Niveaux d'organisation sociale chez le corbeau freux, une espèce d'oiseau monogame

Palmyre Boucherie

To cite this version:

Palmyre Boucherie. Niveaux d'organisation sociale chez le corbeau freux, une espèce d'oiseau monogame. Animal biology. Université de Strasbourg, 2016. English. NNT : 2016STRAJ107 . tel-01565996

HAL Id: tel-01565996
https://theses.hal.science/tel-01565996
Submitted on 20 Jul 2017

UNIVERSITE DE STRASBOURG

ECOLE DOCTORALE DES SCIENCES DE LA VIE ET DE LA SANTE

IPHC, Département Écologie, Physiologie et Éthologie

THÈSE Présentée par:

Palmyre BOUCHERIE

Soutenue le: 23 September 2016,
Pour obtenir le grade de : **Docteur de l'Université de Strasbourg**

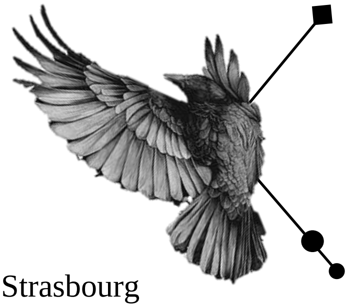
LAYERS OF SOCIAL ORGANISATION IN ROOKS, A MONOGAMOUS BIRD SPECIES

THÈSE dirigée par:

Dr. Valérie DUFOUR	Chargée de recherche HDR, CNRS, Université de Strasbourg

RAPPORTEURS :

Pr. Thomas BUGNYAR	Professeur, Université de Vienne
Dr. Claudia WASCHER	Lecturer, Université Anglia Ruskin



EXAMINATEUR :

Dr. Bernard THIERRY	Directeur de recherche, CNRS, Université de Strasbourg

A mon grand-père, toujours avide d’apprendre.

TABLE OF CONTENTS

ACKNOWLEDGMENTS

Je tiens tout d'abord à remercier les membres de mon jury, le Pr Thomas Bugnyar, le Dr Bernard Thierry, et le Dr Claudia Wascher, pour avoir accepté de lire et d'évaluer ce travail.

Bien sûr je tiens à remercier Valérie Dufour, ma directrice de thèse, pour m'avoir donné l'opportunité d'effectuer cette thèse. Merci aussi de m'avoir laissé le temps précieux de la réflexion lors de mon voyage. Merci Valérie pour ta confiance, depuis le master jusqu'à la fin de cette grande aventure.

Je tiens également à remercier Christelle Roy pour m'avoir accueillie au sein de l'IPHC, François Criscuolo, responsable du DEPE, et Odile Petit pour m'avoir accueillie au sein de l'équipe d'Éthologie Évolutive.

Je remercie aussi tous mes collaborateurs, sans qui ce travail n'aurait pas pu voir le jour. Céline Bret, qui m'a guidé et conseillé lors de mes premiers pas. Un très grand merci à Mylène Mariette, co-auteur elle aussi sur mon tout premier papier et notre chapitre oiseaux, mais aussi membre de mon comité de thèse. Merci pour tout le temps si précieux que tu m'as consacré, tous tes conseils et tes encouragements. Nos échanges m'auront beaucoup appris. (Merci aussi pour le café à Paris, à charge de revanche lors de de ta prochaine visite). Merci à Christophe Bousquet, pour cette si belle collaboration scientifique, ta plume (et notamment ce magnifique premier jet écrit dans un moment de grande inspiration sur le trajet de la maison). Merci pour tous tes petits coups de pouce (notamment dans la dernière ligne droite), ta générosité et ta bonne humeur. Merci à Christof Neumann et Julie Duboscq, pour toutes les réunions skype transfrontalières, et ces heures de discussion si précieuses où j'ai tant appris. Merci à Cristian Pasquaretta bien sûr, pour ta bonne humeur, ton italian style, ton enthousiasme sans failles, mais aussi pour notre belle collaboration. Merci à Sebastian Sosa, une très belle rencontre scientifique, qui a mené à une collaboration simple et fructueuse. Merci aussi à Emilio Rojas pour tout nos incroyables brainstorming scientifiques, l'un des plus beau fou rire de travail, et cette énergie si pimentée ! À vous tous, merci, et j'espère que nous aurons encore l'occasion de travailler ensemble.

Merci bien sûr à Joanna, ma copie-éditrice préférée. Merci pour tes corrections, ta curiosité et surtout ton humour corrosif!

Un merci tout particulier à Bernard. Merci de m'avoir transmis ton savoir et ta curiosité. Merci pour tous ces échanges qui ont construit ma pensée scientifique d'aujourd'hui, et continueront de nourrir mes projets de demain. Merci pour aussi les noms d'indiens, les évadées Napoléoniennes, et les dégustations de grands crus. Merci pour ta présence et ton soutien tout simplement.

Bien entendu un immense merci à tous les habitants du DEPE.

Merci à toute l'équipe d'éthologie, et tout particulièrement aux trois 150naires (ça sonne presque comme mousquetaires), Bernard, Odile et Valérie, mais aussi bien sûr Pierre et

Hélène, tout particulièrement pour votre aide auprès des oiseaux. Merci notamment à Pierre pour tes inventions de Macgyver.

Merci bien sûr à François, Yan, Cédric, Thierry, J-P, Yves, Nico, Jean-Yves, Yannick, pour votre bonne humeur, votre soutien et les moments partagés. Et pour les mêmes raisons, bien sûr, merci aux filles, mais aussi parce que vous êtes les petits rayons de soleil du laboratoire : Sylvie (et ta chevelure de rêve), Claudine, Caro, Brigitte, et bien sûr Martine, sans qui mes aventures à l'étranger n'auraient pas été possibles, et qui a toujours une solution magique aux petits tracas administratifs (notamment l'envoi de fiches de payes en Bolivie…).

J'en profite pour remercier tout particulièrement François et Cédric pour votre aide et votre gentillesse dans les derniers moments de rédaction. Merci François d'être un boss si chouette et à l'écoute. Merci Cédric pour nos échanges scientifiques et nos discussions.

Merci aussi à Ivan, et Carsten, pour votre aide et vos conseils lors de la rédaction.

Sylvie bien sûr, qui aura été la toute première personne à me faire confiance, en m'acceptant dans le master de Strasbourg. Mais merci surtout d'être toi, une si belle personne si pleine de vie.

Évidemment, évidemment, vous tous, les copains, les amis, les confidents, les trublions, les joyeux lurons, les potes de galère et d'infortune, les compères de fiesta. Je pense bien sûr à vous. Mathilde, Vincent (mon colloque préféré), Amélie, Emilio, Amandine, Quentin (mon colloque préféré), Christophe, Nancy, Agnès, Ivan, Valeria, Fanny, Mathieu, Xavier, Philippine. Merci pour votre présence tout simplement, pour cette belle énergie de groupe et le plaisir de tous nos moments partagés. Merci pour votre soutien dans les moments difficiles, votre réconfort, mais aussi votre joie de vivre et toutes les festivités!

Mathilde, à l'heure où j'écris ces lignes tu viens tout juste de quitter la maison, et vraiment je ne sais pas comment j'aurais fait sans toi. Merci pour ta générosité sans borne et ton écoute. Cette belle énergie qui fait de toi quelqu'un de si particulier et de si précieuse. Merci aussi pour les covoiturages, et nos interminables discussions. Merci.

Merci de tout cœur à Vincent, tout d'abord pour les chouettes moments de partage durant les quelques semaines qui tu auras passé à la maison. Merci à l'ami et merci au grand scientifique. Merci pour ton aide et ton soutien, depuis le premier jour jusqu'à la toute fin de cette aventure.

Merci Nancy pour tous tes conseils et ton aide si précieuse en statistiques, je n'en serais pas là aujourd'hui sans toi ! Merci aussi pour les vitamines et ton pétillant !

Merci à Amélie, Fanny, et Manfred, mes trois colocataires de bureau, mais tellement plus aussi. Merci pour votre présence à ces différentes étapes de ma thèse, et votre soutien. Merci Amélie pour l'escalade, les soirées à la belle, les terrasses, les discussions dans les pâquerettes et nos si beaux échanges. Merci Fanny pour ton éclat de rire si communicatif, et ta générosité. A special thanks to Manfred, pour toutes nos discussions sur le monde qui nous entoure, et aussi pour ta patience dans mes derniers moments de rédaction.

Merci aussi à Aurèlie Hranitzky, et Sophie Calibre pour les bons soins prodigués à nos chers petits pensionnaires. Merci aussi à tous les stagiaires et étudiants, Florence, Julie, Vincent, Thimothé, Mathilde, Zoé, Alexy, Estelle, Thibaut, Pauline, Raphael, Perrine, Marjolaine, Pierre, Mathieu, Heide, qui ont donné de leur temps pour nous aider à mieux comprendre nos protégés. Merci à JP et Christophe pour votre aide et votre coup de filet!

J'ai aussi eu la chance d'être entourée des personnes remarquables en dehors du laboratoire.

J'ai bien sur une pensée tendre pour Suzanne, Alba & Romain, Haribo, Sophie, Amaelle & Adrien, vous tous qui m'avez avec patience et bienveillance écoutée et soutenue dans les moments de doutes, mais surtout qui avez aussi été là pour partager les réussites, les petites et les grande joies, et les festivités de toute sortes. Merci pour votre amitié.

Merci Alba et Romain pour l'échappée belle en Sardaigne, et toutes celles à venir.

Merci à Sophie, ma pote.

Et merci encore ma belle Suzy blue, pour tout.

Merci bien sûr à ma famille, et tout particulièrement à mes parents, pour m'avoir appris la curiosité, l'envie de lire, d'écouter, d'apprendre, d'ouvrir grand les yeux, et de tout questionner. Merci bien sûr de m'avoir permis d'arriver jusqu'ici, en m'offrant de si longues études, mais aussi en me soutenant toujours dans mes choix (parce que bon, c'est toujours pas très clair l'endroit où ça va me mener tout ça ☺).

J'ai bien sur une pensée toute particulière pour chacun d'entre vous. Mes trois petits amours de frères et sœurs, Auguste, Hippolyte et Garance. Ma petite maman. Mon papa. Ma belle-mère préférée, Sarah. Merci pour votre amour et votre soutien toutes ces années.
Vous êtes tout ; mon oxygène et ma force.

Merci aussi à ma belle-famille, Béatrice, Pascal, Marie et Bat, qui avez toujours été présents, à l'écoute et enthousiastes.

Merci à toi, papi, pour nos longues discussions, ta présence à mes côtés ces dernières années. Merci pour ta curiosité sans bornes, ta soif d'apprendre et de découvrir le monde, qui j'en suis certaine, continuera longtemps de m'inspirer. Merci pour ta liberté et ton courage. Et merci pour ton dernier cadeau, qui m'a fait pousser des ailes.

Et bien évidement toi, Philippe. L'amoureux. Le meilleur ami. Mon compagnon de route, de vie, de voyage. L'oreille attentive, et mon soutien sans failles. Merci pour notre si belle complicité. Les éclats de rire, la tendresse. Merci pour ta force et ta capacité à rendre les choses si légères. Merci d'être toi. Merci pour ton écoute et ton réconfort, ta patience infinie, et toutes les belles surprises et les petits plats concoctés avec amour. J'ai hâte de découvrir plus encore la vie avec toi.

Avant de terminer, ou plutôt de commencer, mes pensées vont bien sûr vers vous mes chers corbeaux. Kafka, Brain, Pinky, Merlin, Hugo, Noah, Zazou, Osiris, Jonas, Elie, Tom, Shani, Sihoban, Bashir, Carmen, Pom, Gigi.

PUBLICATIONS

Articles

Boucherie P.H., Mariette M.M., Bret C., Dufour V. (2016) Bonding beyond the pair in a monogamous bird: impact on social structure in adult rooks (*Corvus frugilegus*). Behaviour. DOI: 10.1163/1568539X-00003372

Boucherie P.H., Poulin N., Dufour V. Behavioural mechanisms of divorce and pair bond formation in long-term pairing rooks (*Corvus frugilegus*). *Submitted.*

Boucherie P.H., Sosa S., Pasquaretta C., Dufour V. (2016) A longitudinal network analysis of social dynamics in rooks (*Corvus frugilegus*): repeated group modifications do not affect social network in captive rooks. Current zoology, Institute of zoology, Chinese academy of sciences, 2016. DOI: 10.1093/cz/zow083

Boucherie P.H., Dufour V. Temporal and behavioural dynamics in dominance hierarchies in rooks (*Corvus frugilegus*). *Submitted.*

Boucherie P.H., Rojas E., Dufour V. Patterns of allofeeding in adult rooks (*Corvus frugilegus*). *In prep.*

Book chapter

Boucherie P.H., Mariette M.M., Rat M., Heeb P., Doutrelant C., Bousquet C. (2014) Application de l'analyse des réseaux sociaux chez les oiseaux. In *Analyse des réseaux sociaux appliquée à l'éthologie et l'écologie*. (Ed. Matériologiques.) pp. 161-204 DOI: 10.13140/RG.2.1.4100.5601

COMMUNICATIONS

1st Workshop SNAAS (Social Network Analysis in Animal Societies). 3–4th of July 2013, Collège Doctoral Européen, University of Strasbourg, Strasbourg, France.
Boucherie P.H., Dufour V. *"Social network in a social corvid, the rook"*. Oral Communication

7th European Conference on Behavioural Biology (ECBB 2014). 17–21th of July 2014, Czech University of Life Sciences, Prague, Czech Republic.
Boucherie P.H., Bret, C., Dufour V. *"Effect of social perturbations on the social network of captive rooks"*. Poster

Journées de l'Ecole Doctorale 2015. 26th of February 2015, University of Strasbourg, Strasbourg, France.
Boucherie P.H., Mariette M.M., Bret, C., Dufour V. *"Social structure and social dynamics in rooks"*. Oral Communication

Colloque SFECA 2014. 21-24th of May 2015, University of Strasbourg - CNRS Cronenbourg - IPHC DEPE, Strasbourg, France.
Boucherie P.H., Mariette M.M., Bret, C., Dufour V. *"The characteristic of intra and extra pair social bonds in a monogamous bird, the rook (Corvus frugilegus)"*. Oral Communication

Gottinger Freilandtage 2015, from Cohesion to Norms. 08-11th of Decembre 2015, Behavioural Ecology & Sociobiology Unit at the German Primate Centre, Gottingen, Germany.
Boucherie P.H., Mariette M.M., Bret, C., Dufour V. "Monogamous birds can bond outside the mated pair: Social relationships and group cohesion in adult rooks (*Corvus frugilegus*)*"*. Oral Communication

Behaviour, Evolution, Ecology and Physiology Seminar Strasbourg, IPHC, DEPE, Strasbourg. 20th of May 2016, University of Strasbourg - CNRS Cronenbourg - IPHC DEPE, Strasbourg, France.
Boucherie P.H., Social complexity of dynamics in rooks (*Corvus frugilegus*)*"*. Oral Communication

8th European Conference on Behavioural Biology (ECBB2016). 12–15th of July 2016, University of Vienna, Vienna, Austria.
Boucherie P.H., Sosa S., Pasquaretta C., Dufour V. "A longitudinal network analysis of social dynamics in rooks (Corvus frugilegus): repeated group modifications do not affect social network in captive rooks". Poster

