, adding the maximum value to the minimum value and dividing the sum between two. In order to be categorized as a harmonic pair, a raven pair's loading values had to exceed at least two threshold values for at least two of the three components. Note that in the case of component 2 the threshold value actually had to be undercut for harmonic pairs as it consisted of agonistic behavioural variables and thus had to be treated inversely. Following this approach, five raven pairs could be categorized as harmonic, while four raven pairs were classified as inharmonic (Annex: Figure 1).

3.2. Factors Influencing Relationship Quality

An additional general linear model analysis was carried out to detect possible influences of life-history traits on the extracted components. However, neither mate choice possibility (F = 0.675; p = 0.673), nor relationship tenure (F = 0.369; p = 0.919) nor breeding success (F = 0.006; p = 0.537) had a significant influence on the extracted components. The only significant influence was found for age difference (Wilks-Lambda: F = 17.63; p = 0.02). A test of between-subject effects revealed that this significant influence concerned only component 4 (F = 37.94; p = 0.007).

3.3. Use of Communicative Signals

On the whole, 24 different signal types were observed in 2404 communicative interactions. In 68.9% of all cases the observed signal was a gesture, as it fulfilled all three criteria for the definition of gestures used in primate research. In order to be defined as gesture, a signal had to be (1) directed to a recipient, (2) mechanically ineffective and (3) open to a voluntary response by the recipient (Pika 2008). All 24 signal types as well as the proportions of signals which fulfilled each single criterion for being defined as a gesture are comprised in Table 3 in the annex. Ten signal types were found to be used as gestures only, while three signal types were used as mechanically effective non-gestural signals exclusively. Beyond that, four signal types were found to be frequently used both as gesture and as mechanically effective nongestural signal. To investigate whether harmonic pairs used a signal more often as gesture or rather non-gestural signal than inharmonic pairs and vice versa, the use of such signals was compared between the two groups. However, no significant difference was found when the respective frequencies per hour were subjected to a Mann-Whitney-U-Test (Table 3). Note that in six signal types their use as gesture or non-gestural signal could not be decided in some cases as the recipient was out of sight in a distance of more than 3 m to the signaler. This made it impossible to determine if the signal was performed in the recipient's direction. In one signal type ("snap") a voluntary response could not be expected in a small proportion of cases so that these signals could not be defined as gestures. I will go into it in more detail in the signal type's discussion.

Signal	proportion of signals used as gesture		Mann- Whitney- U-Test		proportion of signals not used as gesture		Mann- Whitney- U-Test	
	Н	I	U	р	н	I	U	р
grab	69.81%	85.53%	10.0	0.571	30.19%	14.47%	5.0	0.571
poke	76.47%	68.75%	3.5	0.571	23.53%	31.25%	6.5	0.571
push	8.33%	40.0%	3.5	0.571	91.67%	60.0%	6.5	0.571
touch	49.02%	49.25%	10.0	1.0	50.98%	50.75%	5.0	0.286

Table 2: Statistical values for comparison of signals being used both as gestural and mechanically effective non-gestural signals between harmonic (H) and inharmonic (I) raven pairs.

3.3.1. General Use of Gestures

Before pertaining to individual signal types, the use of gestural signals in general was analyzed. Prior to carrying out the analyses in this section, all signals which did not fulfill the criteria for being defined as gestures were excluded from the data set. The first question concerned whether harmonic pairs use on average a larger diversity of gestural signals than inharmonic pairs. To investigate this issue, the average number of gestural signal types was compared between harmonic and inharmonic pairs applying a Mann-Whitney-U-Test. Harmonic pairs used on average 15 (mean: 15.4 ± 2.97) different gestures for communicative purposes, while inharmonic pairs used on average 12 different gestures (mean: 11.75 ± 6.60). There was no significant difference concerning gesture diversity between harmonic and inharmonic pairs (Mann-Whitney-U-Test: U = 6.0; p = 0.413; Figure 8).



GESTURE DIVERSITY

Figure 8: Total number of different signal types used (gestures only) in all nine raven pairs.

As the diversity of signals was not found to differ between harmonic and inharmonic pairs, there was still the possibility of a difference in the average number of gestural signals between the two groups. In other words, harmonic pairs may use on average more gestural signals for communicative purposes than inharmonic pairs or vice versa. To investigate this hypothesis, gestures were assigned to four signal categories (tactile, visual, tactile and auditory as well as visual and auditory; see 2.4.2.) and the frequencies of gestures per hour within each signal category were compared between harmonic and inharmonic pairs. However, there was no significant group effect (test for between-subject effects: F = 0.022, p = 0.887). Both harmonic and inharmonic pairs used on average six tactile gestures per hour (harmonic mean: 6.11 ± 4.65 ; inharmonic mean: 5.81 ± 5.89). Referring to visual gestures, harmonic pairs used on average eight gestures per hour (mean: 8.23 ± 3.68), while inharmonic pairs used seven (mean: 7.39 ± 4.89). Concerning tactile and auditory gestures, harmonic pairs used just one signal per hour (mean: 1.34 ± 2.68) while inharmonic pairs used less than one signal (mean: 0.31 ± 0.61). Finally, when analyzing visual and auditory gestures, harmonic pairs used four gestures per hour (mean: 3.83 ± 2.64) while inharmonic pairs used seven (mean: 7.39 ± 6.22). There were no significant differences in the frequencies of gestures in the four signal categories when applying the Mann-Whitney-U-Test, either (for tactile gestures: U = 11.0, p =1.0; for visual gestures: U = 8.0, p = 0.730; for tactile and auditory gestures U = 8.5, p =0.730; for visual and auditory gestures U = 13.0, p = 0.556; Figure 9).



GESTURAL SIGNAL CATEGORIES

Figure 9: Average frequency of gestures per hour for harmonic and inharmonic pairs in four signal type categories: tactile signals, visual signals, tactile and auditory signals as well as visual and auditory signals. Error bars indicate the s.d.

Concerning gestures used in different signal categories, it was additionally analyzed whether harmonic pairs use gestural signals more flexibly than inharmonic pairs by adjusting their signals to the attentional state of the recipient. This would be the case if harmonic pairs performed visual gestures more often towards an already attending recipient or tactile gestures more often when the recipient was not visually oriented towards the signaler. Furthermore, signals with an additional auditory component could be performed more often towards a recipient that was not attending in order to gain its attention. To investigate these hypotheses, the proportion of signals in each of the defined signal categories towards an attending recipient (Annex: Figure 2) as well as towards a not attending recipient was compared between harmonic and inharmonic pairs. However, there was neither a significant group effect (test for between-subject effects: recipient attending: F = 0.951, p = 0.362), nor were there any significant differences between the two groups when applying the Mann-Whitney-U-Test. All mean proportions as well as the statistical results for the Mann-Whitney-U-Tests are comprised in Table 3.

signal category	attentional state of	proportion of all signals (mean ± SD)			Mann- Whitney- U-Test	
	recipient	н	I	U	р	
tactile	attending	29.57% ± 9.17%	29.01% ± 6.16%	8.0	0.730	
	not attending	0.78% ± 0.28%	0.99%*	5.5	0.286	
visual	attending	42.95% ± 10.83%	39.37% ± 8.68%	9.0	0.905	
	not attending	2.44% ± 1.77%	0.76 ± 0.46%	5.5	0.286	
tactile +	attending	9.66% ± 13.04%	2.73%*	8.5	0.730	
auditory	not attending	0.53% ± 0.13%	0%	6.0	0.413	
visual +	attending	17.86% ± 7.9%	34.45% ± 9.12%	18.0	0.063	
auditory	not attending	2.72% ± 0.42%	3.08% ± 2.23%	8.5	0.730	

Table 3: Proportions of signals used in different signal categories towards an attending or a not attending recipient in harmonic (H) and inharmonic (I) pairs as well as statistical results for differences between the two groups.

*no standard deviation as there was only one inharmonic pair which actually used these signals

Communicative success between individuals may be assessed by investigating the average number of gestural signals used within a communicative bout. The lower the number of gestural signals used to achieve a communicative goal within a communicative bout, the more successful is the communication between signaler and recipient. Consequently, in harmonic pairs the signaler should use less gestural signals per communicative bout than would be the case for the signaler in inharmonic pairs, if communicative success was higher

former group. To test in the this hypothesis, the average number of gestures communicative used per bout was compared between harmonic and inharmonic pairs. Harmonic pairs used on average two gestures per communicative bout (mean: 2.43 \pm 0.29), while inharmonic pairs used on average three gestures (mean: 2.83 \pm 0.08)per communicative bout. There was no significant difference between harmonic and inharmonic pairs (Mann-Whitney-U-Test: U = 17.0, p = 0.111; Figure 10).



Figure 10: Average number of gestures used per communicative sequence in harmonic and

inharmonic pairs. Error bars indicate the s.d.

For each gesture occurring in an agonistic context, an escalation level was determined. This could either be low, medium or high (see 2.4.2.). To investigate whether gestures occurred less often in communicative bouts with medium and high escalation levels, but more often in communicative bouts with a low escalation level in harmonic pairs, the average frequencies of gestures per hour in all three escalation levels were compared between harmonic and inharmonic pairs. However, no significant group effect on was found (Test of between-subject effects: F = 0.001, p = 0.981). Both harmonic and inharmonic pairs used on average one gesture per hour in an agonistic context with a low escalation level (harmonic mean: 0.55 ± 0.33 ; inharmonic mean: 1.16 ± 0.56 ; Mann-Whitney-U-Test: U = 16.0, p = 0.190), three gestures per hour in an agonistic context with moderate escalation level (harmonic mean: 3.32 ± 2.73 ; inharmonic mean: 2.74 ± 1.54 ; Mann-Whitney-U-Test: U = 10.0, p = 1.0) and less than one gesture per hour in an agonistic context with high escalation level (harmonic mean: 0.34 ± 0.47 ; inharmonic mean: 0.36 ± 0.72 ; Mann-Whitney-U-Test: U = 8.0, p = 0.730; Figure 11).

GESTURES PER SEQUENCE


GESTURES WITH ESCALATION LEVEL

Figure 11: Average frequency of agonistic gestures per hour for harmonic and inharmonic pairs in each of the three defined escalation levels. Error bars indicate the s.d.

3.3.2. Use of specific communicative signals

In a second analysis the use of specific communicative signals, i.e. different signal types, was compared between harmonic and inharmonic pairs to analyze if at least certain signals were used more often in harmonic than in inharmonic pairs or vice versa.

When analyzing the average frequencies per hour in each signal type, no significant differences were found between harmonic and inharmonic raven pairs. This applies to the signal types' average frequencies per hour in an affiliative and agonistic context as well as for both contexts together (total frequency per hour). All 24 analyzed signal types as well as their average frequencies per hour and the corresponding statistical values are given in Table 4.

