Social strategies and tool use in wild corvids

Thèse présentée à la Faculté des Sciences

Institut de Biologie, Université de Neuchâtel

Pour l'obtention du grade de docteur ès sciences

Par Di Lascio Felice Elias

Acceptée sur proposition du jury :

Prof. Redouan Bshary, directeur de thèse

Prof. Thomas Bugnyar, rapporteur

Prof. Klaus Zuberbühler, rapporteur

Présentée et soutenue le 28. 01. 2014

Faculté des sciences
Secrétariat-décanat de Faculté
Rue Emile-Argand 11
2000 Neuchâtel - Suisse
Tél: + 41 (0)32 718 2100
E-mail: secretariat.sciences@unine.ch

IMPRIMATUR POUR THESE DE DOCTORAT

La Faculté des sciences de l'Université de Neuchâtel autorise l'impression de la présente thèse soutenue par

Monsieur Felice Di Lascio

Titre:

"Social strategies and tool use in wild corvids"

sur le rapport des membres du jury composé comme suit:

- Prof. Redouan Bshary, Université de Neuchâtel, directeur de thèse
- Prof. Klaus Zuberbühler, Université de Neuchâtel
- Prof. Thomas Bugnyar, Université de Vienne, Autriche

Neuchâtel, 25 février 2014

Le Doyen, Prof. P. Kropf

Content (1/2)

Content (2/2)

Content **Pages**

Summary

Crows and ravens have attracted increasing attention because of the advanced cognitive capacities these birds seem to possess, which have earned them the nickname of “feathered apes”. Indeed, the work carried out in the last two decades has shown that corvids possess abilities that can rival those of monkeys and apes. Birds within this family tend to form long-term monogamous bonds, where pair partners support each other in agonistic encounters, collaborate to raise descendants, i.e., cooperate in a variety of contexts. The strong interdependency between mating partners and the high-qualitative nature of these relationships have been proposed to be the ground for the evolution of their higher intelligence; because in such relationships, pair partners need to coordinate their activities and eventually understand each other’s needs or intentions. In parallel, other experiments have shown that rooks (*Corvus frugilegus*) and New Caledonian crows (*Corvus moneduloides*) might use this intelligence to make use of tools and to understand the functional properties of these tools, even though rooks are not known to use tools in nature. Based on these two main species, currently, the most widely accepted idea is that tool use is not a specialized capacity present only in a few species of this group but rather a capacity that is shared among many representatives of this family. To date, the link between these remarkable capacities, their intelligence, presumably acquired in the context of pair bonding, remains contentious because most previous studies were carried out on small groups of captive birds. The aim of this thesis was to complement those previous studies with field observations / experiments to better understand whether laboratory results reflect the typical capacities of free-ranging birds by studying two different species of corvids, rooks and carrion crows (*Corvus corone corone*) in their natural habitat. Rooks are colonial breeding birds that live in dense colonies where conflicts over nesting material, females and nesting position are frequent. This first species is hence ideal to study conflicts and what cooperative strategies these birds use to limit the occurrence and consequences of conflicts. In chapter one we describe how rooks steal nesting material from other nests within the colony and studied whether close nesting pairs (neighbours) cooperate by avoiding to steal each other’s nesting material. Additionally, we studied how mating partners

coordinate between guarding the nest and collecting the required materials and whether this influences the frequency of thefts received at nest. In chapter two we examined in more details how rooks behave after a conflict. In particular we quantified the frequency of affiliative behaviours exchanged among former opponents (reconciliation) and between the victim or the aggressor and a third-party (consolation). Finally in chapter three, we studied whether wild carrion crows are able to solve a simple tool use task. The experimental apparatus consisted of a Plexiglas tube fixed on a wooden frame and placed in the field in which we inserted a piece of food. The crows had at their disposal the tools (hooked sticks) to extract the reward. The main results of chapter one are that rooks mainly stole twigs form neighbouring nests and that better coordinated pairs received fewer thefts. In chapter two pair partners exchanged higher frequencies of affiliative behaviours after a conflict happened compared to control situations whereas no such phenomenon was observed between former opponents. Finally, in chapter three our main finding is that carrion crows were unable to use the tools provided even having received several rewarded trial. Overall, the first two chapters indicate that rooks mainly cooperate with their mating partners and that other social relationships are less important given that they neither cooperated with close neighbours nor reconciled with former opponents. These findings confirm previous results on captive birds that all showed that rooks have a limited tendency to cooperate with other individuals than their mating partners. In contrast the findings of chapter three rather tend to strengthen the idea that tool use is a specialized capacity of some species and not a widespread capacity among corvids as has been suggested previously.

Key words: Group-living ● social cognition ● cooperation ● conflict management ● Dear enemy effect ● tool-use ● rooks ● carrion crows

Résumé

Les corvidés ont suscité un intérêt croissant ces dernières années à cause des capacités cognitives très développées que ces oiseaux semblent posséder. Ceci leur a valu le surnom de « singes à plumes ». En effet, les travaux de recherches menés ces deux dernières décennies ont montré que les corvidés possèdent des capacités cognitives qui pourraient rivaliser avec celles de certains singes. Les oiseaux au sein de cette famille ont tendance à former des couples monogames sur le long terme. Dans ces relations les partenaires se soutiennent mutuellement lors de conflits avec d'autres individus, collaborent pour élever leurs descendants, en bref, coopèrent dans une variété de contextes. La forte interdépendance entre partenaires de reproduction ainsi que la nature hautement qualitative de ces relations ont été proposées comme étant la base ayant servi à l'évolution de l'intelligence supérieure de ces oiseaux, car dans une telle relation, les partenaires doivent coordonner leurs activités et donc comprendre les besoins ainsi que les intentions de l'autre. En parallèle, d'autres expériences menées en captivité ont montré que les corbeaux freux (*Corvus frugilegus*) et les corbeaux de Nouvelle-Calédonie (*Corvus moneduloides*) pourraient faire usage de cette intelligence pour se servir et comprendre les propriétés fonctionnelles d'outils, alors qu'étonnamment les corbeaux freux ne se servent pas d'outils dans la nature. Sur la base des observations faites sur les deux espèces susmentionnées, à l'heure actuelle, l'idée la plus largement acceptée est que l'utilisation d'outils n'est pas une capacité spécialisée présente uniquement chez quelques espèces au sein de ce groupe mais bien une capacité partagée par la plupart des espèces de cette famille d'oiseaux. A ce jour, le lien entre ces capacités remarquables, leur intelligence, vraisemblablement acquise dans le contexte de la vie de couple, reste controversé car la plupart des expériences précédemment menées, ont porté sur de petits groupes d'oiseaux élevés en captivité. Le but principal de cette thèse était par conséquent de compléter ces études antérieures grâce à des observations et des expériences menées sur le terrain de façon à mieux comprendre si les résultats obtenus en laboratoire reflètent les capacités d'oiseaux vivant en liberté en étudiant deux espèces de corvidés : les corbeaux freux et les corneilles (*Corvus corone corone*) dans leur habitat naturel. Les

corbeaux freux sont des oiseaux qui vivent et se reproduisent dans des colonies densément peuplées ce qui a pour conséquence que les conflits pour le matériel de nidification, l'accès aux femelles ou encore les sites de nidification sont fréquents. Cette première espèce est donc idéale pour étudier et mieux comprendre les conflits et les stratégies coopératives mis en œuvre par ces oiseaux afin d'en réduire la fréquence ainsi que les conséquences. Dans le chapitre un, nous décrivons en détail comment les corbeaux freux volent le matériel de nidification sur les nids d'autres couples au sein de la colonie. En outre, nous avons étudié si les couples nichant à proximité les uns des autres (voisins) coopèrent dans ce contexte en évitant de se voler réciproquement. De plus, nous avons étudié la manière dont les partenaires au sein du couple se coordonnent de manière à surveiller le nid et à collecter les matériaux nécessaires à la construction du nid. Nous avons cherché à comprendre dans quelle mesure la coordination du couple influe sur la fréquence à laquelle ils se font voler. Dans le deuxième chapitre, nous avons examiné plus en détail la façon dont se comportent les corbeaux freux à la suite d'un conflit. Plus spécifiquement, nous avons cherché à quantifier la fréquence des comportements affiliatifs échangés entre anciens adversaires (réconciliation) ainsi que la fréquence de ces comportements amicaux entre la victime ou l'agresseur et une troisième partie (consolation). Finalement, dans le chapitre trois, nous avons étudié si des corneilles sauvages sont capables de résoudre un problème nécessitant l'utilisation d'un outil. A cette fin, nous nous sommes servis d'un tube de plexiglas fixé sur un cadre en bois. Ce dernier était placé à différents endroits sur le terrain. Dans le tube, nous avons ensuite inséré un morceau de nourriture et les corneilles avaient à leur disposition des outils (branche pourvue à l'une de ces extrémités d'un crochet) afin d'extraire la nourriture du dispositif expérimental. Les principaux résultats du chapitre un indiquent que les corbeaux freux volent des branches principalement sur les nids voisins et que les couples les mieux coordonnés étaient ceux qui se faisaient voler du matériel de nidification le moins fréquemment. Dans le chapitre deux, les résultats indiquent que les partenaires au sein du couple échangeaient des comportements affiliatifs à des fréquences plus élevées à la suite d'une agression que dans des situations contrôles. A l'inverse, un tel phénomène n'a pas été observé entre anciens adversaires. Finalement, les résultats du troisième et dernier chapitre indiquent que les corneilles ne sont pas en mesure de se servir des outils que nous leurs avons mis à disposition et cela même après avoir reçu plusieurs essais récompensés. Dans

l’ensemble, les deux premiers chapitres indiquent que les corbeaux freux coopèrent principalement avec leurs partenaires de reproduction et que d’autres relations sociales sont moins importantes étant donné qu’ils n’ont ni coopéré avec leurs voisins ni ne se sont réconciliés avec leurs anciens adversaires. Ces découvertes confirment les résultats d’études antérieures menées sur des oiseaux captifs, c’est-à-dire, que ces animaux ont une tendance limitée à coopérer avec d’autres individus de leur espèce en dehors de leur partenaire de reproduction. A l’inverse, les résultats du chapitre trois tendent à renforcer l’idée que la capacité à utiliser des outils est limitée à certaines espèces au sein de ce groupe plutôt qu’une capacité plus largement répandue parmi le groupe des corvidés comme cela a été suggéré précédemment.

Mots-clés: Vie de groupe ● cognition sociale ● coopération ● gestion de conflits ● utilisation d’outils ● corbeaux freux ● corneilles

General introduction

(a) Cooperation and group living

Cooperation and group living is widespread among animals including humans and apparently poses a challenge to the theory of natural selection proposed by Darwin more than 150 years ago (Darwin 1859). His theory emphasises that individuals will compete over resources in order to maximise their own fitness. Therefore, cooperative behaviours will strongly be selected against if co-operators and selfish individuals coexist within the same population. This is not what we observe in nature and the large scale cooperation in human societies is certainly the most striking counter-example since we interact in a positive way with our family members, friends, colleagues and to some extent, even with totally unknown and unrelated persons (West et al. 2006; Dubreuil 2008). Hence, why do we observe seemingly altruistic acts in humans and non-human animals? Since Hamilton's seminal publication (Hamilton 1964[a,b]) a large body of theoretical and empirical work has shown that cooperative acts can be understood within the framework of the inclusive fitness theory (Reviewed in: Lehmann and Keller 2006; West et al. 2007). This theory predicts that individuals will only help others when they either receive indirect genetic benefits by helping relatives (Hamilton 1964[a,b]) or direct benefits from the receiver they were interacting with (Trivers 1971) or via third-parties (Alexander 1987, Nowak and Sigmund 1998, Wedekind and Milinski 2000; Nowak & Sigmund 2005). Hence, the work carried out during the last decades has shown that altruism, defined as an act that increases the fitness of the receiver and that decreases the fitness of the performer, is under negative selection, and that apparently altruistic acts are in most cases underpinned by benefits, even if they are not obvious at first glance. One of the major actual challenges for scientists interested in cooperation, group living or more generally behavioural ecology, is to better understand the mechanisms that maintain cooperation in nature.

(b) Costs and benefits of group living

When living and cooperating in groups, individuals, at very least, need to coordinate their behaviours as otherwise social groups would not be maintained. Hence, group living in its simplest form (Selfish herd: Hamilton 1971), already involves costs in the form of coordination efforts (Noe 2006). Furthermore, when living in dense aggregations individuals often compete and conflict over resources or space (e.g., rooks: Henderson and Hart 1991) what represent additional costs. On the other hand there are also numerous benefits that emerge as a by-product form the life within a group, such as enhanced predator defence (Sridhar et al. 2009) or improved food localisation (Ward and Zahavi 1973; Brown 1986; Green 1987; Marzluff et al. 1996). The overall benefits should outweigh the costs of sociality as otherwise we would not observe animal societies in nature (Krause and Ruxton 2002). Nevertheless, as conflicts cannot be avoided, particular behavioural responses or mechanisms that tend to reduce or limit the costs of conflicts must be under positive selection.

(c) Conflict management strategies as a way to reduce the costs of group living

Hierarchies are a first mechanism by which individuals can reduce the costs of sociality. By knowing where they stand within the group, individuals can avoid useless struggles (Schjelderup-Ebbe 1922). Additionally it has also been documented in some species that social tolerance is increased among close neighbours a phenomenon known as the dear enemy effect (Fisher 1954). The higher social tolerance among neighbours is a second mechanism by which individuals can avoid the costly consequences of agonistic encounters with their conspecifics, i.e., neighbours do not constantly fight over the borders of their territories or other resources (reviewed in: Temeles 1994). This second phenomenon has been studied mainly in solitary living species, but might also apply to group living animals that occupy small sub-territories within the group, such as colonial breeding birds. While these two first mechanisms might contribute to reduce the costs of group living, conflicts still happen. Conflicts that result from competitive situation are detrimental to all individuals involved and one way to restore disturbed relationships or to offset the costs after struggles is to reconcile with one former opponent (Aureli et al. 2002) or to be consoled by third-parties (de Waal and Van Roosmalen 1979; Watts et al. 2000). In some species both types of conflict management mechanisms coexist whereas in others, individuals do not reconcile, depending on the social systems of the species of interest (Aureli et al. 2002). These have been called post-conflict affiliative behaviours and were first studied in monkeys and apes (Aureli and de Waal 2000). The overall result of these adaptations is social stability, where by pursuing a self-serving goal, each individual will contribute to the success of own group (Roberts 2005, Bergmüller and Taborsky 2005; Bshary and Bergmüller 2008).

(d) Group living and cognition

Group living has also been of interest for many scientists interested in social cognition because sociality has been suggested to be associated with larger brains compared to solitary life-styles (Dunbar and Shultz 2007). While this might be a general trend observed in many social mammalians since ancestral times (Shultz and Dunbar 2010[a]), the first species that were studied in this regard were primates.

Indeed it seems that group living played a major role in the evolution of their higher cognitive abilities (Jolly 1966; Humphrey 1976; Barton 1996; Dunbar 1998) whereas other factors (the physical world, the feeding ecology etc) played only a secondary role (However see: van schhaik et al. 2012). This is well illustrated by the work of Dunbar (1992) where he showed that the neocortex size of primates, thought to reflect high cognitive abilities, relativized by the size of other brain parts, is positively correlated with the social group size of those species. This has been called the social brain hypothesis (Dunbar 1998) and can be summarized as follows: because behaviours in the social world are hard to predict, individuals need achieve high brain power to remember who is whom, who did what to whom or what is the relative rank of a given individual within a particular social group to behave appropriately, i.e., to behave in a socially competent way. Intriguingly, the relationship between the size of social groups and relative brain sizes, expected to predict higher cognitive abilities, revealed to be untrue for certain species, in particular for birds (Emery et al. 2007).

(e) Group living and cognition in birds

When investigating, the factors that favoured the evolution of higher intelligence in birds, it seems that monogamy, rather than group size, predicts the smartness of species (Emery et al. 2007, Shultz and Dunbar 2010[b]). In other words, and contrast to primates, rather than number of relationships within the group it is the quality of long-term relationships that likely favoured the evolution of high cognitive capacities in birds because individuals need to coordinate their behaviours and eventually understand each other's needs or intentions (Emery et al. 2007, Shultz and Dunbar 2010[b]). However this claim remains contentious (See: Scheiber et al. 2008; Shettleworth 2010).

When looking closer at the relative brain sizes of species within avian taxa it seems that two groups clearly detach form the rest: Corvids and Parrots (Emery et al. 2007, Shultz and Dunbar 2010[b], Jonsson et al. 2012). Species of both groups indeed show intriguing capacities (Emery et al. 2007). Hence, while the cognitive capacities of these birds arouse independently, our current state of knowledge suggests that corvids and primates converged in their cognitive capacities (Emery and Clayton 2004; Emery 2006). This gave corvids the nickname of "feathered apes". Next to their convergent evolution in their cognitive capacities with monkeys and apes, it seems that a range of other behavioural adaptations tended to become strikingly similar to the latter in the course of evolution. For instance, one interesting aspect of corvids social life is that when being confronted with aggressive encounters, individuals seem to show post-conflict affiliative behaviours that are similar to those observed in other social vertebrates (rooks: Seed et al. 2007; ravens: Fraser and Bugnyar 2010[a,b]; Fraser and Bugnyar 2011; comparative studies on jays, jackdaws and rooks: Logan et al. 2013; Logan and Clayton 2013). These post-conflict friendly interactions seem to reduce costs of aggression in group living species as outlined earlier. Corvids are an interesting group to study in this respect because in this family, its representatives show different social systems, varying from strictly territorial to colonial breeding species, with varying conflict management mechanisms (See: Logan et al. 2013, Logan and Clayton 2013). For instance studies in captivity have shown that ravens, a territorial species, are consoled by their affiliates and that they reconcile with former opponents (Fraser and Bugnyar 2010[a,b]; Fraser and Bugnyar 2011). In contrast rooks, that are colonial breeders only affiliate with pair partners (Seed et al. 2007). These were until relatively recently mainly studied in captivity with very little information at hand about wild birds (However see: Braun and Bugnyar 2012; Braun et al. 2012).

(f) Cognition and tool use

Tool use, defined as the use of an external object for the achievement of a particular goal (Beck 1980), is a capacity that is widespread across taxa but nevertheless relatively rare if considering the number of species that exhibit this kind of behaviours (Hansell and Ruxton 2008). Again, some corvid species seem to be surprisingly similar to other big brained species that use tools. Among corvids, New Caledonian crows seem to be the most prolific tool users in this group. Indeed previous studies have shown that these birds flexibly use tools in the wild and in captivity when being tested for it (For a review on tool use in New Caledonian crows see: Rutz and St Clair 2012). This corresponds to the observation that tool use is an ecologically relevant capacity in this species that use hooks to extract larvae from decaying tree trunks in their natural habitat (Bluff et al. 2010). More surprising are the capacities of rooks (*Corvus frugilegus*), that have shown to be good tool users when being tested in controlled conditions in captivity even though they are not known to use tools in the wild (Bird and Emery 2009[a,b]). To explain the unexpected capacities of rooks, some authors have proposed that corvids are generally smart birds and that as a by-product, these birds are able to use, modify or combine tools when needed (Bird and Emery 2009[a]; see also: Jonsson et al. 2012). As outlined earlier, it seems that their higher intellect has emerged as a consequence of long-term bond lifestyle (Emery et al. 2007, Shultz and Dunbar 2010[b]; However see also Scheiber et al. 2008 for a divergent opinion). Hence, the link between the capacity to use tools and their superior intelligence has been implicitly suggested (Bird and Emery 2009[a]). To better understand why corvids have evolved high cognitive abilities and may utilize this intelligence to understand the functional properties of tools and whether the capacity to use tools is as widespread as has been suggested more species in the corvid family need to be tested in this respect.

(g) Captive vs wild studies: the importance of studying corvids in their natural habitat

While pioneer studies on ravens were carried out mainly with wild birds and / or had a high ecological validity (Marzluff and Heinrich 1996; Bugnyar and Kotrschal 2001, 2002, 2004) more recent studies on rooks and other corvid species were largely conducted using a small number of trained individuals on ecologically less relevant questions (Helme et al. 2006; Seed et al. 2008; Bird and Emery 2009[a,b]; 2010, Di Lascio et al. 2013) where most current hypothesis are based on the latter studies. For instance, rooks (*Corvus frugilegus*) were studied in captivity for two main aspects: (i) first they were studied for their conflict management strategies (Seed et al. 2007; Logan et al. 2013; Logan and Clayton 2013) and second (ii) for their capacity to use tools (Bird and Emery 2009[a,b]). These studies revealed that rooks have evolved interesting conflict management strategies comparable to other social species and that they were surprisingly good at understanding the functional properties of tools. However, when summarizing the state of knowledge at the moment, it seems that very little is actually known about other species in this group with respect to tool use. In fact mainly two species were studied in this respect; rooks and New Caledonian crows, where the former were only tested in captivity. Furthermore, with respect to conflict management and the ontogeny and maintance of their social bonds, rooks were exclusively studied in captivity (Emery et al. 2007).

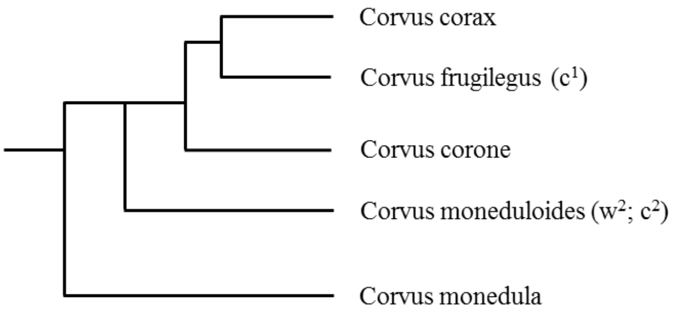

Figure 1. Simplified phylogenetic tree of the five main studied species in the corvus genera. c if for studied in captivity, w is for studied in the wild. Are considered only those studies that aimed at testing the capacity to use tools. [1]Bird and Emery 2009; [2]Rutz and St Claire 2012.