LIST OF TABLES

GENERAL METHODS

CHAPTER 3

CHAPTER 4

CHAPTER 5

CHAPTER 6

APPENDIX 1

APPENDIX 2

LIST OF FIGURES AND PICTURES

INTRODUCTION

GENERAL METHODS

CHAPTER 3

CHAPTER 4

CHAPTER 5

CHAPTER 6

DISCUSSION

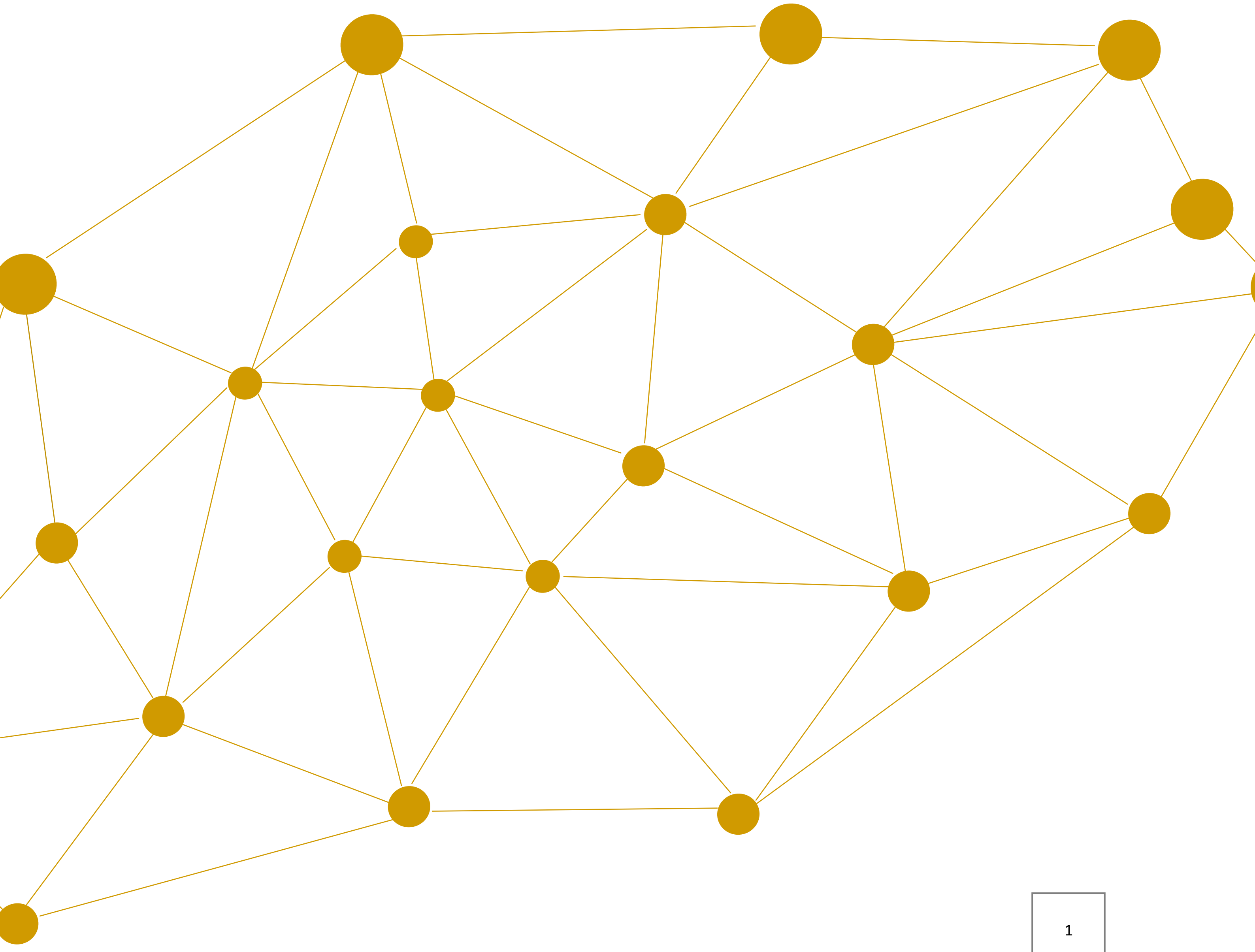
APPENDIX 1

APPENDIX 2

APPENDIX 3

1

INTRODUCTION



“The whole is greater than the sum of its parts.”

– **Aristotle** –

---

1. LIVING IN GROUPS

1.1. Competition and cooperation: costs and benefits of group living

The term of "animal society" is often used to define any type of population structure arising from repeated interactions between conspecifics (Thierry, 2008). In its simplest form, an animal society may be an aggregation of individuals (e.g. fish schools, bird flocks, locust swarms; Sumpter, 2006), but more complex forms of sociality also exist, characterised by the emergence of social relationships among group members. Group living is ultimately advantageous for individuals, as it represents an optimal solution to environmental pressures (Dunbar, 1989; Krause and Ruxton, 2002). Group living can indeed be seen as an adaptive strategy conferring clear fitness benefits in terms of minimizing predation risk, increasing foraging efficiency, and a facilitated access to reproductive partners (Krause and Ruxton, 2002). Individuals are indeed less likely to be predated when they are associated with others than alone (i.e. dilution effect; Dehn, 1990; Foster and Treherne, 1981; Wrona and Dixon, 1990). In addition, predators are expected to be less efficient when attacking a multitude of similar preys than a single individual (i.e. confusion effect; Landeau and Terborgh, 1986; Milinski, 1984). Increased group size also results in a decrease of vigilance rates per individual, but increased efficiency of predator detection at the group level (Pulliam, 1973). Group members can inform others of the presence of a predator (Dehn, 1990; Pulliam, 1973; Rubenstein, 1978; Schaik et al., 1983; Zuberbühler et al., 1997), and part of the group can even play the role of sentinels, watching over the surrondings while others can invest in other activities (Ridley et al., 2013; Wrigh et al., 2001). In some species, individuals can collectively mob or harass predators (Arroyo et al., 2001; Berger, 1979; Maklakov, 2002). Living in groups can also facilitate the access to local information, notably for food resources, or breeding sites. According to the "public information" hypothesis, individuals can indeed use the performance of conspecifics (e.g. for finding food or reproducing) to make decisions (Aplin et al., 2012; Boulinier et al., 2014; Brown, 1986; Doligez et al., 2003, 2002). For instance, in birds or bats, colonies or roosts can be seen as information centres where individuals exchange and transfer information about food patches, by observing or interacting with each other (e.g. recruitment behaviour; Brown, 1986; Danchin and Wagner, 1997; Ratcliffe and Ter Hofstede, 2005; Richner and & Heeb, 1996; Ward and Zahavi, 1973). In primates or canids, group members may also display more complex forms of cooperation, such as collaborative hunting, which increases the probability of catching larger preys (Boesch, 2002; Creel, S., & Creel, 1995; Stander, 1992; Vail et al., 2013). Last but not least, gathering in groups also facilitates the access to reproductive partners, and represents a solution to improve offspring survival or share parental care (e.g. in birds: cooperative breeding, Baglione et al., 2002b; formation of juveniles crèche, Le Bohec et al., 2005).

Living with others also require to deal with the cost of gregariousness, and the resulting competition between conspecifics (Emlen, 1997; Rubenstein, 1978; West-Eberhard, 1979). For instance, competition can arise for the access to reproduction or mating partners, food resources, or more broadly for the use of space (Clutton-Brock and Huchard, 2013; Schradin et al., 2010; Sterck et al., 1997; Wrangham, 1980). Thus, group living often increases survival and reproduction of individuals displaying stronger competitive or fighting abilities to obtain a larger share of resources compared to other individuals (West-Eberhard, 1979). From the asymmetry of benefits can then arise conflicts and aggressions, which are ultimately costly for individuals in terms of energy and can result in injuries. Recurrent conflicts can also induce social stress, which in turn, can have physiological implications (e.g. modulation of heart rate; Viblanc et al., 2012; Wascher et al., 2010, 2009). Social stress can even result from the simple observation of other interactions, in particular conflicts involving affiliates (e.g. modulation of heart rate in greylag geese, *Anser anser*; Wascher et al., 2008). In addition, living in close proximity with others also increases the risk of parasite or disease transmission (Duboscq et al., 2016; Romano et al., 2016).

However, in most social species, the benefits of group living generally overweight its costs. In addition, the formation of relationships among group members can compensate part of the costs associated with group living. Indeed, although forming relationships is time- and energy- consuming, the formation of affiliative structures reduces the overall frequencies of aggressions in a group (van Schaik and Aureli, 2000; de Waal, 1986). More recently, direct fitness benefits were also found to correlate with the formation of affiliative relationships, endorsing the adaptive function of group living (Silk, 2007a, 2007b). In female baboons, social bonding correlates with increased individual longevity (Archie et al., 2014) and offspring survival (Silk et al., 2010, 2003). Similarly, in chimpanzees or macaques, the formation of coalitionary relationships increases males reproductive success (Gilby et al., 2013; Schülke et al., 2010). In rhesus macaques males have a higher probability of paternity with affiliated females (*Macaca mulatta;* Kulik et al., 2012). Comparable results were also found in non-primate species, like in feral horses (*Equus ferus*) or bottlenose dolphins (*Tursiops truncates*), in which females bonding increases reproductive success (Cameron et al., 2009; Frère et al., 2010). Group living thus imposes to compromise between the benefits and the costs of gregariousness, which generate opposite forces responsible for the emergence/maintenance or the dissolution of groups, and therefore for an amazing diversity of shape and dynamics in animal societies.

1.2. From simple aggregations to sociality

In simple aggregations, individuals gather because of converging interests for the use of space, or for similar motivations (i.e. see the above). This is for instance the case for cockroaches (Ame et al., 2004; Jeanson et al., 2005), birds flocks (Couzin et al., 2002; Heppner and Grenander, 1990), fish schools (Mackinson, 1999; Parrish et al., 2002), or locust swarms (Despland et al., 2000). In those gregarious species, individuals can synchronise their activity, or move collectively. Interactions can either be frequent or occasional, according to the density and the size of the aggregation, but individuals do not appear to show specific preferences towards particular congeners. The repetition of simple interactions between conspecifics and rules-of-thumb at the individual level can lead to the emergence of more complex patterns at the group level, without requiring complex social behaviours (e.g. flying patterns and synchronicity in birds murmurations, fish schools, construction of termites mounts; Couzin and Krause, 2003; Herbert-Read et al., 2011; King and Sumpter, 2012; King et al., 2011a; Sumpter, 2006). Those collective patterns, often termed as “self-organised”, are underpinned by simple rules of attraction, alignement and repulsion between individuals (Sumpter, 2006), and often relate to the size of aggregations and the number of direct neighbours surrounding a given individual (Couzin and Krause, 2003; Mirabet et al., 2007). Bird flocks in flight or fish school, for instance, can be explained by simple rules-of-thumb, according to which individuals (i) move away from their very nearby neighbours to maintain a minimal distance; (ii) adopt the same direction as those nearby; (iii) and avoid becoming separated from the others (Couzin et al., 2002). Variations in those rules can create different shape and dynamics of grouping patterns (Czirok and Vicsek, 2000; Gueron et al., 1996; Mirabet et al., 2007; Okubo, 1986).

The simplicity of those interactions, make them relatively easy to quantify and monitor (King and Sumpter, 2012). However, individual interactions do not always follow simple rules, and more complex forms of group living also exist. Those are typically characterised by the emergence of regular social interactions among group members, leading to the emergence of social relationships (e.g. carnivores, de Villiers et al., 2003; primates, Hohmann et al., 1999; Silk et al., 2004; Sterck et al., 1997; horses, Sigurjónsdóttir et al., 2003; elephants Wittemyer et al., 2005; bats, Vonhof et al., 2004; whales, Baird and Whitehead, 2000; birds, Aplin et al., 2012). Those social relationships form the basis of more complex social patterns, which vary in their degree of sophistication and in the diversity of social behaviours that are expressed by group members (Bergman and Beehner, 2015; Silk et al., 2013; Wey et al., 2008). For instance, in highly social species, intricate collective behaviours or processes such as cooperative hunting (chimpanzees, *Pan troglodytes*; Boesch, 2002, 1994), cooperative breeding (meerkats, *Suricatta suricaatta*; Clutton-Brock, 2002; carrion crows, *Corvus corone*, Baglione et al., 2002a,b), social learning and imitation (keas, *Nestor notabilis*, Huber et al., 2001), or cultural transmission (dolphins, *Tursiops sp.*, Krützen et al., 2005) may emerge among group members. An interesting case where sociality is perhaps brought to its paroxysm is that of eusociality. Eusocial species (mainly social insects: termites, ants, wasps) are characterised by communal or cooperative brood care (i.e. caring for offspring from other group members), the overlap of at least two different generations in the same group, and the division of labour into reproductive and non-reproductive casts (Bonabeau et al., 1998; Charnov, 1978; Queller, 1989). Individuals can even be morphologically differentiated according to their specialization in the colony with accentuated differences between workers and reproducing individuals (Bourke, 1999; Grüter et al., 2012). In eusocial species, individuals do not exactly adjust their behaviour to others individuals, but more to their casts (i.e. recognised through pheromone signals), interacting similarly with all individuals of a given cast (Bergman and Beehner, 2015). As illustrated by these examples, the complexity of a given society can arise from different mechanisms: be it just a simple rule based on advance chemical signalling or a more complex form of interactions between individuals. In what follows, I will focus on societies involving this later type of interactions.

1.3. Role of kinship and reciprocity in cooperative relationships

All benefits arising from group living result from more or less complex cooperative behaviours (strategies) among group members. Cooperation is expected to be enhanced by a high degree of tolerance (Hare et al., 2007; Melis et al., 2006), and the establishment of valuable relationships among partners (Berghänel et al., 2011; Drea and Carter, 2009; Seed et al., 2008). Cooperation has been extensively studied in a wide range of species. It can be: i) mutualistic, if beneficial to both the initiator and the receiver; ii) altruistic, if beneficial to the receiver but detrimental or energetically costly to the initiator (West et al., 2007a, 2007b). For instance, allo-grooming behaviour can be considered an altruistic behaviour, as grooming another individual decreases the donor’s fitness (e.g. energy used, time taken from other activities like foraging and decreased vigilance to predators), while increasing the recipients’ fitness (e.g. decreased parasite load and stress; in baboons, *Papio hamadryas,* Wittig et al., 2008; in impala, *Aepyceros melampus,* Mooring and Hart, 1995). Similar reasoning can be applied to other affiliative behaviours such as food-sharing, or support in conflicts. For more collective behaviours, such as predator harassment, or collaborative hunting, all individuals involved can in general be considered as donors and recipients, with costs and benefits likely to vary according to the degree of participation of the individuals. For instance, in the case of cooperative breeding, as found in meerkats (Clutton-Brock et al., 2001), the cost of cooperation can be extremely high, as it may lead to the suppression of the donors’ reproduction, while increasing the reproductive success of the receivers (i.e. reproducing pair; Young et al., 2006). However, helping kin is also usually a better option in fitness terms than trying to reproduce alone when facing habitat saturation.