As "kick" could occur either as tactile signal, where the signaler contacted the recipient's body with its foot, or as visual signal, where no body contact was observed, this gesture was additionally analyzed separately in each of the signal categories. Both harmonic and inharmonic raven pairs used this gesture in almost equivalent proportions: Harmonic pairs used the tactile "kick" in 38.89% of all cases while inharmonic pairs did it in 36.36% of all cases. On the contrary, harmonic pairs used the visual version of kick in 61.11% of all cases while inharmonic pairs did it in 63.64% of all cases.

	no.				statistical values				
Behaviour	raven pairs using it	conte xt	e total frequency per hour obs. (mean ± SD)			Ma Whit U-1	nn- tney- `est	between subjects test	
	(H/Ī)			н	I	U	р	F	р
		AF	9	-	1.0	-	-		
begging*	0/1	AG	0	-	-	-	-	-	-
		total	9	-	1.0	-	-		
hent un		AF	8	-	0.99	-	-		
display*	0/1	AG	0	-	-	-	-	-	-
		total	8	-	0.99	-	-		
bowing display [▲]	5/4	total	185	2.63 ± 1.98	1.75 ± 1.61	6.0	0.413	-	-
anuda hilling		AF	4	0	0.11 ± 0.16	15.0	0.286		
(no gosturo)	3/2	AG	13	0.18 ± 0.20	0.11 ± 0.22	8.0	0.730	0.05	0.836
(no gesture)		total	17	0.18 ± 0.20	0.22 ± 0.38	9.0	0.905		
		AF	83	0.62 ± 0.39	1.47 ± 1.79	11.5	0.730		
grab	5/3	AG	19	0.16 ± 0.26	0.34 ± 0.40	11.0	1.0	1.2	0.310
		total	102	0.78 ± 0.51	1.81 ± 2.07	13.0	0.556		
arab		AF	14	0.16 ± 0.17	0.17 ± 0.23	10.0	1.0		
(no gesture)	3/2	AG	13	0.19 ± 0.36	0.11 ± 0.22	8.5	0.730	0.04	0.845
(no gesture)		total	27	0.34 ± 0.48	0.29 ± 0.34	9.0	0.905		
head up display [▲]	3/3	total	170	0.38 ± 0.47	4.08 ± 4.82	14.0	0.413	-	-
		AF	13	0.04 ± 0.06	0.31 ± 0.61	9.5	0.905		
hold	4/1	AG	10	0.16 ± 0.21	0.06 ± 0.11	7.0	0.556	0.11	0.746
		total	25	0.24 ± 0.28	0.36 ± 0.72	6.5	0.413		
		AF	105	1.57 ± 1.90	0.87 ± 0.84	8.5	0.730		
hold beak	4/3	AG	6	0.11 ± 0.11	0.03 ± 0.06	6.0	0.413	0.54	0.486
		total	111	1.68 ± 1.96	0.90 ± 0.87	8.5	0.730		
		AF	13	0.23 ± 0.22	0.06 ± 0.11	5.0	0.286		
kick	5/1	AG	34	0.51 ± 0.50	0.25 ± 0.50	5.5	0.286	1.27	0.297
		total	47	0.74 ± 0.40	0.31 ± 0.61	4.0	0.190		
		AF	11	0.19 ± 0.18	0.06 ± 0.11	5.0	0.286		
kick (visual)	4/1	AG	18	0.26 ± 0.30	0.14 ± 0.28	7.0	0.556	1.58	0.249
		total	29	0.45 ± 0.28	0.19 ± 0.39	6.5	0.413		
kick (tactile)	5/1	total	18	0.29 ± 0.21	0.11 ± 0.22	4.0	0.190	-	-
		AF	61	0.45 ± 0.73	1.10 ± 1.24	12.0	0.730		
open beak	5/4	AG	66	1.0 ± 0.99	0.61 ± 0.54	7.0	0.556	0.05	0.837
		total	134	1.56 ± 1.74	1.77 ± 1.66	10.0	1.0		
open up beak		AF	37	0.50 ± 0.71	0.40 ± 0.58	9.0	0.905		
(no gesture)	4/2	AG	8	0.15 ± 0.10	0.03 ± 0.06	3.5	0.111	0.21	0.659
(total	45	0.65 ± 0.77	0.43 ± 0.63	7.0	0.556		
		AF	33	0.50 ± 0.58	0.25 ± 0.50	4.0	0.190		
poke	5/2	AG	4	0.04 ± 0.05	0.07 ± 0.15	9.5	0.905	0.33	0.582
		total	37	0.54 ± 0.62	0.33 ± 0.47	7.0	0.556		
poke		AF	7	0.16 ± 0.14	0	2.0	0.063		
(no gesture)	4/2	AG	6	0.02 ± 0.06	0.18 ± 0.29	13.0	0.556	0.002	0.965
		total	13	0.18 ± 0.19	0.18 ± 0.29	9.0	0.905		
present	3/1	total	16	0.23 ± 0.35	0.15 ± 0.30	7.0	0.556	0.14	0.719

Table 4: Frequencies per hour and corresponding statistical values for all observed behaviours. H = harmonic pairs, I = inharmonic pairs, obs. = observations

	no.					statistical values			
Behaviour	raven pairs using it	conte xt	total obs.	frequency (mean	Mann- Whitney- U-Test		between subjects test		
	(H/I)			н	I	U	р	F	р
pull		AF	17	0.41 ± 0.75	0	4.0	0.190		
(no gosturo)	4/1	AG	10	0.20 ± 0.26	0.04 ± 0.07	6.0	0.413	1.27	0.298
(no gesture)		total	29	0.63 ± 0.98	0.07 ± 0.15	4.5	0.190		
push	2/1	total	6	0.08 ± 0.11	0.06 ± 0.11	9.5	0.905	1.69	0.235
		AF	35	0.67 ± 0.82	0.05 ± 0.09	3.5	0.111		
push (no gosturo)	4/3	AG	11	0.21 ± 0.40	0.04 ± 0.07	8.5	0.730	1.69	0.235
(no gesture)		total	46	0.88 ± 1.21	0.08 ± 0.10	5.0	0.286		
		AF	71	1.04 ± 1.0	0.57 ± 0.90	6.0	0.413		
raise beak	5/3	AG	28	0.40 ± 0.38	0.24 ± 0.32	8.0	0.730	0.62	0.457
		total	99	1.48 ± 1.31	0.81 ± 1.18	6.0	0.413		
rattle beak [▲]	1/1	total	30	0.15 ± 0.33	0.67 ± 1.34	11.0	1.0	-	-
shrug display [▲]	3/2	total	13	0.22 ± 0.04	0.11 ± 0.22	8.5	0.730	-	-
small thin		AF	3	0.07 ± 0.17	0	8.0	0.730		
small thin	2/1	AG	5	0.06 ± 0.09	0.06 ± 0.11	9.5	0.905	0.46	0.521
posture		total	8	0.14 ± 0.22	0.06 ± 0.11	8.5	0.730		
		AF	98	0.18 ± 0.83	1.23 ± 1.59	8.0	0.730		
snap	5/3	AG	32	0.55 ± 0.34	0.15 ± 0.17	3.0	0.111	0.35	0.571
		total	130	1.85 ± 0.86	1.38 ± 1.53	7.0	0.556		
stare down [■]	5/3	total	25	0.41 ± 0.21	0.20 ± 0.27	5.0	0.286	-	-
thick head [▲]	5/4	total	181	2.01 ± 1.22	2.53 ± 0.57	14.0	0.413	-	-
tilt head	5/3	total	20	0.29 ± 0.11	0.17 ± 0.14	3.0	0.111	-	-
touch		AF	254	3.59 ± 3.98	2.41 ± 2.24	10.0	0.662		
	5/3	AG	43	0.57 ± 1.0	0.49 ± 0.60	9.0	0.905	0.21	0.662
		total	297	4.19 ± 4.95	2.91 ± 2.67	9.0	0.905		
		AF	300	4.69 ± 4.90	2.52 ± 3.37	5.5	0.286		
touch (no gesture)	5/3	AG	9	0.06 ± 0.08	0.22 ± 0.45	9.5	0.905	1.08	0.334
		total	309	4.74 ± 4.87	2.74 ± 3.17	6.0	0.413		

* observed just in one inharmonic pair, thus statistical analysis not possible

^A context could not be decided for a large number of signals, thus only total frequency per hour analyzed

[•] sample size in at least one context category too small, thus only total frequency per hour analyzed

If the proportion of signals in an undecided context was high, i.e. > 10% of all signals for a certain signal type, only the total frequency per hour and duration per occurrence were analyzed. However, if the context could not be decided for less than 10% of all cases, those signals with an undecided context were simply excluded from analysis.

For state behaviours, the average durations per occurrence were additionally compared between the two groups to investigate whether some signals were performed longer in harmonic than in inharmonic pairs or vice versa. As already done for the frequencies per hour, the average durations per occurrence were analyzed in an affiliative and agonistic context as well as in both contexts together (total duration per occurrence). However, no significant differences were found between the two groups, except in one case:

When comparing the total duration per hour between harmonic and inharmonic pairs a significant result was obtained (Mann-Whitney-U-Test: U = 0.0, p = 0.016; Figure 12). The signal was observed on average for 19.24 s \pm 5.36 s in harmonic pairs, while it was for 4.06 s \pm 4.44 s in inharmonic pairs. Thus, harmonic pairs performed "stare down" significantly longer than inharmonic pairs.

The average durations per occurrence in both harmonic and inharmonic pairs as well as the corresponding statistical values for all state behaviours are given in Table 5.



STARE DOWN DURATION

Figure 12: Average duration per occurrence of "stare down" in both contexts together (affiliative + agonistic) as means \pm standard deviations in harmonic (n = 5) and inharmonic (n = 4) pairs. Error bars indicate the s.d.

			statistical values				
Behaviour	cont ext	duration per o (mean	Ma Whit U-T	nn- tney- Test	between subjects test		
		Н	I	U	р	F	р
	AF	-	3.22 ± 2.95	-	-		
begging*	AG	-	-	-	-	-	-
	total	-	3.22 ± 2.95	-	-		
	AF	-	141.0 ± 110.0	-	-		
bent up display*	AG	-	-	-	-	-	-
	total	-	141.0 ± 110.0	-	-		
bowing display [▲]	total	9.26 ± 7.97	5.93 ± 6.56	6.0	0.413	-	-
	AF	0	0.67 ± 0.82	15.0	0.286		
crude billing	AG	0.80 ± 0.78	0.44 ± 0.88	7.5	0.556	0.02	0.894
(no gesture)	total	0.80 ± 0.78	0.68 ± 0.84	8.5	0.730		
head up display [▲]	total	3.16 ± 4.45	7.28 ± 7.01	14.0	0.413	-	-
	AF	12.96 ± 12.22	4.41 ± 3.08	4.0	0.190		
hold beak	AG	5.70 ± 8.09	2.5 ± 5.0	7.0	0.556	2.14	0.187
	total	12.75 ± 11.94	4.48 ± 3.13	4.0	0.190		

Table 5: Durations per occurrence and corresponding statistical values for all observed state behaviours. H = harmonic pairs, I = inharmonic pairs, obs. = observations

			statistical values				
Behaviour	cont ext	duration per o (mean	Mann- Whitney- U-Test		between subjects test		
		Н	I	U	р	F	р
	AF	1.0 ± 1.22	1.59 ± 1.60	13.0	0.556		
open beak	AG	3.12 ± 2.04	2.91 ± 1.56	10.5	1.0	0.01	0.926
	total	3.35 ± 2.12	2.68 ± 1.51	8.0	0.730		
present	total	22.26 ± 25.74	4.13 ± 8.25	5.0	0.286	-	-
rattle beak [▲]	total	3.63 ± 8.12	1.84 ± 3.69	10.0	1.0	-	-
shrug display [▲]	total	5.63 ± 10.02	2.88 ± 5.75	8.5	0.730	-	-
small thin	AF	0.80 ± 1.79	0	8.0	0.730		
	AG	1.0 ± 1.41	2.63 ± 5.25	9.5	0.905	0.18	0.688
posture	total	1.3 ± 1.79	2.63 ± 5.25	9.5	0.905		
stare down	total	19.24 ± 5.36	4.06 ± 4.44	0.0	0.016	-	-
thick head [▲]	total	44.4 ± 21.39	43.0 ± 11.83	9.0	0.905	-	-
tilt head	total	17.15 ± 11.82	11.0 ± 9.59	6.0	0.413	-	-

* observed just in one inharmonic pair, thus statistical analysis not possible

▲ context could not be decided for a large number of signals, thus only total frequency per hour analyzed

sample size in at least one context category too small, thus only total frequency per hour analyzed

In the following the results concerning response behaviour and communicative success shall be illustrated. To assess communicative success in each signal type it was necessary to define a communicative goal for each signal type first. The results concerning communicative goals are listed on the following pages. However, it was not possible to determine a communicative goal for all signal types, as response behaviour was very variable in some cases. The respective signal types are marked with " a " in Table 6 which comprises all signal types as well as their communicative goals and the results of the Mann-Whitney-U-Tests for the comparison of communicative success between harmonic and inharmonic pairs. To sum up, there were no significant differences in communicative success between harmonic and inharmonic pairs, except in one case: When "stop action" was defined as communicative goal to "raise beak" (p. 48, Figure 23) and communicative success was compared between harmonic and inharmonic pairs, a significant difference was found (Mann-Whitney-U-Test: communication successful: U = 15.0, **p** = **0.036**; communication not successful: U = 0.0, **p** = **0.036**).