Studies on conflict management in other species, for instance primates, have shown that sometimes animals show higher rates of affiliations when studied in enclosures than when being observed in their natural habitat (reviewed in: Colmenares 2006). Furthermore, when studying animals on their cognitive capacities, it seems that generally, captive animals are better at solving these problems than their wild counterparts. In particular, phenomena like enculturation or higher rates of exploration (boldness) have been proposed to account partly for the better performance of hand raised individuals (Thornton and Lukas 2012).

(h) Aims of the project

The aim of this thesis was to study wild corvids in order to complement captive studies on conflict management strategies and tool use abilities. In the context of tool use, testing wild animals allows excluding confounding effects such as previous experience, given that wild birds are very likely naïve regarding such experiments. We studied two species of free living corvids: (i) rooks that are colonial breeders where conflicts over nesting position or other resources are frequent during the breeding season (Coombs 1960), hence ideal to study conflicts and the mechanisms used to reduce those costs and the possible cooperative strategies used by these birds in competitive situations; (ii) carrion crows for their capacity to use tools. Carrion crows were chosen as second species because in contrast to rooks they were willing to interact with the experimental set up. They seem to be a suitable study species due to their close relatedness to rooks (Jonsson et al. 2012) and because they have a similar ecology to the former (Haffer and Bauer 1993). To our knowledge carrion crows were never tested before on their capacity to use tools. Given their relatively closer phylogenetic relationship to rooks than to New Caledonian crows they are a good species to test the hypothesis of Bird and Emery (2009[a]) that the general cognitive tool box of corvids allows them to solve tool-use tasks independently of ecological relevance.

(i) Specific questions of this thesis

In chapter one, we studied one interesting behaviour rooks show during the breeding season. Rooks build their nests in dense colonies by either collecting nest material from surrounding trees or by stealing branches from other nests (Coombs 1960). During nest construction, mating partners alternate roles between guarding the nest to prevent theft and collecting branches. Interestingly, nests are usually constructed in close proximity to a neighbour, leading to multiple opportunities for cooperation or resource competition between close neighbours. We focussed our study on neighbourhood relationships in a naturally occurring colony of wild rooks by studying the stealing patterns in this species. We described the frequency of nest material stealing in order to address two main questions. First, we quantified the stealing behaviour and frequency of breeding pairs with respect to neighbour vicinity/proximity which we used then to determine whether neighbour avoid stealing each other nesting material or if they would eventually cooperate by defending mutually their territories. Second, we also asked whether the presence of pair partners at the nest influences the frequency of thefts received. In other words we asked whether cooperation (coordination of behaviour) between mating partners helps preventing thefts. Overall chapter one aimed at quantifying some of the costs of colonial breeding and identifying the cooperative strategies used by these birds to limit those costs, either between pair partners or with close neighbours to better understand the sociality of this species in the wild.

In chapter two, we studied the conflict management strategies used by rooks in the wild following an aggression. We quantified the frequency of affiliative behaviours exchanged between former opponents (reconciliation) and between combatants and third-parties (consolation) after an aggression happened. Those strategies have been studied in many details in captivity previously and the results described in chapter two are a first comparison with wild animals.

In chapter three, we studied the capacity of wild carrion crows to use sticks as tools in order to obtain high quality food that was otherwise inaccessible. The food was placed inside a Plexiglas tube. In the first part of the experiment we placed the tools next to the apparatus to measure whether the crows would spontaneously start using the tool. In case of initial failure, we would pre-insert the tools into the apparatus in subsequent steps to increase the likelihood that animals would start using the tools offered.

Previous studies in captivity on rooks have shown that these birds mainly cooperate among pair partners and that other relationships are less important (Emery et al. 2007; Seed et al. 2007; Seed et al. 2008). However, a certain disadvantage to these studies is that they were based on a small number of captive birds where individuals are forced to live together and where relatedness between group members probably doesn’t reflects what happens in nature. In contrast early anecdotes have suggested that neighbours collaborate to defend their territory (Yeates 1934; Coombs 1960). Based on recent studies, we predict that at very least, pairs partners should cooperate in both contexts: (a) defending their nest and (b) following aggression by affiliating at higher rates. Whether or not neighbouring pairs will cooperate by not stealing each other’s nesting material or by cooperatively defending their territory is harder to predict.

Regarding tool use in carrion crows, we expected that because of their close relatedness with rooks (Jonsson et al. 2012) they would be able to solve our artificial tool use task though we were agnostic on whether they could solve the task spontaneously or after receiving extra training. We hope that the current thesis will contribute to a better understanding of rooks’ sociality and complement recent experiment on tool-use in corvids and give us a broader picture of the presence of this capacity in this group of birds.

(j) References general introduction

Alexander, R.D. 1987. The biology of moral systems. Aldine de Gruyter, New York.

Aureli, F. & de Waal, F. B. M. 2000. *Natural conflict resolution.* Berkley: University of California Press.

Aureli, F., Cords, M. & Van Schaik, C. P. 2002. Conflict resolution following aggression in gregarious animals: a predictive framework. *Anim. Behav.*, 64, 325-343.

Barton, R. A. 1996. Neocortex size and behavioural ecology in primates. *Proceedings of the royal society of London Series B*, 263, 173-177.

Beck, B. B. 1980. Animal tool behaviour: the use and manufacture of tools by animals. Garland STPM Publishing, New York, NY.

Bergmüller, R. & Taborsky, M. 2005. Experimental manipulation of helping in a cooperative breeder: helpers 'pay to stay' by pre-emptive appeasement. *Anim. Behav.*, 69, 19-28.

aBird, C. D. & Emery, N. J. 2009. Insightful problem solving and creative tool modification by captive nontool-using rooks. *PNAS*, 106, 10370-10375.

bBird, C. D. & Emery, N. J. 2009. Rooks use stones to raise the water level to reach floating worm. *Curr. Biol.*, 19, 1410-1414.

Bird, C. D. & Emery N. J. 2010. Rooks perceive support relations similar to six-month-old babies. *Proc. R. Soc. B.*, 277, 147-151.

Bluff, L. A., Troscianko, J., Weir, A. A. S., Kacelnik, A. & Rutz, C. 2010. Tool use by wild new caledonian crows Corvus moneduloides at natural foraging sites. *Proc. R. Soc. B.*, 277, 1377-1385.

Braun, A. & Bugnyar, T. 2012. Social bonds and rank acquisition in raven nonbreeder aggregations. *Anim. Behav.*, 84, 1507-1515.

Braun, A., Walsdorff, T., Fraser, O. N. & Bugnyar, T. 2012. Socialized sub-groups in a temporary stable raven flock? *J. Ornithol.*, 153, 97-104.

Brown, C. R. 1986. Cliff swallow colonies as information centres. *Science*, 234, 83-85.

Bshary, R. & Bergmüller, R. 2008. Distinguishing four fundamental approaches to the evolution of helping . *J. Evol. Biol.*, 21, 405-420.

Bugnyar, T. & Kotrschal, K. 2001. Movement coordination and signalling in ravens (corvus corax): an experimental field study. *Acta. Ethol.*, 3, 101-109.

Bugnyar, T. & Kotrschal, K. 2002. Scrounging tactics in free-ranging ravens, corvus corax. *Ethol.*, 108, 993-1009.

Bugnyar, T. & Kotrschal, K. 2004. Leading a conspecifc away from food in ravens (Corvus corax)? *Anim. Cogn.*, 7, 69-76.

Colmenares, F. 2006. Is postconflict affiliation in captive nonhuman primates an artifact of captivity? *International Journal of Primatology*, 27, 1311-1336.

Coombs, C. J. F. 1960. Observations on the rook corvus frugilegus in southwest Cornwall. *Ibis*, 102, 394-419.

Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London.

de Waal, F. B. M & van Roosmalen, A. 1979. Reconciliation and consolation among chimpanzees. *Behavioral Ecology and Sociobiology*, 5, 55-66.

Di Lascio, F., Nyffeler, F., Bshary, R. & Bugnyar T. 2013. Ravens (Corvus corax) are indifferent to the gain of conspecific recipients or human partners in experimental tasks. *Anim. Cogn.*, 16, 35-43.

Dubreuil, B. 2008. Strong reciprocity and the emergence of large-scale societies. *Philosophy of the social sciences*, 38, 192-210.

Dunbar, R. I. M. 1992. Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, 20,469-493.

Dunbar, R. I. M. 1998. The social brain hypothesis. *Evolutionary anthropology*, 6, 178-190.

Dunbar, R. I. M. & Shultz, S. 2007. Evolution in the social brain. *Science*, 317, 1344-1347.

Emery, N. J. & Clayton, N. S. 2004. The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, 306, 1903.

Emery, N. J. 2006. Cognitive ornithology: the evolution of avian intelligence. *Phil. Trans. R. Soc. B.*, 361, 23–43.

Emery, N. J., Seed, A. M., von Bayern, A. M. P. & Clayton, N. S. 2007 Cognitive adaptations of social bonding in birds. *Phil. Trans. R. Soc.* B. 362, 489-505.

Fisher, J. 1954. Evolution and bird sociality. In: Evolution as a process (Huxley, J.,

Hardy, A.C. & Ford, E.B., eds). Allen and Unwin, London, pp. 71-83.

aFraser, O. N., & Bugnyar, T. 2010. Do ravens show consolation? responses to distressed others. *PLoS ONE*, e10605.

bFraser, O. N. & Bugnyar, T. 2010. The quality of social relationships in ravens. *Anim. Behav.*, 79, 927–933.

Fraser, O. N. & Bugnyar, T. 2011. Ravens reconcile after aggressive conflicts with valuable partners. *PLoS ONE*, e18118.

Greene, E. 1987. Individuals in an osprey colony discriminate between high and low quality information. *Nature*, 329, 239-241.

Haffer, J. & Bauer, K. 1993. in *Handbuch der Vögel Mitteleuropas*- teil III Passeriformes, eds Glutz von Blotzheim UN, Bauer KM (Aula-Verlag Wiesbaden) pp1733-1857.

aHamilton, W. D. 1964. Genetical evolution of social behaviour I. *Journal of theoretical biology*, 7, 1-16.

bHamilton, W. D. 1964. Genetical evolution of social behaviour II. *Journal of theoretical biology*, 7, 17-52.

Hamilton, W. D. 1971. Geometry for the selfish herd. *J. Theor. Biol.*, 31, 295–311.

Hansell, M. & Ruxton, G. D. 2008. Setting tool use within the context of animal construction behaviour. *Trends Ecol. Evol*., 23, 73-78.

Helme, A. E., Clayton, N. S. & Emery, N. J. 2006. What do rooks (Corvus frugilegus) understand about physical contact? *J. Comp. Psychol.*, 120, 288-293.

Henderson, I. G. & Hart, P. J. B. 1991. Age-specific differences in the winter foraging strategies of rooks corvus frugilegus. *Oecologia*, 85, 492-497.

Humphrey, N. K. 1976. The social function of intellect. In: Bateson, P. & Hinde, R. A. (eds) *Growing points in ethology* (pp. 303-321). Cambridge: Cambridge University Press.

Jolly, A. 1966. Lemur social behavior and primate intelligence. *Science*, 153, 501-507.

Jonsson, K. A.; Fabre, P. H. & Irestedt, M. 2012. Brains, tools, innovation and biogeography in crows and ravens. *BMC Evol. Biol*., 12:72.

Kacelnik, A. 2009. Tools for though or thoughts for tools? *PNAS*, 106, 10071-10072.

Krause, J. & Ruxton, G. D. 2002. Living in groups. Oxford, UK: Oxford university press.

Lehmann, L. & Keller, L. 2006. The evolution of cooperation and altruism – a general framework and a classification of models. *J. Evol. Biol.*, 19, 1365-1376.

Logan, C. J. & Clayton, N. S. 2013. Rook, but not jackdaw, post-conflict third-party affiliation reduces aggression for aggressors. *Ethol.*, 119, 1-9.

Logan, C. J., Emery, N. J. & Clayton, N. S. 2013. Alternative behavioural measures of postconflict affiliation. *Behav. Ecol.*, 24, 98-112.

Marzluff, J. M., Heinrich, B. & Marzluff, C. S. 1996. Raven roosts are mobile information centres. *Anim. Behav*., 51, 89-103.

Noe, R. 2006. Cooperation experiments: coordination trough communication versus acting apart together. *Anim. Behav*., 71, 1-18.

Nowak, M. A. & Sigmund, K. 1998. Evolution of indirect reciprocity by image scoring. *Nature*, 393, 573–577.

Nowak, M & Sigmund, K. 2005. Evolution of indirect reciprocity. *Nature*, 437, 1291-1298.

Roberts, G. 2005. Cooperation through interdependence. *Anim. Behav.*, 70, 901-908.

Rutz, C. & St Clair, J. J. H. 2012. The evolutionary origins and ecological context of tool use in New Caledonian crows. *Behav. Process*., 89, 153-165.

Scheiber, I. B. R., Weiss, B. M., Hirschenhauser, K., Wascher, C. A. F., Nedelcu, I. T. & Kotrschal, K. 2008. Does „relationship intelligence“ make big brains in birds? *The open biological journal*, 1, 6-8.

Schjelderup-Ebbe, T. 1922. Beiträge zur Sozialpsychologie des Haushuhns. *Z. Psychol.*, 88, 225-252.

Seed, A. M., Clayton, N. S. & Emery, N. J. 2007. Post-conflict third-party affiliation in rooks (Corvus frugilegus). *Curr. Biol.*, 17, 152-158.

Seed, A. M., Clayton, N. S. & Emery, N. J. 2008. Cooperative problem solving in rooks (Corvus frugilegus). *Proc. R. Soc. B.*, 275, 1421-1429.

Shettleworth, S. J. 2010. Clever animals and killjoy explanations in comparative psychology. *Trends in cognitive sciences*, 11, 477-481.

aShultz, S. and Dunbar, R. I. M. 2010. Encephalization is not a universal macroevolutionary phenomenon in mammals but is associated with sociality. *PNAS*, 107, 21582–21586.

bShultz, S and Dunbar, R. I. M. 2010. Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment. *Biological journal of the linnean society*, 100, 111-123.

Sridhar, H., Beauchamp, G. & Shanker, K. 2009. Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Anim. Behav.*, 78, 337-347.

Temeles, E. 1994. The role of neighbours in territorial systems: when are they ‘dear enemies’? *Anim. Behav*., 47, 339-350.

Thornton, A. & Lukas, D. 2012. Individual variation in cognitive performance: developmental and evolutionary perspectives. *Phil. Trans. R. Soc*. B., 367, 2773-2783.

Trivers, R. L. 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.* 46, 35-57.

Ward, P., & Zahavi, A. 1973. The importance of certain assemblages of birds as “Information centres” for food finding. *Ibis*, 115, 517-534.

Watts, D. P., Colmenares, F. & Arnold K. 2000. Redirection, consolation and male policing: How targets of aggression interact with bystanders. In: Natural Conflict Resolution (Ed. by F. Aureli & F. B. M. de Waal), pp. 281-301. Berkeley, California: University of California Press.

Wedekind, C. & Milinski, M. 2000. Cooperation through image scoring in humans. *Nature* 288, 850-852.

West, S. A., Gardner, A., Shuker, D. M., Reynolds, T., Burton-Chellow, M., Sykes, E. M., Guinnee, M. A. & Griffin, A. S. 2006. Cooperation and the scale of competition in humans. *Curr. Biol.*, 16, 1103-1106.

West, S. A., Griffin, A. S. & Gardner, A. 2007. Evolutionary explanations of cooperation. *Curr. Biol.*, 17, 661-672.

Yeates, G. K. 1934: The life of the rook. London.

Chapter 1

Title manuscript 1: Pair partners in rooks (Corvus frugilegus) coordinate to cope with the costs of theft of nest material

Authors: Felice Di Lascio[1]; Redouan Bshary[1]; Anne-Cécile Dagaeff[2] & Ralph Bergmüller[1]

[1]Université de Neuchâtel, 2000 Neuchâtel, Rue Emile-Argand 11, Switzerland

[2]Laboratoire Evolution et Diversité Biologique (EDB), UMR 5174, Université Paul Sabatier, 118 Route de Narbonne, F-31062 Toulouse, France

(a) Abstract

Sociality typically involves conflicts between group members and social relationships are often involved in coping with the resulting costs. Rooks (*Corvus frugileus*) are a colonial species in which social life in the reproductive season is characterised by a high degree of conflict resulting from twig stealing from other pairs' nests within the colony. We studied the patterns and consequences of twig stealing within one colony of free-ranging birds and the potential social strategies the birds use to limit the occurrence of thefts, focussing on social relationships between nest neighbours and on coordination of behaviour between pair partners. Most stealing events occurred while nest owners were absent, suggesting that guarding the nest is of vital importance to prevent thefts. Pairs with higher coordination scores suffered less from thefts than other pairs in the colony and were also faster in constructing their nests. We compared the frequency of thefts among immediate neighbours with thefts at more distant nests to determine whether there is higher tolerance among close neighbours (i.e., a "dear enemy effect"). However, the birds preferentially stole twigs from nearby nests, suggesting they economically optimise travel time from their own

nest. Overall, our results suggest high levels of conflict among colony members and close cooperation only among pair partners, indicating that rooks particularly rely on pair bonds and associated pair nest guarding to cope with the costs of conflicts arising from colony life.

Key words: Group living ● colonial breeding ● Dear enemy effect ● pair coordination ● rooks ● Corvus frugilegus

(b) Introduction

Why individuals live in groups is a fundamental question for understanding the evolution of sociality (Krause & Ruxton 2002). While benefits of group living arise due to reduced risk of predation (Hamilton 1971), increased foraging success (Beauchamp 1998) or the opportunity to share information (Torney et al. 2011), these benefits need to outweigh the involved costs emerging from competition over resources and mating partners (West-Eberhard 1979). In many colonial breeding birds, individuals compete over most resources of their natural environment and colonies may be described as selfish herds (Hamilton 1971), where the costs of sociality often seem obvious, while their benefits are less clear (Roland et al 1998, Danchin & Wagner 1997). For instance, colonial birds frequently steal nesting material form each other's nests (e.g., penguins: Carrascal et al. 1995; Moreno et al. 1995; herons: Afkami & Strassmann 2007; Weavers: Roulin 1999). This behaviour has been described in a range of species and has been suggested to occur more frequently when, for instance, the nesting material is scarce or costly to obtain (Carrascal et al. 1995). A recent review about the energetic costs associated with nest building and their impact on successful reproduction has suggested that these costs can be substantial (Mainwaring & Hartley 2013). The costs of successful nest construction should be particularly high in species in which stealing of nest material from the nest is common. Costs result from collecting new material and from defending the nest against thieves. In such a situation cooperation among mating partners might be crucial (Emery et al. 2007). For instance, in rooks (*Corvus* *frugileus*) it has been reported that pair partners will typically alternate their roles between guarding the nest and collecting the required materials during the nest construction period, especially when competition over nesting material is intense (Coombs 1960).

While kleptoparasitism of nesting materials has been studied in detail in some species, most reports of the phenomenon remain largely anecdotal (e.g., penguins: Carrascal et al. 1995; Moreno et al. 1995; herons: Afkami & Strassmann 2007; Weavers: Roulin 1999). Most studies considered the potential causes and consequences of these behaviours on a colony level (group size, density etc.) but rarely considered the structure of the colonies and the individual interactions involved in the thieveries (i.e. who steals from whom). Colonies are seldom uniform units and pairs of individuals that occupy small sub-territories within the group (e.g. neighbouring nest sites), may have particular social relationships. These factors might have an influence on how cooperative or tolerant individuals are with some of their conspecifics, especially with close neighbours.

Hence, even though individuals compete on a colony level, there may be variation in the degree of competition on a smaller scale. For instance, close neighbours may be less competitive among each other, because of benefits emerging from neighbourhood relationships reducing the costs of conflict. Individuals of many species have been observed to reduce their aggression level towards familiar conspecifics neighbours in contrast to unfamiliar ones (reviewed in: Temeles 1994), a phenomenon also known as the “dear enemy effect” (DEE) (Fisher 1954).

The opposite effect has also been described. In some species individuals were more aggressive towards neighbours compared to non-neighbours (Müller & Manser 2007; Brunton et al. 2008; Schradin et al. 2010); termed the “nasty neighbour effect” (NNE) (Müller & Manser 2007). This effect has been proposed to occur more frequently in species where neighbours represent a greater threat than strangers (Temeles 1994).

Finally, in the absence of social effects of neighbours on nest stealing individuals should behave economically. In this case, individuals should exploit nests that are closest to their own nest and reduce the frequency of nest stealing at other nest with increasing distance from their own nest.

The DEE and the NN-effects have been studied in territorial species with all-purpose territories. Assuming that nests can be regarded as sub-territories within a colony, we apply these concepts to study the social effects of stealing of nest material among members of a colony of rooks.

A further aspect that should be important in the context of stealing of nesting material is the question whether pair partners cooperate by coordinating their nest attendance to minimise the loss of nest material at their nest. Other colony members can remove the nest material of an unattended nest in only a few minutes of time (Yeates 1934, Coombs 1960, own observations). The presence of at least one bird at the nest has been suggested to reduce the likelihood of twig stealing by other colony members considerably (Coombs 1960.). To construct and preserve a nest for breeding, pair partners need to resolve the trade-off between searching for new nest material to enhance the nest, and guarding the nest to avoid nest destruction by other colony members. Enhancing the nest can be maximised if both birds search for new nest material (at the cost of loosing nest material due to twig stealing by others) and protecting the nest can be maximised if both birds are present at the nest (at the cost that no new nest material can be acquired). Hence, a solution to optimise the benefits from guarding the nest and from acquiring new nest material is that pair members coordinate each other so that one bird remains at the nest most of the time.