Several mechanisms have been proposed to explain the occurrence of altruism, and the adaptive function of this type of cooperation. Chief amongst those is kin selection which suggests that by cooperating with closely related partners, individuals indirectly increase their inclusive fitness (Hamilton, 1964). In species with delayed dispersal of offspring, affiliations and coalitions often occur among siblings (Beisner et al., 2011; Loretto et al., 2012; Smith et al., 2010). In cooperatively breeding species for instance, helpers are often close relatives (Baglione et al., 2003; Eberle and Kappeler, 2006; Komdeur, 1994). However, in numerous species helpers are not necessarily related, and more and more studies suggest that kin-based cooperative breeding may just be a consequence of limited opportunity for the dispersal of mature juveniles (Clutton-Brock, 2002). Beside kin-selection, reciprocal altruism characterises cooperative events and affiliations among unrelated individuals and at a cost for the donor (Brosnan and Waal, 2002; Trivers, 1971). Reciprocal altruism involves a cost when producing the cooperative behaviour. The only possibility for this type of cooperative behaviour to be maintained in a given population is if a favour is received in return at a later time, implying a delay between the immediate cost and the future benefits of cooperation (Kappeler, 1993; Langergraber et al., 2007; Mitani et al., 2000; Moore, 1992). Thus, the occurrence of reciprocity may well very much depend on the time individuals spend together, their degree of affiliation, and the nature of past interactions that occurred between the two partners (Brosnan and Waal, 2002). In numerous social species, affiliations are often found to be reciprocal (e.g. grooming, support in conflicts; Seyfarth & Cheney, 1984; Hemelrijk, 1994; de Waal & Luttrell, 1988; Watanabe, 1979). Individuals can reciprocate by exchanging similar or different goods or services (Hemelrijk, 1990a, b). For instance, in chacma baboons, female can trade grooming for grooming (Barrett et al., 1999). In vervet monkeys, grooming between unrelated individuals increases the probability to receive support in future conflicts (i.e. *Cercopithecus aethiops*, Seyfarth and Cheney, 1984). In tufted capuchin monkeys (*Cebus apella nigritus*) grooming positively correlates with tolerance over food resources (Tiddi et al., 2011). In passerines, unrelated nesting neighbours can reciprocate mobbing, meaning that they are more inclined to join neighbours that helped them previously when harassing predators (Krams et al., 2006; Wheatcroft and & Price, 2008). Overall, it must be noted that these two types of cooperation are not mutually exclusive, but can act synergistically in a group. Because cooperation compensates part of the costs of intra-group competition, ultimately increasing individual fitness (i.e. survival and reproduction), it is one of the processes that should ensure group cohesion and stability.

2. SOCIAL ORGANISATIONS AND SOCIAL STRUCTURE

2.1. Defining a species' social organisation

A species' social organisation results from a combination of its social structure, its demographic structure, and its mating system. Whereas the social structure is defined by the network of relationships existing between all group members (Hinde, 1976), the demographic structure relates to the size and composition of the group (i.e. age, sex of individuals, philopatry and sex dispersal) and the mating system defines the type of reproductive behaviour (e.g. monogamy, polygyny, polyandry). Variations in either one of those components (social, demographic, or reproductive) may induce changes in the others, resulting in changes in social organisation. For instance, hamadryas baboons (*Papio hamadryas*) and gelada baboons (*Theropithecus gelada*) both live in multi-male multi-female groups. However, they are characterised by different dispersal regimes. There is a female-biased dispersion in hamadryas, and a male-biased dispersion in geladas. This induces differences in the strength of intra- and inter-sexual relationships, with strong female-female relationships in geladas, and strong male-female and male-male relationships in hamadryas (Grueter et al., 2012). This example highlights the importance of considering all components of social organisation and entails the necessity to properly characterize a species' social structure, as it largely affects social patterns and group dynamics. If the demographic structure and mating system of a group are relatively easy components to evaluate from direct observations, establishing a species' social structure requires an in depth-analysis of individuals' social interactions.

If social organisations vary across species, similar organisations can sometimes be found in very different taxa. For instance, eusociality is found in many social insects, but also in two mammalian species, the naked mole-rat (*Heterocephalus glaber*) and the Damaraland mole-rat (*Fukomys damarensis*; Jarvis et al., 2008; Reeve et al., 1990). This illustrates well that organisations can be selected because they are the most-cost effective strategies to a given set of external and internal pressures.

2.2. Levels of social structure

We can distinguish two different levels in a species' social structure: (1) the social interactions, and (2) the social relationships between individuals. First, interactions that occur in the present time can be described by the behaviours expressed by the individuals. Those include affiliative behaviours (e.g. grooming, food sharing), agonistic behaviours (e.g. aggressions, threats), but also vocal communications, postures, or facial expressions. From the interactions then arise the relationships, characterised by the type and the temporal pattern of repeated interactions among individuals known to each other (Hinde, 1976). Indeed, in a succession of repeated social interactions, a given social interaction might influence the next one. Consequently, relationships are dynamic and vary in strength and stability over time (Hinde, 1976; Silk et al., 2006a, 2006b). This highlights the need to include a temporal dimension in the study of social relationships. Overall, two main types of social relationships can be described, namely affiliative and agonistic relationships (i.e. or dominance relationships). By definition, the establishment of a relationship requires that individuals recognise each other and remember past interactions (Barrett and & Henzi, 2002; Hinde, 1976). The social structure in turn is defined by the network of all relationships connecting group members. To summarise, the social structure is characterised by the type (i.e. affiliative, agonistic, and neutral) of social relationships among individuals and also their temporal pattern (i.e. how they are distributed in the group, and how this distribution varies with time; Hinde and Simpson, 1975; Hinde, 1976).

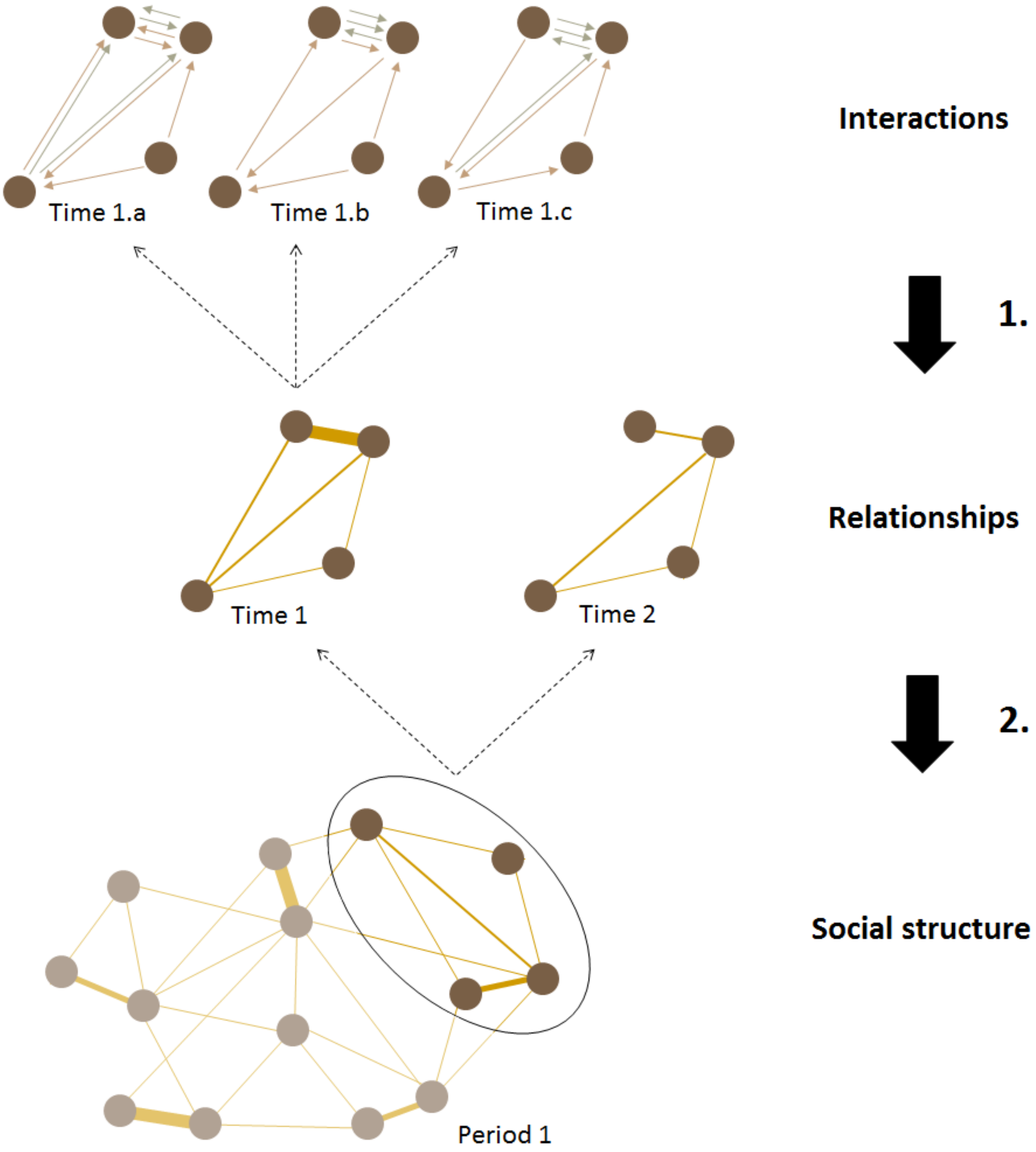


Figure 1.Schematic representation of two levels in the social structure: interactions and relationships. 1) The relationships are characterised by the type and the temporal pattern of repeated interactions among individuals. 2) Then, the social structure arises from the network of all potential relationships in the group, characterised by their type and their temporal pattern i.e. how they are distributed in the group, and how this distribution varies with time.

2.3. Affiliative relationships and associated structures

Two individuals frequently associated or interacting in a positive manner (beneficial for both individuals) are considered to be affiliated (Alexander, 1974). Spatial association indices generally attest of positive relationships – indeed, it may be risky to spend time in close proximity of potential aggressors or competitors – and often correlate with positive interactions. According to the species, affiliated individuals can interact in various manners: they may either engage in mutual grooming (vervet monkeys, Seyfarth, 1980) or preening (corvids, Emery et al., 2007), tolerate each other at a food resource (baboons, *Papio ursinus*, King et al., 2011b), share food or actively transfer food items (bats, *Desmodus rotundus*, Wilkinson, 1984; rooks, *Corvus frugilegus*, Scheid et al., 2008), jointly manipulate objects (keas, *Nestor notabilis*, Tebbich et al., 1996), engage in social play (wolves; *Canis lupus*, Cordoni, 2009), support each other in conflicts (baboons, *Papio cynocephalus*, Silk et al., 2004), reconcile after conflicts (ravens, *Corvus corax*, Fraser and Bugnyar, 2011; chimpanzees, *Pan troglodytes*, de Waal and van Roosmalen, 1979), or form coalitions against other individuals (de Villiers et al., 2003; Fraser and & Bugnyar, 2012; Loretto et al., 2012; Schino et al., 2007). Individuals rarely interact in a similar way with all congeners, and privileged relationships between a subset of individuals in the social group often emerge. One of the main reason for this is that social interactions are necessarily time-constrained, and that individuals can only interact with a limited number of partners (Lehmann et al., 2007a). The patterns and contents of affiliative relationships can thus vary substantially within the same social structure, characterizing bonds of different intensity and quality among group members (Silk et al., 2006b). Moreover, affiliative relationships also vary in stability and duration, from short-term or contextual affiliations, to long-term and even life-long relationships, like in primates (Sterck et al., 1997), dolphins (Lusseau et al., 2003), or corvids (Emery et al., 2007). Because not all affiliative relationships are defined by the same affiliative behaviours, the affiliative structure can vary according to the considered behaviours (Whitehead and Dufault, 1999; Whitehead, 2008).

To date, one of the major challenges in the study of social relationships is the objective determination of the relationships content, so that they can be differentiated according to their quality. Indeed, the quality of the relationship is likely to influence the frequency and manner in which future interactions will occur (Aureli et al., 2002; de Waal, 2000; Silk et al., 2013). Several methods were thus proposed to attempt to objectify the content of relationships. Among them, the rate of affiliative behaviour in relation to the rate of agonistic behaviour are often used as a proxy to qualify a given relationship. The term “social bond” for instance, can be used to refer to close and long-lasting relationships, based on frequent spatial associations, affiliative behaviours (i.e. allo-grooming or allo-preening), and some degree of exclusivity in affiliative partners (Dunbar, 2012). However, if the rate of interactions and associations captures essential aspects of the relationship content, it may not fully represent all the dimensions of these relationships (e.g. their temporal dynamics, variation in partners' investment, directionality). Recently, an alternative method emerged from studies of dyadic conciliatory tendencies in primates. Three components are proposed to characterise the quality of relationships: the value, the security, and the compatibility (Cords, M. & Aureli, 2000). The value of the relationships is defined by the benefits associated with the relationships, like the support in conflict or the facilitated access to food resources. The security relates to the degree of consistency interactions between partners: the predictability of the relationships (i.e. changes in strength or stability) over time. Finally, the compatibility relates to the degree of tolerance among partners, it depends notably on the temperament of the individuals and the history of past interactions. The investigation of those three components of relationships has so far been performed on several primates' species (in chimpanzees, *Pan troglodytes* (Fraser et al., 2008; Koski et al., 2012), in japanese macaques, *Macaca fuscata*, Majolo et al., 2010; in barbary macaques, *Macaca sylvanus*, McFarland and Majolo, 2011; in spider monkeys, *Ateles geoffroyi;* Rebecchini et al., 2011), and also in corvids (i.e. in ravens; Fraser and Bugnyar, 2010b). Yet the three components cannot be systematically identified in all species (i.e. see in spider monkeys, Rebecchini et al., 2011). In addition, by comparing results between species, the components extracted are only superficially similar, and may not reflect the same dimensions of relationships. Indeed, they rarely involve exactly the same variables (i.e. the same behaviour) from one study to another (Koski et al., 2012; McFarland and Majolo, 2011; Stevens et al., 2015), precluding reliable comparisons across species.

2.4. Dominance relationships and social hierarchy

When living in groups, individuals can also be brought to compete for food, space or reproduction, and conflicts of interest may arise, leading to agonistic interactions between individuals (Krause and Ruxton, 2002; Rubenstein, 1978). Agonistic interactions can be of various types, from clear aggression to avoidance (i.e. when a subject moves away from an approaching individual), supplantation (i.e. when a subject moves away from an individual that enters in contact with him and takes its place; Bernstein, 1981; Drews, 1993). Group members rarely equally benefit from habitat, resources, or reproduction, as individuals displaying better fighting abilities usually obtain a disproportionate share of the resources (Crook, 1972; Robichaud et al., 1996; White and Wood, 2007). In this context, dominance relationships and more generally social hierarchies can regulate conflicts and compensate part of the effect of the competition and the asymmetry of benefits (Bernstein, 1981; de Waal and & Luttrell, 1985; de Waal, 1986).

Dominance relationships emerge from repetitive agonistic interactions between two opponents: the dominant individual wins while the subordinate individual loses most of the conflicts (Bernstein 1981). Dominance is thus “a relative measure and not an absolute property of individuals” (Drews, 1993). Dominance relationships can be structurally organised into a hierarchy, in which individuals rank from the most dominant to the most subordinate. Hierarchies have been described in many species ranging from vertebrates (mammals, birds) to invertebrates (insects). They are most often found to be linear and transitive (i.e. if A > B and B > C, then A > C; Appleby, 1983; de Vries, 1995). Dominance relationships reflect individual asymmetries in the propensity to win conflicts, which can be more or less marked according to the species (Balasubramaniam et al., 2012; De Vries et al., 2006; Leiva and de Vries, 2014). In addition to linearity, the steepness has been proposed to quantify the symmetry of dominance relationships in a group (De Vries et al., 2006). Indeed, conflicts are not always asymmetrical from dominant to subordinate, and in certain cases subordinates may protest or retaliate, or more rarely win a conflict against a more dominant individual (de Waal and & Luttrell, 1985; Massen et al., 2014a). The proportion of retaliations or protestations often reflects the degree of social tolerance of the species (Balasubramaniam et al., 2012; Duboscq et al., 2013a,b; Demaria and Thierry, 2001; Thierry, 2013). Indeed, if the dominance hierarchy is by definition supposed to be clear and stable (i.e. who dominates whom), tolerant species allow more protests from low-ranking individuals than despotic species. Therefore, steep dominance hierarchies are typically found in despotic species (e.g.

rhesus macaques, *Macaca mulatta*; de Waal and & Luttrell, 1985), while more shallow hierarchies are typical of more tolerant species (e.g. tonkean macaques, *Macaca tonkeana*; De Marco et al., 2010). Stable and linear hierarchies are usually expected in species forming small and cohesive groups, where individuals frequently encounter and necessarily have to cope with competition (Drews, 1993; Shultz and Dunbar, 2009; e.g. in carrion crows, Chiarati et al., 2010; in Florida scrub jays, *Aphelocomu c. coerulescens*, Woolfenden and Fitzpatrick, 1977), or in less cohesive species, but characterised by well-structured social relationships (e.g. African elephants, *Loxodonta africana*, Archie et al., 2006; Wittemyer et al., 2005; in spotted hyenas, Holekamp et al., 2007a; in chimpanzees, Wittig and Boesch, 2003). However, hierarchies are not necessarily linear in all species, and in some species, circular triads or intransitivity of rankings can be found (i.e. A > B and B > C, but C > A; Chase et al., 2002; e.g. in keas, *Nestor notabilis*, Tebbich et al., 1996). In species where the dominance relationships are not linear, dominance relationships are expected to structure the group less than in species displaying strong linearity.