Begging

Concerning "begging", in 44.44% of all cases the signal resulted in being fed by the recipient, while in each 22.22% of all cases there was a vocal response or the individuals engaged in "hold beak". In 11.11% of all cases there was no obvious response. Thus, "feeding" as a response towards "begging" was considered as communicatively successful.

Bent up display

Referring to "bent up display", in 12.5% of all cases the recipient responded with "bowing display" but stopped precisely this signal in 50% of all cases as response to "bent up display". Thus, the latter was defined as the signal's communicative goal. Note that in 37.5% of all cases there was no obvious response.

Bowing display

"Bowing display" was one of these signal types where response behaviour was very variable. Nevertheless, as responses towards display behaviours were analyzed in more detail in order to investigate whether they occurred more often conjointly in either harmonic or inharmonic pairs, the recipient responded with the same display in 7.35% of all cases in harmonic pairs while this happened in 4.97% of all cases in inharmonic pairs. Another display form was used in 5.03% of all cases in harmonic pairs and in 22.51% of all cases in inharmonic pairs. Furthermore, in harmonic pairs the recipient showed in 29.92% of all cases another behavioural response which was not a display. In inharmonic pairs this happened in 22.53% of all cases. Finally, no obvious response was observed in 57.69% of all cases in harmonic pairs and in 50% of all cases in inharmonic pairs. However, no significant differences were found in these response categories between harmonic and inharmonic pairs (Mann-Whitney-U-Test: same display: U = 11.0, p = 1.0; other display: U = 11.0, p = 1.0; other response: U = 11.5, p = 0.730; no response: U = 5.0, p = 0.286; Figure 13).

Finally, when the occurrence of an arbitrary display as response to "bowing display" was compared between harmonic and inharmonic pairs, no significant difference was found, either (Mann-Whitney-U-Test: display as response: U = 14.0, p = 0.413; no display as response: U = 6.0, p = 0.413).



RESPONSE TO BOWING DISPLAY

Figure 13: Response to "bowing display" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "bowing display" signals.

Crude billing

Concerning response behaviour towards "crude billing", in harmonic pairs both individuals engaged in "crude billing" in 55.56% of all cases, while in inharmonic pairs this response was registered in 66.67% of all cases (Figure 14). Thus, a communicative interaction was considered successful, when both individuals engaged in "crude billing" as a response.



RESPONSE TO CRUDE BILLING

Figure 14: Response to "crude billing" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "crude billing" signals.

Grab

When analyzing the response to "grab" as a gesture, response behaviour was very variable for the total of all "grab" signals. This was also the case concerning all "grab" signals occurring in an affiliative context in harmonic and inharmonic pairs. However, in an agonistic context, the recipient responded in 37.5% of all cases with "open beak" in harmonic pairs, while response behaviour was again very variable in an agonistic context in inharmonic pairs (Figure 15). Consequently, "open beak" was defined as communicative goal to "grab" as a gesture in an agonistic context only.



Figure 15: Response to "grab" as a gesture in harmonic and inharmonic raven pairs in an affiliative and agonistic context as well as for both contexts together. Shown are percentages of responses to all observed "grab" signals.

"Open beak" was also the response behaviour which occurred in 31.25% of all cases towards the mechanically effective, non-gestural "grab" in harmonic pairs and in 18.18% of all cases in inharmonic pairs. In all the other cases the response was again very variable (Figure 16). Thus, "open beak" was defined as communicatively successful response in the mechanically effective "grab", too.



Figure 16: Response to non-gestural "grab" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "grab" signals.

Head up display

Referring to the response towards "head up display", in 39.23% of all cases the recipient responded with a "head up display" itself in inharmonic pairs. Thus, this response was considered as communicative goal to this gesture. In harmonic pairs this response was observed in 10.03% of all cases only. However, there was no significant difference in communicative success between harmonic and inharmonic pairs (Mann-Whitney-U-Test: same display/signal communicatively successful: U = 14.0, p = 0.413). Another display form was used as response in 15.05% of all cases in harmonic pairs and in 5.45% of all cases in inharmonic pairs. Furthermore, a different behavioral response was shown in 31.64% of all cases in harmonic pairs. Finally, no obvious response was registered in 43.28% of all cases in harmonic pairs and in 22.43% of all cases in inharmonic pairs. No significant differences were found between harmonic and inharmonic pairs up = 1.0; other response: U = 15.5, p = 0.190; no response: U = 15.0, p = 0.286; Figure 17).

There was also no significant difference when the occurrence of an arbitrary display as response to "head up display" was compared between harmonic and inharmonic pairs (Mann-Whitney-U-Test: display as response: U = 5.0, p = 1.0; no display as response: U = 4.0, p = 1.0).



RESPONSE TO HEAD UP DISPLAY

Figure 17: Response to "head up display" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "head up display" signals.

Hold

The response to "hold" was very variable in harmonic pairs. In most cases (33.33%) the recipient even avoided the signaler. Nevertheless, in the inharmonic pair, the recipient tolerated the signaler's foot on its body in 53.85% of all cases (Figure 18). Thus, tolerating the gesture was determined as communicative goal to "hold".



RESPONSE TO HOLD

Figure 18: Response to "hold" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "hold" signals.

Hold beak

Concerning the response to "hold beak", in harmonic pairs the recipient reciprocated the gesture in 96.25% of all cases, while in inharmonic pairs this response was registered in 82.35% of all cases (Figure 19). Thus, a communicative interaction was determined as successful, when both individuals engaged in "hold beak" as a response.



RESPONSE TO HOLD BEAK

Figure 19: Response to "hold beak" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "hold beak" signals.

Kick

When analyzing the response to "kick", in harmonic pairs the recipient avoided the signaler in 30.56% of all cases while other behavioural responses were very variable. In inharmonic pairs the recipient responded with "open beak" in 72.73% of all cases (Figure 20). Thus, "open beak" was defined as communicative goal to "kick".



RESPONSE TO KICK

Figure 20: Response to "kick" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "kick" signals.

Concerning the response to the visual version of "kick", in harmonic pairs the recipient in most cases avoided the signaler (36.36% of all cases) as was already the case for all "kick" signals. Other behavioural responses were again very variable. In inharmonic pairs the recipient responded with either "raise beak" (42.86% of all cases) or "open beak" (57.14% of all cases; Annex: Figure 5). Consequently, communicative success was tested with both signals as communicative goal.

Referring to the tactile version of "kick", in harmonic pairs response behaviour was very variable. However, in inharmonic pairs the recipient always responded with "open beak" (Annex: Figure 7). Thus, "open beak" was defined as communicative goal to the tactile version of "kick".

Open beak

Response behaviour towards "open beak" signals was very variable in an agonistic context as well as in both contexts together. However, when analyzing responses in an affiliative context, in harmonic pairs both signaler and recipient subsequently engaged in "billing" in 31.58% of all cases. Other behavioural responses were again very variable which applied for response behaviour in inharmonic pairs, too (Figure 21). Thus, "billing" was defined as communicative goal to "open beak" in an affiliative context.



RESPONSE TO OPEN BEAK

Figure 21: Response to "open beak" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "open beak" signals.

Poke

When analyzing the response to "poke" as a gesture, in 30.77% of all cases the recipient oriented himself in the signaler's direction following the signal in harmonic pairs, while this happened in 27.27% of all cases in inharmonic pairs. Other behavioural responses were rather variable, especially concerning harmonic pairs (Figure 22). Thus, orienting towards the signaler was defined as the communicative goal to "poke".



RESPONSE TO POKE

Figure 22: Response to "poke" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "poke" signals.

Present

Regarding the response to "present", in harmonic pairs the recipient started to preen the signaler in 75% of all cases (Figure 23). Thus, allo-preening was defined as communicative goal to the "present" gesture and subsequent preening by the recipient was considered successful communication. Note that in 41.67% of all cases the chest was the body part presented to the recipient in harmonic pairs, while in 25% of all cases it was the head. Beak, throat, neck and back were each presented in 8.33% of all cases. However, inharmonic individuals presented the head in 75% of all cases while in 25% of all cases it was the neck.



RESPONSE TO PRESENT

Figure 23: Response to "present" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "present" signals.

Pull

When analyzing the response to "pull", in harmonic pairs the recipient responded with "snap" in 37.04% of all cases and with various behavioural responses in all the other cases. In inharmonic pairs the recipient either retreated (50% of all cases) or showed no obvious response (50% of all cases; Annex: Figure 14). Because of the small number of "pull" signals in inharmonic pairs, communicative success was not tested for this behaviour.

Push (no gesture)

Concerning the response to "push", in harmonic pairs the recipient responded with "raise beak" in 46.51% of all cases, while this response did not occur in inharmonic pairs at all. However, in inharmonic pairs the recipient responded with "open beak" in 66.67% of all cases (Annex: Figure 15). Thus, it was not possible to define a communicatively successful interaction.

Raise beak

Referring to response behaviour towards "raise beak", in harmonic pairs behavioural responses were rather variable (Figure 24). However, in inharmonic pairs "raise beak" stopped an action in 37.93% of all cases while in harmonic pairs this happened in 4.17% of all cases. Thus, "stop action" was determined as communicative goal to "raise beak".



RESPONSE TO RAISE BEAK

Figure 24: Response to "raise beak" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "raise beak" signals.

Rattle beak

Regarding the response to "rattle beak", in harmonic pairs the recipient responded with "thick head" in 50% of all cases while this occurred in 41.7% of all cases in inharmonic pairs (Figure 25). As these values referred to one raven pair each, communicative success was not statistically tested in this case.



RESPONSE TO RATTLE BEAK

Figure 25: Response to "rattle beak" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "rattle beak" signals.

Shrug display

Concerning "shrug display", in harmonic pairs the recipient retreated in 11.1% of all cases while no obvious response was observed in 88.9% of all cases. The latter was the case in 100% of all cases in inharmonic pairs (Annex: Figure 8). Thus, communicative success could not be assessed for this gesture.

Stare down

When analyzing the response to "stare down", in harmonic pairs the recipient started to preen the signaler in 47.37% of all cases while other behavioural responses were rather variable (Figure 26). Thus, allo-preening was defined as the gesture's communicative goal and interactions with allo-preening as outcome as communicatively successful interactions.



RESPONSE TO STARE DOWN

Figure 26: Response to "stare down" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "stare down" signals.

Tilt head

When analyzing the response to "tilt head", in harmonic pairs the recipient responded with allo-preening in 57.14% of all cases (Figure 27). Thus, allo-preening was defined as the signal's communicative goal.



RESPONSE TO TILT HEAD

Figure 27: Response to "tilt head" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "tilt head" signals.

Touch (no gesture)

When analyzing the response to the mechanically effective "touch", in both harmonic pairs and inharmonic pairs no obvious response occurred in more than 80% of all cases (Annex: Figure 16). Thus communicative success could not be compared between harmonic and inharmonic pairs for this signal.