We studied rooks (*Corvus frugilegus*), a colonial breeding corvid (Gerber 1956; Patterson 1971; Goodwin 1976). During the breeding season (From March to late June), rooks build their nests by either collecting nest material from surrounding trees or by stealing branches from other nests. Nests are usually constructed in close proximity to each other creating opportunities for cooperation or resource competition between close neighbours. While it has been suggested that neighbours might form social bonds and avoid stealing from each other’s nests (Yeates 1934, Coombs 1960), studies on captive birds suggest that the most important social relationship in rooks is their mating partner and that other social relationships appear to be absent (Emery et al. 2007). In line with this, no cooperative interactions have been observed between other individuals than the pair partners during agonistic encounters (Seed et al. 2007). However, as these results were obtained under captive conditions, field data are required.

Here we studied the social effects on stealing of nest material in a colony of free-ranging rooks. To better understand whether neighbour effects are important in shaping the patterns of stealing of nest material, we quantified the stealing behaviour and frequency of breeding pairs with respect to proximity to neighbours. Furthermore, we investigated whether the presence of pair partners at the nest influences the frequency of thefts received and whether pair partners may coordinate their presence at the nest to optimise nest construction and protection.

Considering that neighbours interact more often among each other than non-neighbours, we expect that social effects may be important in shaping stealing of nest material within a colony. In this case the pattern of stealing towards neighbours should differ from the pattern expected by pure economic behaviour (minimising the travel distance to other nests). If rooks merely minimise their travel distance, we predict a negative correlation between thefts and distance to other nests. In case of a DEE-effect rooks should tend to avoid stealing from close neighbours. In case of a NNE-effect rooks should tend to prefer stealing from close neighbours. As stealing of nest material involves severe costs, we predict that nests are rarely left unattended. To optimise the trade-off between nest construction and protection we expect that pair partners coordinate each other, which would be reflected by only one bird present at the nest most of the time. Pairs with better coordination should suffer less from twig stealing from their nest and should have higher success in nest construction.

(c) Materials and methods

Study site

The colony studied was located in Neuchâtel, Switzerland. The colony consists of a two hundred year old plane tree (*Platanus spec.*) on which 45 nests were counted in the year 2010. From year to year rooks used this rookery in numbers varying from 50 to 100 individuals per year. The colony was surrounded by roads and located in an urban environment ideally situated for study, in front of the battlements of the castle of Neuchâtel from which the observations were carried out (6°55 E, 46°59 N). The observer was located in front of the nests at a distance of 25-30 meters and made all observations with binoculars.

Data collection

Observations were carried out between the 1st of March and the 27th of April 2010 by FD. The observations were stopped at the end of April because leaves started to appear on the tree, which made further precise observations impossible. At this time the pairs had completed the construction of their nests. The behaviours were recorded on a Dictaphone and later transcribed into an excel sheet. Observations were carried out almost daily either in the morning or in the afternoon. The timing of the observation period on any given day was randomly determined. Each observation session lasted two hours, for a total of 140 hours of observations, i.e., 70 observation sessions. Before each observation session, the observer took a picture of the colony, which was later used to identify the locations of the nests (see below).

Behaviours sampled

First, we wanted to know which individuals were stealing from which other individuals. We considered a nest as receiving a stealing event when an individual removed a branch from a particular nest and reintegrated the branch within another nest. The nest to which the branch was returned was considered to be the nest of the bird that stole the twig. Given that the birds were not marked, nest locations were used as an indicator of the identity of the pairs involved. All stealing events where the stolen nest or the robbing bird could not be identified were ignored (this happened in 8.5% of our observations). Second, the observer noted for each stealing event whether one, two or no birds were present on the nest during the stealing event. A nest was considered as guarded when at least one bird was present and as unguarded when no bird was present at that moment. Third, the observer noted which nests were under construction. A nest was considered to be under construction if within an observation session at least one twig was brought back to the nest, this twig was either stolen from another nest or collected elsewhere. The construction duration for each nest was then calculated as the amount of time between the first day when a pair was seen carrying branches and the first feeding event of the female by the male. We decided to define the first feeding event of the female as the end of the construction of the nest, because pairs reaching this stage usually stop carrying branches or do so only at very low frequencies. During the observation session the observer sampled ad libitum the behaviours mentioned previously. Additionally, every 10 minutes, the observer counted the total number of birds present within the colony and made a quick scan sampling through the nests and noted how many birds were present on each nest. This information was used to calculate the coordination scores (See the coordination score section for more details).

Nest location, distance between nests

The locations of the nests were determined with the help of a picture of the colony. A number was assigned to each nest. These locations were assumed to be reliable indicators of the identity of the pairs. Measures of the absolute distances between the nests were not possible. Instead, we ranked the proximity of nests relative to the others. Hence, the closest nest to the focal nest received rank 1, the second closest rank 2, the third closest rank 3 and so on, for each nest in the colony.

Coordination score

In each observation session, that lasted 120 minutes, we performed 12 counts (one count every ten minutes) of the number of birds present on each nest (scan sampling). The total number of counts for each nest varied between 85 and 150 depending on how long each pair needed to complete the construction of its nest. During these counts we noted whether there were one, two or no birds present at the nest. We converted these counts into pair coordination scores, where no bird present received a score of 0, two birds a score of 1 and one bird a score of 2. These scores are based on the following reasoning: to construct and preserve a nest for breeding, pair partners need to resolve the trade-off between searching for new nest material to enhance the nest and guarding the nest. In the absence of at least one bird other birds could destroy a whole nest in only a few minutes of time (own observations). On the other hand, the presence of one bird was typically sufficient to prevent thievery (nest were guarded by one bird in 88 percent of our counts). Hence, we assumed that when both birds stay away from the nest, this reflects the lowest level of coordination (and highest risk) (score = 0). When both birds are present at the nest, this should involve the lowest risks of twig stealing, but also involve no further supply of new nest material (score = 1). Finally, we assumed as the best solution to optimise the opportunity to enhance the nest by acquiring new material and to protect the current nest when one bird is present at the nest (score = 2). If the birds behave randomly and uncoordinated, we would expect average score values around 1 (equal likelihood that no, one or two birds are at the nest). In case pair partners coordinate their presence at the nest so that one bird is mostly present at the nest, we would expect values close to 2. Finally, higher coordination scores should be associated with a lower risk of thefts and with shorter periods of nest construction.

We calculated an average coordination score for each pair. Thus, each pair received a single presence score which was then used in all subsequent analysis. Finally, to be considered for the analysis the nests (pairs) had to meet two criteria: (1) the content of the nest had to be clearly visible to the observer (i.e. nests at the highest part of the tree crown were ignored). (2) The male started feeding the female before the end of our last observations session, i.e., the pair had reached the final stage of the construction before the 27th of April (thereafter observations were obstructed by leaves of the tree). In the end the final sample size considered for all analysis concerning presence scores was 24 nests.

Data analysis

Data were analysed with the statistical program SPSS 16.00. All tests were non parametric and two tailed.

(d) Results

Frequency of twig stealing during the breeding season

At the beginning of March thefts had already started and were observed until April 22^{nd}. A total of 45 nests were counted in the breading season 2010. Each nest received an average of 20 thefts during the two months of observations but the frequency at which pairs were stolen varied between 0 and 120 thefts. (Mean=20; SD=29.80; min=0; max=120; n=45). There was a seasonal pattern of stealing frequency within our colony: thefts were most frequent between the 15^{th} and the 21^{st} of March (n=447) our third observation week. The number of nests destroyed peaked one week later (n=11), between the 22^{nd} and 28^{th} of March. Moreover, the number of nests destroyed and the number of thefts were strongly correlated over our observation period (r_s=0.912, n=8, p=0.002; Fig.1a). Additionally, pairs seemed to prefer to steal from nests that were unguarded. This is supported by two results: first, the number of birds present in the colony was negatively correlated with the number of stealing events observed (r_s=-0.38, n=70, p=0.01; Fig1b) second, only 42 out of 1064 (3.94%) thefts happened when nests were guarded.

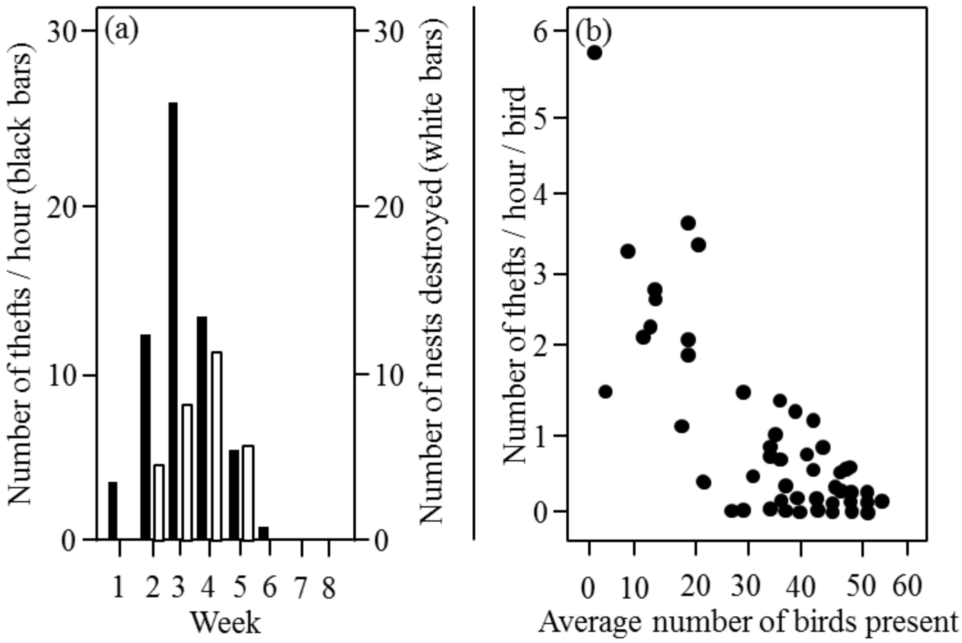

Figure 1a-b. General stealing patterns during the breeding season. (a) Total number of thefts observed during the season according to the observation week during which the observations were carried out (black bars) and the total number of nests destroyed for each observation week (white bars). The first observation week started on 1st of March, the last ended on 25th April. (b) Relationship between the frequency of thefts (per bird and per hour) and the average number of birds present during each observation session.

Do rooks refrain from stealing from their closest neighbours, i.e., do we observe a "dear enemy effect"?

Overall, the total number of thefts observed decreased with distance to the nest as suggested by the negative correlation between the number of thefts and the rank. This correlation applied for the stealing events when the nests were unguarded and when they were guarded (guarded: r_s=-0.84, n=9, p<0.01; unguarded: r_s=-1, n=9 p<0.01; Fig. 2). Our data indicate that there is no "cease fire" between immediate neighbours given that the total number of thefts observed between the closest and second closest neighbours did not significantly differ (Chi-square test: X^2=0.02, df=1, n=98, p=0.89). Furthermore, pairs seemed to steal at higher frequencies from their five closest neighbours (ranks 1 to 5) than from more distant nests, as the total number of branches stolen among the five closest neighbours was significantly higher than the amount of branches stolen from the next five neighbours (ranks 6 to 10) (X^2=9.06, df=1, n=358, p=0.003; Fig. 2).

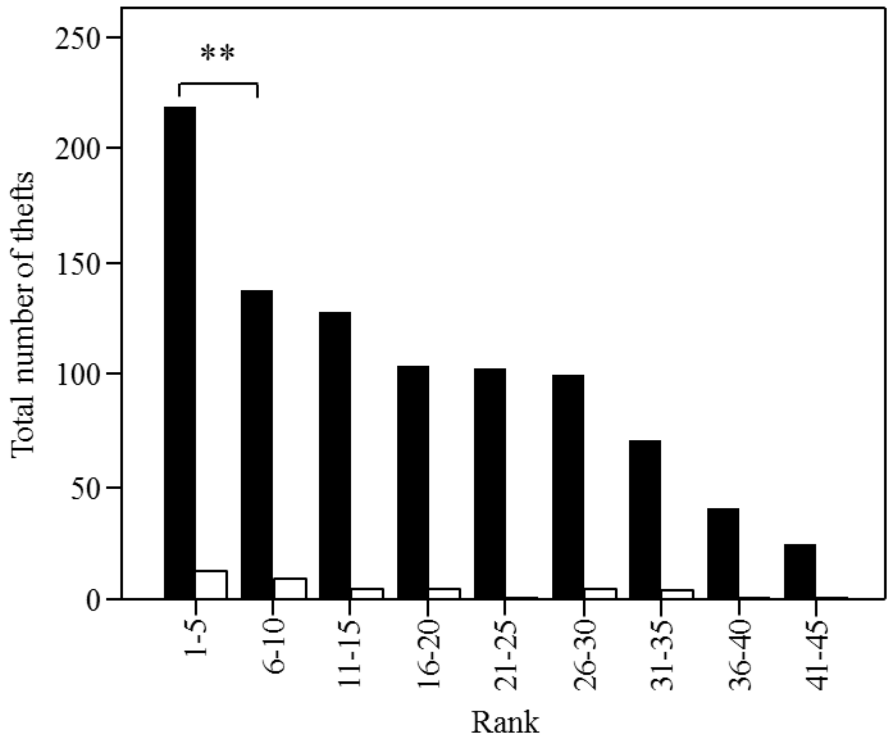

Figure 2. Relationship between the total amount of branches stolen by the pairs and the rank of nests from which the branches were stolen (the data are pooled in categories of five ranks); depending on whether the nests were guarded (white bars) or unguarded (black bars). Two asterisks indicate p<0.01.

Do rooks overexploit their closest neighbours, i.e., do we observe a "nasty neighbour effect" in our study species?

The slopes of the regression lines between distance between nests and frequency of thefts were significantly more likely to be negative than what would be predicted by chance (X^2=7.631, df=1, p=0.0057) confirming the overall negative trend between frequency of thefts and distance. The frequency at which pairs were stealing branches form their five closest neighbours however, did not differ significantly from what would be predicted by the distance to the focal nests, i.e., the expected values predicted by the regression equations (Wilcoxon test: z=-0.82, n=45, p=0.935).

Did better coordination reduce the risk of theft?

Most stealing events occurred while nest owners were absent. 1022 thefts out of 1064 (96%) happened while nests were unguarded (X^2=572.797, df=1, p<0.0001). The coordination scores were significantly negatively correlated with the frequency of received thefts (r_s=-0.702, n=24, p<0.01; Fig. 3a) suggesting that pairs with better coordination were at lower risk of experiencing thefts. Furthermore, presence scores were significantly negatively correlated with construction duration (r_s=-0.655, n=24, p<0.01; Fig. 3a), indicating that well-coordinated pairs needed less time to finish their nest. Finally, the frequency of thefts received was positively correlated with the time needed for nest completion (r_s=0.503, n=24, p=0.012; not shown).

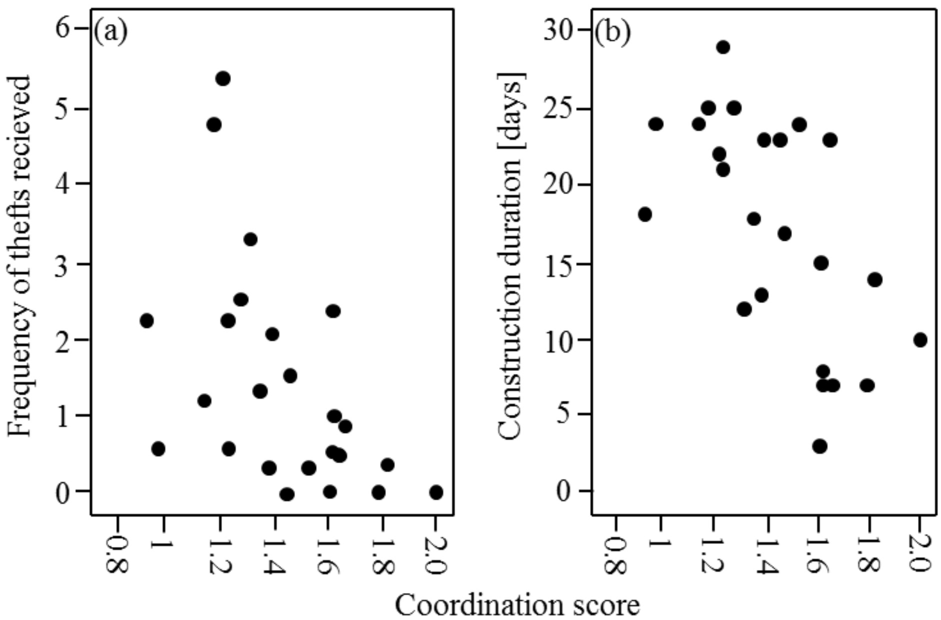

Figure 3a-b. Correlations between the coordination score and (a) the frequency at which pairs experienced thefts and (b) the construction duration of each nest in days; each dot represents one pair.

(e) Discussion

Our results suggest that competition over nesting material is intense in rooks and continues throughout the breading season. Received nest stealing was frequent and often lead to complete nest destruction. The number of thefts decreased with distance to the nest and there was no evidence for the hypothesis that close neighbours may be treated differently (neither worse nor better than expected). Hence, social effects among neighbours affecting the likelihood of stealing appear to be absent. However, guarding the nest appears to be important for successful nest completion. Only about four percent of the thefts occurred while the nests were guarded. Pairs with higher coordination scores suffered less from twig stealing and needed less time for nest completion. Overall, nest building and competition over nest material has costly consequences on successful breeding in colonial rooks. Our results suggest that coordination among pair partners might be important to cope with these costs of coloniality.

Neighbours are competitors not “dear enemies”

Our findings indicate that immediate neighbours do not avoid stealing branches from each other’s nests, which suggests neighbours do not cooperate in this context. In contrast, our results suggest that neighbours are intensively competing for nesting material and that rooks use an economical strategy for twig stealing that is based on the distance to their own nest as it has been reported for Bowerbirds (Doerr 2009). Hence, in contrast to most studies on vertebrates, where the authors reported a DEE or a NNE, our results rather support the idea of the optimal pilfering strategy. The nasty neighbour effect, where individuals behave more competitively / aggressively toward neighbours than toward non-neighbours, has been explained with the relative threat hypothesis (Temeles 1994). This hypothesis states that aggressiveness among neighbours or strangers is mainly determined by the threat imposed by each of the category of individuals, the responses of individuals being conditional on the relative threat imposed by neighbours compared to strangers. Considering this hypothesis, in species where neighbours pose a greater threat than non-neighbours, individuals should respond more aggressively toward the former. For instance, one potential treat, is to loose paternity in favour of a neighbour. Schradin and colleagues (2010) have shown that in striped mice, where males were five times more aggressive toward neighbours than non-neighbours, 28% of siblings were indeed sired by neighbours in comparison to only 7% for non-neighbours. Interestingly, in wild rooks, males intensively compete over access to females and extra-pair copulations are common in colonies of wild rooks (Coombs 1960; Roskaft 1983), hence this might also apply to our study species. However, rooks did not overexploit their neighbours, as the frequency of thefts decreased almost linearly with distance. In conclusion, in line with studies conducted in captive birds (Emery et al. 2007; Seed et al. 2007) our results seem to confirm that rooks do not form coalitions with other individuals than their mating partners.

Well-coordinated pairs receive fewer thefts

Our results suggest that intra-pair coordination is essential for successful nest construction and eventually breeding success as shown by the negative relationships between the coordination score and both the frequency of thefts received and the construction duration. Better coordinated pairs have been shown to have a higher nestling survival (Mariette & Griffith 2012) a higher chance of keeping the same partner on the subsequent year (Davis 1988; Black 2001) or a reduce the risk of predation when coordinating feeding visits (Raihani et al. 2010). Our results add some evidence to the hypothesis that behavioural synchrony among mating partners, especially in monogamous birds, is essential for achieving successful reproduction (Hirschenhauser 2012).

In captive rooks, pairs with higher tolerance levels tended to show higher success rates in an experiment where individuals had to pull a platform by coordinating with the help of a partner to access a reward (Seed et al. 2008). The current result is in line with these previous results: pair coordination seems to be a component that is essential for gaining access to resources and reproduction in rooks as it has been suggested by Emery et al (2007). Future studies are needed to investigate how coordination is achieved, whether particular communication is involved and whether coordination becomes better with increasing age and duration of pair partnership.

Conclusion

Rook social life during the breeding season is characterised by a high degree of conflict over nest material. While there is no evidence that close neighbours cooperate within the colony, pair coordination was essential for the establishment of a nest. Hence, our results fit the idea that the basic most important unit of cooperation in rooks is the pair bond and that these birds particularly rely on their mating partners to cope with the intense competition within the colony during the breeding season.

(f) Acknowledgements

We thank the Fondation Pierre Mercier pour la Science for funding this study (to R. Bergmüller). We thank also the authorities of the city of Neuchâtel allowing us to observe the colony form the battlements of the castle. These observations were conducted in agreement with the Swiss law on animal ethics.

(g) References

Afkami, M. E. & Strassmann, J. E. 2007. Adult yellow-crowned night-herons face in opposite directions at the nest. *The Wilson Journal of Ornithology*, 119, 747-749.

Beauchamp, G. 1998. The effects of group size on mean food intake rate in birds. *Biol. Rev.*, 73, 449–472.