The social hierarchy can play a strong structural role that constraints individual interactions and regulates conflicts (Bernstein, 1981; Drews, 1993; Thierry et al., 2004). One of the major consequences of hierarchies is the establishment of an order of priority to resources, which usually follows individual rankings (Alanärä et al., 2001; Amsalem and Hefetz, 2011; Bell et al., 2012; Stahl et al., 2001). In chacma baboons (*Papio ursinus*) for instance, a high rank facilitates the monopolisation of females (Alberts et al., 2003; Bulger, 1993). By regulating conflicts, hierarchies and dominance relationships help reducing agonistic interactions and the cost (e.g. injuries, stress) inherent to constant competition among group members (Bernstein, 1981; de Waal and & Luttrell, 1985; de Waal, 1986). In non-human primates, two types of social hierarchies can be distinguished (de Waal and & Luttrell, 1985): the real hierarchy directly issued from actual conflicts, and the formal hierarchy detectable from ritualized signs of submissions. Those submissive behaviours are performed unidirectionnally by subordinates towards dominants (de Waal and & Luttrell, 1985; de Waal, 1986).

2.5. Group constraints on relationships

2.5.1 Relatedness

Relatedness between group members is considered as a major factor influencing the distribution of affiliative and agonistic interactions, and thus social structures (Bernstein et al., 1993; Hatchwell, 2009; Viblanc et al., 2016). In the vast majority of species, affiliative relationships primarily emerge between relatives, and in particular between mother and offspring (i.e. in particular in mammals; Dunbar, 2012; Shultz and Dunbar, 2010a). Groups can then be composed of one or several co-existing families (i.e. sub-groups of relatives, most often parents and offspring). For instance, in numerous primate species, the social structure is arranged around matrilines (i.e. subgroup composed of one female and her daughters; Chapais et al., 1991; Kutsukake, 2000). Females that belong to the same matriline usually show higher rates of coalitions together than with other group members (Chapais et al., 1991; Isbell and Young, 2002; Silk, 2002b; Watanabe, 1979), and individuals inherit the rank of their “matriline” (Chapais et al., 1991; Kutsukake, 2000). Matrilines are also found in other mammalian species, like whales (Williams and Lusseau, 2006), elephants (Charif et al., 2005), or hyenas (Holekamp and Smale, 1991).

2.5.2. Mating system: the case of monogamy

Privileged relationships can also primarily occur between reproductive partners, in particular in monogamous species (Emery et al., 2007; Shultz and Dunbar, 2010b). In fact, the simplest form of social organisation is the monogamous pair with its juveniles. The pair inhabits and defends a territory against other pairs, as in titi monkeys (*Callicebus sp.*; Mendoza and Mason, 1986), prairie voles (*Microtus ochrogaste*; Sue Carter et al., 1995) or as in numerous birds species such as barn owls (*Tyto alba;* Roulin, 1999), or ravens (Marzluff and Heinrich, 1991).

Contrary to mammals, where most social species are polygynous (i.e. but social mammals also show monogamy, uni-male group, or promiscuity; Clutton-Brock, 1989), more than 85% of the birds species are monogamous (Greenwood, 1980). Bi-parental care is also particularly widespread in avian species compared to mammals (i.e. both sex contribute to offspring provisioning; in 81% of the species; Cockburn, 2006). Reproductive success thus strongly depends on the strength of the pair bond, and the efficiency of partners in cooperating and synchronising their behaviour. Depending on the species, the style of the monogamy can vary according to: i) the duration of the pair bond (e.g. from one season of reproduction to a lifetime), ii) the exclusivity of matings/copulations (Griffith, 2002); and iii) the type of parental care (e.g. mono- or bi-parental care; provisioning up to nutritional independence or after, Clutton-Brock, 1991; Cockburn, 2006). Bi-parental care indeed requires individuals to synchronise their behaviour and adjust their efforts to the investment of their partner and the needs of juveniles (Mariette and Griffith, 2015, 2012). In some species, partners may even negotiate with one another to adjust their effort (Johnstone, 2006). The duration of partnership positively influences reproductive success, as with time, long-term partners tend to increase their behavioural synchronicity and therefore their efficiency in providing parental care (Davis, 1988; Emery et al., 2007; Ens et al., 1996; Mariette and Griffith, 2015, 2012; Sánchez-Macouzet et al., 2014). Thus, in species forming long-term pair bonding (i.e. the pair bond may last over several reproductive seasons), the relationship between the mated partners often goes far beyond the reproductive function (e.g. geese, albatrosses, swans, corvids, parrots; Emery et al., 2007). This long-term bond is akin to the long-term alliances that can be found in highly social mammals like primates, elephants, or dolphins (e.g. jackdaws, *Corvus monedula*; rooks, *Corvus frugilegus*; ravens, *Corvus corax*; Clayton and Emery, 2007; Fraser and Bugnyar, 2011; Scheid et al., 2008; Spoon et al., 2004). In those species, mated partners spend a substantial amount of time in association and interact frequently through an array of affiliative behaviours (e.g. preening, food sharing, allofeeding, joint manipulation of objects; de Kort et al., 2006, 2003; Emery et al., 2007; Scheid et al., 2008). They can also support each other during and after conflicts (Fraser and Bugnyar, 2012, 2011, 2010a; Logan et al., 2012; Seed et al., 2007), and reconcile after conflicts (i.e. in non-breeders' ravens reconcile among valuable partners, Fraser and Bugnyar, 2011).

However, the formation of such strong and long-lasting relationships is likely to have major consequences on the diversity and number of social relationships an individual may be involved in. Indeed, the investment required for long-term pair bonding, and the behavioural synchronicity needed to share parental care (Mariette and Griffith, 2015, 2012; Spoon et al., 2006) are both highly time-consuming, and may leave little time to interact outside the pair.

2.5.3. Group composition

Social structures are strongly influenced by group demographic composition. Indeed, individuals' physical abilities, needs, experiences, or activity-budget will vary according to their sex or age. In mammals, offspring strongly depend on their mother for provisioning, and as they grow older, they gradually start interacting with others. At first they are often subordinate to adults, but gradually acquire a dominance rank, for instance through maternal inheritance or by challenging older subordinates (e.g. in spotted hyenas, *Crocuta crocuta*, Holekamp and & Smale, 1991; in macaques, *Macaca fuscata*, Kutsukake, 2000). In addition, an individual's age will also affect its behavioural repertoire, and juveniles will exhibit a different behavioural repertoire from adults. For instance, in canids and primates, juveniles engage more often in social play (Bekoff, 1974; Bloomsmith et al., 1994; Feddersen-Petersen, 1991). Similarly, individual sex will also have a major influence on behaviour, as males and females often display different behavioural repertoires (Clutton-Brock et al., 1982). In addition, inter- and intra-sexual relationships may vary substantially in strength and occurrence according to the species (Grueter et al., 2012). In numerous primates for instance, the form taken by the social structure largely depends on the type and distribution of relationships among females (Henzi et al., 2009; Sterck et al., 1997; Wrangham, 1980). Social structures can thus significantly vary according to group composition and inter-individual variations in sex and age, and can finally be made more complex by the number of different generations coexisting in the same group (Thierry, 2008).

2.6. Multi-level social organisations

Overall, the degree of sociality of a given species can be related to: i) the diversity of differentiated relationships (i.e. type of relationships: affiliative and dominance, diversity of partners), and ii) the extent to which social relationships occur beyond the privileged family units (e.g. relatives and reproductive partners). Indeed, relationships between non-reproductive partners and unrelated individuals lead to additional layers of relationships in the overall social structure that will make it more complex. In primates, elephants, dolphins or hyenas, individuals usually interact with numerous social partners, both related and unrelated individuals, with whom they may engage in different types of relationships (Connor, 2007; Holekamp et al., 2012; Kappeler, 1993; Langergraber et al., 2007; Mitani et al., 2000; Moore, 1992; Silk, 2002a; Wittemyer et al., 2005). This lead to the emergence a multi-level organisation, as found for instance in hamadryas or gelada baboons, that are characterised by one-male-multi-females core reproductive units, nested in a larger structure composed of clans and bands; Grueter et al., 2012; Kummer, 1968). Those clans and bands are respectively formed by alliances and associations between males and by the aggregations of several clans. In addition, in hamadrya baboons there is a high degree of fission-fusion dynamics. The level of group cohesion is adjusted to the activity and the context, with individuals gathering against predators at night and around water points, and disbanding to forage one their own during the day (Grueter et al., 2012). Doing so, they cope more efficiently with patchily distributed food resources. This type of society appers to fulfill several group functions relative to reproduction and juvenile rearing (i.e. mostly one-male-multi-females unit), but also predation vigilance and the management of food resources (i.e. clans and bands; Grueter et al., 2012; Kummer, 1968; Thierry, 2008).

2.7. Spatio-temporal cohesion, dynamics of social structures

Social structures are vary “in spatial cohesion and individual membership over time” (Aureli et al., 2008). Each species can be characterised according to the extent to which it expresses fission-fusion dynamics, defined by the temporal variation in spatial cohesion among group members, and in sub-unit size and composition (Aureli et al., 2008). Depending on species, associations of group members can be more or less permanent (Kappeler and Van Schaik, 2002). Sometimes, groups regularly split into temporary sub-units, when the needs and motivations of all individuals do not meet (Aureli et al., 2008). The frequency of splitting relates to the type of activity undertaken by each individual (e.g. foraging, sleeping) and the prevailing environmental conditions (e.g. food availability; Lehmann et al., 2007b; McFarland Symington, 1990; Silk. et al., 2014). The expression of fission-fusion varies between species, but marked variations can also be found within species (Aureli et al., 2008; Silk. et al., 2014). So far, a high degree of fission-fusion dynamics has been reported in species with high levels of innovation and advanced skills in social cognition like chimpanzees (Lehmann and Boesch, 2004), spider-monkeys (Ramos-Fernández et al., 2009), but also spotted hyenas (Smith et al., 2008), elephants (de Silva et al., 2011), bottlenose dolphins (Lusseau et al., 2006), bats (Kerth et al., 2011), and to a certain extent some birds species (e.g. tits or chickadees, Aplin et al., 2012; corvids, Clayton and Emery, 2007; Emery, 2004). Such dynamics are expected to have major implications on the management of relationships over time and space, and to be cognitively demanding for individuals, as the degree of fission-fusion largely affects an individual’s opportunity to interact and meet others conspecifics (Aureli et al., 2008). The memory of past interactions or the ability to use transitive inferences are supposed to be enhanced in species expressing high degree of fission-fusion, although the correlation between fission-fusion dynamics and cognitive abilities still needs to be investigated.

2.8. Link between advanced cognition and complex sociality

2.8.1 Cognition and sociality in mammalian and avian species

Highly social species – and among them species expressing a high level of fission-fusion dynamics – appear to present advanced cognitive skills (e.g. primates, dolphins, elephants, canids, corvids and parrots). In line with this, the social intelligence hypothesis (independently proposed by: Jolly, 1966; and Humphrey, 1976), proposes that the variability and complexity of the social environment have been a major evolutionary force in the development of advanced cognitive skills (Dunbar, 1998; Kudo and Dunbar, 2001; Pérez-Barbería et al., 2007). While any individuals have to deal with the day-to-day challenges and variability of their physical environment, group-living individuals additionally have to cope with the variability and unpredictability of their social environment. Living in social groups would have induced an arm race which requires individuals to constantly adapt their behaviour to social partners to deal with the balance of competition and cooperation. This may have favoured the evolution of greater information-processing abilities. A positive relationship between group size and relative brain size was found first in primates (Dunbar, 1992), and then in various other insectivores and carnivores species (Dunbar et al., 1998), in hyenas (Holekamp et al., 2007a, b), and in cetaceans (Connor, 2007), supporting the role of the social environment in the evolution of cognitive skills. The quantity of relationships that an individual can keep track of appears to be essential for the emergence of complex cognitive skills (Dunbar 1992, 1998; Dunbar et al., 1998).

However, the link between cognition and sociality is not necessarily systematic and clear across all species (Holekamp, 2007b). Although sophisticated cognitive abilities seem to globally correlate with sociality in birds, it does not correlate with group size (Beauchamp and Fernández-Juricic, 2004; Emery et al., 2007; Shultz and Dunbar, 2010b, 2006). In fact, if avian sociality is often expected to be less complex than in mammals regarding the number and diversity of their social relationships, this is not necessarily true regarding the quality and stability of their relationships (Dunbar and Shultz, 2007; Dunbar, 2012; Emery et al., 2007; Shultz and Dunbar, 2010b). It was proposed that relative brain size in birds is linked to the formation of long-term pair bonding rather than group size (e.g. long-term pair bonding in corvids or parrots; Emery et al., 2007). Consistently, Shultz and Dunbar (2010b) found that in birds, “relative brain size strongly correlates with bi-parental care, pair-bonding, and stable relationships”. The formation and maintenance of such a sophisticated relationship may be indeed cognitively demanding for individuals (i.e. relationship hypothesis; Emery et al., 2007).

Yet again, the relationship intelligence hypothesis may not explain all the variation observed between avian species (Scheiber et al., 2008). This hypothesis posits that differences in the quality and complexity of the pair bond can explain differences in cognitive abilities, notably between corvids/parrots and geese. It supposes notably that small-brain bird species like geese do not possess any form of relationship intelligence (Emery et al., 2007). However, numerous studies indicate that geese relational features are certainly much more complex than supposed by Emery and collaborators (Emery et al., 2007; see also Scheiber et al., 2008). Indeed, geese form affiliative and dominance relationships (Frigerio et al., 2001; Weiß et al., 2004), keep track of those relationships among other group members (Wascher et al., 2008; Weiß et al., 2010; Weiß and Scheiber, 2013), coordinate their behaviour and physiology with their partner (Schneider & Lamprecht, 1990; Weiß et al., 2005; Scheiber et al., 2006;) or support them in conflicts (Frigerio et al., 2003; Weiß et al., 2004; Scheiber et al., 2005). Therefore, if the relationship intelligence hypothesis can be valuable for social corvids or parrots, it is not necessarily true of all birds’ species. In addition, it suggests that complex relational features are not only restricted to bigger brains bird species, which questions the cause and effect link between long-term pair bonding and cognitive skills. For instance, bird species with larger brains do not necessarily live in groups or form sophisticated pair bonding (e.g. solitary owls; Burish et al., 2004).