		Mann-Whitney-U-Test					
Signal	communicative goal (recipient's response)	commu succ	inication cessful	communication not successful			
		U	р	U	р		
begging*	"feeding"	-	-	-	-		
bent up display*	stop "bowing display"	-	-	-	-		
bowing display	-	-	-	-	-		
crude billing (no gesture)	reciprocate gesture	3.0	1.0	3.0	1.0		
grab [▲]	-	-	-	-	-		
grab (agonistic context)	"open beak"	4.0	1.0	2.0	0.800		
grab (no gesture)	"open beak"	3.0	1.0	3.0	1.0		
head up display	"head up display"	14.0	0.413	-	-		
hold	tolerate gesture	4.0	0.400	0.0	0.400		
hold beak	reciprocate gesture	3.0	0.400	0.08	0.629		
kick	"open beak"	5.0	0.333	0.0	0.333		
kick (visual)	"raise beak"	4.0	0.400	0.0	0.400		
	"open beak"	4.0	0.400	0.0	0.400		
kick (tactile)	"open beak"	5.0	0.333	0.0	0.333		
open beak	-	-	-	-	-		
open beak (affiliative context)	"billing"	5.0	1.0	4.0	1.0		
open up beak (no gesture) 🔺	-	-	-	-	-		
poke	orientate towards signaler	6.0	1.0	4.0	0.857		
poke (no gesture) [▲]	-	-	-	-	-		
present	"allo-preening"	1.0	0.400	3.0	1.0		
pull (no gesture)	-	-	-	-	-		
push	-	-	-	-	-		
push (no gesture)	not clear	-	-	-	-		
raise beak	stop action	15.0	0.036	0.0	0.036		
rattle beak	thick head	-	-	-	-		
shrug display	-	-	-	-	-		
small thin posture	-	-	-	-	-		
snap	-	-	-	-	-		
stare down	"allo-preening"	1.5	0.071	13.5	0.071		
thick head	-	-	-	-	-		
tilt head	"allo-preening"	2.0	0.143	13.0	0.143		
touch	-	-	-	-	-		
touch (no gesture)	-	-	-	-			

Table 6: Signal types with their communicative goals and statistical values for the comparison of communicative success between harmonic and inharmonic raven pairs. Signal types used for assessment of overall communicative success (see below) are marked by bold font.

* observed just in one inharmonic pair, thus statistical analysis not possible

▲ see explanation in the text (p. 35)

sample size too small to analyze response behaviour

It the previous section communicative success had already been assessed and compared between harmonic and inharmonic pairs using the average number of gestures per communicative bout. In a final analysis, another method was applied for this purpose: the average number of gestures used within a communicative sequence/bout in order to achieve a signal type's communicative goal was compared between the two groups. All signal types which were used in this analysis are marked by bold font in Table 6. Although featuring a communicative goal, "Hold" as well as "Hold beak" were not included because in both cases the goal was to reciprocate or rather tolerate the gesture. Concerning "Bent up display", as the communicative goal was to stop a "bowing display" in the recipient, only the number of gestures was determined from there on where a "bowing display" occurred in the recipient. Harmonic pairs used on average 1.22 ± 0.37 gestural signals per communicative bout in order to achieve a communicative goal while inharmonic pairs used on average 1.35 ± 0.23 gestural signals. There was no significant difference in the average number of gestures used to attain a communicative goal between the two groups (Mann-Whitney-U-Test: U = 11.0; p = 0.393; Figure 28). Note that one pair ("Innsbruck") had to be excluded from the analysis as there were no communicatively successful interactions within the data set.



NO. OF GESTURES USED TO ACHIEVE

Figure 28: Average number of gestures used per communicative sequence in order to achieve a specific communicative goal in harmonic and inharmonic pairs. Error bars indicate the s.d.

4. Discussion

The present study was conducted to answer two research questions concerning monogamous raven pairs. First of all we wanted to know whether raven pairs differ in pair bond quality. Based on the outcome, the aim was to investigate whether pair bond quality has an influence on communicative exchange between pair-partners. Concerning the latter, a special focus was to be laid on gestural communication within raven pairs.

To answer the first question, affiliative and agonistic social interactions between the pairpartners as well as proximity patterns were subjected to a PCA which resulted in the extraction of three principal components of relationship quality in these raven pairs. These components enabled the classification of raven pairs into five harmonic and four inharmonic couples. However, when the two groups were subsequently compared regarding their use of communicative signals, no significant differences were found, with the exception of two cases. These results will be discussed in the following.

Relationship quality components

Application of the PCA method led to the extraction of three principal components which matched the number of components extracted in preceding studies of relationship quality. This was, on the one hand, a study by Fraser, Schino and Aureli (2008) assessing relationship quality in chimpanzee groups and, on the other hand, a study by Fraser and Bugnyar (2010) who did the same in common raven groups. Both preceding studies labeled their components "Value", "Compatibility" and "Security", following the theoretical framework of Cords and Aureli (2000) for relationship quality components.

"Value" refers to the direct benefits gained as a result of the relationship, such as agonistic support or food sharing. In other words, this principal component comprises what the subject gains from its relationship with a partner, which depends on what the partner has to offer, how willing the partner is to offer it and how accessible the partner is (Cords & Aureli 2000). In the present study, the first component was not composed of entirely the same variables as in the preceding studies of relationship quality (Fraser, Schino & Aureli 2008; Fraser & Bugnyar 2010). Nevertheless, it showed high loadings of behavioural variables with a benefit to at least one pair-partner and may be labeled "Value" as well. These beneficial variables were "contact sit" and "close proximity", in agreement with both preceding studies of relationship quality, as well as "approaching" was defined as approximating an individual with "contact sit" as an outcome. Thus, this variable may be considered as beneficial, because both partners enjoy

close proximity as a result. In the case of "billing" and "billing duration", the benefit may lie in occasional food transfer from beak to beak. Moreover, the longer the billing situation prevailed, the more food could theoretically be passed on. "Courtship feeding", which could be interpreted similarly to "successful begging" in the preceding studies, did not match the criteria required to be subjected to the PCA as discrete behavioural variable but was therefore included in an "affiliative behaviours" variable. This variable summarized all affiliative behaviours observed, even those which occurred in fewer cases than required to be used as discrete variables. Next to "courtship feeding" these were "sharing" and "transfer", further behaviours which can be considered as beneficial to the partner as it gains either food or an object from the interaction. Given this information, it was not surprising that the "affiliative behaviours" variable showed a high positive loading on the first component, too.

The second component, "Compatibility", represents the general tenor of social interactions within the dyad which may result from both the temperament of the partners and their shared history of social exchanges. Apart from the compatibility of the dyad, it measures the level of tolerance and affiliation between the partners and reflects the ease with which partners can interact (Cords & Aureli 2000). In both preceding studies of relationship quality (Fraser, Schino & Aureli 2008; Fraser & Bugnyar 2010) this component comprised variables which represented the incompatibility of the dyad in first instance, but for the ease of interpretation the signs for the scores obtained for each dyad were subsequently inversed. As this was not done in the present study, the discussion will refer to an "Incompatibility" component. Taking into account all variables with high loadings on the second component in the present study, this component may indeed be interpreted as measuring the lack of tolerance and affiliation between the pair-partners and be labeled accordingly, i.e. "Incompatibility". The respective behavioural variables were "agonistic behaviours", "displacement", "chasing away" and "moderate to low proximity" (individuals 1 m - 3 m apart from each other). The former summarized aggressive and submissive behaviours which did not meet the criteria to be treated as discrete variables, similar to the "affiliative behaviours" variable in the first component. Next to "displacement" and "chase away" it included pecking the partner and chasing it in flight. Thus, the "agonistic behaviours" variable can be interpreted similar to the "aggression" variable which showed a high loading on the "Incompatibility" component in the preceding studies. This variable was used to measure the frequency of aggressive conflict in general. Interestingly, other studies have measured compatibility of a dyad in terms of the amount of time spent grooming (Arnold & Whiten 2001; Preuschoft et al. 2002; Koski, Koops & Sterck 2007; Cooper, Bernstein & Hemelrijk 2005). Consequently, the inverse case for the second component in the present study would be a high negative loading for "preening". This does not apply to the duration of allo-preening in the present case, but at least to its frequency. In other words, incompatible dyads engage less frequent in mutual preening in the present study. This, too, may be due to a lack of tolerance towards the partner.

The third theoretical component, "Security" is about the perceived probability that the relationship with the partner will change. This relates to the consistency of the partner's behavioural response: in a secure relationship the partner's behavioural responses are predictable (Cords & Aureli 2000). Relationship security can be assessed using behaviours which indicate a lack of stability or predictability and a high degree of inequality between social partners. Nevertheless, the observation period was too short and the data set too small for using the same behavioural variables as done by Fraser, Schino and Aureli (2008) and Fraser and Bugnyar (2010) to assess relationship security. According to Castles, Aureli and de Waal (1996) less secure relationships may be indicated by approaches that often result in negative outcomes, e.g. avoidance. If this is case, less secure relationships should show higher rates of "displacement" behaviour. However, this could not be confirmed, as the "displacement" variable had a high positive loading on the "Incompatibility" component only. On the whole and contrary to the preceding studies of relationship quality, the third component in the present study did not show any characteristics of the theoretical "Security" component. The most probable reason may be that no suitable measure for relationship security was included in the variable set subjected to the PCA. Instead, the third component in the present study was characterized by high positive loadings of "allo-preening", "contact sit duration", "billing duration" and "close proximity". These variables, except "contact sit duration", have already been defined as beneficial behaviours in the discussion of the first component and/or in both preceding studies of relationship quality. Concerning "Contact sit duration", this variable is very similar to "close proximity", the former being defined as the average duration per contact sit in seconds, while the latter measures the proportion of time spent within reaching distance (= contact sit). Thus, both variables can be interpreted in a similar way, namely as beneficial towards at least one partner. Considering this interpretation as well as those for the other variables with a high positive loading here, the third component may be treated as additional measure for the direct benefits gained from the relationship. Accordingly, it shall be labeled "Value 2" in the present study.

In summary, two of three extracted components indeed seemed to match previously hypothesized qualities of social relationships and thus could be labeled following Cords and Aureli's (2000) theoretical proposal for relationship quality components: "Value" and "Incompatibility". The third component, "Value 2", appears to be an additional measure for the direct benefits gained from the relationship and may result from the higher diversity of behavioural variables used in the PCA. The lack of a security component, however, may not be due to the nonexistence of a security component in monogamous raven relationships but rather to the present study's methodological approach. Actually, the lack of an appropriate measure for relationship security may be responsible for its deficiency. Components of relationship quality in monogamous raven pairs may still be analogous to those in chimpanzee and raven groups but a larger data set is needed to confirm this theory.

Referring to limitations, the quality of a relationship may not be the same for both partners of a dyad as most interactions between individuals within the same dyad are not likely to be symmetrical (Cords & Aureli 2000). Thus, one partner may benefit more than the other which leads to the relationship being assessed differently from each partner's perspective (Fraser, Schino & Aureli 2008). This is why data should be analyzed on the individual rather than the dyadic level, i.e. using a separate score for each partner in any dyad. However, the size of the data set in the present study prohibited analyses at the individual level. Nevertheless, this issue should be addressed in future studies of relationship quality.

Harmonic and inharmonic raven pairs

Concerning the classification of raven pairs into harmonic and inharmonic couples, the loading values for each extracted component for each dyad yielded a threshold value which was subsequently used to identify relationship quality in each observed raven pair. To be classified as clearly harmonic couple, the loading values in a raven pair had to exceed both threshold values for the two value components and fall below the threshold value for the incompatibility component. This was the case in three raven pairs ("Seewiesen", "Hanau", "Bayrischer Wald"). Accordingly, these three pairs did not only seem to benefit from their relationships, but they also seemed to feature a high level of tolerance and affiliation between pair-partners. However, the classification of harmonic pairs was not that straightforward for all raven pairs. Two couples apparently showed high levels of tolerance and affiliation between pair-partners, but nevertheless they seemed to benefit only from one of the two value components. When examining the frequencies of the variables with a high loading on the missed value component in these two pairs, in one pair ("Wels") it was found that almost all

frequencies were only slightly higher than the mean value for all pairs while two frequencies were even higher than the mean value. This pattern was mirrored by the pair's loading value for this component, which did not lie far from the threshold value. Thus, this pair was a harmonic one, but its frequencies for the variables with a high loading on the missed value component were apparently not high enough to exceed the corresponding threshold value. In the second case ("Haag") the cause was much easier to find: almost all frequencies fell below the mean value for all pairs and two variables were even missing in this pair (i.e. "billing" and "billing duration"). Nevertheless, this pair featured the second highest contact sit duration of all pairs which may explain why at least one of the threshold values for the two value components was exceeded.