Black, J. M. 2001. Fitness consequences of long-term pair bonds in barnacle geese: monogamy in the extreme. *Behav. Ecol.*, 12, 640-645.

Brunton, D. H., Evans, B., Cope, T. & Ji, W. 2008. A test of the dear enemy hypothesis in female New Zealand bellbirds (Anthornis melanura): female neighbors as threats. *Behav. Ecol.*, 19, 791-798.

Carrascal, L. M., Moreno, J. & Amat, J. A. 1995. Nest maintenance and stone theft in the Chinstrap penguin (Pygoscelis antartica). 2. Effects of breeding group size. *Polar Biology*, 15, 541-545.

Cockburn, A. 2006. Prevalence of different modes of parental care in birds. *Proc. R. Soc.*, 273, 1375-1383.

Coombs, C. J. F. 1960. Observations on the rook corvus frugilegus in southwest Cornwall. *Ibis*, 102, 394-419.

Danchin, E. & Wagner, R. H. 1997. The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology & Evolution*, 12, 342-347.

Davis, L. S. 1988. Coordination of incubation routines and mate choice in Adélie penguins (Pygoscelis adeliae). *Auk*, 105, 428-432.

Doerr, N. R. 2009. Stealing rates in the great bowerbird (Ptilonorhynchus nuchalis): effect of the spatial arrangement of males and availability of decorations. *Emu*, 109, 230-236.

Emery, N. J., Seed, A. M., von Bayern, A. M. P. & Clayton, N. S. 2007. Cognitive adaptations of social bonding in birds. *Phil. Trans. R. Soc. B.*, 362, 489-505.

Fisher, J. 1954. Evolution and bird sociality. In: Evolution as a process (Huxley, J., Hardy, A.C. & Ford, E.B., eds). Allen and Unwin, London, pp. 71-83.

Gerber, R. 1956. *Die Saatkrähe*. Leipzig: A. Ziemsen Verlag

Goodwin, D. 1976. *Crows of the world.* London, UK: British museum (Natural history) Press.

Hamilton, W. D. 1971. Geometry for the selfish herd. *J. Theor. Biol.*, 31, 295–311.

Hirschenhauser, K. 2012. Testosterone and partner compatibility: evidence and emerging questions. *Ethology*, 118, 799-811.

Krause, J. & Ruxton, G. D. 2002. Living in groups. New York, NY: Oxford University Press.

Mainwaring, M. C. & Hartley, I. R. 2013. The energetic costs of nest building in birds. *Avian Biology research*, 6, 12-17.

Mariette, M. M. & Griffith, S. C. 2012. Nest visit synchrony is high and correlates with reproductive success in the wild Zebra finch Taeniopygia guttata. *J. Avian Biol.*, 43, 131–140.

Moreno, J., Bustamante, J. & Vinuela, J. 1995. Nest maintenance and stone theft in the Chinstrap penguin (Pygoscelis antartica). 1. Sex roles and effects on fitness. *Polar Biology*, 15, 533-540.

Müller, C. A. & Manser, M. B. 2007. Nasty neighbours rather than dear enemies in a social carnivore. *Proc. R. Soc. B.*, 274, 959-965.

Patterson, I. J., Dunnet, G. M. & Fordham, R. A. 1971. Ecological studies of the rook, Corvus frugilegus L., in North-east Scotland. Dispersion. J. appl. Ecol. 8, 815-833.

Raihani, N. J., Nelson-Flower, M. J., Moyes, K., Browning, L. E. & Ridley, A. R. 2010. Synchronous provisioning increases brood survival in cooperatively breeding pied babblers. *J. Anim. Ecol.*,79, 44–52.

Roland, C., Danchin, E. & Fraipont, M. 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. *American Naturalist*, 151, 514-529.

Roskaft, E. 1983. Male promiscuity and female adultery by the Rook Corvus frugilegus. *Ornis. Scand.*, 14, 175-179.

Roulin, A. 1999. Stealing of nest material in Ploceus cucullatus nigriceps: costs and benefits of coloniality. *Ostrich: Journal of African Ornithology*, 70, 152-152.

Schradin, C., Schneider, C. & Lindholm, A. K. 2010. The nasty neighbour in the striped mouse (*Rhabdomys pumilio*) steals paternity and elicits aggression. *Front. Zool.*, 7, 19.

Seed, A. M., Clayton, N. S. & Emery, N. J. 2007. Post-conflict third-party affiliation in rooks (Corvus frugilegus). *Curr. Biol.*, 17, 152-158.

Seed, A. M., Clayton N. S. & Emery, N. J. 2008. Cooperative problem solving in rooks (Corvus frugilegus). *Proc. R. Soc. B.* 275, 1421-1429.

Temeles, E. 1994. The role of neighbours in territorial systems: when are they 'dear enemies'? *Anim. Behav.*, 47, 339-350.

Torney, C. J., Berdahl, A. & Couzin, I. D. 2011. Signalling and the evolution of cooperative foraging in dynamic environments. *PLoS Comput. Biol.* 7(9): e1002194.

West-Eberhand, M. J. 1979. Sexual Selection, Social Competition, and Evolution. *Proc. Am. Philos. Soc.*, 123, 222–234.

Yeates, G. K. 1934: The life of the rook. London.

Chapter 2

Title manuscript 2: Conflict management in free ranging rooks

Authors: Felice Di Lascio[1]; Redouan Bshary[1]; Anne-Cécile Dagaeff[2]; Ralph Bergmüller[1]

[1]Université de Neuchâtel, 2000 Neuchâtel, Rue Emile-Argand 11, Switzerland

[2]Laboratoire Evolution et Diversité Biologique (EDB), UMR 5174, Université Paul Sabatier, 118 Route de Narbonne, F-31062 Toulouse, France

(a) Abstract

Conflict management is a means to offset the costs arising from competition over resources in social species. While conflict management mechanisms have been described in a range of species, the social conditions favouring their evolution are still unclear, especially for free living species. Here we investigated whether wild rooks (*Corvus frugilegus*), which are socially monogamous colony breeders and show extensive conflicts over nesting material before and during the breeding season, show friendly post conflict behaviours. We studied two colonies of wild rooks with 60 and 150 individuals, respectively, and used a modified version of the post-conflict / matched control methodology to assess the presence of reconciliation and consolation. As predicted, no reconciliation was observed between former opponents. However, pair partners engaged in a higher frequency of affiliative behaviours (bill twinning) after they were involved in a conflict with others compared to before the conflict (consolation). Mutual displays, which are behaviours associated with situations of conflict, occurred equally frequent before and after conflicts, suggesting they signal elevated social tension. Victims (individuals that were attacked in a conflict) were more likely to be unpaired than aggressors. Even though social

interactions are characterised by a high degree of conflict among members of a colony, behaviours used for conflict management in rooks are primarily exchanged among third parties in the conflict (pair partners). Our results suggest that post-conflict affiliative behaviours among rook pair partners serve for consolation by advertising social bonds to third parties.

Key words: post-conflict affiliation ● third-party affiliation ● group living ● rooks ● Corvus frugilegus

(b) Introduction

Social life almost invariably involves conflicts. Conflicts occur over access to food or mating partners, and involve costs including injuries, enhanced stress levels or degradation of important social relationships which, in the extreme may lead to exclusion from the group (Kutsukake and Clutton-Brock 2008; Aureli et al. 2002; Aureli and Smucny 2000; de Waal 2000).

In response, animals have evolved behavioural adaptations that enable them to cope and mitigate the detrimental effects of conflicts. Conflict management strategies help to avoid conflicts, prevent escalation, or resolve conflicts by repairing social damages, or alleviate the stress resulting from enduring conflicts (Aureli et al. 2002). Conflict management has been studied mainly in primates (Aureli et al. 2002) but also in various other vertebrate taxa such as spotted hyenas (Wahaj et al. 2001), bottlenose dolphins (Weaver 2003), domestic goats (Schino 1998), dogs (Cools et al. 2008) and fishes (Bshary & Würth 2001). Different types of friendly post-conflict interactions (conflict resolution) have been described. These include “reconciliation”, which refers to a friendly contact between former opponents shortly after a conflict and “consolation” which is an increase in unsolicited affiliative interactions initiated by a third party towards the victim of a conflict (de Waal and Vanroosmalen 1979). “Solicited consolation” refers to an affiliative contact initiated by the victim towards a third-party (Watts et al. 2000). Behaviours involved in conflict resolution have been shown to reduce the likelihood of renewed post conflict aggression (Norscia and Palagi 2011; Fraser and Bugnyar 2010a; Leone and Palagi 2010; Palagi and Cordoni 2009; Palagi et al. 2006; Aureli and van Schaik 1991) and restore tolerance between former opponents (Aureli et al. 2002; Cords and Aureli 2000; de Waal 2000).

Engaging in a friendly interaction with another individual during or shortly after a conflict involves costs and therefore constitutes an investment. Thus, from an evolutionary perspective the key question that needs to be addressed is: why should an individual invest in conflict resolution? Investments in conflict resolution have been proposed to (a) protect or restore relationships that are particularly important to individuals such as alliances, partnerships or friendships (the "valuable relationship hypothesis" (de Waal & Aureli 1997), (b) as honest signals to social partners that indicate that a conflict is over (Silk et al. 2000), or (c) to support the well being of a valuable social partner such as kin or other individuals with strong mutual attachments such as "friends" or pair partners (consolation, Watts et al 2000).

Reconciliation appears widespread among vertebrates (Aureli et al. 2002). Apart from mammals, the best evidence for reconciliation has been reported in corvids. For example, there is evidence for both consolation and reconciliation in ravens (*Corvus corax*), where these post-conflict affiliative behaviours were more likely to happen between individuals sharing a valuable relationship (Fraser and Bugnyar 2010[a,b]; 2011).

In contrast, evidence for consolation remains relatively rare. In primates, consolation has so far been described in chimpanzees (de Waal and van Roosmalen 1979; de Waal and Aureli 1996) and other great ape species (gorillas: Cordoni et al. 2006, Mallavarapu et al. 2006; bonobos: Palagi et al. 2004) but rarely in monkey species (de Waal and Aureli 1996). In captive rooks (*Corvus frugilegus*), only consolation has been reported and reconciliation was not observed (Seed et al. 2007; Logan et al. 2013a, 2013b).

Rooks are a highly social species of corvid, which roost and nest communally (Haffer and Bauer 1993). There is intense conflict over reproduction (Roskaft 1983, own observations) and nesting material (Roskaft 1981, own observations). Therefore, mechanisms to reduce the costs of conflict should be expected.

In rooks the pair bond appears to be the critical social relationship (Roskaft and Espmark 1982, Emery et al. 2007). Pair interactions are characterised by a high degree of affiliative contact, such as food-sharing, bill twining and allopreening (Emery et al. 2007). Pair members also aide one another in fights (either ganging together against a common victim or passive social support or intervening in a current dispute), attacking the aggressor of their partner or their aggressor's partner, and directing affiliative behaviour towards their partner after they had been the victim or aggressor in a fight (Seed et al. 2007, Logan et al. 2013a,b).

These studies in captivity found no evidence for reconciliation. In contrast, there is evidence of third-party affiliation after conflicts when analysing the pattern of "mutual displays" (two birds engage in a synchronized bowing and tail fanning display accompanied by caws) and a very specific behaviour called "bill twinning" (two birds interlock the mandibles of their beaks) (Seed et a. 2007). As the latter behaviour rarely occurred during the control period, the authors concluded that this might be a very specific behaviour serving for conflict resolution (third party affiliation / consolation). Affiliative behaviours among pair partners after a conflict with a third individual could have several effects such as reducing the stress level of the partner in the conflict, strengthening the pair bonds or advertising the pair alliance to third parties to reduce the likelihood of a renewed attack (Seed et al. 2007). To better understand conflict management in free-ranging rooks we investigated the following questions: (i) Do rooks engage in post conflict affiliative behaviours? (ii) Are former opponents involved (reconciliation) or only third parties (consolation)? (iii) Is there a difference in the likelihood of post conflict affiliation between victims and aggressors? (iv) Are certain affiliative behaviours specific to post conflict situations?

There is no evidence for individualised valuable relationships other than among pair partners in rook sociality (Emery et al. 2007) and pair partners do not appear to engage in conflicts with each other (Seed et al. 2007, own observations). Therefore, according to the valuable relationships hypothesis, we predict that reconciliation should be absent in rooks. As there is intense conflict among colony members and because the long term pair partner is of high value in rook sociality, we expect that pair partners invest in conflict mitigation when their partners are involved in a conflict. Therefore, we predict friendly post-conflict interactions among pair partners, after one partner was involved in a conflict with others (i.e. third-party affiliation / consolation).

(c) Methods

Studied animals

We observed rooks in two colonies that were mainly composed of adult individuals and located in Neuchatel, Switzerland. Adult individuals can easily be hold apart from birds in their first year because in the latter the base of the beak is bare (Gerber 1956). The first colony (~60 individuals) was located in “La Collegiale” (6°55 E, 46°59 N) on a single Plane tree of about 100 years of age. The second colony (~150 individuals) was located in a distance of 4 km close to the museum “Le Latenium”(6°58 E, 47°00 N) on Ash trees. Both colonies were surrounded by roads in an urban environment. The rooks use these rookeries every year.

Data collection and analysis

Data were collected by recording 8 videos of 10 minutes duration each observation session, where each video was focused on a different part of the tree. Recordings were done by one or two observers (ACD and FDL) almost daily between 7:30 and 9:00 a.m. These hours were chosen because they correspond to the arrival time of the rooks coming from the sleeping trees and their departure for foraging. Observations were carried in 2011 and 2012 at the end of January and February before of the nesting season, which is the time at which the birds are fighting for their personal territory and the future location of nests on the tree. Therefore, this is the optimal period to observe conflicts. Each video recording was focused on one of 6 predefined sections of the tree. The order of observation of tree section was randomised to avoid order effects and observer bias. In case no bird was present in the assigned area, the next area on the list was chosen. The videos were recorded using a Canon EOS 60D camera with HD resolution (1920×1080 pixels) and a 135 mm telephoto lens. At the beginning and the end of each video, the total number of birds present in the rookery was recorded. The observers observed from elevated points at a distance of approximately 30 meters form the trees. At this distance, birds appeared to be undisturbed of the observer presence.

A modified version of the standard PC-MC methodology was used to analyse post conflict behaviours. According to the PC-MC methodology (de Waal and Yoshihara 1983, Veenema et al. 1994), the affiliative behaviours of individuals are recorded after an interaction with unambiguous aggression, called the Post Conflict (PC) period, with a special attention to contacts between former opponents. The next possible day, at the closest possible time of the day of the first observation, the behaviours of the involved individuals are recorded as a Matched Control (MC) (with the condition that no aggressive interactions have occurred during a given time preceding the observation). PC and MC periods are then compared.

As the birds we observed were not individually marked, we slightly modified this method by comparing the period following the first aggression (PC) with the period immediately before the conflict (BC). This provided two advantages: first, it removed much of the variation emerging from different conditions between two observation days. Second it assured that the same birds were observed before and after the conflict. Frequencies of behaviours were compared between these periods rather than latency to the first affiliative contact, a method used by Logan and colleagues in a captive setting (2013a).

In studies on primates, the likelihood of post conflict behaviours typically has a peak within the first minute after the beginning of the conflict. Seed et al. (2007) found the same in captive rooks. Therefore, we recorded all behaviours during 90 seconds for the PC period to be certain to see all the post conflict behaviours. Additionally, this removed the problem that following the birds for much longer than 90 seconds was almost impossible during our observations as the birds were leaving the trees very frequently. During the observations all birds involved in the conflict and their partner (if present) were followed on the video and their behaviour was recorded. The same duration of time (90 seconds) was used for the BC period (i.e., in total we had 180 seconds for the BC PC comparisons). During the BC period, the same birds as in the PC period were followed. We excluded videos from the analysis if they did not fulfil the two following criteria: first, an obvious conflict with physical attack occurred and second, all the involved individuals were visible during the 90 seconds preceding and following the conflict. The bird, which initiated the conflict, e.g. by pecking first or initiating the displacement, was called “aggressor”, the first bird which was attacked was called “victim”; any other birds involved were also followed and their behaviour was described. As pair partners in rooks studied in captivity do not show aggressive behaviours among each other (Emery et al. 2007, Seed et al. 2007) we defined individuals as "paired" when they showed affiliative behaviours, or were sitting in close contact with another individual than the aggressor or the victim. If none of these behaviours was observed and no bird was seen in proximity (within 1m) of the focal birds they were defined as temporarily single which we call "single" hereafter. The behaviours of all interacting individuals (opponents and partners) were recorded from the movies with the time of their occurrence. Additionally, we recorded the frequency of affiliative behaviours outside the context of conflict by focusing on two birds in contact sitting (likely paired partners) that were selected as focal individuals, provided that no aggressive interactions had occurred on the video during the 300 previous seconds. If it was possible to observe more than one pair on the video, each one was assigned a number, then the followed couple was picked at random. We made these additional observations to obtain information about baseline levels of affiliative behaviours. For each conflict, we selected a "matched" baseline observation at the next possible day. The baseline observations were analyzed according to the same procedure as for the BC and PC periods.

Behaviours observed

The behaviours we observed in our videos were classified as either aggressive or affiliative. To this end we followed the description and classification previously used for a study on rooks in captivity (Seed et al. 2007). Below we provide a table with the aggressive and affiliative behaviours and the corresponding descriptions that were observed in the current study.

Table 1: Description of the behaviours observed in the wild rooks, following the definitions given by Seed et al. 2007* and Emery et al. 2007**

Category	Behaviour	Description
Affiliative	Bill twinning	Two birds interlock the mandibles of their beaks.*
	Mutual displaying	Two birds engage in a synchronized bowing and tail-fanning display, accompanied by harsh vocalizations.*
	Allo-preening	One bird slowly nibbles or strokes the feathers of another with the beak.*
	Contact sitting	The birds are sitting in contact or at a beak-length of the other bird.**
Aggressive	Pecking	A bird hits another one with his beak on a part of his body.
	Displacement with contact	A bird approaches and touches the other one with his beak or body (pecking, pushing) which retreats.
	Aerial aggression	A bird aggresses another one with a flight into his direction, and either hits him with his claws or his beak.

Statistics

Non-parametric statistics were used because the data were not distributed normally. All tests were conducted using the software IBM SPSS Statistics 20 and were two-tailed. For the comparison between behaviours in the BC and PC period, Wilcoxon signed-ranks tests were used; in all other cases we used Fisher’s exact tests. The initial alpha level was set at 0.05 however, in order to adjust the critical alpha level for multiple comparisons, we used the false discovery rate (FDR) correction method as described by Benjamini and Hochberg (1995). According to the FDR method we defined three families of hypotheses in our study, where the first corresponds to the comparisons between the BC and PC periods, the second to the comparison of aggressors and victims and last to the comparisons between the PC periods and the baseline observations. Hence, the first family included four comparisons, the second and the third family five comparisons each. Accordingly, based on the p values obtained within each family of hypotheses, the alpha levels were set at 0.025 for the first set of hypothesis, at 0.01 for the second and at 0.03 for the third. The analyses were based on 30 videos, which we treated as independent samples. However, for the comparisons between PC and BC or between PC and baseline observations, for those conflicts where the aggressors or the victims were categorized as “alone” were excluded from the analysis. Accordingly, the actual sample size for the victims and aggressors was 17 and 28, respectively. Because we could not individually identify the birds between days, we used a random computer permutation test (1000 trials per run) to calculate how many different individuals we could expect to have been sampled twice. Expected values vary between 33.7 % for the population of “la Collégiale” and 12.3% for the population of “le Laténium”. Because we selected different locations within the tree crown for our observations, we are confident that significant results are unlikely caused by pseudo-replication (Hurlbert 1984).

(d) Results

Is there reconciliation or third party affiliation in wild rooks?

The affiliative behaviours we observed were “bill twinning” and “mutual displaying”. No other types of affiliative behaviours were observed. Both never occurred between former opponents but exclusively between pair partners. Both, aggressors and victims showed a higher frequency of “bill twinning” in the PC than in the BC period (Figure 1; Wilcoxon test: aggressors, $z=-2.236$, $n=28$, $p=0.019$; victims: $z=-2.570$, n=17, p=0.01). In contrast, pair partners were not performing mutual displays at higher rates after the first aggression (PC) than before (BC) the first aggression occurred (Wilcoxon test: aggressors: z=-0.605, n=28, p=0.545; victims: z=-0.259, n=17, p=0.796).