Overall, neither group size nor pair bonding appear as the most relevant measures of social complexity in birds (Beauchamp and Fernández-Juricic, 2004; Holekamp, 2007b). Thus, although we lack of empirical data on bird social organisations to better understand the link between cognition and sociality in birds, the number of differentiated relationships or the size of social networks might be a good proxy of social complexity in birds (Bergman and Beehner, 2015; Wey et al., 2008). Consistently, Burish et al. (2004) found that birds’ brain architecture and size positively correlates with various socio-structural traits (e.g. collective nest defence, hierarchies, social flights, communal roosting, fission-fusion dynamics), it especially correlates with the occurrence of “between-individuals social interactions or socially transferable cognitive tasks” such as individual recognition, social learning, social play and cooperative alliances, mainly reported in corvids or parrots, but not only (Burish et al., 2004).

2.8.2 How individuals do picture the relationship?

At this point, it should be noted that relationships and social structures are both constructed and deduced from repeated interactions. Although individuals can individually recognise conspecifics and keep track of interactions, this does not necessarily imply that they have a mental representation of the type of relationship, and much less of the social structure they are living in. Such social and cognitive capacities are particularly expected in species living in stable social structure, where all individuals regularly meet each other. The understanding of third-party relationships has so far been studied in primates (i.e. in baboons, *Papio cynocephalus ursinus*, Cheney and Seyfarth, 1999; Cheney et al., 1995; in vervet monkey, *Chlorocebus aethiops pygerythrus*, Borgeaud et al., 2013), but some evidences were also found in spotted hyneas (i.e. Engh et al., 2005), and more recently in ravens (i.e. *Corvus corax*, Massen et al., 2014a). In more details, ravens respond differently to playback following or violating (rank reversal) the dominance relationships of other group members or neighbouring individuals (i.e. who dominates whom; Massen et al., 2014a). In addition, when they concerned their own group members, rank reversals appeared to be more stressful for individuals (Massen et al., 2014a). Thus, by observing others, ravens may actually acquire some knowledge about their relationships (i.e. their type and quality; Massen et al., 2014a). However additional studies on mental representation of third-party relationships are needed on a wide range of species to better appreciate how individuals understand social relationships (i.e. in which they are involved, but also relationships between others), and to evaluate the prevalence of this ability across species and organisations.

3. INTER AND INTRA-SPECIFIC VARIATIONS OF SOCIAL ORGANISATIONS

3.1. External constraints

3.1.1 Inter-specific variability

Ecological factors can either favour group spatio-temporal cohesion or impair it (Schradin et al., 2010). The environment can affect group composition but also individual patterns of interactions - thus, social structure -, the reproductive strategies – thus, mating system -, and ultimately the entire social organisation (Chapman et al., 1995; Clutton Brock & Harvey, 1977; Isbell and Young, 2002; Janson and van Schaik, 1988; Smith et al., 2008; van Schaik, 1989; Wrangham, 1980).

The distribution and the quality of food resources generally influences group size and group composition (i.e. in non-human primates species, Wrangham, 1980; Chapman et al., 1995; Janson and van Schaik, 1988; in African antelopes, Jarman, 1974; in chamois, *Rupicapra pyrenaica parva*, Pérez-barbería & Nores, 1994; in whales, *Orcinus orca*, Foster et al., 2012). For instance, in wild spider monkeys or chimpanzees, the size of the group is a function of travel costs, which are determined by the density, quantity and distribution of the food resources (Chapman et al., 1995). This also appears to be the case in spotted hyenas, which express a high degree of fission-fusion dynamics, and for which the dynamics of short- and long-term grouping patterns depend on fluctuations in local ressources (Smith et al., 2008). In killer whales, the degree of inter-connectivity and cohesion of the social structure is strongly impacted by food availability: a lower food availability results in an increase in foraging effort, and consequently, in a decrease in the time allocated to social activities (Foster et al., 2012). In birds, the distribution and quality of food resources and the degree of predation also influence group size and coloniality, but also foraging tactics in numerous species (Elgar, 1989; Elgar and Catterall, 1981; Martin, 1988; Minias, 2014; Rolland et al., 1998). In primates, socio-ecological models have been proposed to explain the observed variations in female social bonding patterns, according to the distribution of food resources and the risk of predation (Sterck et al., 1997; van Schaik, 1989; Wrangham, 1980). In chimpanzees for instance, external pressures underlie differences in females hierarchies across groups (i.e. food competition and predation risk; Wittig and Boesch, 2003). Socio-ecological models predict that in primates, females should form more “despotic” hierarchies (i.e. strict, linear and stable), when the competition for food resources is higher (Sterck et al., 1997; van Schaik, 1989; Wrangham, 1980).

3.1.2 Intraspecific variability

Social organisations can strongly vary within a given species (Lott, 1991; Schradin, 2013). Different populations of the same species can express different social organisations according to the combination of external (e.g. food distribution and predation risk) and internal factors (e.g. food or reproductive competition), emphasising the fact that many species do not have a fixed form of social organisation. The carrion crow for instance (*Corvus corone*) shows geographic variations in its social organisation. Although this species usually breeds in isolated pairs, a part of the Spanish population regularly exhibits cooperative breeding (Baglione et al., 2002a, 2002b). In some species, intra-specific variations can also be observed at the population level (Lott, 1991). Within one population, alternative forms of social organisation can be expressed, depending on the variations in the set of ecological and internal pressures experienced at given time periods. For instance, the social organisation of breeding striped mice (*Rhabdomys pumilio*) is a function of habitat saturation, group living being favoured when at high population density, and solitary living being favoured at low population density, when indviduals can avoid reproductive competition by solitary breeding (Schradin et al., 2010). In this species, a given population can thus adapt to variations in the balance between the benefits of communal breeding (i.e. improvement of thermoregulation and decrease of predation risk), and the costs of reproductive competition (e.g. increased chances of female aggressions and infanticides; Schradin et al., 2010).

Overall, some species can exhibit remarkable plasticity of their social behaviour according to fluctuations of ecological factors. In addition to genetic variations (i.e. inducing local adaptation between populations), and developmental plasticity, the demographic structure and the social organisation of a population is likely to be affected by how plastic individuals are in their social behaviour (i.e. called flexibility; Schradin, 2013; Schradin et al., 2012). However, the proximate mechanisms underlying the shift from one organisation to another remain largely unknown.

3.2. Internal constraints

Because species do not show the same degree of variation in their organisations, we may wonder whether the diversity of forms taken by social organisations is limited or not. To date, if numerous studies have been interested on the variation of social organisations according to ecological factors, surprisingly little is known on the processes that stabilise social structures. Yet understanding sociality, and more broadly its evolutionary determinants, requires to understand not only how social organisations adapt to environmental conditions, but also the processes stabilising them over time, across environmental contexts and changes in group composition (Jacobs and Petit, 2011; Thierry, 2007).

In this respect, the social organisation of macaques (genus *Macaca*) currently represents the best-documented case regarding the robustness of social patterns in animal societies. Macaque species show great variations of their social relationships within common socio-demographic structures (i.e. multi-males multi-females groups, with phylopatric females; Thierry, 2007; Duboscq et al., 2013a,b). However, each species is characterised by a typical social style, defined by the covariation of several social traits (e.g. development of social tolerance, dominance asymmetry, maternal permissiveness; Thierry, 2013). Macaque social styles are remarkably consistent over time, and across groups and environmental conditions (Thierry, 2013, 2007). According to their social style, macaque species can be ordered on a four-grade scale, from “despotic” to “tolerant” species. Tolerant species are mainly characterised by linear but relaxed dominance hierarchies and a weak influence of kinship on social behaviour, while despotic species are characterised by steep hierarchies and a strong nepotism (Balasubramaniam et al., 2012; Duboscq et al., 2013a,b). In addition, within each social style, a number of social traits show strong interconnections (Thierry, 2013). By limiting the changes possible to the social organisation, functional dependency between traits allow only a subset of social styles to arise. For instance, any association between high intensity of aggression and high degree of maternal permissiveness is functionally contradictory, and is consequently never observed in macaques (Thierry, 2013). In strongly intolerant species, mothers are very protective and frequently retrieve their infants from others’ reach, limiting their interactions with other group members to relatives. On the contrary in more tolerant species, mother can without much risk allow infants to interact with other partners, which promotes allomothering care (i.e. care provide by females other than the mother; Thierry, 2007).

Therefore, the functional interdependency of macaques' social traits acts as an internal constraint on social organisations, and ultimately limits the range of organisations that animals can form in response to environmental pressures. Cross-species comparisons of macaques' social styles show that variations in macaques' social organisations are consistent with phylogeny and cannot be solely attributed to socio-ecological differences (Matsumura, 1999; Ménard, 2004; Thierry et al., 2000). In the *Eulemur* genus, socio-demographic structures also correlate with phylogenetic distance between species, but not with environmental factors (Ossi and Kamilar, 2006). Note that several studies showed that phylogenetic relatedness explains a substantial amount of behavioural diversity in non-primate species too (i.e. in birds, Johnson et al., 1999; Prum, 1994; in equids, Linklater, 2000).

The case of macaques' social organisations shows that internal constraints can oppose to ecological constraints, and ultimately modulate their impact on the social structure, by exerting strong stabilising pressures on the individuals' social behaviours, which may induce evolutionary stasis (Thierry, 2013, 2007). This emphasises the fact that both ecology and phylogeny play a role in the evolution of social organisations, and points at the need to integrate the species' phylogenetic history together with the study of environmental factors (Menard, 2004; Thierry, 2013; Thierry et al., 2000). So far, the study of ecological determinants on social organisations variations, have eclipsed the study of the robustness of social patterns. One might expect similar resilience of social organisations in other highly social species. It would be necessary to investigate the robustness of the social patterns in non-primate species forming individualised and differentiated social relationships, and also in species expressing a high degree of fission-fusion dynamics, where individuals are faced with constant changes in of group structure (Couzin and Laidre, 2009; Kerth et al., 2011; Wittemyer et al., 2009). Understanding the processes that modulate and stabilise social organisations across taxa, would help us to understand the evolution and ultimate function of sociality, and more importantly, the different mechanisms sustaining intra- and inter-specific variations. However, the set of social traits and their patterns of covariation are likely to differ from species to species, as the costs and benefits of group living are rarely expressed in the same currencies in all species. In-depth study of the species' social organisations are therefore necessary to investigate the diversity of forms taken by sociality across species, and the relative share of ecology and phylogeny in the evolution of social behaviour.

4. The study of social relationships and social structure in birds

It is now necessary to extend the sampling of empirical data on animal social organisations. However, a major issue inherent to the study of animal sociality is that it is strongly taxa-biased. Studies on the social organisation of birds for instance are clearly underrepresented in comparison to studies on mammals. This may be due to the fact that most birds are socially monogamous (more than 85% of the species; Greenwood, 1980), which seemingly decreases the diversity of social relationships that could emerge outside of the pair (i.e. see above; see also Dunbar and Shultz, 2007). Yet numerous avian species are good candidates to study the emergence of more complex forms of sociality. This includes species showing advanced cognitive skills like corvids or parrots, but also species living in groups all year long, where individuals necessarily have to cope with both costs and benefits of group living, e.g. colonial and cooperatively breeding species. In addition, the formation of long-term pair bond also attests of a species' ability to establish and maintain valuable relationships (e.g. in raven, *Corvus corax*, Fraser and Bugnyar, 2010b; in jackdaws, *Corvus monedula*, de Kort et al., 2006; in New Caledonian crow, *Corvus moneduloides*, Holzhaider et al., 2011; in cockatiels, *Nymphicus hollandicus*, Spoon et al., 2004; in monk parakeets, *Myiopsitta monachus*, Hobson et al., 2014). A few studies suggest that multi-level societies, similar to those of mammals, can emerge in birds. In monk parakeets for instance - a colonial parrot species – individuals can bond out of the pair, and groups are characterised by multiple layers of relationships, composed of both an affiliative and a dominance structure (Hobson et al., 2014). Yet if the current paradigm shift in bird socio-biology is slowly acknowledging the fact that social structures are far more complex than simple aggregations, numerous assumptions on bird sociality remain untested (Bergman and Beehner, 2015). For instance, whether the strength and the duration of the pair bond is either negatively or positively correlated to extra-pair relationships in avian species remains largely unknown. Although numerous bird species are likely candidates for the emergence of more complex forms of sociality, to date we lack empirical and quantitative data on the diversity and dynamics of social relationships that may emerge out of privileged family unit in avian species (i.e. reproductive partners and their juveniles), and little is known about the degree of complexity of avian social organisations. Studies on avian social organisations should investigate on how such a strong bond (pair) can integrate in a social structure, and how it varies according to the strength and dynamics of extra-pair relationships. Considering that cognitive abilities and sociality may have co-evolved in numerous species, bird species displaying advanced cognitive skills represent the best candidates for multi-level/complex social organisations. Therefore, we should target bird species that: i) live in groups part of the year or even all year long, which would favour the emergence of more intricate social processes to cope with the balance of the costs and benefits of social living; ii) form sophisticated and long-term partnerships, attesting of individuals' ability to establish and maintain valuable bonds, and iii) display advanced cognitive skills.

4.1. Diversity of birds' social organisations and collective behaviours

Avian species have for long been considered as less complex than mammals regarding their social organisations. Consistently, most studies focused on the strength of the pair bond and its fitness correlates (Black, 2001; Spoon et al., 2006; van de Pol et al., 2006), often neglecting the social complexity that may arise out of the family unit in some avian species (e.g. colonial or cooperative breeding species). However, numerous bird' species gather in groups during winter or the breeding season (Greenwood, 1980), and sometimes all year long like rooks or jackdaws (Goodwin, 1955; Roell and Bossema, 1982). Moreover, birds express a large range of social organisation (e.g. territorial pairs, coloniality, communal roosting, cooperative breeding; Cockburn, 1998; Ekman, 2006; Hatchwell, 2009). In addition, they display a wide range of complex collective behaviours, from the construction and use of collective nests (Brosset, 1978; Riehl and Jara, 2009), the collective harassment of predators (Krams et al., 2006), sentinel behaviours (Arnold, 2000; Ridley et al., 2013), complex synchronized swarms in flight (Okubo, 1986; Sridhar and Shanker, 2013), or crèching behaviour (Le Bohec et al., 2005). Some of those collective behaviours can certainly be explained by simple rules of attraction and repulsion between group members, or similar motivations and shared benefits (Ballerini et al., 2008; Heppner and Grenander, 1990). Yet there is also growing evidence that in some avian species, collective behaviours are sustained by the establishment of social relationships among group members, and not just by simple rules of aggregation. For instance, the structuration of bird flocks in flight, depends on the dominance status of individuals, and social preferences for conspecifics and mated partners (i.e. in pigeons, *Columba livia*, Nagy et al., 2010; in mixed flocks of rooks and jackdaws, Jolles et al., 2013a; Kasprzykowski, 2003). In addition, non-random associations and interactions occurring out of the privileged family unit, have been reported in various bird species (e.g. New Caledonian crows, *Corvus moneduloides*: Rutz et al., 2012; great tits, *Parus major*: Aplin et al., 2013; cockatiels, *Nymphicus hollandicus*: Seibert & Crowell-Davis, 2001;

Spoon et al., 2007; zebra finches, *Taeniopygia guttata*: Elie et al., 2011; common guillemot, *Uria aalge*: Lewis et al., 2007), and notably in cooperatively breeding species (Radford & Fawcett, 2014; Gaston, 1977; Carlisle & Zahavi, 1986). Indeed, it is known that in cooperatively breeding species, including in birds, individuals can cooperate and affiliate with different partners, refuting the possibility that they simply aggregate and interact randomly (Baglione et al., 2006; Carlisle and Zahavi, 1986; Cockburn, 1998).