Concerning the inharmonic pairs, in one case ("Innsbruck") the pair-partners seemed not to have any benefits from their relationship, but they also did not exceed the threshold value for the incompatibility component. A closer look at the frequencies for the variables with a high loading on this component revealed that in all but one case they either fell below the mean value for all pairs or a specific agonistic behaviour did not occur at all. Thus, despite the apparent lack of benefits, the pair-partners seemed to show little aggressive behaviour towards each other in this inharmonic pair. Interestingly and contrarily to the harmonic pairs, there was no clearly inharmonic pair which did not seem to benefit from any of the two value components and additionally showed a low level of tolerance and affiliation between the pairpartners. This may be due to the small sample size in the present study but nevertheless it rises the question if such pairs exist at all.

Furthermore, the analysis yielded two inharmonic pairs ("Munich", "Heidelberg") with a seemingly low level of tolerance and affiliation between the pair-partners but an apparent benefit from their relationship due to exceeding the threshold value for at least one of the two value components, namely "Value 2". When a detailed look was taken at the frequencies and durations of variables showing a high loading on this component in these two raven pairs, contact sit durations which exceeded the mean value for all pairs were again revealed. Therefore, in all but one case the other frequencies and durations were lower than their mean values for all pairs. This seems to confirm the assumption that exceeding the mean value for "Contact sit duration" is sufficient to exceed the threshold value for "Value 2". Indeed, "contact sit duration" shows the highest loading value on this component, followed by "billing duration" and "allo-preening". This may also be the reason, why the threshold value for "Value 2" was not exceeded in the last inharmonic pair. Here, both allo-preening frequency and contact sit duration were lower that the mean value for all pairs while the

"billing duration" and "close proximity" variables showed frequency values slightly higher than the mean. Nevertheless, while apparently showing a low level of tolerance and affiliation between pair-partners, this raven pair seemed to benefit at least from the first value component as the respective threshold value was exceeded.

Factors influencing relationship quality

Following the extraction of principal components for relationship quality, the effects of lifehistory traits on each of the extracted components were investigated, in order to determine possible sources of variation therein. Nevertheless, no significant results were obtained, except in one case:

Age difference was found to show a significant influence on the fourth principal component. As this component comprised only two variables, "allo-preening duration" and "following" and explained only a small amount of the overall variance in the data set, it was not consulted for the classification of raven pairs into harmonic and inharmonic couples. The positive effect of age difference on this component implies that raven pairs with a larger age gap between pair-partners show higher following frequencies and allo-preening durations. Why this is the case, remains to be solved.

In ravens, there was no significant effect of age difference on none of the value components as had been found in chimpanzees by Fraser, Schino and Aureli (2008). They discovered chimpanzee individuals of similar age to have more valuable relationships which is supported by de Waal and Luttrell's (1986) "similarity principle". This principle states that similar needs, access to resources and power qualify individuals of the same age to provide and exchange higher fitness benefits than individuals with an age gap. Additionally, Fraser, Schino and Aureli (2008) found individuals of a similar age to show more secure relationships. As there was no security component in the present study, this aspect could neither be confirmed nor disclaimed in ravens. Nevertheless, the reason for the lack of a significant influence of age difference on at least one of the value components in the present study does not necessarily mean that such a relationship does not exist in ravens but may again be due to the small sample size.

According to Kummer (1978), social relationships are investments which maximize the longterm gain for both partners from the relationship with each other. Consequently, individuals who have interacted over longer time periods should display more valuable and more compatible relationships than those who have spent less time together. This is supported by Marzluff and Angell (2013) who state that it is the constant, close contact for years which enables raven pairs to coordinate. In fact, Fraser, Schino and Aureli (2008) found relationship tenure, i.e. time spent together since introduction to the pair-partner, to have a significant positive effect on both "Value" and "Compatibility" in chimpanzees. Moreover, a significant negative influence of relationship tenure on "Security" was found. Thus, despite seeming to have more valuable and compatible relationships, individuals that had spent more time together apparently had less secure relationships that those which were together in the group for a shorter time. As there was no "Security" component in the present study, the effect of relationship tenure on relationship security could not be tested. Concerning the other components, again no significant effect was found. However, personal observations give rise to the guess that a larger sample size may indeed reveal a significant effect of relationship tenure. A good example may be the "Innsbruck" pair, where the pair-partners seemed not to benefit from their relationship but apparently featured a low level of aggression towards each other. As they had been brought together recently, a valuable relationship may yet have been to develop. The supposition of a change in the relationship is not unlikely as already Fraser and Bugnyar (2010) assumed the behaviour and complexity of raven relationships to have changed over the course of just one study period. However, one suspicious case is not enough to make any assumptions and a larger sample size may even result in different conclusions.

Furthermore, a possible effect of mate choice possibility on the relationship quality components was investigated. As they bond for life, ravens need relatively long time-periods to find and choose the right partner (Gwinner 1964; Heinrich 1999). However, most captive ravens do not have the possibility to choose a partner from a group of birds but are simply brought together with an unbonded member of the opposite sex. Thus, there is no guarantee that the pair-partner's temperaments are actually matching. As temperament is described to have an influence on the compatibility of pair-partners (Cords & Aureli 2000), a significant negative effect of mate choice possibility on "Incompatibility" was probable. Nevertheless, no significant effect was found. One explanation may be that there actually is no such effect because of raven individuals simply adjusting to each other, even if their temperaments are not matching well. This may also be the reason why both Heinrich (1999) and Lorenz (1935) observed raven pairs to form partnerships "of convenience" which were quickly dissolved when a better matching partner was found. However, a larger sample size is needed to confirm this theory.

Finally, the effect of reproductive success on the extracted relationship quality components was tested to analyze if raven pairs with high reproductive success were those with valuable and compatible relationships. This was suggested as raven pairs rely heavily on cooperation between pair-partners in order to obtain and defend high quality territories, begin reproduction early in the season and coordinate incubation and nestling care (Bradbury & Vehrencamp 2011). Such cooperation is assumed to imply at least a certain level of tolerance between the pair-partners. Furthermore, in two other avian species with long-term pair bonds, cockatiels (*Nymphicus hollandicus*; Spoon, Millam & Owings 2007) and guillemots (*Uria aalge*; Zahavi 1977) a higher allo-preening rate, categorized as clearly beneficial behaviour (Fraser & Bugnyar 2010), was found to be positively correlated with reproductive success does not depend on mutual benefits or partner compatibility. Being bonded still seems enough to reproduce successfully, at least in captivity. Of course, the small sample size in the present study is not sufficient to make any predictions concerning this topic and the results may point in a different direction if more raven pairs are investigated.

So far, the extraction of three relationship quality components, "Value", "Incompatibility" and "Value 2", has been discussed as well as their use for the classification of raven pairs into five harmonic couples and four inharmonic couples which, to some degree, even differed in the characteristics of their relationships within the group. Nevertheless, these differences could not be ascribed to specific life-history traits which may be due to the small sample size in the present study. In the following, harmonic and inharmonic pairs' use of communicative signals shall be discussed.

General use of gestures

Based on parameters applied in primate research, common ravens were found to use a various range of gestures for communicative purposes in the present study. To discern gestural signals from non-gestural signals, each potential gesture was checked for being directed to a recipient, mechanically ineffective and open to a voluntary response, following the definition for gestures in primate literature (Pika 2008). Signals which did not match these criteria were not included in further analysis or treated separately when analyzing the specific use of communicative signals.

Concerning the diversity of gestural signals used, there was no significant difference between harmonic and inharmonic pairs. In other words, harmonic pairs used on average not significantly more different gestural signals for communicative purposes than inharmonic pairs. The opposite might have been the case if communication in harmonic pairs was assumed to be more elaborate than in inharmonic pairs. Nevertheless, there seemed to be no influence of relationship quality on gesture diversity. Note that in the "Innsbruck" pair only three different gestural signals were used which may have been due to the female's recent introduction to the male. The diversity of communicative signals in this pair may rise when the pair-partners get accustomed to each other.

Depending on the perceptual system to receive them, gestural signals were assigned to four signal categories: "tactile", "visual", "tactile and auditory" and "visual and auditory". A difference in the use of at least tactile signals was assumed as inharmonic pairs were supposed to show lower spatial proximity between pair-partners and this may have promoted the use of visual (and maybe also visual and auditory) signals which do not require spatial proximity between signaler and recipient. However, this was not the case. Harmonic and inharmonic pairs did not differ significantly in the average number of gestures they used in different signal categories. This was also the case when the average number of gestures used per communicative bout was analyzed. This analysis was carried out to compare communicative success between harmonic and inharmonic pairs based on the assumption that using a lower number of gestural signals per communicative bout indicates higher communicative success. According to Bradbury and Vehrencamp (2011), successful cooperation between partners requires learned responsiveness to partner signals. When assuming that harmonic pairs cooperate better, their responsiveness to partner signals may be higher so that less signals are needed to achieve a communicative goal. However, relationship quality seemed not to have any significant influence on communicative success. This was also the case when a different approach was used for its assessment. After determining communicative goals for several signal types, the average number of gestures used per communicative bout in order to achieve a signal type's communicative goal was calculated and compared between harmonic and inharmonic pairs. Contrarily to the previous analysis of communicative success, now only those communicative bouts were analyzed which included a signal type and its communicative goal. However, this approach did not perform better concerning significant results. On the one hand, the reason for both non-significant results may be that in raven pairs communicative success indeed does not depend on the quality of bond as either no learned responsiveness to partner signals is needed to communicate successfully or the learned responsiveness does not depend on relationship quality. On the other hand, the sample size may simply be too small to reveal a significant effect.

As three of four inharmonic pairs seemed to feature a low level of tolerance and affiliation between the pair-partners, assessed using the frequencies of agonistic interactions, there was the possibility that they used gestures more often in an agonistic context with high escalation level compared to harmonic raven pairs. The respective analysis showed that this was not the case. Altogether, the frequency of gestures used in agonistic contexts with high escalation level was rather low in both groups compared to gestures used in agonistic contexts with low and moderate escalation level. This finding was mirrored by the intensity of agonistic social interactions: Behaviours which involved physical hitting of an individual, were either observed in very few cases (here: "pecking") or not at all during the whole observation time (e.g. "fighting", i.e. hitting each other with feet and beaks, often while jumping in the air).

Furthermore, harmonic and inharmonic pairs were compared concerning the flexibility of gesture use, inspired by the study of Pika and colleagues (2005) in five primate species: All studied species were found to use visual gestures more often when the recipient was directed bodily towards the signaler than when the recipient's back was turned. Tactile gestures, therefore, were found to be used more often when the recipient's back was turned. Nevertheless, no significant effect of relationship quality on the flexibility of use was found in common raven pairs. Both harmonic and inharmonic pairs seemed to perform similarly concerning the use of gestures in different signal categories towards attending or not attending recipients. According to Pika and colleagues (2005), adjustments in gesture use as those observed in primates, may indicate that the signaler knows something about how its signal is being perceived by the recipient. If this is also the case in ravens, at least this knowledge does not seem to differ between harmonic and inharmonic pairs.

To sum up, relationship quality seemed not to have any significant influence on the general use of gestural signals in raven pairs. One explanation may be that there indeed exists no influence of relationship quality on communicative exchange concerning the use of gestures. Both harmonic and inharmonic pairs may communicate equally successful using comparable ranges of gestural signals as well as similar amounts of gestural signals in different signal categories, showing similar escalation levels concerning agonistic gestures and adjusting their gesture use comparably to the attentional state of the recipient. Of course, the non-significant results may also have their origin in the small sample size in the present study and more raven pairs as well as longer observation periods are needed to define the precise cause.

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The observation that the general use of gestures was not influenced by relationship quality did not exclude the possibility that there was a significant difference in the use of specific gestural signals between harmonic and inharmonic pairs. Accordingly, the use of specific communicative signals was compared between harmonic and inharmonic pairs and shall be discussed in the following. The definitions for raven communicative signals were phrased as non-interpretative as possible. Thus, the labeling simply describes the observed action, without ascribing it to specific categories, such as threat behaviour or submissive behaviour. This shall be done in the following, when comparing the observed behaviours with descriptions of raven behaviour by Gwinner (1964).