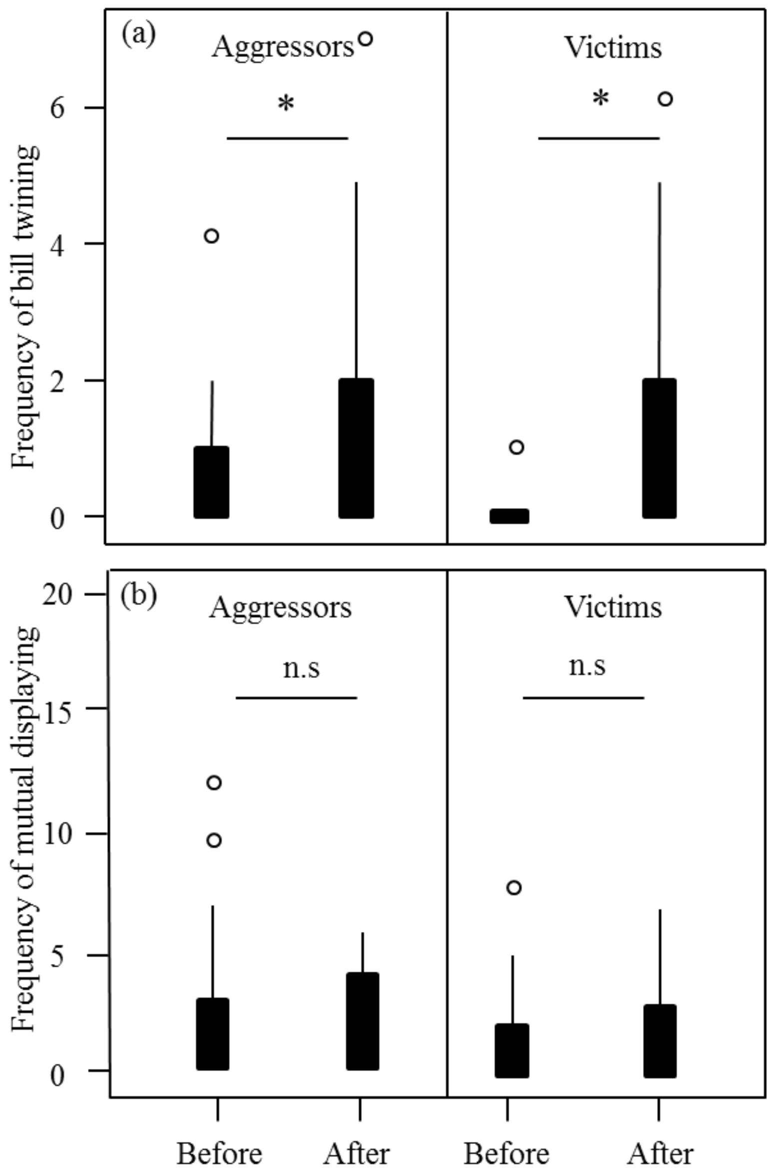

Figure 1. Comparison of the frequency of bill twinning in the 90 seconds preceding the first aggression (Before) with the frequency of this behaviour for the 90 second following the first aggression (After), for the aggressors (a) and the victims (b). Box plots with the median and the interquartile and the range are shown. Circles indicate outliers. One asterisk is for p<0.025.

Do victims show more affiliative behaviours compared to aggressors?

There was no significant difference between the frequency at which aggressors and paired victims were bill twining, neither in the BC period (Wilcoxon test: z=-1.186, n=15, p=0.236) nor during the PC period (Wilcoxon test: z=-0.513, n=15, p=0.608). Furthermore, aggressors and victims engaged in mutual displaying at similar frequencies in the BC period (Wilcoxon test: z=0, n=15, p=1) and in the PC period (Wilcoxon test: z=-0.776, n=15, p=0.438). However, victims were significantly more often categorized as "single" (no pair partner present) than aggressors who had a partner in the interaction (victims: 13 alone vs 17 with partner; aggressor: 2 alone vs 28 with partner; Fishers' exact test: p=0.002).

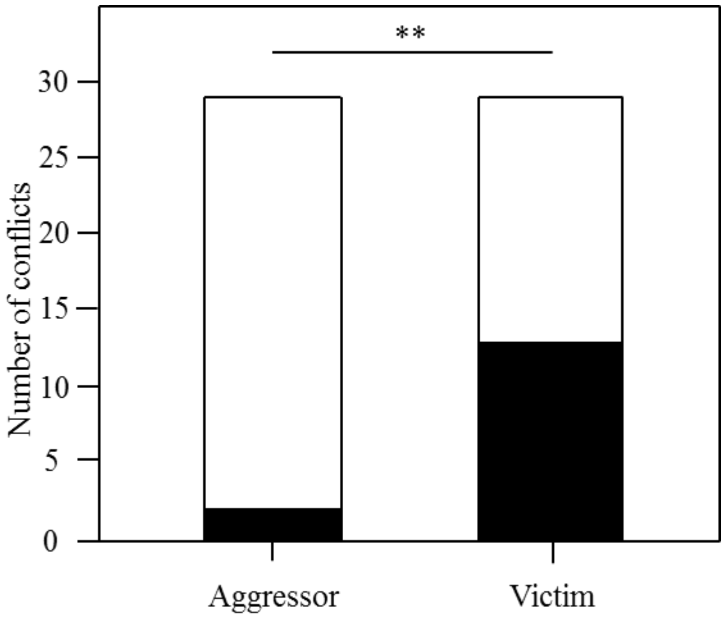

Figure 2. Number of conflicts involving either single (black) or paired (white) individuals according to whether they were the aggressor or the victim of the conflict. Two asterisks are for p<0.01

Do affiliative behaviours occur more often following an aggression?

Bill twinning occurred more often after an aggression (aggressors: 13 out of 28 (46%); victims: 9 out of 17 (53%)) compared to the baseline observations (4 out of 30 (13%)) (Fishers' exact test: aggressor, p=0.008; victims, p=0.006). In contrast, there was no increase in the likelihood of mutual displays after an aggression (aggressors: 15 out of 28 (54%); victims: 11 out 17 (64%)) compared to the baseline situation (14 out of 30, i.e. 47% during the baseline observations) (Fishers' exact test: aggressors: p=0.793; victims: p=0.362).

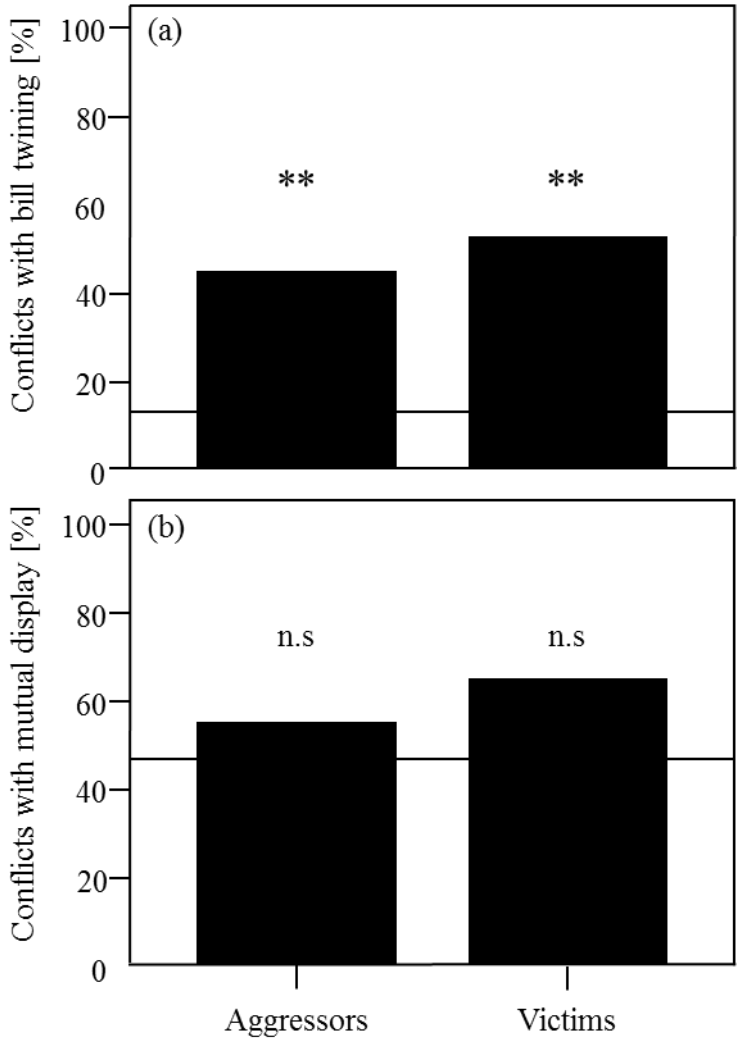

Figure 3a-b. Percentage of post-conflict observations where (a) bill twining and (b) mutual displaying was observed for the aggressors and the victims. The black solid lines are for the baseline levels of these behaviours in the control observations. n.s is for non significant differences, two asterisks are for p<0.01.

(e) Discussion

While there is a high level of conflict among individuals of a colony of rooks, friendly post conflict behaviours (bill twinning) occurred only among pair partners after one of them was involved in a conflict with others (third party affiliation / consolation) but were not observed between former opponents (reconciliation). Mutual displays, occurred equally frequent before and after conflicts, suggesting they indicate elevated levels of social tension and not as previously suggested affiliation (Seed et al. 2007). Victims (individuals that were attacked in a conflict) were more likely to be categorized as single than aggressors in conflicts. Overall, our results suggest that rooks use two different strategies to manage conflicts: mutual displays serving as signals of social tension that may preclude further escalation and bill twinning among pair partners as a means of consolation. Our results are consistent with earlier studies with captive birds, where the authors report similar findings (Seed et al. 2007; Logan et al. 2013a, 2013b).

Conflict management mechanisms and social system of rooks

These results correspond to the social system of rooks. Like in many other colonial breeding birds the important social relationships in rooks is the pair partner, while relationships with other colony members do not appear individualised and are mainly of competitive nature. (e.g., rooks: Emery et al. 2007; penguins: Carrascal et al. 1995; barn swallows: Fujita and Higuchi 2011, Herons: Afkhami and Strassmann 2007). This is in line with a study in captive birds that suggests juvenile rooks form alliances, support each another in fights, exchange commodities such as food, social support and preening (Emery et al. 2007) mainly with one social partner. In the wild we found not much evidence for other important relationships than the pair partner. For instance, a recent study investigating whether nest neighbours would support each other to prevent the stealing of nesting material by other birds did not find any evidence support among neighbours (Di Lascio et al. in prep). While rooks live in stable pair bonds throughout the year, nesting colonies and winter foraging flocks that meet at rookeries can be large consisting up to many thousands individuals

(Gerber 1956). It seems therefore unlikely that individuals maintain particular individualised relationships that would favour reconciliation in such large groups.

The findings in rooks are contrast to observations in closely related ravens (*Corvus corax*), where consolation and reconciliation among former opponents has been reported (Fraser and Bugnyar 2010a; 2011). In contrast to rooks, ravens may postpone reproduction for up to 10 years and social interactions involve the formation of coalitions in groups of non-breeding birds (Fraser and Bugnyar 2010b, Braun and Bugnyar 2012; Braun et al. 2012). Therefore, the presence of reconciliation in ravens appears to result from individualised valuable relationships in non-breeding groups.

Do victims show more affiliative behaviours compared to aggressors?

Consolation has been suggested to support the well being of a valuable social partner such as kin or other individuals with strong mutual attachments such as “friends” or pair partners (consolation, Watts et al 2000). This can potentially be done by dampening the stress level of the partner in the conflict, by strengthening the pair bond or by advertising the pair alliance to third parties to reduce the likelihood of a renewed attack (Seed et al. 2007).

If post-conflict affiliation would only be performed to reduce stress levels of the pair partner, we would expect that the pair partner not involved in the conflict would initiate the friendly interaction. However, both partners usually initiate bill twinning simultaneously (Seed et al 2007, Own observations). Therefore, bill twining does not appear to be a behaviour that one pair partner performs solely for the benefit of the partner in a conflict.

We suggest that bill twinning should be important in signalling the alliance with the pair partner to third parties. Such advertising of the alliance could reduce the likelihood of renewed attacks from third parties. Several findings suggest this is the case in rooks.

First, victims and aggressors affiliated at similar frequencies with their partners after a conflict with others, which corresponds to what has been found in captive rooks

(Seed et al. 2007). This suggests that both opponents benefit from affiliative interactions with their partners after a conflict.

Secondly, lone birds were attacked more frequently compared to paired birds. This suggests that the risk of receiving attacks can be reduced when birds signal they are not alone.

Third, the risk of renewed aggression has been observed to be lower when the rooks were affiliating with their pair partner (Logan et al. 2013b), even though this protective effect was only observed for aggressors but not for the victims in captive conditions.

How specific are the affiliative behaviours observed to the period following an aggression?

We observed bill twinning almost exclusively in situations of conflict but not in control situations. This is similar to what has been observed in captive birds (Seed et al. 2007) which suggests that bill twinning is a specific affiliative behaviour used in situations of conflict, as has been reported in chimpanzees (de Waal and van Roosmalen 1979) and spectacled leaf monkeys (Arnold and Barton 2001).

We did not observe a significant difference in the occurrence of mutual displaying before compared to after a conflict. We performed our observations shortly before the breeding period, at time at which conflicts primarily occurred at the nesting trees. As mutual displays rarely occurred when birds were not at the nesting tree (own observations), mutual displays appear to signal arousal resulting of the tension at the nesting site, rather than affiliation. In this sense they may be important in reducing the likelihood of conflict escalation, by indicating that further escalation might lead to an aggressive conflict.

Conclusion

As predicted we did not observe reconciliation in rooks, but report evidence for post-conflict third party affiliation that might serve to reduce the likelihood of renewed attacks by signalling alliances among pair partners to third parties. Mutual displays may be important in signalling the level of social tension to others to preclude further conflict escalation. Our observations on free ranging birds support the results from captive studies that conflict management in rooks is centred around the pair bond as key social unit in this colony breeding bird.

(f) Acknowledgements

We thank the Fondation Pierre Mercier pour la Science for funding this study (to R. Bergmüller). We thank also the authorities of the city of Neuchâtel allowing us to observe the colonies form the battlements of the castle and form the roof of the Laténium. These observations were conducted in agreement with the Swiss law on animal ethics.

(g) References

Afkami, M. E. & Strassmann, J. E. 2007. Adult yellow-crowned night-herons face in opposite directions at the nest. *The Wilson Journal of Ornithology*, 119, 747-749.

Arnold, K. & Barton, R. A. 2001. Postconflict behavior of spectacled leaf monkeys (Trachypithecus obscurus). II. Contact with third parties. *International Journal of Primatology*, 22, 267-286.

Aureli, F. & van Schaik, C. P. 1991. Post-Conflict behavior in long-tailed macaques (Macaca fascicularis) : I. The social events. *Ethology*, 89, 89-100.

Aureli, F. & Smucny, D. 2000. The role of emotion in conflict and conflict resolution. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 199-224. London: University of California Press.

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

Benjamini, Y. & Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the royal statistical society series B-methodological*, 57, 289-300.

Braun, A. & Bugnyar, T. 2012. Social bonds and rank acquisition in raven nonbreeder aggregations. *Animal Behaviour*, 84, 1507-1515.

Braun, A., Walsdorff, T., Fraser, O. N. & Bugnyar, T. 2012. Socialized sub-groups in a temporary stable raven flock? *Journal of Ornithology*, 153, 97-104.

Bshary, R. & Würth, M. 2001. Cleaner fish *Labroides dimidiatus* manipulate client reef fish providing tactile stimulation. *Proceedings of the Royal Society of London, Series B,* 268, 1495-1501.

Carrascal, L. M., Moreno, J. & Amat, J. A. 1995. Nest maintenance and stone theft in the Chinstrap penguin (Pygoscelis antartica). *Polar Biology*, 15, 541-545.

Cools, A. K. A., van Hout, A. J. M. & Nelissen, M. H. J. 2008. Canine reconciliation and third-party-initiated postconflict affiliation: Do pacemaking social mechanisms in dogs rival those of higher primates? *Ethology*, 114, 53-63.

Cordoni, G., Palagi, E. & Borgognini, T. S. 2006. Reconciliation and consolation in captive Western gorillas. *International Journal of Primatology*, 27, 1365-1382.

Cords, M. & Aureli, F. 2000. Reconciliation and relationship qualities. In: *Natural Conflict Resolution*, (Ed. by F. Aureli & F. B. M. de Waal), pp. 177-198. London: University of California Press.

de Waal, F. B. M & van Roosmalen, A. 1979. Reconciliation and consolation among chimpanzees. *Behavioral Ecology and Sociobiology*, 5, 55-66.

de Waal, F. B. M, & Yoshihara, D. 1983. Reconciliation and redirected affection in rhesus monkeys. *Behaviour*, 85, 224–241.

de Waal, F. B. M. & Aureli, F. 1996. Consolation, reconciliation and a possible cognitive difference between macaques and chimpanzees. In: Reaching into thoughts: The mind of great apes. (Russon A. E., Bard, K. A. & Parker, S. T. Eds). Cambridge University Press, Cambridge, pp. 80-110.

de Waal, F. B. M. & Aureli, F. 1997. Conflict resolution and distress alleviation in monkeys and apes. In: *The Integrative Neurobiology of Affiliation*, (Ed. by C. S. Carter, B. Kirkpatrick & I. I. Lederhendler), pp.317-328. New York: Annals of the New York Academy of Sciences.

de Waal, F. B. M. 2000. The first kiss: Foundations of conflict resolution research in animals. In: *Natural Conflict Resolution*, (Ed. by F. Aureli & F. B. M. de Waal), pp.15-33. London: University of California Press.

Emery, N. J., Seed, A. M., von Bayern, A. M. P. & Clayton, N. S. 2007. Cognitive

adaptations of social bonding in birds. *Philosophical Transactions of the Royal*

Society B, 362, 489-505.

aFraser, O. N. & Bugnyar, T. 2010. Do ravens show consolation? Responses to distressed

others. *PLoS ONE*, 5, e10605.

bFraser, O. N. & Bugnyar, T. 2010. The quality of social relationships in ravens. *Animal Behaviour*, 79, 927–933.

Fraser, O. N. & Bugnyar, T. 2011. Ravens reconcile after aggressive conflicts with

valuable partners. *PLoS ONE*, 6, e18118.

Fujita, G. & Higuchi, H. 2011. Effect of neighbour visibility on nest attendance patterns of Barn Swallows Hirundo rustica in loose colonies. *IBIS*, 153, 858-862.

Gerber, R. 1956: Die Saatkrähe. Leipzig: A. Ziemsen Verlag.

Haffer, J. & Bauer, K. 1993. *Handbuch der Vögel Mitteleuropas- teil III Passeriformes* (Ed. by Glutz von Blotzheim U. N. Bauer KM (Aula-Verlag Wiesbaden) pp1733-1857.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, 54, 187–211.

Kutsukake, N. & Clutton-Brock, T. H. 2008. Do meerkats engage in conflict management following aggression? Reconciliation, submission and avoidance. *Animal Behaviour*, 2008, 75, 1441-1453.

Leone, A. & Palagi, E. 2010. Reconciling conflicts in a one-male society: the case of geladas (*Theropithecus gelada*). *Primates,* 51, 203-212.

aLogan, C. J., Emery, N. J. & Clayton, N. S. 2013 Alternative behavioral measures of postconflict affiliation. *Behavioral ecology,* 24, 98-112.

bLogan, C. J., Ostojic, L. & Clayton, N. S. 2013. Rook, but not jackdaw, post-conflict third-party affiliation reduces aggression for aggressors. *Ethology*, 119, 1-9.

Mallavarapu, S., Stoinski, T. S., Bloomsmith, M. A. & Maple, T. L. 2006. Postconflict behavior in captive Western lowland gorillas (Gorilla gorilla gorilla). *American Journal of Primatology*, 68, 789-801.

Norscia, I. & Palagi, E. 2011. Do wild brown lemurs reconcile? Not always. *Journal of Ethology*, 29, 181-185.

Palagi, E. Paoli, T. & Borgognini, T. S. M. 2004. Reconciliation and consolation in captive bonobos (Pan paniscus). *American Journal of Primatology*, 62, 15-30.

Palagi, E., Cordoni, G. & Borgonini Tarli, S. M. 2006. Possible roles of consolation in captive chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology,* 129, 105-111.

Palagi, E. & Cordoni, G. 2009. Postconflict third-party affiliation in *Canis lupus*: Do wolves share similarities with the great apes? *Animal Behaviour,* 78, 979-986.

Roskaft, E. 1981. Territorialism, neighbour conflicts and social interactions in the rooks corvus frugilegus during the breeding season. *Fauna Norv. Ser. C. Cinclus*, 5, 5-9.

Roskaft, E. & Espmark, Y. 1982. Vocal communication by the Rook Corvus frugilegus during the breeding season. *Ornis Scandinavica*, 13, 38-46.

Roskaft, E. 1983. Male Promiscuity and Female Adultery by the Rook Corvus frugilegus. *Ornis Scandinavica*, 14, 175-179.

Schino, G. 1998. Reconciliation in domestic goats. *Behaviour*, 135, 343-356.

Seed, A. M., Clayton, N. S. & Emery, N. J. 2007. Postconflict third-party affiliation in rooks, *Corvus frugilegus*. *Current Biology*, 17, 152-158.

Silk, J. B., Kaldor, E. & Boyd, R. 2000. Cheap talk when interests conflict. *Animal Behaviour*, 59, 423-432.

Veenema, H. C., Das, M., & Aureli, F. 1994. Methodological improvements for the study of reconciliation. *Behavioural Processes* 31, 29–37.

Wahaj, S. A., Guse, K. R. & Holekamp, K. E. 2001 Reconciliation in the Spotted Hyena (Crocuta crocuta). *Ethology*, 107, 1057-1074.

Watts, D. P., Colmenares, F. & Arnold K. 2000. Redirection, consolation and male policing: How targets of aggression interact with bystanders. In: Natural Conflict Resolution (Ed. by F. Aureli & F. B. M. de Waal), pp. 281-301. Berkeley, California: University of California Press.

Weaver, A. 2003. Conflict and reconciliation in captive bottlenose dolphins, Trursiops truncatus. *Marine Mammal Science*, 19, 836-846.