4.2. Group living in birds: comments on coloniality

One of the most striking form of group living in birds is the massive aggregation of breeding pairs in colonies, where individuals breed in a densely distributed territory, which usually contains no other resources than nesting sites. Coloniality mainly occurs in seabirds (i.e. on average 95% of seabird species; Danchin and Wagner, 1997; Rolland et al., 1998), but also in a few terrestrial birds like rooks (Griffin, 1999; Griffin and Thomas, 2000). Avian colonies are mainly organised around nesting behaviour. Living and in particular breeding with such a high density of conspecifics close by necessarily comes with fitness costs for individuals (e.g. competition for nest sites, mates, food, transmission of parasites, cannibalism and infanticide), but also results in fitness benefits such as reduction of predation risk, thermoregulation, or increased foraging efficiency (Danchin and Wagner, 1997; Møller, 1987; Rolland et al., 1998). Colonial breeders can also use conspecific breeding/foraging success as cues to assess habitat or nest site quality (i.e. public information theory, Boulinier et al., 2014; Doligez et al., 2003, 2002; Richner and & Heeb, 1996). Individuals are indeed more likely to be attracted by sites already occupied, which would attest of good nesting conditions or of the proximity of good foraging sites (Doligez et al., 2002). However, all those benefits (e.g. thermoregulation, decreased predation, and increased foraging success) do not necessarily require individuals to bond with conspecifics, and so far, we don’t know how the emergence of social bonds between colonial breeders could impact the balance of costs and benefits of colonial living.

4.3. Bird cognition and social complexity

Numerous bird species are well-known for their cognitive abilities, and in particular corvids (Emery, 2006; Emery and Clayton, 2004; Lefebvre et al., 2004), which may have important implications in terms of social complexity. Corvids are mostly known for their aptitudes in physical cognition, in link with their abilities in food storing and extraction of food from complex and challenging environments (Grodzinski and Clayton, 2010; Taylor and Källander, 2010). In western scrub-jays notably, individuals can anticipate and plan for the future, in particular when caching food for latter consumption, and this independently of their current motivational state (Correia et al., 2007). Crows and ravens are also able to successfully delay gratification in an exchange task, in order to wait for a reward of a better quality (Dufour et al., 2012; Hillemann et al., 2014; but see Wascher et al., 2012a). Several studies have also highlighted the ability of corvids to manufacture and use tools for specific foraging tasks either in the lab or in the wild (especially New Caledonian crows; Bluff et al., 2007; Chappell and Kacelnik, 2004; Hunt and Gray, 2003). Other corvid species are also known to be able to solve complex tasks such as trap-tube problems (Seed et al., 2006), or the use of stones to raise water level (Bird and Emery, 2009a) without training. Despite the fact that they do not appear to use tools in the wild, rooks are also able to shape tools and use them in a sequential order to gain access to a reward (Bird and Emery, 2009b). In addition, individual rooks may team up to solve a problem, although it seems that they do not utterly understand the role of the partner in the task (i.e. string pulling task; Seed et al., 2008).

Recent studies have shown that corvids may display complex social abilities (Clayton et al., 2007; Clayton and Emery, 2007). In rooks, individuals can differentiate individuals, and more precisely they can discriminate affiliates from non-affiliates (Bird and Emery, 2008). In jackdaws, although nestlings do not beg selectively at parents, they quickly discriminate conspecifics from others, and may even discriminate parents from neighbours (Zandberg et al., 2014). Similarly, ravens and carrion crows discriminate conspecifics from others (i.e. familiar against unfamiliar; in ravens, Boeckle and Bugnyar, 2012; in carrion crows, Wascher et al., 2012b). Raven even differentiate affiliates from unaffiliated three years later (Boeckle and Bugnyar, 2012). More broadly, corvids can be attentive to others, adjusting their behaviour according to the behaviour and identity of conspecifics (Bugnyar et al., 2007; Clayton et al., 2007; Dally, 2006). Western scrub-jays for instance, display protective behaviours toward their caches, but they only do it once they have been pilfered by another conspecific (Emery and Clayton, 2001). Ravens are also known to adjust their behaviour according to the social context. For instance, they can differentiate potential competitors which have, or do not have, information about hidden food (Bugnyar, 2011), or can selectively engage or not in pilfering behaviour according tot the type of competitor they are facing (Bugnyar & Heinrich 2006). More recently, it was also shown that raven preferentially observe and thus learn more from their affiliates than from other conspecifics (i.e. in an artificial foraging task), indicating that in aggregations of juvenile ravens, the affiliative structure can strongly influence the spread of information in the group (Kulahci et al., 2016).

4.4. Rooks' social-ecology: Pair bonding and colonial living

Among corvids, the rook (*Corvus frugilegus*) is an ideal species to investigate multi-level organisation and social dynamics in birds. On top of their advanced cognitive abilities (Emery, 2004; Emery et al., 2007; Scheid and Noë, 2010; Seed et al., 2008), they form strong and stable pair-bonds that may last for a lifetime (Emery et al., 2007). They also permanently live in groups and breed in colonies, insuring that individuals regularly meet other conspecifics and renders possible the emergence of complex social relationships not restricted to the pair. In this species, individuals thus face both the challenges of pair-bond requirements, and the necessity to deal with numerous potential collaborators/competitors. In addition, they are thought to express a high degree of fission-fusion dynamics: individuals have to deal with constant changes in group composition and size, with a high turnover with respect to individual group (colony) membership.

Early in life (i.e. before the first reproductive attempt), rooks form long-term monogamous pair bonds (Emery et al., 2007). Before sexual maturity, young rooks interact with several partners in order to choose their mate, including same-sex partners and siblings (Emery et al., 2007; Scheid et al., 2008). Among juveniles, social interactions include food sharing, allopreening and close contact (rooks: Emery et al., 2007; Scheid et al., 2008; jackdaws, *Corvus monedula*: de Kort et al., 2003, 2006), all of which are behaviours believed to participate in the process of pair formation. Indeed, during the pair formation process, rooks gradually interact with non-siblings and individuals of the opposite sex, shifting from one preferred partner to another (Røskaft & Espmark, 1984; Emery et al., 2007; von Bayern et al., 2007). In doing so, they gradually select one privileged partner to pair up with, and with whom they interact in an exclusive manner (Emery et al., 2007). These behaviours are assumed to be exclusive to the pair in adults (rooks: Emery et al., 2007; jackdaws: von Bayern et al., 2007).

Furthermore, although they form strong and long-term pair bonds, rooks breed in colonies which can vary widely in size from tens to tens of thousands of individuals closely nesting. The size of the colony is affected by both the distribution of resources and the degree of competition with other colonies (Griffin and Thomas, 2000). Out of the breeding season, rooks also gather and roost collectively, sometimes together with jackdaws. In autumn and winter, astonishing swirling masses of rooks and jackdaws can be seen in flight at dawn and dusk (Picture 1). Rooks' colonial dynamics are best described as mimicking fusion-fusion societies, with individuals alternatively merging and splitting from the colony to forage or flight in smaller subgroups during the day. Whether those subgroups of individuals are stable over time, and from one season to another, is still unclear. If so, we may expect subgroups to be formed according to individual motivations and needs, but also eventually according to individual affiliations. However for social relationships to emerge, individuals have to meet regularly. Considering the dynamics and the size of some rook colonies, we may wonder how relationships could actually emerge and endure over time. Numerous studies describe the high fidelity of rooks to their roosting colonies and even nesting sites. Thus, nesting neighbours may remember each other from one year to the next (Goodwin, 1955; Richardson et al., 1979). Further, some juveniles are thought to stay within their native colony when they start breeding (Griffin, 1999). Thus, in addition to the pair bond unit, relatedness and affiliations are two layers of social relationships that could sustain social structure in rooks.

Picture 1. Rooks and jackdaws gathering at dusk in Norfolk. Photo by Martin Argles for the Guardian.

Several studies suggest a certain degree of structuration of rook colonies, which highlights some form of regulation for collective behaviours. For instance, nest location appears influenced by individuals’ competitive abilities, and the best competitors usually choose the highest roosting positions to avoid predation by mammals (Kasprzykowski, 2008), except in case of severe weather, when they favour sheltered position in the canopy to minimise heat loss (Swingland, 1977). Rooks’ flock composition also varies with the age of composing individuals. Once they are nutritionally independent, juveniles tend to join small aggregations of 30 individuals on average, while adults are more often seen in larger flocks (i.e. >50 individuals; Henderson, 1991). Juveniles usually favour flocks composed of few adult individuals, which are expected to be dominant over juveniles, and more efficient while foraging (Henderson, 1991; East, 1988; Dunnet et al., 1969). Besides, several studies suggested that rooks can use social information to locate and search for food (Chantrey, 1982; Waite, 1881; Fear, 1974).

Overall, because rooks live and breed in very close proximity with others, in huge colonies, they necessarly have to cope with both the benefits and costs greggariouness. In addition, they also have to deal with constant modifications of group composition, from day to day, or from season to season (i.e. fission-fusion dynamics). Therefore, we could expect the emergence of a multi-level social organisation to be beneficial to individuals in this species, as it may alleviate the effects of competition arising from colonial living, and allow dealing with constant modifications in colony composition. Indeed, the formation of relationships (dominance and affiliations) can compensate part of the costs associated with group living, for instance by reducing the asymmetry of benefits among group members, or by limiting the risk of injuries, or by favouring cooperation among partners (e.g. for resources management, protection against predators, juveniles rearing). Yet if rooks’ social complexity has often been assumed, few studies have focused on its social organisation.

5. AIM OF THIS THESIS

This thesis focuses on the diversity and dynamic of social relationships in a group of captive adult rooks over three years. It aims to investigate the behavioural mechanisms underlying the emergence and maintenance of different levels of social organisation, and understand how different categories of social relationships can form a group structure. By fostering our knowledge of rooks' social organisation, the thesis will also contribute to the establishment of a comparative framework in corvids, necessary to a better understanding of the evolution of animal sociality.

The thesis will address four problems:

In a first study (Chapter 3), I investigate the nature of social relationships in rooks. I examine the possibility of extra-pair (i.e. secondary affiliations) and same-sex relationships, using various measures of spatial association, affiliation, sexual behaviour and aggression, to differentiate and characterise each type of relationships. In case extra-pair relationships occurred, I also look whether pairs actually represent the core of the structure, and if additional layers of relationships may be present.

In a second study (Chapter 4), I analyse the consequences of secondary affiliations on the strength and stability of pairs. From the monitoring of variations in the strength of relationships over time, I test the occurrence of variations in partnership, in particular after demographic changes (i.e. losses and addition of individuals). Having shown that variations in partnership do occur, I then scrutinize the mechanisms underlying divorce and formation of new pairs, and the respective responsibility of each individual in the process.

In a third study (Chapter 5), I explore the temporal dynamics of relationships - both pairs and secondary affiliations - over the three years. More precisely I inquire whether the removal and formation of relationships follow consistent patterns. This allows to test the robustness of the social patterns in this group and the resilience of the network, both across time and demographic changes.

In a fourth study (Chapter 6), I investigate the prevalence and strength of the dominance hierarchy in rooks. To do so, I analyse the structural characteristics of the hierarchy (i.e. linearity, steepness, directionality of conflicts), and their stability over time. Then, I examine the determinants of dominance relationships, and their dynamic over time.

2

GENERAL METHODS

1. SOME INFORMATION ABOUT ROOKS (*CORVUS FRUGILEGUS*)

1.1. General information

Rooks belong to the Corvus Genus in the Corvidae family and the passerine order. The Latin appellation *frugilegus*, means “fruit-gathering”. The Corvidae family includes more than 120 species, including crows, ravens, rooks, jackdaws, jays, magpies, choughs, and nutcrackers, distributed worldwide, except from the southern tip of South America and the polar caps (Figure 1). The Corvus genus regroups over a third of the Corvidae family, it includes jackdaws, crows, ravens and rooks, species which generally have black plumage, possible with some grey or white variations. Among them, rooks can be found in a large number of locations, including Asia, Russia, and Europe (Figure 1). Thus they occupy a large variety of habitat from farmland, flooded grassland, deciduous or mixed forest but also urban habitats, often favouring the vicinity of cultivated area to roost. On the IUCN wildlife conservation classification of species, rook species is evaluated as least concern (http://dx.doi.org/10.2305/IUCN.UK.2012-1.RLTS.T22705983A38368499.en).

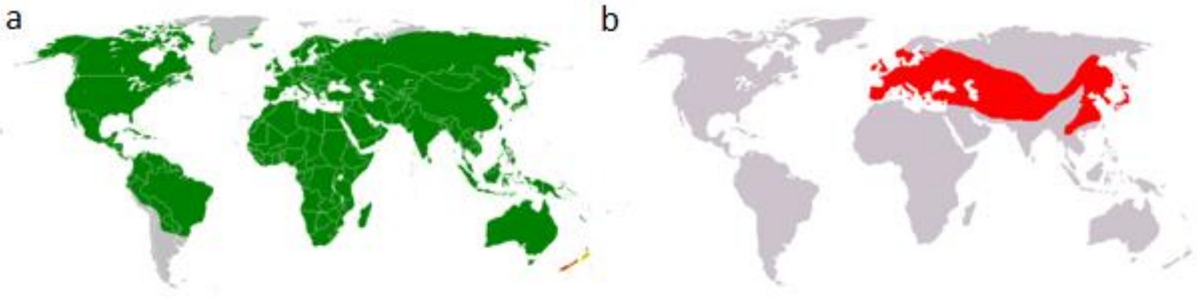


Figure 1. Distribution maps of the a) Corvidae family, and b) the rooks (*Corvus frugilegus*).
Source : *https://en.wikipedia.org/wiki/Corvidae#/media/File:Corvidae.png, https://en.wikipedia.org/wiki/Rook_(bird)#/media/File:Rook_range_map.PNG*, maps computed from Madge & Burn (1993) and Goodwin (1976).

Rooks generally measure 45cm length, and 80 to 95 centimetres wingspan. They weight from 380 to 520 grams and can live up to 20 years. They are characterised by glossy black feathers with some blue sheen in the light. The beak is grey and the skin is also white-grey around the beak and the eyes (Picture 1). Rooks are opportunist birds, but mainly eat worms or insects, cereal grains, and fruits, but also food rubbish in urban habitats, and possibly small mammals or eggs (Waite, 1948; Feare et al., 1974; Feare, 1961; Kasprzykowski, 2003). Rooks usually forage in small groups composed of on average of ten individuals (i.e. both adults and juveniles after the breeding season; East, 1988), but can also reach hundreds of individuals (Kasprzykowski, 2003).

Picture 1. Male adult rook starting courtship (Tom). Photo by Palmyre Boucherie.

1.2. Reproduction

Rooks breed and roost all year long in colonies, building nests in the very top of tree branches in large colonies ranging from tens to tens of hundreds of individuals (Benchley, 1986; Kasprzykowski, 2008; Ogilvie, 1951). The season has a strong impact on the activity and the areas used, and in and out of the breeding season, rooks usually roost in different sites (Marshall and Coombs, 1957). The breeding season usually starts at the end of February or early March, and last until the end of May (Lincoln et al., 1980; Figure 2; see also Owen, 1959). Note that a resurgence of sexual activity can be seen in September, before the breeding season (Lincoln et al., 1980; Figure 2). Before the reproduction, usually in February, individuals increase their visits to the rookery. At this stage, individuals can frequently engage in fights with others congeners, likely for the location of the future nests (Marshall and Coombs, 1957). At the end of February, they start building nests (Owen, 1959). There are some evidences that the choice of the nest is attributed to the males (Richards, 1976) and is often associated with an increase of the general level of activity of the colony (e.g. frequent vocalisations, manipulations of branches; Marshall and Coombs, 1956; Richards, 1976). At this stage, pairs frequently display bowing or tail fanning behaviours, associated with cawing of high intensity (Marshall and Coombs, 1957; Ogilvie, 1951; Richards, 1976). Rooks usually lay 3-5 eggs, between March and April (Lincoln et al., 1980; Owen, 1959; Lockie, 1955). The female mostly incubates the eggs, during 15-20 days (Owen, 1959). However, parents share the parental care, and both male and female alternatively feed the young, and the partner (i.e. when incubating or surveying the nest; Lockie 1955). Young usually fledge after about 30-33 days (Owen 1959). Parents stop providing food to their offspring in July, after their reach nutritional independence (East, 1988).