Use of specific communicative signals

Harmonic and inharmonic pairs used most gestures in both affiliative and agonistic contexts. This corresponds with observations by Tomasello and colleagues (1994, 1997) as well as Arbib, Liebal and Pika (2008) in chimpanzees. They were found to use gestures in multiple contexts, sometimes even across widely divergent behavioural domains. Thus, similar to chimpanzees, ravens seem to use their gestures flexibly.

"Begging" is described to occur both as response towards the male's courtship feeding and spontaneous in order to appease another individual (Gwinner 1964). In the present study it was observed in one single pair and in an affiliative context only, where it was followed by courtship feeding in most cases. Indeed, it was the female which begged while the male supplied it with food. According to Huber (1991), begging for feeding purposes never occurs in males, but the gesture is used as appeasement behaviour by both male and female. A possible function as appeasement gesture could not be confirmed in the present study. Interestingly, the signal was observed in an inharmonic pair only, although it would have been supposed to rather occur in harmonic pairs because of being associated with courtship feeding, a beneficial behaviour which tends to occur in valuable relationships (see discussion: "Relationship quality components"). Because of the small number of "begging" observations in the present study, this gesture can only be supposed of not being influenced by relationship quality and a larger sample size will be needed to review this supposition. More observations may even be obtained, when feeding time recordings are included in the analysis, as "begging" frequency is reported to rise after food has been provided (Gwinner 1964). Apart from that, courtship feeding is described as being more common during the breeding season (Gwinner 1964), which is approximately from the end of January to mid-June (Haffer et al. 1993). Thus, "begging" behaviour may also be more common in this time span. Because the present study was carried out outside the breeding season, several other behaviours with a function in reproduction could not be analyzed either. This was on the one hand precopulatory behaviour, e.g. soliciting postures, and on the other hand copulatory behaviour. According to Gwinner (1964) sexually motivated behaviours are constricted to courtship feeding or impressing behaviours ("Imponierverhaltensweisen") outside the breeding season.

An example for sexually-motivated impressing behaviour is the "bowing display" or "Verbeugungszeremonie" (Gwinner 1964). Displays are ritualized behaviour patterns being based on emotionally motivated intention movements (Huxley 1966). In ravens, they are described as being highly variable concerning the body movements as well as the vocalizations uttered, the latter often being displaced by learned vocalizations (Gwinner 1964). This was also the case in the present study. Especially the vocalizations were different from animal to animal and they often resembled human words or environmental sounds. Mated pairs are reported to perform joint displays together, often as a highly synchronized duet (Lorenz 1940; Gwinner 1964; Bradbury & Vehrencamp 2011). Furthermore, individuals in other bird species were observed to either alternate the use of display elements or to produce the elements in concert, depending on the context (Emery et al. 2007). As some displays in birds are assumed to function as an emotional bond between the mated pair (Huxley 1966), it may be interesting for future studies to analyze individual differences in display behaviour within and between pairs and to assess how much synchronization there actually is between raven pair-partners. Gwinner (1964) describes the "bowing ceremony" as being probably the most striking behaviour within the common raven behavioural repertoire. Similarly elaborate displays are reported in various other bird species, e.g. in rooks (Corvus frugilegus; Coombs 1978), members of the genus Phasianidae (Schenkel 1958) and in the openbill stork (Anastomus oscitans; Huxley 1962). Regarding the influence of relationship quality on "bowing display", it was assumed that high quality relationships show higher rates of joint displays because of their function in mating behaviour which should involve a higher level of tolerance and affiliation between the individuals. Consequently, the response behaviour towards displays was analyzed in more detail to check for such an influence. However, no significant effect could be found. Harmonic pairs did not seem to perform joint displays significantly more often than inharmonic pairs. This applied to both performing the same display together as well as performing different forms of displays towards each other. "Bowing display", next to "feather ears" and "thick head", is described as being one of three distinct elements with two different functions which follow each other with rising intensity in signaling (Gwinner 1964). According to Gwinner, these three elements may either be motivated sexually and be performed in the context of courtship display to stimulate and synchronize the partner, or they may be motivated by aggression and performed in an agonistic context, e.g. in order to suppress a rival. Specifically these characteristics may have been responsible for the difficulties in determining the context for impressing behaviours in the present study. Furthermore, the dual function of impressing behaviours may also account for the lack of an influence of relationship quality on the frequencies and durations of "bowing display" and "thick head" ("Dickköpfiges Imponieren", Gwinner 1964). The latter is described by Gwinner to usually precede a "bowing display" which can be affirmed for the present study. Both "bowing display" and "thick head" may be used in an affiliative courtship context in harmonic pairs and, on the contrary, in an agonistic context in inharmonic pairs or vice versa. Their function in an agonistic context would especially apply to the "Innsbruck" pair where the female started performing "thick head" as well as "bowing display" towards the male as soon as the male approached her within 1 m. When the male continued to approach her, she immediately retreated. Similar sequences were observed in the inharmonic "Heidelberg" pair.

The third impressing behaviour, "Feather ears", where feathered parts atop the eyes are erected, was not recorded in the present study, as it was difficult to detect viewing the twodimensional video material, especially for the females where they are not as distinct as in the males (Gwinner 1964). Additionally, the observer had to be quite close to the study subjects in order to detect "feather ears", which was not always possible. The "feather ear impressing posture" ("Federohrimponierhaltung", Gwinner 1964), was not observed, either, as this behaviour occurs predominantly between males in order to intimidate a rival and the present study included only mixed-sex dyads. This also applies for the "feather ear attack posture" ("Federohr-Angriffshaltung", Gwinner 1964).

Concerning displays, four other visual and auditory gestures were observed in the present study, which had not been described by Gwinner (1964). One of these is "head up display". As there was no influence of relationship quality on neither the frequency, nor the duration of "head up display", this behaviour may be another form of impressing behaviour with two different functions. However, it did not necessarily occur together with "thick head", as was the case for "bowing display". Moreover, inharmonic pairs performed this signal as joint display almost three times as often as was the case in harmonic pairs. Given that inharmonic pairs apparently show a low level of tolerance and affiliation towards each other, its function may rather be to challenge the partner about one's own superiority, similar to the function of

"bowing display" in the "Innsbruck" pair. The response behaviour towards "head up display" may also be a crucial clue that, although not being described by Gwinner, this behaviour was indeed a display and not just a vocalization. The latter could be suggested when taking into account that the wing bows are also strut apart and the tail is fanned when vocalizations are uttered which require much effort (Haffer et al. 1993). Being oriented towards the partner may have been just accidental while performing the signal which would also explain why in several cases the signal occurred when the other individual was more than 3 m apart from the signaler. This difficulty in discerning displays from simple vocalizations also applies to "rattle beak", "shrug display" and "bent up display". Concerning "rattle beak", an additional argument for its use as a display may be that it evoked other forms of impressing behaviour, "thick head" as well as "bowing display", or potentially impressing behaviour ("head up display") as response in both harmonic and inharmonic pairs. Furthermore, its use was not influenced by relationship quality, either. This did also account for "shrug display". However, in this case the behaviour may indeed be just a vocalization, regarding the response behaviour: In most cases there was no obvious response and the only other response was the recipient's retreat. Nevertheless, the sample size is too small to decide this for sure. Referring to "bent up display", response behaviour points towards a function as impressing behaviour because the recipient either responded with a "bowing display" or with stopping a "bowing display". As this behaviour was observed only in one inharmonic pair, no definite classification can be made.

Another behaviour, where the function was difficult to deduce, was "hold beak". Haffer and colleagues (1993) mention this behaviour shortly while Gwinner (1964) categorizes it as part of courtship feeding after observing it in one raven pair. In contrast, "hold beak" did not show any link to courtship feeding in the present study and thus was described as distinct behaviour. The most common response to "hold beak" was that both individuals locked their beaks and stayed in this position for several seconds. Furthermore, it was used to stop an action in the recipient in harmonic pairs. However, relationship quality was not found to have any influence on this behaviour which also applied to "hold". "Holding one another's feet" is also mentioned by Savage (2005; p. 59) who describes it as typical behaviour of pair-partners. As in both "hold beak" and "hold" maintaining close proximity is inalienable for communicative success, an affiliative function may be deduced. Consequently, both behaviours would be supposed to occur more often in harmonic than in inharmonic pairs because of close proximity having a high loading on the "Value" component of relationship quality. However, this is not the case. One possible explanation may be that both "hold" and

"hold beak" have an additional function as appeasement behaviours. Such behaviours are usually used following an agonistic interaction. To confirm an additional function in appeasing the partner, it would be necessary to analyze which signals occur directly before and after these two behaviours and whether they are primarily agonistic. This, in turn, points to a major difficulty in the present study's analysis of response behaviour. It would be necessary to improve the coding scheme in order to analyze whole sequences of behaviours in order to define a signal's meaning, i.e. "the response selected by the recipient from all the responses open to it" (Cherry 1955, p. 114), more accurately. This would additionally allow to assess goal-directedness for all observed behaviours which may be used as additional criterion to discern gestural from non-gestural signals as well as displays from simple vocalizations.

In order to resolve conflicts, animals need at least two agonistic signals: an aggressive threat signal and a submissive or de-escalation signal (Bradbury & Vehrencamp 2011). According to Gwinner, the former applies to the "Kopf-Vorwärts-Drohstellung" which signalizes the individual's superiority as well as its intention to attack and corresponds with "open beak" in the present study. Thus, "open beak" would be supposed to occur less often in harmonic than in inharmonic pairs because of the apparently low level of tolerance and affiliation between pair-partners in the latter group. However, this is not the case. Relationship quality seemed not to have any significant influence on "open beak" in the present study. A possible explanation may be that "open beak" is used for different purposes as indicated by highly variable response behaviour towards this signal. In other words, "open beak" may have different meanings. According to Smith (1965), a signal's meaning may be peculiar to a recipient individual. Thus, it is not unlikely that it may have distinct meanings in different raven pairs. Moreover, the meaning may also differ within a raven pair. Cartmill and Byrne (2010) found primate gestures to be "multi-purpose" with an average individual using a gesture for approximately five different functions. Such multifunctionality could also apply to raven gestures and to "open beak" in the present study. Concerning different meanings, learned responsiveness to the partner's signals may ensure that communication is still successful within each raven pair (Bradbury & Vehrencamp 2011). Analyzing response behaviour in each raven pair separately may at least provide an answer to the question whether signal meanings differ between raven pairs. However, the small sample size in the present study did not allow a finer analysis. Beyond that, Smith (1965) stresses that a signal's meaning should be analyzed with reference to context, as specificity may come from context. In the case of "open beak", the number of observed signals was large enough to conduct an additional analysis of response behaviour in both context categories. In fact, the signal seemed to be used to initiate billing in an affiliative context. Nevertheless, again no significant effect of relationship quality was found on communicative success.

Another aggressive threat behaviour described by Gwinner (1964) is the "Frontaldrohen" or "frontal threat" where the individual fluffs its feathers in erected body posture and holds its beak either diagonally or directed towards the ground while the intertarsal joints are bent. Additionally the wings may be extended and the tail may be fanned. Gwinner observed this behaviour when an individual defended its nest during breeding time only which may be the reason why it was not recorded in the present study. Contrarily to "frontal threat", "kick" was not described by Gwinner explicitly but may be additionally categorized as aggressive threat behaviour, taking into account its prevalent occurrence in an agonistic context as well as the response behaviour towards "kick" signals. The respective response behaviour was either predominantly an avoiding response in harmonic pairs, or an "open beak" as well as a "raise beak" in inharmonic pairs. Categorizing "kick" as aggressive signal also coincides with Gwinner mentioning this behaviour as aggressive response of a male towards a courting female when describing courtship behaviour. Because of its categorization it is surprising that there was no significant influence of relationship quality on this signal's use and it occurred in one inharmonic pair only. The opposite would have been more probable, taking into account the seemingly lower level of tolerance and affiliation in inharmonic pairs compared to harmonic pairs.