Chapter 3

Title manuscript 3: Spontaneous performance of wild crows on a simple multistep tool use task

Authors: Felice Di Lascio[1], Stéphane Rizzo[1], Noélie Nodiroli[1], Ralph Bergmüller[1] & Redouan Bshary[1]

[1]Université de Neuchâtel, 2000 Neuchâtel, Rue Emile-Argand 11, Switzerland

(a) Abstract

The capacity to use tools has been described in a broad range of species ranging from insects to higher vertebrates, including birds. Among birds, corvids seem to be an outstanding group as many of their representatives have been shown to flexibly use tools and to have some understanding about the functional properties of these tools. However, most studies carried out to date with corvids have been conducted in captivity using extensively trained animals, whereas studies on wild animals are virtually absent. Here we tested wild carrion crows (*Corvus corone corone*) in Western Switzerland on a tool use task where the animals needed to extract a piece of food from a Plexiglas tube fixed on a wooden frame, with the help of a stick. Out of 23 birds, only seven could be habituated to participate. None of the tested animals spontaneously used the sticks that were at their disposal, first near the apparatus and in a second step already inserted. Even after a third phase of successful foraging due food being attached to the stick, animals were unable to successfully use inserted sticks though they were more likely to remove the sticks, indicating that they had associated sticks with food rewards. The current results seem to indicate that crows have a limited tendency to use tools when being tested in the wild. In the current report we discuss what we think could be the most plausible explanations of these negative findings.

Key words: Tool-use ● Corvus corone ● Crows ● Chimpanzees ● Cognition

(b) Introduction

In certain circumstances animals need the help of others or the use of objects for the attainment of their objectives. These goals might consist of extracting food from a substrate, to capture preys efficiently, to win a contest or to use an object for their physical maintenance (Bentley-Condit and Smith 2009). Chimpanzees, for instance, have been shown to use tools in a variety of contexts, for example to extract termites with sticks, break nuts with the help of stones, chase competitors with the help of a larger branch that is used as an arm, or with the help of an ally (reviewed in: Boesch and Boesch 1990). While most people would instantly appreciate whether, what an animal does resembles tool use, its definition remains largely arbitrary and several definitions have been proposed (Bentley-Condit and Smith 2009). One of the most widely cited and accepted definitions of tool use that we will refer to, throughout this text, is that of Beck (1980), where he defines it as: "*the employment of an object to alter the form, position or condition of another object, organism or the user itself*". According to this definition, many species use tools in the wild and in captive environments. Indeed, whereas chimpanzees have been a species of primary interest because of their common ancestry with humans and because of the apparently complex modes by which these behaviors are transmitted, resembling those of our own species (Biro et al. 2003; Whiten et al. 2005), recent studies on tool use in diverse taxa have shown that outside primates some species employ tools as accurately as our closest relatives (e.g., birds: Emery and Clayton 2004; Seed and Byrne 2010). Indeed, from a wide phylogenetic perspective, it seems that the capacity to use unanimated objects evolved several times in distantly related species that differ depending on the ecological conditions they evolved in and their cognitive or physical (pre)-adaptations (Bentley-Condit and Smith 2009) (e.g., physical pre-adaptations in New Caledonian crows: Troscianko et al. 2012). The question of why some species use tools whereas others do not is still hard to answer because interpreting the differences between such distantly related species is sometimes challenging, not to say impossible. One way to circumvent the problem of comparing distantly related species is to restrict the study of tool use to a subset of species that are more closely related such as a family or a genus where for instance, the past phylogenetic history is easier to infer (Kacelnik 2009). This reduces the risk of misinterpreting the differences we observe between the species we compare. The corvid family, is such a unit and has until now been studied to a large extent, amongst other things for their capability to use tools. According to Bentley-Condit and Smith (2009) in the genus corvus about 60% of the representatives use tools in captive and / or wild environments, which makes them ideal candidates to study and better understand the evolution of tool use. Among corvids, New Caledonian crows are certainly the most prominent tools users; they have been shown to be capable of selecting the right tools depending on the experimental tasks (Taylor et al. 2011), using tools in a sequence to reach food (Meta tool-use) (Taylor et al. 2007) and to modify tools when necessary (Weir et al. 2002, Weir & Kacelnik 2006). New Caledonian crows are not solely gifted tool users under captive conditions but show these behaviors also in the wild where they depend on tools to extract larvae from decaying candlenut tree trunks (Bluff et al. 2010). In fact, their performances in captivity mirror what they do under wild conditions. More unexpected are however the performances of captive rooks, a social species of corvid (Coombs 1960, Yeates 1934), that have been tested in recent years on similar paradigms and that seemed to be capable to use, select and modify tools in a comparable manner as their New Caledonian counterparts (Bird and Emery 2009[a,b]). In contrast to their close relatives, rooks are not known to use tools under natural conditions. This finding is surprising because, the natural history of a species is usually a good predictor of a species specific cognitive capacities measured in such tasks, something that we call hereafter the ecological approach. For instance, when comparing the performance of caching and non-caching corvids on a spatial task, where individuals had to cue on landmarks to orient themselves, Jones et al. (2002) found that, the caching species was better / faster at solving this experiment than the non-caching corvid. This example illustrates that sometimes, the natural history of a species explicates better the divergences / convergences of the cognitive capacities of species than phylogeny. In this perspective, the finding that rooks use tools in captivity even though they do not show this kind of behavior in nature, are difficult to explain by the ecological approach only. Indeed, if the capacity to use tools is a specific adaptation then the discrepancy between the performances of captive and wild rooks needs to be explained in a different manner. This apparent paradox lead Emery and colleagues (2009[a]) to propose that the capacity to use tools is likely to be a capacity that is common to most corvids that emerges as a by-product from a general form of intelligence rather than being a domain-specific capacity that evolved to solve tool related problems. This hypothesis is indirectly supported by a recent finding that suggests that the capacity to use tools in corvids is unrelated to their relative brain size (Jonsson et al. 2012). In fact, these results suggest that as all corvids have relative large brains compared to other birds, they all have the capacity to use tools, or innovate, when needed. However, results in the cognitive field, especially when approaching complex forms of learning and reasoning in the physical domain are prone to criticisms and alternative explanations (Shettleworth 2009, 2010, 2012). One recurrent criticism is that the performances of captive animals, reared by humans and tested serially in a range of similar experimental tasks, are unlikely to be illustrative of the natural capacity of the species of interest (Thornton and Lukas 2012). This is notably supported by a handful of studies that either directly compared the performance of wild vs captive animals (Benson-Amram et al. 2013) or field studies that complemented laboratory studies (Laidre 2008). These studies indicate that commonly, wild animals are not as good as captive animals when being tested in tool use experiments. Even in nature performances of animals can differ between populations if local conditions are influenced, for instance, by human presence. van de Waal and Bshary (2010) compared the performance of 6 wild groups of vervet monkeys on their technical skills by exposing them to experimental boxes which the animals could open in different ways. What their study shows is that the two groups of animals that had within their territory access to human facilities were also those that were faster and better at opening the boxes in comparison to the four other groups that lived in a habitat undisturbed by humans. This suggests that contact with humans, or at very least human made objects, may have increased their manipulative, technical performances in response. An interesting approach is to consider captivity as being an environment with specific selection pressures (Mason et al. 2013). Indeed, captive animals need to cope with this novel environment, where space is restricted and humans are present. Those animals surviving in captivity might be less fearful, have a lower stress response to human presence (Mason et al. 2013) or unfamiliar objects (e.g., birds: Greenberg 1983, 2003) and might be more likely to explore, manipulate and as a consequence of all that, are able to solve tool related tasks easier (Thornton and Lukas 2012). While the comparison of wild vs captive subjects is an interesting research question per se, we think that when trying to understand what the typical capacities of a species are, testing them in their natural habitat should be a priority and might be a good way to avoid the effects of enculturation (Call and Tomasello 1996), previous experience on experimental tasks (Shettleworth 2009), or the risk of testing a subset of animals that are not representative of wild animals.

In the corvid family the picture of their capacity to use tools is still incomplete predominantly for wild birds. To our knowledge, New Caledonian crows are the only species of this family that have been tested in both their natural habitat and in strictly controlled conditions in captivity (For a review on tool use in New Caledonian crows see: Rutz and St Clair 2012). Here we decided to test wild corvids on a tool use task that is well established in the laboratory to test the spontaneous performance on these tasks without previous experience. In our study area we had both rooks and carrion crows (*Corvus corone corone*). As it turned out only carrion crows were willing to approach and interact with the experimental apparatus, and the study thus exclusively focuses on them. Crows are a corvid species that is omnivourous and widespread all over the Palearctic region and that seems to be easily adaptable to the newly created anthropomorphized environments (Haffer and Bauer 1993), being especially abundant in urban and agricultural landscapes. Crows are also a sympatric species of rooks and are known to forage in mixed flocks with the former with whom they also share sometimes sleeping trees in winter. Finally, crows are phylogenetically relatively close to rooks with whom they shared a common ancestor some 11 millions years ago, and with whom they also share a relative residual brain size that is similar (Jonsson et al. 2012). Because of all these similarities, we think that carrion crows are good candidates for a first comparison of the capacity to use tools in the wild and also because, to our knowledge, there are to date no studies on tool use in crows, neither in the wild nor in captivity. In the first phase of the experiment we asked whether the animals would spontaneously use tools at their disposal to extract food from an apparatus where the reward was not accessible otherwise. In case of failure, we asked whether the crows would solve the task if the association between the tool and the food was made more conspicuous by pre-inserting the tool in the apparatus, or in the ‘worst-case’ scenario after exposure to a series of trials in which the food was attached to the stick, so that pulling out the stick would be enough to solve the task. Based on the resemblances with other corvids and the positive evidence published in recent years in this family, we predicted that crows should be able to solve the current experiment eventually, while it seemed difficult to predict whether they would need help initially and if so how much.

(c) Methods

Animals and study sites

The experiments were carried out between April and August 2012 in three different cantons, Bern, Neuchâtel and Vaud, in Switzerland. Before being tested, the animals had to be habituated to human presence while they were eating at a given site. For this reason, the observer went on a site where crows were observed repeatedly, deposited food and waited for a maximum of 60 minutes at a distance of approximately 30 metres. This was repeated almost daily during a period of a maximum of 4 weeks prior to commencing the experiment described below. If subjects refused to eat while the experimenter was present within that time, they were not further tested. Only the results for the individuals that were successfully habituated are described and discussed in the current report. Because individuals were not marked, study sites were chosen within the territory of adult individuals. We assumed that the same individuals were present throughout the experiment in each location. On each study site, individual recognition was possible with the help of naturally occurring markings on the plumage, the legs or the beak. Carrion crows, like other corvid species, are known to be a neophobic species that are unlikely to approach novel objects or persons rapidly (e.g., ravens: Heinrich 1988, Heinrich et al. 1995). During the period of testing, corresponding roughly to the breeding period of this species, individuals defended their territory intensively (Haffer and Bauer 1993). For these reasons, we believe it is rather unlikely that other individuals then those initially habituated interfered with our subjects. The exact age, sex or reproductive statuses of the individuals are unknown.

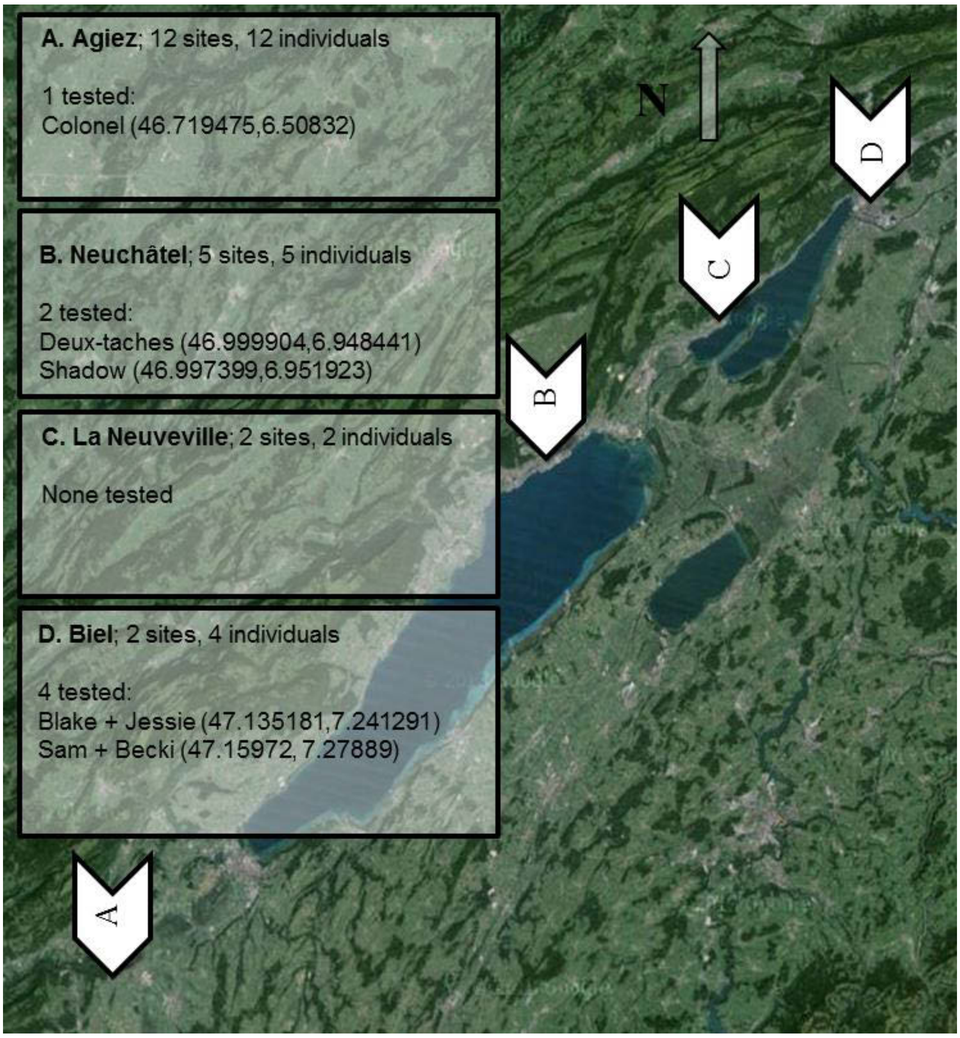

Figure 1. Map of the study area. In the white rectangles on the left of the map are indicated the number of sites and individuals tested in each location. Additionally, are mentioned the decimal coordinates of the exact location of their territory. Each location in which one or more individuals were tested are highlighted by the white arrows containing the capital letters from A to D. They indicate approximately the centre of the studied territories.

Apparatus

We used a Plexiglas tube fixed on a wooden block by two legs of about 10 centimetres. The apparatus was placed on our study sites, fixed to the ground with the help of two 30 centimetres long nails passing through two holes drilled in the wooden block. From the first phase of our experiment, we placed next to the apparatus five natural, more or less straight branches collected in the surrounding trees that were: 20 cm long and 1 cm thick with a side branch at one end of about 1 cm that worked as a hook. The exact measures of all the elements of the apparatus are shown in figure 2.

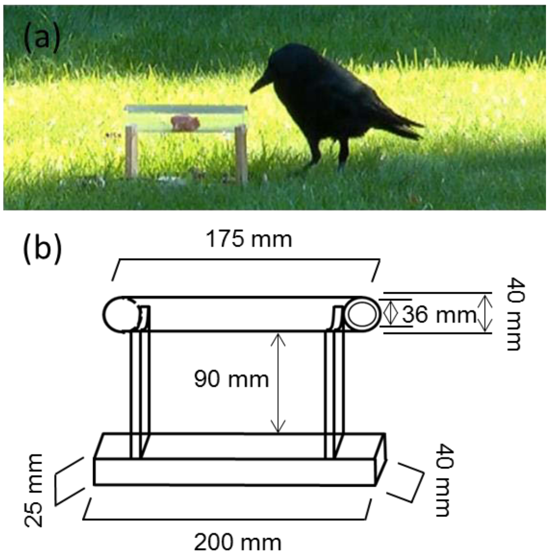

Figure 2a-b. Apparatus. **a** Picture of the apparatus baited with a food reward placed in the center of the Plexiglas tube with the crow “Blake” approaching the tube from the side. **b** sketch of the apparatus with measures. Sizes are given in millimetres.

Experimental procedure

The experiment was divided in six successive phases (See figure 3a-f). During each phase, data were collected either in the morning or the afternoon depending on the presence or absence of the tested individuals. Whenever individuals were present and participated in the experiment, they were tested in one session per day. Sessions lasted for a maximum of 10 trials, but typically lasted for about 3. Each trial lasted for a maximum of 10 minutes, if individuals were not able to solve the task within 10 minutes, the trial was considered as failed. In such a case, the observer approached the apparatus, extracted the reward and placed another piece of food in the tube. The next trial started when the test subject touched the apparatus or manipulated a stick. Given that the number of trials and specific passing criterions varied between phases we described them below for each phase in its own section.

A summary of the number of individuals and the number of trials each individual received are given in table 1 on the next page. Data were collected by 4 different observers; Noélie Nodiroli (NN), Stéphane Rizo (SR), Felice Di Lascio (FD) and Rémi Aubrun (RA) on six different sites in Switzerland. During the experiment, the subjects were either filmed with a camera (FD , RA) or observed directly by the observers (NN, SR). Usually, the observer arrived at the study site, checked for the presence of the sticks next to the tube, placed some food near or inside the tube depending on the experimental phase, and stayed at a distance of 20 to 30 meters from the tube. When the experiments were filmed, the observer placed next to him a camera that was fixed on a tripod. On two sites (Biel) more than one individual were tested simultaneously. On these two sites, individuals were very likely pair partner with one individual being dominant over the other, i.e., one individuals had priority of access to the food, as is typical for carrion crows (see: Chiarati et al. 2012). In most cases it was the same individual approaching first and being tested first. The observer had no influence on which individual he would be able to test first. In rare cases (~5% of all trials), both individuals were interacting with the apparatus simultaneously. In these trials only the behaviours of the bird that approached first were noted. Each phase is briefly described in its own section below.

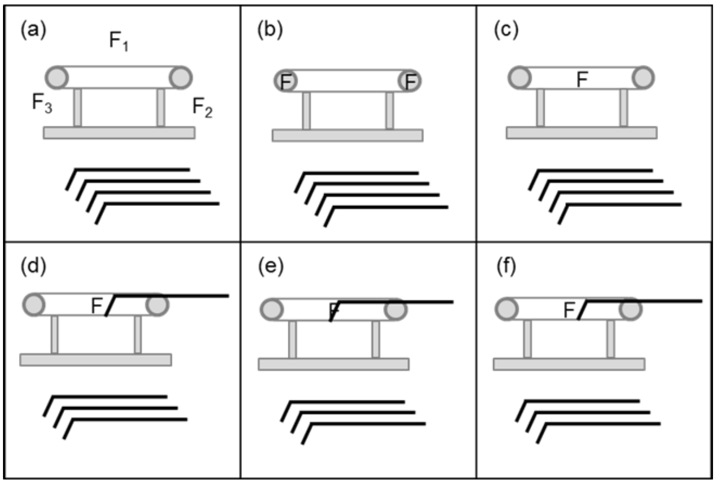

Figure 3a-f. Summary of the experimental phases. Phase 1 (a), phase 2 (b), phase 3 (c), phase 4 (d), phase 5 (e), phase 4.1 (f). In phase 1, F_{1-3} indicate three different types of food offered. In phase 2 the F placed at the ends of the tube indicates the type of food that was preferred in phase 1 and that was used to bait the tube in this and all subsequent phases. The black solid lines placed at the bottom of the apparatus in the phases 1 to 4.1 indicate the hooked sticks (tools). In phase 4 and 4.1 one of the hooked sticks is pre-inserted in the tube and can be used to extract the meat by either pulling or pushing the meat out of the apparatus. In step 5 the stick that overlaps the F indicates that the food was connected to the tool.

Table 1: Summary table of the number of individuals that were tested in each step. For each step are given the name of the individuals that were tested. Between brackets next to the names are indicated the number of trials each test subject received. In the third column are indicated the locations in which individuals were tested. The locations are given as decimal coordinates.

Exp. Steps	Individuals	Locations
1	Sam (9), Becki (8), Blake (15), Jessie (5), Shadow (37), Deux-taches (25)	Sam and Becki (47.15972, 7.27889) Blake and Jessie (47.135181,7.241291) Shadow (46.997399,6.951923) Deux-taches (46.999904,6.948441) Colonel (46.719475,6.50832)
2	Sam (18), Becki (10), Blake (18), Jessie (7), Shadow (31), Deux-taches (22), Colonel (11)	
3	Sam (14), Becki (12), Blake (20), Jessie (4), Deux-taches (10), Colonel (23)	
4	Sam (14), Becki (19), Blake (14), Jessie (15), Deux-taches (10), Colonel (35)	
5	Sam (24), Becki (21), Blake (25), Jessie (21), Deux-taches (23), Colonel (29)	
6	Sam (20), Becki (20), Blake (23), Jessie (22), Deux-taches (24), Colonel (25)	

Phase 1: food test preference

The aim of this first step was to determine the food preference of our study subjects. For this, we offered them three different types of food: bread, dog food and red meat. For each test trial the 3 types of food were deposited simultaneously in equal quantities and at an equal distance to the apparatus. Over test sessions the distance between the food and the apparatus was gradually decreased. In the first session the food was deposited at approximately 5 meters from the apparatus whereas in the last session the food was in contact with the apparatus. The type of food that was eaten first was considered as the preferred type of food. The type of food that was preferred in this first experimental phase was then used in all subsequent phases.

Phase 2: tube baiting

In phase 2, we habituated the animals to eat from the Plexiglas tube. For that we inserted two pieces of the preferred food at both extremities of the Plexiglas tube. The food was inserted in such a manner that the individuals could easily extract the reward with their beak. A trial was considered as completed if the individual extracted at least one piece of food. This second phase was stopped when individuals were eating form the tube without any noticeable reactions of fear, i.e., when birds showed no sudden backward motion while extracting the meat.