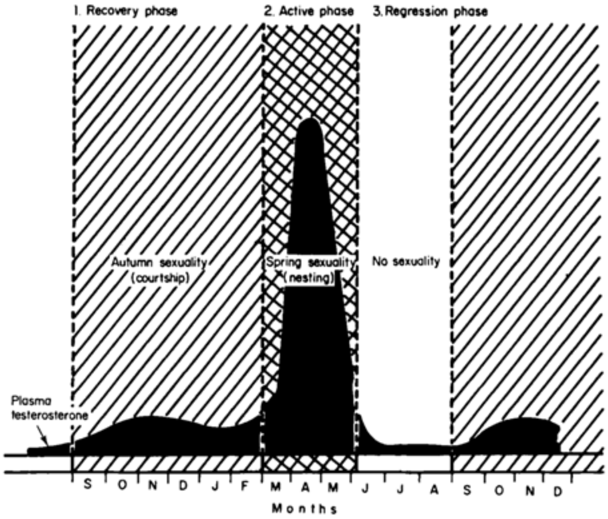


Figure 2. Figure taken from Lincoln et al. (1980), representing how the breeding season of rook starts in autumn with the increase in activity of the pituitary/gonadal axis and consequent changes in behaviour (autumn sexuality). Full gonadal development occurs in spring along with full sexual behaviour (spring sexuality) and then the birds enter a sexually quiescent phase when the feather moult occurs and body weight returns to normal”.

Out of the breeding season, rooks also gather and roost in huge flocks (Lincoln et al., 1980), which can reach tens of thousands of individuals. They can sometimes roost together with other birds’ species, often jackdaws (*Corvus monedula*). Those congregations into very large flocks can sometimes display impressive aerial ballets at dawn and dusk.

2. METHODS

2.1. Subjects

In 2012, the original group was composed of 11 individuals (9 males, 2 females), taken from the nest in a wild local colony in 2006 and 2007 (i.e. individuals were 2 to 4 weeks old; Table 2). Two dyads of those individuals were nest-mates, and all other individuals were singletons (i.e. with no nest-mates; Table 1). During hand-rearing, nest-mates were kept together in a nest box. Among the five singleton, two were added in the same box of one of the two dyads of nest-mates. Two others singleton were put together in the same nest box, the three others were alone in their boxes (Table 1).

In April and June 2013 two birds escaped after rodents damaged the aviary (h, male; p, female). Following this, in October 2013, six new birds all rescued from hunting traps in southern Alsace, were added to the original group (i.e. 1 juvenile male and 5 females, Table 2). Before being added to the group, birds were kept together in quarantine for two months (i.e. from August to October 2013). When added to the original group, in order to avoid conflicts, the two sub-groups of individuals were first kept isolated by a central mesh separating the two main compartments of the aviary (Figure 3). However, individuals could see and hear each other's, and limited contacts could still occur through the separating mesh. The mesh was removed after one month, and all individuals could freely associate and interact. Soon after this, one of the newly introduced female escaped from the aviary (w; December 2013), and was thus not included in the analysis. Finally, two other birds died of natural causes in the end of May and in early August 2014 (z, male c; female). The evolution of the group composition and sex-ratio over time is resumed in Table 2.

Individuals	**Sex**	**Date of capture**	**Nest origin**	**Nest box**
a	♂	08/2013		
b	♂	05/2006	1	1
c	♀	08/2013		
e	♂	05/2006	2	2
g	♀	08/2013		
h	♂	05/2006	3	3
j	♀	05/2006	2	2
k	♂	05/2006	4	1
m	♂	05/2006	5	4
n	♂	05/2006	6	1
o	♂	05/2006	7	4
p	♀	08/2013		
s	♀	08/2013		
t	♂	05/2006	8	5
w	♀	08/2013		
y	♀	05/2006	1	1
z	♂	04/2007	9	6

Table 1. Individuals' sex, date of capture, nest origin and nest-box number during the hand-rearing period. Original group members are colored in green and newly introduced members in orange. The nest origin and nest box are only reported for original group members, which were collected from the nest. Newly introduced individuals were mostly captured as adults (i.e. one juveniles).

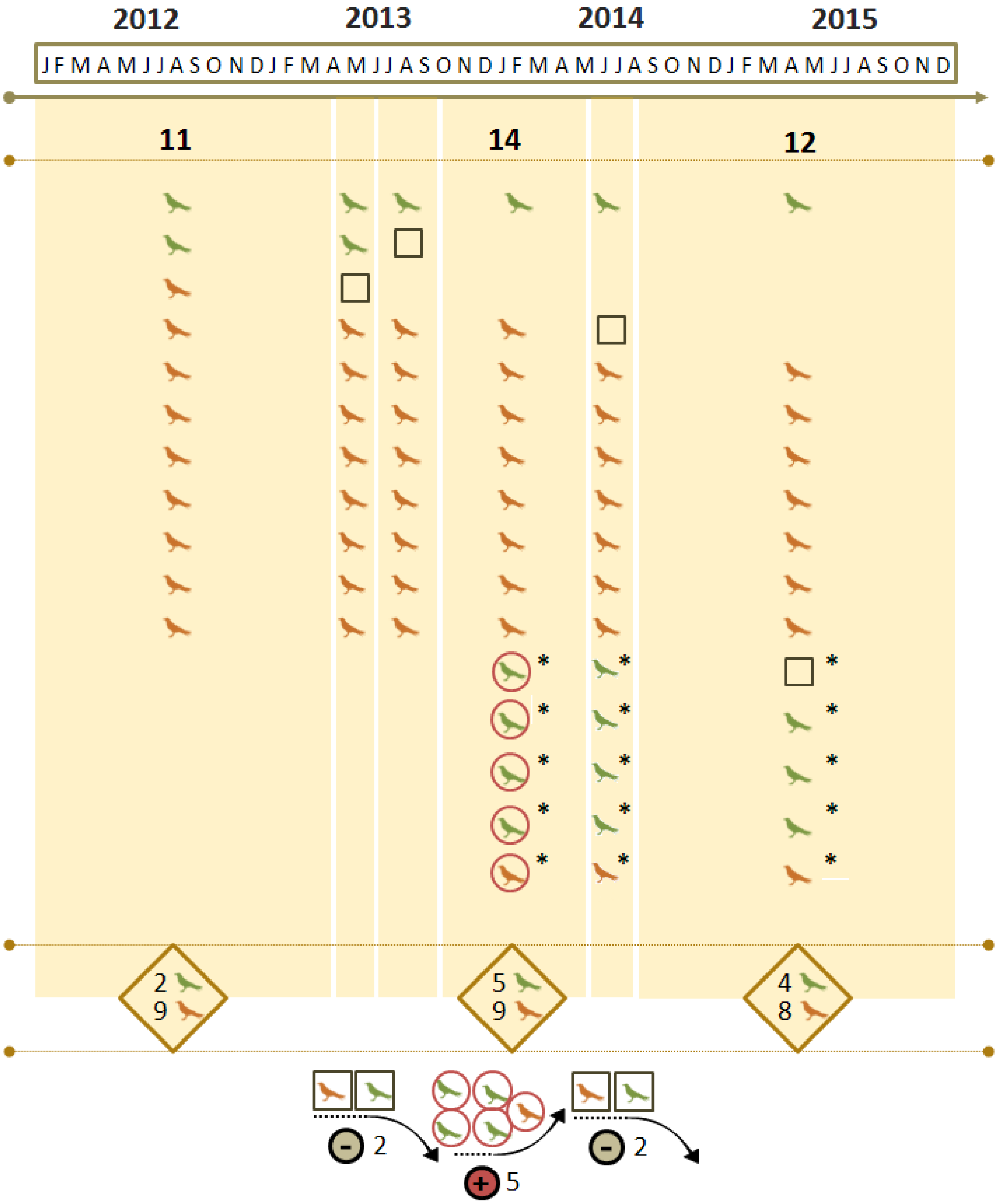


Figure 3. Modifications of group composition and sex-ratio over time. Asterisks indicate newly introduced group members. A square indicates the loss of an individual, and a circle indicates the addition of an new individual in the group (i.e. newly introduced group members). Females are coloured in green and males in orange. In 2012, the group composition was stable since 2010. In April and June 2013, two individuals escaped after rodents damaged the aviary (h, male; y female). In October 2013, six new individuals were

added to the group (a, juvenile male; c, g, p, s, w, females), one of which escaped a few days afterwards and thus do not appear in the table (w, female). Finally, two other birds died of natural causes in the end of May and in early August 2014 (z, male; c, female).

2.2. Housing conditions

All subjects were housed together in a large outdoor aviary in the CNRS campus of Cronenbourg, Strasbourg, France. The aviary 18 × 6 × 3.5 meters was divided in 6 compartments, two main compartments, appending three smaller ones (Picture 2 and Figure 3). All compartments were separated by a mesh and a door, allowing if necessary to isolate individuals. However all spaces were constantly left open and individuals could freely choose where to forage, perch or nest. The aviary contained several wood perches, platforms, ropes, tree branches for perching, and food tables (Picture 2). The ground was covered with gravel. The aviary was also furnished with sticks and small branches for nests construction, two water pools for bathing, as well as small plastic toys for enrichment. Individuals had ad libitum access to food, a fresh mix of pellets and yogurts, and water.

Picture 2. Housing aviary at the CNRS campus of Cronenbourg, Strasbourg, France.

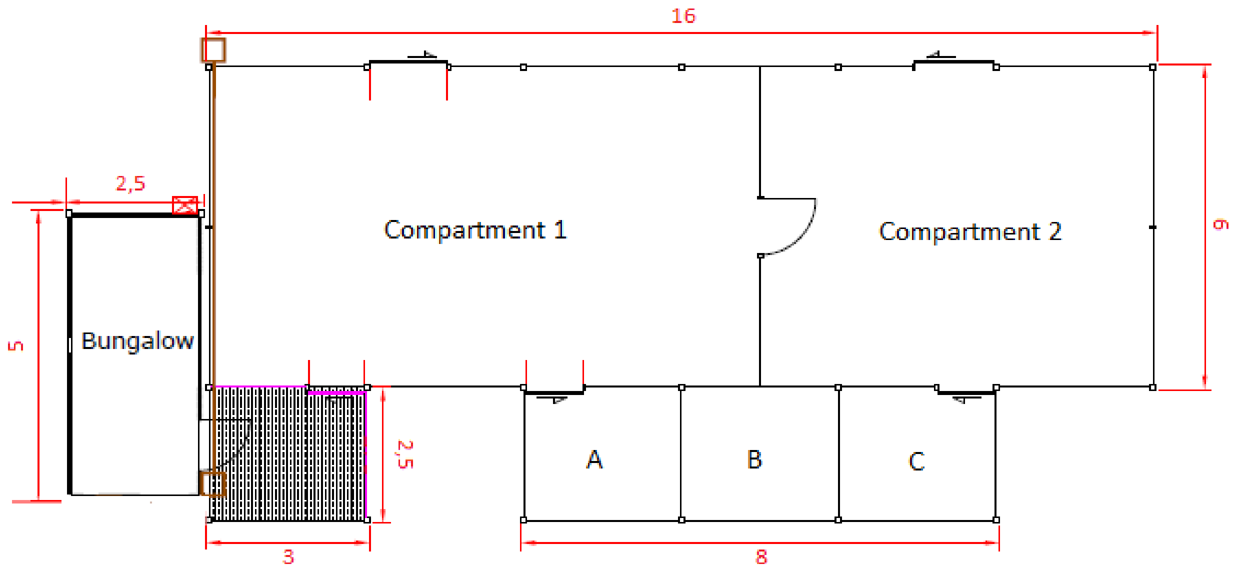


Figure 4. Illustration of the aviary design. The aviary was composed of two main compartments, attended by three smaller compartments (A, B and C), and a bungalow for animal care and food storing. Dimensions are given in meters.

2.3. Observation procedure and data collection

Data were collected over three different years: i) from January to the end of April 2012, 55 observation sessions; ii) from January to the end of September 2014, 83 observation sessions; iii) from January to the end of September 2015, 83 observation session[1]. Those periods included the breeding season (i.e. March to June; see also Figure 2). More precisely, for this group, the breeding season was defined by the beginning of nest building (usually in early March), and stopped as soon as individuals started dismantling nests (i.e. usually at the end of May). Observation sessions were performed once a day, between 08:00 and 18:00 hours. As far as it was possible, the observation sessions were evenly distributed on the morning (i.e. 08:00 to 12:00) and the afternoon (i.e. 12:00 to 18:00) within each observation period. I always stayed outside the aviary (i.e. approximately 2 meters away from the mesh) and waited for about 5 to 10 minutes before starting the first focal observation. This ensured that the recorded behaviours were not impacted by my recent arrival. Then, I stayed as still as possible during the whole observation session. More generally, all individuals were habitued to the daily presence of students or keepers for at least 3 hours a day. During each session, all

---

[1] Data were collected in 2012 during P.B. master's degree, and in 2014 and 2015 during P.B. PhD, which started in October 2013.

individuals were observed once, randomly one after the other using 10-minutes individual focal sampling (Altmann, 1974).

During the focal sampling, I recorded spatial proximities (i.e. ground proximity and perch proximity), affiliations (i.e. contact-sit, allofeeding, allopreening, and bill-twining), the tolerance at the food source (i.e. co-feeding events), agonistic behaviours (i.e. peck, charge, chase, avoid, supplant, threat), and sexual behaviours (i.e. mounting and courtship). In addition to focal sampling, I used ad libitum sampling to record the rarest behaviours (i.e. allofeeding, co-feeding, courtship and mount; see Ethogram): those behaviours were therefore recorded for all group members during each focal observation (Altmann, 1974). The direction of all behaviours was recorded in 2014 and 2015 (i.e. identity of the emittor and receiver of the behaviour). I recorded the number of occurrence for all behaviours (i.e. frequency), and when possible, I also recorded the duration for: spatial proximities, contact-sit, allopreening, and co-feeding events. All observations were performed using a windows tablet saving immediately all data in excel software

2.4. Ethogram

Analysis performed in this thesis mainly focused on spatial proximities (i.e. ground proximity and perch proximity), affiliations (i.e. contact-sit, allofeeding, allopreening, and bill-twining), co-feeding events, agonistic behaviours (e.g. peck, charge), and sexual behaviours (i.e. mounting and courtship). See Table 3 for the complete list of recorded behaviours and their definition.

Behaviour	**Definition**
	Spatial proximities
At perch	Individuals are located from 10 cm to 50 cm apart on the perch
On the ground	Individuals are located from 0 m to 1 m apart on the ground
	Affiliations
Contact-sit	Individuals are less than 10cm apart on the perch
Allofeeding	One subject actively transfers a food item from its beak to the beak of another subject

Allopreening	One subject runs its beak thought the feathers of another subject
Bill twining	Two subjects gently clatter their beaks together
	Tolerance at the food source
Co-feeding	Two subjects eat together at the same food source (a round platform measuring 1m in diameter)
	Agonistic behaviours
Peck	The subject hits another individual with his beak.
Charge	The subject rushes toward another individual, without contacting him. His body and particularly the head is directed toward the receiver. The covered distance is less than 1m.
Chase	The subject pursues another individual on the ground or by flying.
Avoid	The subject moves away from an approaching individual, either walking or running on the ground, or by flying away. The two individuals do no enter in contact.
Supplant	The subject moves away from another individual who enters in contact with him and takes his place (i.e. by walking, running or flying).
Threat	The subject lightly pecks another individual that is approaching or already in body contact without touching it. The signal can be accompanied with vocalizations and puffed feathers.
	Sexual behaviour
Mount	The subject perches on top of another subject (usually a male on a female) and attempts copulation. Behaviour generally produced at the nest.
Courtship	The subject usually adopts a horizontal posture. Wings are slightly spread and horizontal. The tail can be slightly raised and quiver. Feathers from the neck and the head are raised. The subject inviting courting can also move around the courted subject in this posture. Courtship is generally accompanied by vocalisations. This behaviour is generally followed by mounting but not necessarily. It is usually performed on the ground or at the nest.