Apart from aggressive threat behaviours which are influenced by the intention to attack, Gwinner (1964) describes defensive threat behaviours which, in turn, are influenced by the intention to escape. They are reported to belong to the most frequent behaviours shown within a social group where low-ranking birds have to face high-ranking conspecifics. One of these behaviours is "Schnabelklappen". It is described as a rather weak form of defensive behaviour where the individual opens and closes its beak repeatedly and in an arrhythmic manner towards the other individual, its head feathers meanwhile being fluffed. This definition resembles that of "snap" in the present study. However, "snap" was recorded as an event rather than a state here and it usually occurred independently of "thick head". Although being categorized as aggressive behaviour by Gwinner, and thus supposed to occur more often in inharmonic raven pairs, "snap" was not influenced by relationship quality, either. Moreover, it was observed both in an affiliative and agonistic context. Its categorization may thus be

questionable which is supported by response variability towards "snap" signals. Similar to "open beak", "snap" may have different functions which are context-dependent. As mentioned in the results section, some "snap" signals could not be defined as gestural signals due to not being open to a voluntary response from the recipient's viewpoint. The reason was that in these cases a "snap" was performed towards a retreating individual, i.e. simultaneously to the recipient jumping towards another branch. However, it could not be settled why the signaler used a "snap" in these situations.

Apart from "Schnabelklappen", Gwinner (1964) describes the "Abwehrhaltung" as further defensive threat behaviour. Here, the individual fluffs its head feathers as well as some feathered parts of the back and opens its beak widely towards the other individual while uttering defensive vocalizations. In its most extreme form, the "Blockstellung", the individual ruffles all its feathers while facing the other individual. Gwinner observed this behaviour directly before an individual was attacked by a higher-ranking bird. This behaviour may not have been seen in the present study as there is usually no real dominance hierarchy within a pair bond (Gwinner 1964). Furthermore, forms of agonistic behaviour which involved physical hitting occurred very rarely in the present study. Concerning fighting behaviour, where the individuals hit each other with feet and beaks, often accompanied by jumping in the air, there were even no occurrences at all.

As already mentioned above, apart from aggressive threat signals, submissive signals or deescalation signals are needed in an animal's signal repertoire, in order to deal with conflicts (Bradbury & Vehrencamp 2011). In the common raven this may account for the "small thin posture". However, this signal was observed only in very few cases in the present study which may be due to the relatively small number of signals used in agonistic contexts, especially concerning agonistic contexts with moderate and high escalation levels. The observed individuals may not have been dependent on the signal's frequent use as they did not need to deescalate situations in most cases. This, again, would apply to both harmonic and inharmonic raven pairs as relationship quality seemed not have any influence on "small thin posture" and would match the result that there already was no significant influence of relationship quality on the use of gestures in the three escalation levels. The definition of "small thin posture" corresponds with that of Gwinner's "Klein-Dünn-Werden". In agreement, Gwinner (1964) categorized it as a form of appeasement behaviour which is used to avert the threat of a fight by pretending to be small or turning away potentially dangerous body parts, such as the beak.
Nevertheless, the signal's function could only be guessed in the present study due to the small number of signals observed.

According to Gwinner, "Klein-Dünn-Werden" is often followed by "Schnabelhochstellen" which corresponds with "raise beak" in the present study. It is reported to represent appeasement behaviour of higher intensity. However, this did not seem to apply to "raise beak" in the present study as it was quite common in the observed raven pairs, despite the relatively small number of signals used in an agonistic context. Furthermore, "raise beak" is described by Gwinner as dominance signal because the body size is enlarged in order to signalize superiority. In general, dominance signals are signals of fighting ability and motivation with an added component reflecting prior experience (Bradbury & Vehrencamp 2011). Thus, they would be supposed to occur more often in pairs with an apparent low level of tolerance between pair-partners, namely in inharmonic pairs. However, statistical analysis showed that this signal's use was not influenced by relationship quality. Moreover, inharmonic pairs seemed to use it to stop the recipient from performing a signal/behaviour. This, in turn, was not observed in inharmonic pairs. One explanation may be that the "raise beak" has a different function in harmonic pairs. Alternatively, harmonic pairs may not tend to stop their partners and tolerate their behaviour instead. Either way, in this case there was a significant difference in communicative success between harmonic and inharmonic pairs when "stop action" was defined as communicative goal to raise beak.

Another form of appeasement behaviour is "Wegsehen", which may be translated as "look away": The individual turns its beak slowly, almost accidentally sideways and may turn it back again or start preening its wing feathers, cleaning its bill or pecking the ground (Gwinner 1964). As this closely resembles non-intentional behaviour in response to some environmental stimulus, the signal's observation proved to be quite difficult in the present study. This difficulty is affirmed by Gwinner who observed it to occur in various other situations, too, where no appeasement was necessary. Consequently he could not determine its function and motivation thoroughly. Because of the problems concerning the observation of "look away", the behaviour was not included in the analysis.

Therefore, "stare down", another potential appeasement behaviour, was analyzed. Its definition resembles Gwinner's "Herabstarren" where the individual lowers its head jerkily until the beak is directed vertically towards the ground. Gwinner observed this behaviour to be performed mainly by low-ranking individuals when they were watched by a higher-ranking individual while uttering appeasement sounds. Consequently, he categorized it as appeasement behaviour and supposed it to be another gesture for scaling the body size down,

similarly to "small thin posture". Moreover, he found it to occur at most for two seconds before the individual straightened up again or engaged in other actions. This, however, did not apply to "stare down" in the present study. Here the behaviour could be performed up to 103 seconds and there even was a significant difference in stare down duration between harmonic and inharmonic pairs. The cause may be found in the signal's function. Gwinner was not sure about the expressional function of "Herabstarren" but when response behaviour was analyzed for "stare down" in the present study, its function as preening solicitation in harmonic pairs could be deduced. This is in concurrence with reports by Heinrich (1999) who describes a bird to perch close to another and bend its head down to solicit preening. Nevertheless, the same function did not seem to account for inharmonic pairs, where no obvious response was observed in most cases. A different meaning in the two groups would explain the significantly longer performance of "stare down" in harmonic pairs as the signaler awaited the recipients preening as response while this was not the case in inharmonic pairs. This may also be the reason why, despite the discrepancy in behavioural responses, there was no significant difference in communicative success between harmonic and inharmonic raven pairs. Furthermore, although looking exactly the same, "stare down" and "Herabstarren" may be two different kinds of behaviour, the difference to be found in the signals' duration as well as their functions. However, the possibility that the analysis was biased by two different behaviours being recorded as "stare down" in the present study is rather unlikely as only in one case a duration of less than two seconds was recorded. "Herabstarren" may simply not have been observed in the present study because of its resemblance to non-intentional behaviour.

Another signal which seemed to be used as preening solicitation in harmonic pairs only, was "present". Gwinner (1964) describes this signal as being part of a whole sequence of behaviours which solicit preening in the recipient. In most cases in the present study the recipient responded with allo-preening towards "present in harmonic pairs while in inharmonic pairs no obvious response was most common. However, this discrepancy in the signal's function was not significant between harmonic and inharmonic pairs. The reason may be that certain signals, which usually function as preening solicitations, were also observed to occur within bonded raven pairs as affiliative gestures which not necessarily imply the desire to be preened (Gwinner 19654). This would additionally explain why there was no significant influence of relationship quality on "present", neither concerning its frequency nor its duration. Given that this gesture can be used independently from the desire of being preened, response behaviour does not necessarily need to include allo-preening which is described as

highly beneficial behaviour and thus tends to occur more often in high quality relationships (Fraser & Bugnyar 2010). Apart from that, Gwinner observed ravens to preen each other predominantly on the head, neck and throat but also around the eyes and the beak. This coincided with the body parts which were predominantly presented in inharmonic pairs, namely head and neck. In harmonic pairs, in turn, the chest seemed to be the preferred spot for being preened, as it was presented almost twice as often to the recipient as the head. These two body parts were followed by beak, throat neck and back in harmonic pairs.

A signal which is described by Gwinner to precede "present" in a sequence of signals to solicit preening is "poke". However, Gwinner did not distinguish between mechanically effective and mechanically ineffective "pokes". The mechanically ineffective, gestural "poke" seemed to be used in order to direct the recipient's attention towards oneself in both harmonic and inharmonic pairs. Using "poke" in order to get the other individual's attention makes sense as its attention is inalienable for a preening solicitation. Be that as it may, no significant influence by relationship quality on neither the use of "poke" nor its communicative success was found which coincides with the result for "present", in case these two signals are indeed linked to each other. To confirm such a link, it would be necessary to improve the coding scheme and to analyze whole sequences of behaviours as already mentioned above.

A signal which was used to solicit preening in both harmonic and inharmonic pairs, contrarily to "stare down" and "present", was "tilt head". Neither its frequency, nor its duration proved of being influenced by relationship quality. However, in harmonic pairs the recipient responded with preening the signaler in more than half of all cases while this happened not quite as often in inharmonic pairs. In general, preening solicitations are suggested to function in order to test the partner's attention (Gwinner 1964) and being preened after having solicited preening signalizes the partner's interest in providing satisfaction. Thus, despite the difference not being significant, in harmonic pairs the individuals obviously tended to provide satisfaction to their partner more often than in inharmonic pairs. However, because of its link to allo-preening, a comparably frequent behaviour in valuable relationships (Fraser & Bugnyar 2010), it would not have been surprising to find a significant difference concerning communicative success between harmonic and inharmonic pairs. The lack of such an effect may again be due to the small number of "tilt head" signals observed in the present study.

Furthermore, several tactile event signals, not being mentioned in Gwinner's work, were analyzed in the present study. Some of them were used both as gestural and non-gestural signals, depending on their mechanical effectiveness. However, none of them proved to be influenced by relationship quality. This was not only the case concerning their frequencies but also concerning the communicative success. Nevertheless, one of these tactile signals, "touch", has yet to be mentioned as it was combined with a vocalization in some cases. This vocal component may have been used to increase the signal's intensity which is especially interesting taking into account that this is supposed to have been done by the primate ancestors of humans, too: They are presumed to have used grunts and cries, which were at first largely emotional and involuntary, in order to punctuate gestural communication, adding emphasis and emotional tone (Corballis 2002). Corballis suggests that it may have been the final switch from a mixture of gestural and vocal communication to an autonomous vocal language which finally distinguished *Homo sapiens* from other primates. Thus, a detailed analysis of such tactile and auditory signals, when they occur and which function they have, would be an interesting topic for further studies of gestural communication in the common raven.

On the whole, all analyzed gestures were dyadic gestures, i.e. gestures involving two individuals, being used to attract the attention of others to the self and /or to request actions from others (Pika 2008). This is surprising, as Pika and Bugnyar (2011) already observed raven individuals to use triadic signals, showing and offering, where the recipient's attention was attracted to a third entity referentially. Both signals were used mainly towards already attending recipients from the opposite sex, which would even be encouraged in the present study, as only mixed-sex dyads were investigated here. Thus, the present study could not confirm Pika and Bugnyar's finding that ravens use non-vocal signals triadically and referentially, similarly to pre-linguistic human children and great apes. The reason may be found in the study subject's relationships. While Pika & Bugnyar analyzed gestural communication in raven groups, where pair bonds may not yet have been established, the present study analyzed gestures in already established monogamous pairs. Pika suggested raven referential gestures to function as "testing signals" to evaluate the interest of a potential partner and/or to test and strengthen an already existing bond. The present study's findings support the former: as there was no potential partner anymore but an established pair-partner, there may have been no need to use testing signals anymore. Of course, the lack of referential gestures may again be due to the small sample size and more raven pairs as well as longer observation periods are needed to confirm or discharge this presumption.