Phase 3: spontaneous tool use

In this third phase, the aim was to test whether subjects would spontaneously use the hooked sticks lying next to the apparatus to extract the meat from the tube. Each test session started with a motivation trial where the food was placed at the extremities of the tube as described in step 2. In the subsequent trials, the food was placed in the middle of the tube so that subjects could see but not reach the food directly with their beak. The only way to access the food for individuals was to use the sticks at their disposal close to the apparatus. A trial was considered as successful when test subjects were able to extract the meat by pulling or pushing the food reward out of the tube with the help of the tool. This first experimental phase was stopped when the observers noticed that the motivation of the animals to participate started to decrease, i.e., when the delay to approach the apparatus increased.

Phase 4: tool pre-inserted

As in the previous phase, food was placed in the middle of the apparatus. This time however, one of the hooked sticks was inserted in the tube before the trial started, so that it was in contact with the reward but not hooked to it. To extract the food individuals had to manipulate the stick so that it was hooked to the food and then to pull or to push the reward out of the tube. As in previous step, for each test session the first trial was a motivation trial. A trial was considered as successful when individuals extracted the reward with the help of the tool by either pulling or pushing it out. Each individual received a minimum of 10 trials in total but those individuals that were still motivated to participate despite constant failure were tested longer. In any case, no individual was tested for more than 35 trials in total.

Phase 5: reward attached

The aim of this phase was to increase the association between the tool and the food for those study subjects that would have failed to retrieve food in the previous steps. For that, we placed the food in the middle of the apparatus with the tool inserted in the tube and hooked to the tool. Consequently, each time the animal pulled or pushed the stick out of the tube, the trial was automatically rewarded. A trial was considered as successful when the subject ate the reward fixed at the tool. Individuals had to extract the food successfully on a minimum of 20 trials before being tested in the next phase.

Phase 6: repetition of step 4

The aim of this step was to test whether individuals would behave differently than in step 4 after having received 20 rewarded trials in step 5. Because of the stronger association between the tool and the reward we expected individuals to manipulate tools at a higher frequency in this step than in step 4. As in phase 5, individuals received a minimum of 20 trials to solve the task. Otherwise the experimental procedures were identical to those described for phase 4.

Data analysis

Data were analysed by using the statistical programme IBM SPSS Statistics 20. As results were binomial for each trial (succeed or fail) we used binomial tests, if not stated otherwise, to identify cases of significant performances. Tests were two-tailed and α level was set at 0.05.

(d) Results

Phase 1: food preference

Out of a total of 23 individuals that were initially included in the habituation phase, only 7 individuals (30.45% of the individuals) started eating when the observer was present and were subsequently included in this study.

In phase 1 a total of 6 individuals (Sam, Becki, Blake, Jessie, Shadow, Deux-taches) participated in this first phase between the 10th of April and the 8th of May 2012. The time during which they were tested was a median of 9 days (range: 2-18 days). 4 out of the 6 individuals developed a significant preference for the meat (Sam, $n=9$, $p=0.004$; Blake, $n=15$, $p=0.007$; Deux-taches, $n=25$, $p=0.043$; Shadow, $n=37$, $p=0.008$), one individual was close to a significant preference (Jessie, $n=5$, $p=0.063$) and the last subject (Becki) showed a non-significant preference for the meat ($n=8$, $p=0.289$).

Phase 2: tube baiting

7 individuals participated in the second phase of the experiment (Sam, Becki, Blake, Jessie, Shadow, Deux-taches, Colonel) between the 18th of April and the 21th of

May 2012. Indeed one individual (Colonel), directly started the experiment in this second phase. The second phase lasted for a median of 12 days (range: 6-18 days) and subjects required a median of 18 trials (range: 7-31 trials) before eating from the tube without showing obvious reactions of fear when extracting the meat.

Phase 3: spontaneous tool use

6 out of the 7 individuals that participated in step 2 proceeded in step 3 (Sam, Becki, Blake, Jessie, Colonel, Deux-taches). One individual (Shadow) was not tested in this and subsequent steps because it left the study site for an unknown reason. Individuals were tested between the 27th of April and the 13th of June for a median of 6 days (range: 4-9) and received a median of 13 trials to solve the task (range: 4-23). While none of the individuals ever manipulated the tools to direct them to the tube, 5 out of the 6 tested individuals touched the sticks disposed close to the tubes at least once during the time they were tested. A dominant strategy for all individuals was to reach the food by directly pecking at the tube or inserting their beaks into the tube extremities on majority of trials. They did so on a median of 100 % of the trials (range: 78-100).

Phase 4: tool pre-inserted

The same 6 individuals that participated in the previous phase took part in phase 4 and were tested between the 1st of May and the 14th of June. The subjects were tested for a median of 15 days (range: 7-17 days) and received a median of 17 trials to solve the task (range: 10-35). Individuals extracted the tool from the tube on more than half of the trials on a median of 66% of the trials (range 50-100), but never manipulated the stick to pull or to push the meat out of the apparatus. Individuals persisted on reaching the food directly with the beak by directly pecking at the tube or inserting the beak into the tube. This happened on a median of 75% of the trials (range: 40-89). The percentage of trials in which they tried to reach the food in the tube with their beaks was however significantly lower than in step 3 (Wilcoxon test: -2.201, n=6, p=0.028). None of the individuals ever directed the stick previously extracted from the tube or another stick close to the tube toward the apparatus.

Phase 5: reward attached

As in the previous phase the same individuals underwent testing in this fifth step. They were tested between the 8th of May and the 29th of June and required a median of 14 days (range 5-17) to reach our criterion of 20 trials. During this time they received a median of 23 trials (range: 20-25). All but one individual successfully extracted the tool with the food reward attached above chance level (binomial test: Sam, n=20, p=0.115; Becki, n=20, p=0.041; Blake, n=23, p=0.011; Jessie, n=22, p=0.017; Colonel, n=25, p<0.001; Deux-taches, n=24, p<0.001).

Phase 6: repetition of step 4

As in previous phases the same individuals were tested during a median of 17 days (range 5-19) and received a median of 23.5 trials (range: 21-29). Individuals extracted the tool from the tube on a higher percentage of trials compared to step 4 (Wilcoxon test: z=-2.023, n=6, p=0.043). However, none of the birds ever removed the stick in such a way that food would be extracted. Instead, the birds simply removed the inserted stick and persisted to reach the food with their beak directly at similar levels as in step 4 (Wilcoxon test: z=-1.572, n=6, p=0.116). Compared to step 4, individuals did not increase the frequency at which they manipulated sticks on the ground or the stick previously extracted (Wilcoxon test: z=-1.214, n=6, p=0.225).

(e) Discussion

We had asked whether wild crows can learn to use a stick as a tool to extract preferred food out of a tube. While only a minority of animals interacted with the apparatus for testing, those subjects seemed to be highly motivated to reach the food. Contrary to our prediction based on studies on other corvids, the crows failed to solve the task, even after having received several trials (in phase 5) where extracting the tool was systematically rewarded. Thus, they were apparently unable to create a representation of the tool as a mean to reach the reward. This result strongly contrasts with studies on corvids carried out to date. New Caledonian crows (Weir et al. 2002, Weir & Kacelnik 2006, Taylor et al. 2007), rooks (Bird & Emery 2009[a,b]) but also Eurasian jays (Cheke et al. 2011) and non-corvid species (e.g., Kea: Auersperg et al. 2011[a,b]) all showed some understanding of the tasks they were confronted when being tested for their capacity to use tools. Below, we discuss various potential explanations for our negative results.

Cognitive specialization?

If the capacity to use tools is related to a domain general capacity that is common to most corvids, then carrion crows should exhibit similar performances to other corvids, especially because there seems to be no fundamental differences in the cognitive capacities between carrion crows and the other species in this family when being tested in standard cognitive experiments (support task: Albiach-Serrano et al. 2012, delayed choice task: Dufour et al. 2012, Object permanence: Hoffmann et al. 2011, Exclusion task: Mikolasch et al. 2012). However, as pointed out by Bird and Emery (2009[a]) whether or not this capacity is expressed in any given species may also depend on the specific ecological conditions each species evolved in. In this perspective, the difference between our results and the extensive capacity to use tools by new Caledonian crows are easily understandable. In contrast, the dissimilarities between the performance of our carrion crows and rooks are however surprising assuming that their ecology seems to be more similar (Haffer and Bauer 1993). Nevertheless, even though, at first glance, the ecology of the two parent species are comparable, we can speculate that there might be subtle differences that may have led to the evolution of cognitive adaptations / specializations in crows, absent in rooks, that may in turn have hindered their capacity to use tools. For instance, one striking difference between rooks and crows, in the context of caching or more generally when feeding, is that crows seem to be specialized in klepto-parasiting other individuals while rooks seem to adopt mainly a producer strategy (Baglione and Canestrari 2009, Kallander 2007). In this context, other individuals, conspecifics or heterospecifics, manipulating food and the food itself seem to have a stronger local enhancing effect for crows than for rooks (Own observations). The competitive strategy adopted by crows in their natural habitat may have led to the suppression of some inhibition capacity when being confronted with food because in that context being attentive and quick when stealing food is certainly of advantage for individuals (Wascher et al. 2012, see also: Mikolasch et al. 2012). One study in captivity that measured the capacity to wait for a better reward when given a less valuable food reward (delayed choice task), in crows and ravens, showed that both species are able to wait for a few seconds, and sometimes up to five minutes, a result that is comparable to performances found for primates (Dufour et al. 2012). One key difference between corvids and primates is that the former tend to hide the primary reward while waiting for the better reward, whereas no such strategy has been reported for primates. The authors explain that this tactic may allow individuals to not be distracted by the food offered first, especially when waiting for several minutes. In our study, the food reward placed in the Plexiglas tube was constantly visible to the individuals. This might have distracted their attention from the tools and interfered with their capacity to solve the task. In contrast for rooks this might be less of a problem because of what we mentioned above. While this hypothesis remains largely speculative, we think that eventually, our results could have been very different if, for instance, we had used opaque tubes.

Ontogenetic effects

Ontogenetic effects might also, at least partly, explicate the poor performances of our subjects that were all adults. For wild animals, especially adult individuals, it might be particularly challenging to acquire novel techniques or more generally behaviours they never used during their developmental phase (Thornton and Lukas 2013, see also:Mason et al. 2013). In captivity, animals usually outperform their wild counterparts (e.g., spotted hyaenas: Benson-Amram et al. 2013, primates: Laidre 2008) and, in this sense, our results are in line with those studies (reviewed in: Thornton and Lukas 2012). Indeed, young individuals that are still in their sensitive phase, experiencing contact with human made objects, tend to become more manipulative and innovative, i.e., they adapt to captivity (e.g., primates: Reader and Laland 2003). Captive animals are usually also less neophobic than wild individuals (Greenberg 1983, 2003), a trait that has been shown to interfere with performances of individuals in cognitive experiment (e.g., spotted hyaenas: Benson-Amram et al. 2013, Apes: Herrmann et al. 2007). This last point might be particularly important when testing corvids given that these birds are known to be particularly fearful when confronted with novel objects or situations (Heinrich 1988, Heinrich et al. 1995). The experience of birds or other animals in previous experiments may also account for their better performances (Shettleworth 2009). This might be important for species that are not known to use tools in the wild, i.e., non-specialized tool users, and where individuals need to develop these specific capacities. For those species where tool use is part of their behavioral repertoire (e.g., New Caledonian crows) individual performances seem to be little affected by previous information or experience with the task, they typically solve the tool tasks relatively spontaneously (Kenward et al. 2005, 2006, von Bayern et al. 2009). Finally, we would like to stress that, to our knowledge, our experiment is the first to test a wild non-tool using corvid species which makes it difficult to interpret our negative results. To tease apart whether our negative results are best explained by the differences between wild and captive animals or by the species differences, more studies of the same species comparing the performances of hand reared and wild animals are needed.

Methodological considerations: small number of animals tested

Usually, most captive studies include only a small number of individuals. This is not really problematic given that most of those subjects typically solved the tasks they were confronted with. In such studies, when individuals solve a given problem that is thought to reflect certain cognitive capacities, scientists tend to accept the idea that this capacity is present and generalizable to the species level, although recent studies started stressing the importance of considering the variation between individuals (Thornton and Lukas 2012, Herrmann and Call 2012). In contrast, using only a small number of individuals, as in our study, when reporting negative results, is more problematic. Indeed, the low number of animals that we tested does not permit us to conclude that on the species level the capacity to use tools does not exist. As outlined earlier, there is usually less variation in the capacities of captive individuals to solve cognitive tasks in comparison to wild animals. For those studies that report tool use from wild populations of animals, typically not all of the individuals or groups of the studied animals exhibit the behaviors of interest (e.g., Chimpanzees and orangutans: Whiten et al. 2001, van Schaik et al. 2003). For instance, Gruber and colleagues (2010) studied tool use in two distinct communities of chimpanzees (Sonso and Kanyawara) in Uganda, where one community regularly uses sticks (Kanyawara) to access food in their natural habitat, whereas the second community (Sonso) only uses sponges but has never been observed using sticks. When provided with sticks to dip in honey that was trapped in an artificially drilled hole in a tree, none of the chimpanzee of the Sonso community used the tool and only 5 out of 12 (~42%) chimpanzees from the Kanyawara community used the sticks provided. Another example for birds is bait fishing. In order to increase their fishing efficiency, some bird species, most frequently Herons, place a bait or a lure (bread, flies or non-edible items) on the water surface near the shore to attract fish to catch them easier. By doing so, they very likely increase the number or quality of preys they capture; a tactic that may be considered as tool use (reviewed in: Ruxton and Hansell 2011). Interestingly, even in the species that adopt this tactic most frequently, the Green-backed Heron (*Butorides striatus*), only few individuals do so, whereas the rest of the population uses direct fishing tactics. There also seems to exist a relationship between the quality of the environment and the frequency at which the individuals use this technic. In fact individuals seem to fish with baits mainly in open habitats, where the environment offers few elements (trees, rocks, bushes) to hide near the shore (Higuchi 1988). These examples show that; (i) the propensity to use tools may vary from region to region or between populations because of differences in their environment and (ii) that even within those groups or populations where tool use is observed on a regular basis, only some individuals use tools. Whether the rarity with which wild animals use tools is best explained by cognitive constraints or because tool use is rarely better than not using tools in the wild, is still a matter of debate (Hansell and Ruxton 2008).

Concluding remarks

Definite conclusions are hard to derive from our negative results given our small sample size and should therefore be considered carefully. Furthermore, before concluding that crows lack the capacity to use tools, we encourage future projects to test them in slightly modified set-ups, especially because slight changes in the set-ups can have major influences on the response of test subjects when being tested in cognitive tests (e.g., Apes in a choice task: Mulcahy & Hedge 2012). Nevertheless, we think that the current findings are informative about the spontaneous performance of this species when being tested in the wild, especially because the locations in which we tested our subjects were several kilometers apart. While a handful of publications report positive evidence for tool use in captive corvids, there is still a gap in the knowledge regarding wild birds. In conclusion, we encourage future projects to focus on animals in their natural habitat and stress the importance of publishing negative results. When studying cognition, the lack of a capacity is probably as informative as the extraordinary unexpected capacities to use tools of some species.

(f) Acknowledgements

We thank the Fondation Pierre Mercier pour la Science for funding this study (to R. Bergmüller). We thank also the authorities of the city of Neuchâtel that allowed us to place the apparatuses in the fields. These observations were conducted in agreement with the Swiss law on animal ethics.

(g) References

Albiach-Serrano, A., Bugnyar, T. & Call, J. 2012. Apes (Gorilla gorilla, Pan paniscus, P. troglodytes, Pongo abelii) versus corvids (Covus corax, C. corone) in a support task: the effect of pattern and functionality. *J. Comp. Psychol.*, 126, 355-367.

aAuersperg, A. M. I., von Bayern, A. M. P, Gajdon, G. K., Huber, L. & Kacelnik, A. 2011. Flexibility in problem solving and tool use of Kea and New Caledonian crows in a multi access box paradigm. *PLoS ONE* 6(6): e20231.

bAuersperg, A. M. I., Huber, L. & Gajdon, G. K. 2011. Navigating a tool end in a specific direction: stick-tool use in kea (*Nestor notabilis*). *Biol. Lett.*, 7, 825-828.

Baglione, V. & Canestrari, D. 2009. Kleptoparasitism and temporal segregation of sympatric corvids foraging in a refuse dump. *Auk*, 126, 566-578.

Beck, B. B. 1980. Animal tool behaviour: the use and manufacture of tools by animals. Garland STPM Publishing, New York, NY.

Benson-Amram, S., Weldele, M. L. & Holekamp, K. E. 2013. A comparison of innovative problem-solving abilities between wild and captive spotted hyaenas, Crocuta crocuta. *Anim. Behav.*, 85, 349-356.

Bentley-Condit, V. K. & Smith E. O. 2009. Animal tool use: current definitions and an updated comprehensive catalog. *Behav.*, 147, 185-221.

aBird, C. D. & Emery, N. J. 2009. Insightful problem solving and creative tool modification by captive nontool-using rooks. *PNAS*, 106, 10370-10375.

bBird, C. D. & emery, N. J. 2009. Rooks use stones to raise the water level to reach floating worm. *Curr. Biol.*, 19, 1410-1414.

Biro, D., Inoue-Nakamura, N., Yamakoshi, R. T. G., Sousa, C. & Matsuzawa, T. 2003. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Anim. Cogn.*, 6, 213-223.

Bluff, L. A., Troscianko, J., Weir, A. A. S., Kacelnik, A. & Rutz, C. 2010. Tool use by wild new Caledonian crows Corvus moneduloides at natural foraging sites. *Proc. R. Soc. B.*, 277, 1377-1385.

Boesch, C. & Boesch H. 1990. Tool use and tool making in wild chimpanzees. *Folia Primatol.*, 54, 86-99.

Call, J. & Tomasello, M. 1996. The effect of humans on the cognitive development of apes. In: *Reaching into thought: the minds of the great apes* (Ed. by A. E. Russon, K. A. Bard & S. T. Parker), pp. 371–401. Cambridge, UK: Cambridge University Press.

Chiarati, E., Canestrari, D., Vera, R. & Baglione, V. Subordinates benefit from exploratory dominants : response to novel food in cooperatively breeding carrion crows. *Anim. Behav.*, 83, 103-109.

Cheke, L. G., Bird, C. D. & Clayton, N. S. 2011. Tool-use and instrumental learning in the Eurasian jay (Garrulus glandarius). *Anim. Cogn*., 14, 441-455.

Coombs, C. J. F. 1960. Observations on the rook corvus frugilegus in southwest Cornwall. *Ibis*, 102, 394-419.

Dufour, V., Wascher, C. A. F., Braun, A., Miller, R. & Bugnyar T. 2012. Corvids can decide if a future exchange is worth waiting for. *Biol. Lett*., 8, 201-204.

Emery, N. J. & Clayton, N. S. 2004. The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, 306, 1903-1907.

Greenberg, R. 1983. The role of neophobia in determining the degree of foraging specialization in some migrant warblers. *American Naturalist*, 122, 444-453.

Greenberg, R. 2003. The role of neophobia and neophilia in the devellopement of invovative behaviours of birds In: *Animal innovation* (Ed. by S. M. Reader and K. N. Laland), pp. 175-196. New York: Oxford University Press.

Haffer, J. & Bauer, K. 1993. in *Handbuch der Vögel Mitteleuropas*- teil III Passeriformes, eds Glutz von Blotzheim UN, Bauer KM (Aula-Verlag Wiesbaden) pp1733-1857.

Hansell, M. & Ruxton, G. D. 2008. Setting tool use within the context of animal construction behaviour. *Trends Ecol. Evol*., 23, 73-78.

Heinrich, B. 1988. Why do ravens fear their food? *The Condor*, 90, 950-952.

Heinrich, B., Marzluff, J.M. & Adams, W. 1995. Fear and food recognition in naive common ravens. *Auk*, 112, 499-503.

Herrmann, E. & Call, J. 2012. Are there geniuses among the apes? *Phil. Trans. R. Soc. B.*, 367, 2753-2761.

Higuchi, H. 1988. Individual differences in bait-fishing by the Green-backed Heron Ardeola striata associated with territory quality. *Ibis*, 130, 39-44.

Hoffmann, A., Rüttler, V. & Nieder, A. 2011. Ontogeny of object permanence and object tracking in the carrion crow, Corvus corone. *Anim. Behav*., 82, 359-367.

Jolles, J. W., Ostojic, L. & Clayton, N. S. 2013. Dominance, pair bonds and boldness determine social-foraging tactics in rooks, Corvus frugilegus. *Anim. Behav.*, 85, 1261-1269.

Jones, J. E., Antoniadis, E., Shettleworth, S. J. & Kamil A. C. 2002. A Comparative study of geometric rule learning by nutcrackers (Nucifraga columbiana), pigeons (Columba livia), and jackdaws (Corvus monedula). *Journal of comparative psychology*, 116, 350-356.

Jonsson, K. A.; Fabre, P. H. & Irestedt, M. 2012. Brains, tools, innovation and biogeography in crows and ravens. *BMC Evol. Biol*., 12:72.

Kallander, H. 2007. Food hoarding and use of stored food by rooks Corvus frugilegus. *Bird Study*, 54, 192-198.

Kacelnik, A. 2009. Tools for though or thoughts for tools? *PNAS*, 106, 10071-10072.

Kenward, B. Weir, A. A. S., Rutz, C. & Kacelnik, A. 2005. Tool manufacture by naive juvenile crows. *Nature*, 433, 121.

Kenward, B., Rutz, C., Weir, A. A. S. & Kacelnik, A. 2006. Development of tool use in New Caledonian crows: inherited action patterns and social influences. *Anim. Behav.*, 72, 1329-1343.

Laidre, M. E. 2008. Spontaneous performance of wild baboons on three novel food-access puzzles. *Anim. Cogn.,* 11, 223-230.

Mason, G., Burn, C. C., Dallaire, J. A. Kroshko, J., Kinkaid, H. M. & Jeschke J. M. 2013. Plastic animals in cages: behavioural flexibility and responses to captivity. *Anim Behav*., 85, 1113-1126.

Mikolasch, S., Kotrschal, K. & Schloegl, C. 2012. Is caching the key to exclusion in corvids? The case of the carrion crows (Corvus corone corone). *Anim. Cogn.*, 15, 73-82.

Mulcahy, N. J. & Hedge, V. 2012. Are great apes tested with an object-choice task? *Anim. Behav.*, 83, 313-321.

Pierce, J. D. 1986. A review of tool use in insects. *Fla. Entomol*., 69, 95-104.

Reader, S. M. & Laland, K. N. 2003. *Animal innovation*. Oxford: Oxford University Press.

Rutz, C. & St Clair, J. J. H. 2012. The evolutionary origins and ecological context of tool use in New Caledonian crows. *Behav. Process.*, 89, 153-165.

Ruxton, G. D. & Hansell, M. H. 2011. Fishing with a bait or a lure: a brief review of the cognitive issues. *Ethol*. 117, 1-9.

Seed, A. & Byrne, R. 2010. Animal tool-use. *Curr. Biol.*, 20, 1032-1039.

Shettleworth, S. J. 2009. Animal cognition: deconstructing avian insight. *Curr. Biol.*, 19, 1039-1040.

Shettleworth, S. J. 2010. Clever animals and killjoy explanations in comparative psychology. *Trends Cogn. Sci.*, 14, 477-481.

Shettleworth, S. J. 2012. Do animals have insight, and what is insight anyway? *Can. J. Exp. Psychol.*, 66, 217-226.

Taylor, A. H., Hunt, G. R. Holzhaider, J. C. & Gray, R. D. 2007. Spontaneous metatool use by New Caledonian crows. *Curr. Biol.*, 17, 1504-1507.

Taylor, A. H., Elliffe, D. M., Hunt, G. R., Emery, N. J. Clayton, N. S. & Gray, R. D. 2011. New Caledonian crows learn the functional properties of novel tool types. *PLoS ONE*, 6(12): e26887.

Troscianko, J., von Bayern, A. M. P., Chapell, J., Rutz, C. & Martin, G. R. 2012. Extreme binocular vision and a straight bill facilitate tool use in New Caledonina crows. *Nature communications*, 3, 1110.

van de Waal, E. & Bshary, R. 2010. Contact with human facilities appears to enhance technical skills in wild vervet monkeys (Chlorocebus aethiops). *Folia Primatol.*, 81, 282-291.

von Bayern, A. M. P., Heathcote, R. J. P., Rutz, C. & Kacelnik, A. 2009. The role of experience in problem solving and innovative tool use in crows. *Curr. Biol.*, 19, 1965-1968.

Wascher, C. A. F., Dufour, V. & Bugnyar, T. 2012. Carrion crows cannot overcome impulsive choice in a quantitative exchange task. *Front. Psychol.* (3) 118.

Weir, A. A. S., Chappell, J. & Kacelnik, A. 2002. Shaping of hooks in New Caledonian crows. *Science*, 297, 981.

Weir, A. A. S. & Kacelnik, A. 2006. A New Caledonian crow (*Corvus moneduloides*) creatively re-designs tools by bending or unbending aluminum strips. *Anim. Cogn.*, 9, 317-334.

Whiten, A. Horner, V. & de Waal, F. B. M. 2005. Conformity to cultural norms of tool use in chimpanzees. *Nature*, 437, 737-740.

Yeates, G. K. 1934. The life of the rook. London.

General discussion

(a) Initial plans of the project

At the beginning of this project our plan was to work with individually marked rooks to better understand their sociality in the wild and to study in much more details, than what we did in chapters one and two, for instance: pair formation, intra-pair cooperation / coordination, pair maintenance across breeding seasons or dispersal of juveniles. This was planned because intra-pair cooperation has been proposed to be a crucial factor in explaining the extraordinary cognitive capacities of rooks (Emery et al. 2007) while in fact little is known about the sociality of this species in their natural habitat (However see: (Roskaft 1981, Roskaft and Espmark 1982, Roskaft 1983). Furthermore, the initial idea was to fully compare laboratory studies on rooks with field observations and field experiments, in particular tool-use experiments, to add some external validity to those previous studies carried out on hand raised individuals (Emery et al. 2007, Seed et al. 2007, 2008, Bird and Emery 2009[a,b]). In fact the experiment presented in chapter three was first intended to be carried out with rooks. Instead, we tested carrion crows because they approached our apparatuses more easily while rooks never showed any interest (Own observations). A second goal of this project was to better understand the mechanisms of dispersal and colony formation because rooks are a newly settled species in our region (Blaise Mulhauser, personal communication) and better understanding those mechanisms could have contributed in managing more efficiently their number, that are constantly increasing in recent years (Frankhauser 2006). Additionally, capturing individuals would have been optimal for taking genetic samples in order to study the importance of relatedness for social interactions (Hamilton 1964a,b). Genetic information would have allowed us to answer several additional questions such as: (i) how closely related are individuals within a colony, (ii) how closely related are individuals between colonies of the same population, (iii) how tightly related are individuals nesting close to each other and finally, (iv) what influence does kinship have on how cooperative individuals are with each other.

(b) Difficulties encountered with capturing rooks

Unfortunately, the capture of individuals that was planned mainly with ladder cages turned out to be much more difficult than we expected. Despite having invested several month in installing these cages in the fields, modifying them, putting decoy birds around and in the cages, varying the type of food used to bait the cages, I was unable to capture these birds. Possible causes of my failure were some missing expertise, the too frequent displacement of the cages, repeated human disturbances or the extremely fearful nature of the individuals in our study population. Corvids are generally accepted as extremely shy (e.g., ravens: Heinrich 1988, Heinrich et al. 1995). Indeed in our study population individuals hardly ever approached our traps, apparatuses of the tool use experiment, or feeders containing high quantities of quality food, even during winter (Guyot 2013, Master thesis). Colleagues succeeded in capturing other populations of wild rooks with the same methods we used (Christine Schwab, personal communication), in countries where the birds appeared to be bolder and approaching faster (e.g., in England: Fletcher and Foster 2010). As mentioned earlier, our study population, contrary to those other populations studied elsewhere, have relatively recently immigrated to Switzerland in 1963 (Frankhauser 2006; Zbinden 2005[a,b]) and even more recently to our region (Canton of Neuchâtel) where they were observed for the very first time some fifteen years ago (Blaise Mulhauser, personal communication). That might explain the particularly shy behavioural phenotype of the rooks in our region and might in itself be an interesting research avenue for future projects.

(c) Basic unit of cooperation in rooks: the pair bond

While we were unable to answer some crucial questions regarding the sociality of our study species in this thesis, the findings of chapter one and two are nevertheless informative and indicate that rooks mainly rely on their pair partner to cope with the cost of competition when breeding in colonies. In chapter one, we found no evidence that rooks form coalitions with other individuals than their mating partners, even between close neighbours. In contrast, coordination between mating partners appeared to be central to defend nests against thefts. These results are coherent with our findings of chapter two were affiliative behaviours were exclusively exchanged among pair partners and were absent between former opponents. Furthermore, the presence of a partner seemed to reduce the likelihood of being aggressed, given that single individuals were more often involved in conflicts than paired individuals, suggesting a protective effect of partner presence. Overall, the results of these first two chapters confirm the results of previous studies in captivity that also showed that rooks mainly cooperate with one single partner (Seed et al. 2007, 2008, Emery et al. 2007, Logan and Clayton 2013, Logan et al. 2013). How this relates to other findings in other species is more extensively discussed in chapter one and two.

One more aspect that is not discussed in those two chapters is the following. In the primate literature but also in other corvids there are examples of reconciliation, i.e., individuals have other important relationships than the one with their mating partner, what contrasts with our study species (review on primates: Aureli et al. 2002, ravens: Fraser and Bugnyar 2010, 2011). But this also involves social support among members of a coalition if one individual of that particular group is aggressed. While it might be of advantage for individuals when living in relatively small groups, to defend allies and form coalitions (e.g., chimpanzees: Gilby et al. 2013), this might have costly consequences for individuals when living in large colonies of many hundreds or thousands of individuals, such as in colonies of rooks (Gerber 1956). In a system were sources of competition are abundant, for instance in colonial breeding birds (Roland et al. 1998), and where the likelihood to enter in a conflict is high because of the density of individuals, I hypothesised that in the absence of control mechanisms that stabilise social groups (e.g., policing: Flack et al. 2006), complex social networks would have as a consequence that conflicts would rapidly escalate to a generalised conflict in the colony, by the play of alliances. Hence, a social network “compartmented” in sub-units of two individuals could also be seen as a simple mechanism that reduces the likelihood that a conflict propagates. The idea that the rooks’ social system is strongly compartmented, at least during the breeding season, is further supported by the fact that when a conflict happens in our studied colonies, by-standers (nearby pairs) seem to be relatively unaffected by the conflict. Indeed, these by-stander pairs did not have an increased chance to enter in a conflict compared to situations without conflicts and did not show higher rates of affiliation (bill twinning) between mating partners when a conflict happened nearby (Bassetti 2013, Bachelor thesis). While the social system of rooks seems to be compartmented and mainly based on cooperation between mating partners, the conclusion is limited by the fact that in the current thesis, we studied this species only during the breeding season. As mentioned several times, this is a highly competitive period for rooks, which might not be ideal to study examples of cooperation between other individuals than mating partners. Examples of cooperation in rooks must exist given that this species not solely breeds in colonies (Patterson et al. 1971), but also forages in groups and coordinates most of their displacements in groups (Coombs 1960). Hence, I think that rooks are a good study species to explore in more details how group coordination helps finding food and whether these colonies work as central information centres as it has been suggested to happen for many other colonial living bird species (Ward and Zahavi 1973; Brown 1986; Green 1987; Marzluff et al. 1996). Furthermore, the means by which birds coordinate their collective actions in for instance, mobbing predators, is a largely unexplored issue. One possible mean by which these birds coordinate feeding flights, predator defences or escape is vocal communication. In fact a catalogue of the vocal repertoire in rooks already exists but has only been loosely related to the contexts in which these calls happen (Roskaft and Espmark 1982). Hence, studying vocal communication in this species and relating it to more specific contexts is a promising research topic for the future.

(d) Tool use in corvids

In chapter 3, the main finding is that our free-ranging crows were unable to use the tools provided and that they did not perceive them as a mean to reach the reward. As discussed in chapter three this might be due to differences between species when comparing our results with those obtained in other species of corvids or due to differences between captive vs wild animals, because most other experiments were carried out in captivity (Bird and Emery 2009[a,b]). If we would have tested rooks, which was our primary intent, then solely could we have distinguished between these two non-mutually excluding explanations. Unfortunately this was not possible in the current project and along with others we encourage future research projects to systematically test the differences between wild and captive individuals before deriving definite conclusions about a species typical behaviour (Thornton and Lukas 2012). In the case of corvids, the capacity to use tools has been proposed to be a shared capacity among representatives of this family (Bird and Emery 2009[a]). Nevertheless this thought-provoking hypothesis is to date only based on two main species of birds in the genus corvus, New Caledonian crows and rooks. Hence, not solely are systematic comparisons between wild and captive animals needed but also a broader range of species within this family needs to be tested. Nevertheless, if extrapolating a bit about our findings of chapter three and taking into account the methodological limitations of our experiment, my personal opinion is that these findings rather support the idea that tool use is a specialized capacity in some corvids species rather than the by-product of a general form of intelligence. Alternatively, I cannot exclude that rooks are special among corvids given that their social system seems to be slightly different from other species of corvids in that they are colonial breeders (Patterson 1971). Nevertheless, as suggested by our findings of the first two chapters, these colonies seem to be mainly simple assemblages of pairs where interactions with other individuals are rare and hence the social complexity in those groups appears to be relatively limited. How this in turn would have driven to a higher intelligence in rooks compared to other species of corvids, as has been suggested between the lines by Bird and Emery (2009[a]), is even harder to grasp. In my sense complexity of social systems are hard to measure in any case, in particular in birds, where a simple measure such as group size is not appropriated (Emery et al. 2007). Furthermore, if going back to our study species, the carrion crows, these are territorial mainly during the breeding season and at adult stages. In contrast, these do also form larger assemblages of birds in other periods of the year (Haffer and Bauer 1993). Moreover, carrion crows form cooperative breeding groups in Spain, where family members help each other' to raise offspring (Baglione et al. 2002[a,b], 2003). This is a level of social complexity not seen in rooks. To conclude, the project presented in chapter three shows that some corvids can be tested in field conditions on such experiments. While the experiments have been logistically challenging, additional populations and other species should be tested in the field to exclude confounding effects such as previous experiences with similar experiments or the risk of testing a subset of individuals that are not representative of wild animals.

(e) Conclusion – Summary

In summary, the first two chapters confirmed the conclusion of studies conducted in captivity that pairs are the key unit for cooperation in rooks: Chapter one described high levels of conflict between neighbours within colonies, while chapter two provided first evidence for third-party affiliation by pair partners in free-ranging rooks. Finally chapter three indicates that crows have a limited tendency to use tools when being tested for it in the wild. Future studies are needed to determine whether this result is due to differences between wild and captive animals, or due to differences between crows and rooks, or even due to population-specific causes, as documented in chimpanzees and orang-utans (Whiten et al. 2001, van Schaik et al. 2003). Progress in animal cognition in general and in our understanding of covids as a specific example will depend on a strong effort to publish also negative results because these are probably as informative as positive results. To conclude, while writing up this document, I realized that there are to date no recent throughout reviews on these fascinating group of birds and I encourage scientists to invest time and effort in such an enterprise.

General acknowledgments

This project would not have been possible without the contributions of many people over all these years. First of all, without the input and advice of my supervisors, Redouan Bshary and Ralph Bergmüller, this project would probably never have come into existence. I would like to thank you for the time, the energy and patience that you have shown over the last few years and past few days. I would like to thank also Thomas Bugnyar and Klaus Zuberbühler that accepted to become member of my thesis jury. I am convinced that your comments will help improving the content of this thesis and help me in publishing parts of this work. Furthermore, I would like to thank many students and field assistants for their help in the field, in the alphabetic order: Aubrun Rémi, Bassetti Alessandro, Dagaeff Anne-Cécile, Guyot Manoel, Huguenin Kévin, Nodiroli Noélie, Rizzo Stéphane and Schürch Roger. In particular I would like to thank Anne-Cécille for her unequalled devotion in the field, without your help I would probably still stand in the field collecting data on conflict management. My special thanks go also to Roger who, in the first months of this project, supported me in the field but maybe most importantly, encouraged and supported my psychologically in a period where the endpoint of this thesis was still a distant horizon. But all that would not have been possible without the support, of my family and friends. I would like to warmly thank all of you starting with Maria, Sanel, my mother, my extended family and friends for your unconditional support during all these years.

References general discussion

Aureli, F., Cords, M. & Van Schaik, C. P. 2002. Conflict resolution following aggression in gregarious animals: a predictive framework. *Anim. Behav.*, 64, 325-343.

aBaglione, V., Marcos, J. M. & Canestrari, D. 2002. Cooperatively breeding groups of carrion crows (Corvus corone corone) in northern Spain. *Auk*, 119, 790-799.

bBaglione, V., Marcos, J. M. Canestrari, D. & Ekman, J. 2002. Direct fitness benefits of group living in a complex cooperative society of carrion crows, Corvus corone corone. *Anim. Behav.*, 64, 887-893.

Baglione, V., Canestrari, D., Marcos, J. M. & Ekman, J. 2003. Kin selection in cooperative alliances of carrion crows. *Science*, 300, 1947-1949.

Bassetti, A. 2013. Do conflict influence the frequency of affilliative behaviours of the closest couple of bystander? Bachelor thesis, University of Neuchâtel.

aBird, C. D. & Emery, N. J. 2009. Insightful problem solving and creative tool modification by captive nontool-using rooks. *PNAS*, 106, 10370-10375.

bBird, C. D. & emery, N. J. 2009. Rooks use stones to raise the water level to reach floating worm. *Curr. Biol.*, 19, 1410-1414.

Brown, C. R. 1986. Cliff swallow colonies as information centres. *Science*, 234, 83-85.

Coombs, C. J. F. 1960. Observations on the rook corvus frugilegus in southwest Cornwall. *Ibis*, 102, 394-419.

Emery, N. J., Seed, A. M., von Bayern, A. M. P. & Clayton, N. S. 2007. Cognitive adaptations of social bonding in birds. *Phil. Trans. R. Soc. B.*, 362, 489-505.

Flack, J. C., Girvan, M., de Waal, F. B. M. & Krakauer, D. C. 2006. Policing stabilizes construction of social niches in primates. *Nature*, 439, 426-429.

Fletcher, K. & Foster, R. 2010. Use of external biometrics to sex carrion crow *corvus corone*, rook *C. frugilegus* and western jackdaw *C. monedula* in Northern England. Ringing & Migration, 25, 47-51.

Frankhauser, T. 2006. *Corbeaux Freux; Feuille d'information pour les personnes habitant près des colonies nicheuses*. ASPO, Nos oiseaux & Station ornithologique Suisse.

Fraser, O. N. & Bugnyar, T. 2010. The quality of social relationships in ravens. *Animal Behaviour*, 79, 927–933.

Fraser, O. N. & Bugnyar, T. 2011. Ravens reconcile after aggressive conflicts with

valuable partners. *PLoS ONE*, 6, e18118.

Gerber, R. 1956: Die Saatkrähe. Leipzig: A. Ziemsen Verlag.

Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J. & Pusey, A. E. 2013. Fitness benefits of coalitionary aggression in male chimpanzees. *Behav. Ecol. Sociobiol.*, 67, 373-381.

Greene, E. 1987. Individuals in an osprey colony discriminate between high and low quality information. *Nature*, 329, 239-241.

Guyot, M. 2013. Conflicts with farmer and study of an non-invasive mean to keep birds away from the crops. Master thesis, University of Neuchâtel.

Haffer, J. & Bauer, K. 1993. in *Handbuch der Vögel Mitteleuropas*- teil III Passeriformes, eds Glutz von Blotzheim UN, Bauer KM (Aula-Verlag Wiesbaden) pp1733-1857.

Hamilton, W. D. 1963. The evolution of altruistic behaviour. *Am. Nat.*, 97, 354-356.

Heinrich, B. 1988. Why do ravens fear their food? *The Condor*, 90, 950-952.

Heinrich, B., Marzluff, J.M. & Adams, W. 1995. Fear and food recognition in naive common ravens. *Auk*, 112, 499-503.

Logan, C. J. & Clayton, N. S. 2013. Rook, but not jackdaw, post-conflict third-party affiliation reduces aggression for aggressors. *Ethol.*, 119, 1-9.

Logan, C. J., Emery, N. J. & Clayton, N. S. 2013. Alternative behavioural measures of postconflict affiliation. *Behav. Ecol.*, 24, 98-112.

Marzluff, J. M., Heinrich, B. & Marzluff, C. S. 1996. Raven roosts are mobile information centres. *Anim. Behav*., 51, 89-103.

Patterson, I. J., Dunnet, G. M. & Fordham, R. A. 1971. Ecological studies of the rook, Corvus frugilegus L., in North-east Scotland. Dispersion. J. appl. Ecol. 8, 815-833.

Roland, C., Danchin, E. & Fraipont, M. 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. *American Naturalist*, 151, 514-529.

Roskaft, E. 1981. Territorialism, neighbour conflicts and social interactions in the rooks corvus frugilegus during the breeding season. *Fauna Norv. Ser. C. Cinclus*, 5, 5-9.

Roskaft, E. & Espmark, Y. 1982. Vocal communication by the Rook Corvus frugilegus during the breeding season. *Ornis Scandinavica*, 13, 38-46.

Roskaft, E. 1983. Male Promiscuity and Female Adultery by the Rook Corvus frugilegus. *Ornis Scandinavica*, 14, 175-179.

Seed, A. M., Clayton, N. S. & Emery, N. J. 2007. Post-conflict third-party affiliation in rooks (Corvus frugilegus). *Curr. Biol.*, 17, 152-158.

Seed, A. M., Clayton, N. S. & Emery, N. J. 2008. Cooperative problem solving in rooks (Corvus frugilegus). *Proc. R. Soc. B.*, 275, 1421-1429.

Thornton, A. & Lukas, D. 2012. Individual variation in cognitive performance: developmental and evolutionary perspectives. *Phil. Trans. R. Soc*. B., 367, 2773-2783.

van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I. Suzuki, A., Utami, S. S. & Merrill, M. 2003. Orangutan cultures and the evolution of material culture. *Science*, 299, 102-105.

Ward, P., & Zahavi, A. 1973. The importance of certain assemblages of birds as "Information centres" for food finding. *Ibis*, 115, 517-534.

Whiten, A., Goodall, J.; McGrew, W. C.; Nishida, T.; Reynolds, V.; Sugiyama, Y.; Tutin, C. E. G.; Wrangham, R. W. & Boesch, C. 2001. Charting cultural variation in chimpanzees. *Behaviour*, 138, 1481-1516.

aZbinden, N., Keller ,V. & Schmid, N. 2005. Bestandsentwicklung von regelmässig brütenden Vogelarten der Schweiz 1990-2004. *Ornithol. Beob.* 102, 271-282.

bZbinden, N. Schmid, H., Kéry, M. & Keller, V. 2005. Swiss Bird Index SBI. Artweise und kombinierte Indices für die Beurteilung des Bestandsentwicklung von Brutvogelarten un Artengruppen in der Schweiz 1990-2003. *Schweizerische Vogelwarte, Sempach.*