Apart from using a larger sample size, future studies should consider including vocalizations in the data set, especially those which are used for communicative purposes between the pairpartners (e.g. "gro" calls, Gwinner 1964). It would be interesting to include the frequency of such intra-pair communication into the PCA. Furthermore, it may be interesting to assess how many vocalizations any observed pair has in common. According to Savage (2005), bird pairs tend to be more companionable and to spend more time socializing and preening one another's plumage, the more song elements they have in common. Thus, the number of common vocalizations may be an additional variable with a high loading on the value component of relationship quality. Beyond that, it would be interesting to assess the proportion of non-vocal signals to vocal signals in raven pairs and compare it between harmonic and inharmonic raven pairs.

It is important to bear in mind that all these results were obtained from captive birds, where interaction patterns are limited by space, and thus may not be representative for wild raven couples. For example, Gwinner (1964) observed captive ravens to preen each other more often than wild ravens which he ascribed to the lack of preoccupation in captivity. Apart from that, one might criticize that two individuals were subadult in the present study. However, this did not seem to influence relationship quality as one subadult female was part of a harmonic pair while the other belonged to an inharmonic pair. Furthermore, both females were already two years old and, according to literature, pair bonding usually occurs by age two, though the pairs are not likely to reproduce until their third or fourth summers at the earliest (Haffer et al. 1993, Savage 2005).

Conclusion

The present study aimed to answer two research questions: The first question concerned whether raven pairs differ in pair bond quality. In this context, it was predicted that subjecting the most common affiliative and agonistic interactions between pair-partners as well as proximity patterns to a PCA would lead to the extraction of specific relationship quality components. These components, in turn, would allow to group raven pairs into harmonic and inharmonic couples. The obtained results confirmed both predictions. Three components of relationship quality were extracted which indeed proved suitable to group raven pairs into harmonic pairs into harmonic pairs and four inharmonic pairs which were even found to differ in the characteristics of their relationships

within the group. Thus, the present study provided a positive answer to the first research question.

The second research question concerned whether relationship quality influences communicative exchange in raven pairs. Regarding this question the frequencies of communicative signals were predicted to differ between harmonic and inharmonic raven pairs. However, this was not the case in the present study. Neither the frequencies, nor the durations of specific communicative signals were found to be influenced by relationship quality, except in one of 24 signal types, where the duration per occurrence was significantly longer in harmonic than in inharmonic pairs. Furthermore, relationship quality did neither have a significant effect on the diversity of gestures, nor on the average number of gestures used in different signal categories. This also applied to the flexibility of gesture use and the escalation level for gestures used in agonistic contexts. Beyond that, no significant differences were found between harmonic and inharmonic pairs concerning communicative success, except for one signal type where harmonic pairs were communicatively more successful than inharmonic pairs. To sum up, there seemed to be no considerable effect of relationship quality on communicative exchange between pair-partners. Thus, the second research question has to be denied, at least according to the results obtained in the present study.

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Statuatory Declaration

I declare that I have authored this thesis independently, that I have not used other than the declared sources / resources – in particular no internet resources that are not named in the list of references – and that I did not submit this thesis to another examination procedure. The submitted version is consistent with that on the electronic storage medium. I agree on the publication of this master thesis.

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Signature

Date

Annex

Table 1: Study subjects

Pair no.	Location	Name	Sex	Status	hatc hing year	Age	origin	rearing	relation ship tenure (yrs)	mate choice	breeding success	if breeding success: reproduction exact (year + number of chicks)	previous partner?
1	MPI Seewiesen	Anton	М	adult	2010	3	Alpenzoo Innsbruck	captive parent	1	no	no	N/A	no
		Elen	F	adult	2010	3	Wildpark Bayrischer Wald	captive parent	-				no
2	Alpenzoo Innsbruck	Paul	М	adult	2004	9	Wildpark Schwarze Berge	captive parent	0	no	no	N/A	yes
		Flora	F	subadult	2011	2	Natur- u. Tierpark Goldau	captive parent	0				no
3	Tierpark Wels	Lo	М	adult	2004	9	KLF Grünau	handreared	7	yes	yes	2007 (3), 2009 (5), 2010 (4), 2012 (3)	no
		Thea	F	adult	2004	9	KLF Grünau	handreared	7				no
4	Tierpark Stadt Haag	Kämpfer	М	adult	N/A	7+	unknown	handreared	3	no	yes	2012 (1)	yes
		Lundi	F	adult	N/A	3-5	wilderness	wild parent	5				N/A
5	Tierpark Hellabrunn	Jakob	М	adult	2004	9	The Prague Zoological Garden The Prague Zoological	captive parent	parent 8		no	N/A	no
		Munin	F	adult	1990	23	Garden	unknown					yes
6	Alte Fasanerie Hanau	Jacob	М	adult	2006	7	Fasanerie Wiesbaden	captive parent	2	no	no	N/A	yes
		Babsi	F	subadult	2011	2	Tierpark Bielefeld	captive parent	-		110		0
7	Zoo Heidelberg	м	М	adult	2011	2	University of Bielefeld	captive parent	1	no	no	N/A	no
		Ivan	F	adult	2009	4	Private Collection	handreared	-				no
8	Naturpark Bayrischer	Gnaihir	М	adult	N/A	N/A	Zoolog. Garten Wuppertal	unknown 6 unknown		N/A	yes	2009 (2), 2010 (5), 2011 (4), 2012 (4),	yes
	Wald	Nemo	F	adult	2004	9	KLF Grünau					2013 (5)	yes
9	MPI Seewiesen	Jakob	М	adult	2010	3	Wildpark Bayrischer Wald	captive parent	parent 1		ves	2013 (3)	no
		Lena	F	adult	2010	3	Private, Kloster Neuburg	captive parent	-	,	yes	2013 (3)	no

V	Component							
variable	1	2	3	4	5			
Approaching	0,955	-0,176	0,024	0,057	0,148			
Contact sit	0,947	-0,201	0,068	0,072	0,123			
Affiliative Behaviours	0,913	-0,277	0,208	0,080	0,140			
Billing	0,828	0,082	0,052	-0,169	0,033			
Close proximity	0,663	-0,370	0,578	0,055	0,021			
Chasing away	-0,089	0,970	0,077	-0,140	0,003			
Agonistic Behaviours	-0,083	0,962	-0,052	0,055	-0,052			
Displacement	-0,253	0,856	-0,145	0,311	-0,104			
Moderate to low proximity	-0,422	0,592	-0,019	0,407	0,521			
Duration contact sit	-0,087	0,167	0,872	0,207	0,357			
Duration billing	0,522	-0,005	0,774	-0,222	-0,216			
Allo-preening	0,075	-0,582	0,718	-0,138	0,161			
Duration allo-preening	-0,237	0,029	0,119	0,949	0,104			
Following	0,399	0,141	-0,123	0,872	-0,043			
Low proximity	-0,392	-0,003	-0,459	-0,255	-0,742			
Close to moderate proximity	0,464	-0,389	0,056	-0,237	0,695			

Table 2: Varimax rotated component matrix. Values represent coefficients of correlation between each variable and each component and are sorted by size. Values of >0.5 or $<_0.5$ (marked in bold) were considered high loadings.

PRINCIPAL COMPONENT ANALYSIS

■ COMPONENT 1 ■ COMPONENT 2 ■ COMPONENT 3

2.75 2.25 1.75 1.25 0.75 0.25 -0.25 -0.75 -1.25 -1.75 HARMONIC INHARMONIC HARMONIC HARMONIC INHARMONIC HARMONIC INHARMONIC HARMONIC INHARMONIC -2.25 Innsbruck Wels Haag Munich Heidelberg Bayrischer Seewiesen 2 Seewiesen Hanau Wald **RAVEN PAIRS** Threshold component 1 Threshold component 3 Threshold component 2

Figure 1: Loading values for the first three components for all raven pairs including threshold values.



SIGNAL CATEGORIES - RECIPIENT ATTENDING

Figure 2: Average proportion of gestures used towards an attending recipient for harmonic and inharmonic pairs in four signal type categories: tactile signals, visual signals, tactile and auditory signals as well as visual and auditory signals. Error bars indicate the s.d.

Table 3: Proportions of signals in three categories which were used for definition of gestures as well as proportions ofsignals used as gesture or as non-gestural signal within a signal type for all specific communicative signals. Bold fonthighlights signal types being used as both gestural and non-gestural signals. unkn. = unknown, undec. = undecided

		cr									
Signal	direct	ed to a rec	ipient	mechanically ineffective		open to voluntary response		used as gesture			
	yes	no	unkn.	yes	no	yes	no	yes	no	undec.	
begging	100%	0%	0%	100%	0%	100%	0%	100%	0%	0%	
bent up display	80.0%	20.0%	0%	100%	0%	100%	0%	80.0%	0%	20.0%	
bowing display	83.4%	3.2%	13.4%	100%	0%	100%	0%	84.8%	2.3%	12.9%	
crude billing	100%	0%	0%	0%	100%	47.1%	52.9%	0%	100%	0%	
grab	100%	0%	0%	79.1%	20.9%	95.4%	4.6%	79.1%	20.9%	0%	
head up display	59.4%	4.6%	36%	100%	0%	100%	0%	60.5%	3.2%	36.4%	
hold	100%	0%	0%	100%	0%	100%	0%	100%	0%	0%	
hold beak	100%	0%	0%	100%	0%	100%	0%	100%	0%	0%	
kick	100%	0%	0%	100%	0%	100%	0%	100%	0%	0%	
open beak	100%	0%	0%	100%	0%	100%	0%	100%	0%	0%	
open up beak	100%	0%	0%	0%	100%	100%	0%	0%	100%	0%	
poke	100%	0%	0%	78.0%	22.0%	86.0%	14.0%	74.0%	26.0%	0%	
present	100%	0%	0%	100%	0%	100%	0%	100%	0%	0%	
pull	100%	0%	0%	0%	100%	27.6%	72.4%	0%	100%	0%	
push	100%	0%	0%	11.3%	88.7%	67.9%	32.1%	11.3%	88.7%	0%	
raise beak	100%	0%	0%	100%	0%	100%	0%	100%	0%	0%	
rattle beak	48.4%	14.5%	37.1%	100%	0%	100%	0%	48.4%	14.5%	37.1%	
shrug display	50%	0%	50%	100%	0%	100%	0%	50%	0%	50%	
small thin posture	100%	0%	0%	100%	0%	100%	0%	100%	0%	0%	
snap	100%	0%	0%	100%	0%	97.1%	2.9%	97.1%	2.9%	0%	
stare down	100%	0%	0%	100%	0%	100%	0%	100%	0%	0%	
thick head	74.7%	1.7%	23.7%	100%	0%	100%	0%	75.1%	2.1%	22.8%	
tilt head	100%	0%	0%	100%	0%	100%	0%	100%	0%	0%	
touch	100%	0%	0%	49.8%	50.2%	84.2%	15.8%	49.1%	50.9%	0%	



RESPONSE TO BOWING DISPLAY

Figure 3: Response to "bowing display" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "bowing display" signals.



Figure 4: Response to "kick" (visual version) in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "kick" signals.



Figure 5: Response to "kick" (tactile version) in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "kick" signals.

RESPONSE TO SHRUG DISPLAY



Figure 6: Response to "shrug display" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "shrug display" signals.



RESPONSE TO SNAP

Figure 7: Response to "snap" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "snap" signals.



RESPONSE TO THICK HEAD

Figure 8: Response to "thick head" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "thick head" signals.



RESPONSE TO TOUCH

Figure 9: Response to "touch" in harmonic and inharmonic raven pairs hour in an affiliative and agonistic context as well as for both contexts together. Shown are percentages of responses to all observed "touch" signals.



RESPONSE TO OPEN UP BEAK

Figure 10: Response to "open up beak" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "open up beak" signals.



Figure 11: Response to "poke" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "poke" signals.



RESPONSE TO PULL

Figure 12: Response to "pull" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "pull" signals.



Figure 13: Response to "push" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "hold beak" signals.



Figure 14: Response to "touch" in harmonic and inharmonic raven pairs. Shown are percentages of responses to all observed "touch" signals.