Table 2. Ethogram

2.5. Sociality index

A sociality index was used throughout the manuscript, in order to identifying and categorizing all potential relationships existing among all group members according to their strength, for different time periods. This sociality index was constructed following Silk et al. (2006a), using spatial proximities (i.e. ground proximity: GP and perch proximity: PP) and affiliations (i.e. contact-sit: CS, allofeeding: Fe, allopreening: Pr) as follow:

$$S_{ij,year} = \frac{\left((GP_{ij} / GP) + (PP_{ij} / PP) + (CS_{ij} / CS) + (Fe_{ij} / Fe) + (Pr_{ij} / Pr) \right)}{5} \times 100$$

With GP_{ij}, the dyadic frequency of ground proximity for dyad ij, divided by GP, which equals to the overall mean frequency of ground proximity for all possible dyads (and similarly for the other variables: PP, CS, Fe, and Pr). The denominator is fixed, and refers to the number of variables. Note that for pratical reasons, the sociality index was multiplied by 100. The value of the sociality index increases with the strength of a relationship (Silk et al., 2006a).

3

Chapter 3

BRILL

Behaviour

brill.com/beh

Bonding beyond the pair in a monogamous bird: impact on social structure in adult rooks (*Corvus frugilegus*)

Palmyre H. Boucherie [a,b,*], **Mylène M. Mariette** [c], **Céline Bret** [d] **and**

Valérie Dufour [a,b]

[a] Institut Pluridisciplinaire Hubert Curien, University of Strasbourg, 23 rue Becquerel, 67087 Strasbourg, France

[b] Centre National de la Recherche Scientifique, UMR 7178, 23 rue Becquerel, 67087 Strasbourg, France

[c] Centre for Integrative Ecology, School of Life & Environmental Sciences, Deakin University, Melbourne, VIC 3216, Australia

[d] German Primate Centre, Leibniz-Institut für Primatenforschung, Kellnerweg 4, 37077 Göttingen, Germany

[*]Corresponding author's e-mail address: palmyre.boucherie@iphc.cnrs.fr

Accepted 22 May 2016

Abstract

The formation of social bonds outside the mated pair is not frequently reported in monogamous birds, although it may be expected in some species like rooks, living in groups all year round. Here we explore the social structure of captive adult rooks over three breeding seasons. We recorded proximities and affiliations (i.e., allofeeding, allopreening, contact-sit) to classify relationships according to their strength. Three categories of relationships emerged: primary (i.e., pairs), secondary and weak relationships. Affiliations and sexual behaviours were not restricted to pairs, and secondary relationships were clearly recognizable. Mixed-sex secondary relationships were qualitatively equivalent to pairs (i.e., same behaviours in the same proportions), although they were quantitatively less intense. Same sex pairs occurred, and were qualitatively equivalent to mixed-sex pairs. Overall we found that rooks social structure is more than just an aggregation of pairs, which highlights the importance of considering extra-pair relationships in socially monogamous birds.

Keywords: corvids, rook, pair bonding, extra-pair relationship, same-sex relationship, social structure

DOI 10.1163/1568539X-00003372

In social species, the nature of social relationships between group members may vary substantially, ranging from rare associations to close social bonding (Silk et al., 2006a,b; Hinde, 1976). In the vast majority of bird and mammal species, social bonding mainly occurs between the reproductive partners or between parents and offspring (Shultz & Dunbar, 2010a; Dunbar & Shultz, 2007). However, in species with complex social systems, social bonds can extend beyond the family unit. Individuals can be involved in several significant relationships characterised by frequent or constant associations and affiliative interactions (Silk et al., 2006a; Lehmann et al., 2007a; Thierry et al., 1990), but also in horses (Cameron et al., 2009), canidae (Palagi & Cordoni, 2009; de Villiers et al., 2003) or dolphins (Lusseau, 2003; Connor et al., 2001). The establishment of close social bonds between group members is believed to promote group cohesion and cooperation (Dunbar, 2012; Lehmann et al., 2007a; Lusseau & Newman, 2004; Berghänel et al., 2011), and may even improve individual reproductive success (Silk, 2007; Cameron et al., 2009; Frère et al., 2010; Schülke et al., 2010) and individual survival (Archie et al., 2014). All these findings highlight the necessity to characterize animal social relationships in order to better understand the selective pressures that operate in social species.

The vast majority of studies on social bonding concern mammals rather than birds. More than 85% of bird species are socially monogamous (Cockburn, 2006), and studies have mainly focused on the strength of the pair bond and its fitness correlates (Spoon et al., 2006; Van De Pol et al., 2006; Black, 2001), often neglecting the diversity of social relationships that may exist outside the pair. However, although bi-parental care is the most common and conspicuous form of cooperation in birds (Clutton-Brock, 1991; Cockburn, 2006), other types of collective behaviours require high levels of social coordination, including cooperative breeding (Hatchwell, 2009), the collective harassment of predators (Arnold, 2000), sentinel behaviours (Ridley et al., 2013), the construction and use of collective nests (Riehl & Jara, 2009; Brosset 1978), or male cooperation for access to females (DuVal, 2007a,b). In addition, non-random associations as well as affiliative interactions have already been described outside the pair or family unit in birds (e.g. new caledonian crows, *Corvus moneduloides*: Rutz et al., 2012; great tits, *Parus major*: Aplin et al., 2013; cockatiels, *Nymphicus hollandicus*: Seibert & Crowell-Davis, 2001; Spoon et al., 2007; zebra finches, *Taeniopygia guttata*: Elie et al., 2011; common guillemot, *uria aalge*: Lewis et al., 2007), particularly in cooperatively breeding species (Radford & Fawcett, 2014; Gaston, 1977; Carlisle & Zahavi, 1986). But, so far, very few studies have investigated whether such extra-pairs associations or affiliations could correspond to strong affiliative bonds in birds.

Interacting with many different partners compels an individual to deal with the challenges of social competition and cooperation. This may be cognitively demanding (Emery et al., 2007; Shultz & Dunbar, 2010a), as predicted by the social brain hypothesis (Dunbar, 1998). Similarly, pair bonding, stable relationships, and bi-parental care are linked to brain size in birds (Shultz & Dunbar, 2010b; Emery et al., 2007; Bond et al., 2003; Emery & Clayton, 2004; Bugnyar & Heinrich, 2006). Thus, social corvids, whose cognitive abilities are often compared to those of primates (Emery et al., 2007; Emery & Clayton, 2004; Seed et al., 2007; Hunt & Gray, 2003), are likely avian candidates for extra-pair social bonding. Indeed, they are attentive to others (Bugnyar & Heinrich 2006; Bugnyar et al. 2007; Stulp et al. 2009; Tornick et al. 2011; Wascher et al. 2014), they can form and keep track of long-term relationships (Emery et al., 2007), support each other's in conflicts (Fraser and & Bugnyar, 2012; Seed et al., 2007), differentiate affiliates from un-affiliates even three years later (Boeckle and Bugnyar, 2012), or assess social relationships between counterparts (Bond et al., 2003). In addition, in some corvid species like rooks (*Corvus frugilegus*), jackdaws (*Corvus monedula*) or young ravens (*Corvus corax*), these socio-cognitive skills could be correlated to the emergence of complex colonial structure and dynamics which resembles fission-fusion dynamics (Emery 2004; Clayton & Emery 2007; Mikolasch et al. 2013; Braun et al. 2012).

Rooks, in particular, live in groups throughout the year, gathering in large colonies during the breeding season which can sometimes reach up to thousands of individuals (Goodwin, 1955; Roell & Bossema, 1982; Swingland, 1977). In this species, coloniality is expected to bring several benefits, such as the decrease of predation risk, increase foraging success, or the reduction of the loss of heat energy, especially for young during the breeding season (Goodwin, 1955; Halupka, 2013; Swingland, 1977). Although they nest in dense colony, rooks breeding parameters are not negatively affected by the close proximity of nests (i.e. clutch size, number of hatchlings Kasprzykowski, 2008). In addition, they are expected to return to the same colony breeding site from one year to the next, and even in the same nest (Goodwin, 1955; Richardson et al., 1979). Bonds should emerge between closely nesting neighbours, contributing to create a safer breeding environment (Jovani & Grimm, 2008; Lewis et al., 2007), although it remains to be formally tested. This would require in adult rooks the social capacity to bond with several partners, as juveniles do. Indeed, before sexual maturity, young rooks can interact with several partners, including same sex partners and preferentially with siblings (Emery et al., 2007; Scheid, et al., 2008). Later, they gradually interact with non-siblings and individuals of the opposite sex with whom they pair, shifting from one preferred partner to another (Roskaft, 1984; Emery et al., 2007; von Bayern et al., 2007). Among juveniles, social interactions include food sharing, allopreening and close contact (rooks: Scheid et al., 2008; Emery et al., 2007; jackdaws, *Corvus monedula*: de Kort et al., 2006; de Kort et al., 2003), all of which are behaviours believed to sustain the process of pair formation. Yet these behaviours are assumed to be exclusive to the pair in adults (rooks: Emery et al., 2007; jackdaws: Von Bayern et al., 2007), and no studies to date have explored bond formation and quality outside the breeding pair in adult rooks .

In this study we performed detailed observations over three years to identify the different types of relationships existing between captive adult rooks, before and during the breeding period. The group composition and the sex ratio were slightly modified to test whether extra-pair bonding occurred across different social contexts. First, we categorised all relationships according to their strength by using the dyadic frequencies of interactions (i.e. spatial proximities and affiliations). We then aimed to further characterise each category of relationship, investigating the patterns of interaction (i.e. relative proportion of proximities compare to affiliations), and the distribution of other significant social interactions (sexual behaviours, co-feeding and aggressions). We also tested whether the sex composition (same-sex/ mixed-sex) or the reproductive status of the dyad had an impact on the characteristics of the relationship. Finally, social network analyses were used to visualise whether pairs were isolated units or were part of higher degree social structures composed of both pair and extra-pair social bonds (Sueur et al., 2011; Wey et al., 2008).

Material and methods

Subject and study site

Data were collected on captive adult rooks housed on the Cronenbourg CNRS campus in Strasbourg, France. In 2012, the flock was composed of 11 birds (9 males and 2 females), collected from the nest in a wild local colony between 2006 and 2007. Among those 11 birds, two dyads of individuals were siblings (i.e. collected from the same nest). Five wild birds (1 juvenile male and 4 adult females) were then added to the flock in 2013 following their rescue from hunting traps in southern Alsace. Between 2012 and 2014, four birds escaped or died of natural causes. Group composition and sex ratio therefore varied over the three years of observation (2012: 9 males, 2 females; 2014: 9 males, 5 females; 2015: 8 males, 4 females). All birds were banded with coloured leg rings for identification. The rooks were all housed together in a single large outdoor aviary (18m x 6 m x 3.5 m), that was divided into two large compartments and three smaller rooms. Birds had free access to all compartments, allowing them to choose which individuals they associated with or avoided. All year round, the aviary contained large wooden perches, platforms, ropes and suspended baskets for nesting. Birds had ad libitum access to water and food (a mixture of pellets and fresh eggs, yogurt and fruits). The aviary was also furnished with two small pools for enrichment and bathing.

Data collection procedure

Data were collected between January and early June in 2012, 2014 and 2015, which included the breeding season (March to June). In each year, we respectively performed 55, 55 and 54 observation sessions. During each session, all individuals were observed randomly one after the other using 10-minute individual focal sampling (Altmann, 1974), totalling 9 hours of focal observation per individual and per year. We never performed more than one observation session per day, and all observations were conducted by a single observer (PB) between 08:00 and 18:00 hours. The observer always stayed outside the aviary (i.e. approximately 2 meters away from the mesh) and waited for about 5 to 10 minutes before starting the first focal. This insured that the recorded behaviours were not impacted by her recent arrival. Then, she stayed as still as possible during the whole observation session (more generally, all individuals were habitued to the daily presence of students or keepers for at least 3 hours a day). We recorded spatial proximities (i.e. ground proximity and perch proximity), affiliations (i.e. contact-sit, allofeeding, allopreening, and bill-twining), co-feedings events (in 2014 and 2015 only), sexual behaviours (i.e. mounting and courtship) and aggressive behaviours (i.e. supplant, peck and chase). The rarest behaviours (i.e. allofeeding, courtship, mount and co-feeding) were recorded ad libitum (for all group members) during each focal observation (Altmann, 1974).

Ethogram and analysed variables

Ground and perch proximity were recorded if two individuals were located 0 to 1 m apart on the ground, and 10 to 50 cm apart on the perch, i.e. the distance at which individuals typically interact in these locations (either positively or aggressively). Contact-sit was recorded if two individuals were less than 10 cm apart on the perch. Allopreening, which helps with plumage maintenance, was defined as one subject running its beak through the feathers of another, and allofeeding as one subject actively putting a food item into the beak of another (Scheid et al., 2008). Bill twining was defined as two individuals gently clattering their beaks together, and co-feeding as two individuals feeding together at the same food source (a round platform measuring 1m in diameter).

In the analysis, given that birds needed to be either in proximity or in contact-sit to allofeed, allopreen or co-feed, we only considered proximities and contact-sit during which no allofeeding, allopreening or co-feeding occurred, so that all proximities and affiliations were mutually exclusives. The durations of spatial proximities and contact-sit were strongly correlated to their frequencies for each of the three years (For all: Dietz R-test $p < 0.001$, Matrix rank correlation > 0.95; performed in Socprog 2.5 for 10000 permutations), so only analyses based on the frequency were reported. Given that they were functionally equivalent behaviours, we grouped together all agonistic behaviours in one variable named 'aggression' (applying the same weighting to each behaviour). Considering the small amount of bill-twining events recorded, bill-twining and allopreening, which are both assumed to strengthen the relationship (Seed et al., 2007), were also grouped together as one variable named 'allopreening' (bill twining behaviour was more scarce, i.e. 1 bill twining for 8 allopreening).

Data analysis

Identifying and categorizing relationships

To categorize the relationships between all the individuals, we considered all potential dyads for each year (2012: 55; 2014: 91; 2015: 66). As the strength of a relationship depends on the type and frequency of interactions, we constructed a sociality index following Silk et al. (2006a), using spatial proximities (i.e. ground proximity: GP and perch proximity: PP) and affiliations (i.e. contact-sit: CS, allofeeding: Fe, allopreening: Pr) as follow:

$$\mathrm{Sij,year} = \frac{((\mathrm{GPij} / \mathrm{GP}) + (\mathrm{PPij} / \mathrm{PP}) + (\mathrm{CSij} / \mathrm{CS}) + (\mathrm{Feij} / \mathrm{Fe}) + (\mathrm{Prij} / \mathrm{Pr}))}{5} \times 100$$

With GPij, the dyadic frequency of ground proximity for dyad ij, divided by GP, which equals to the overall mean frequency of ground proximity for all possible dyads (and similarly for the other variables: PP, CS, Fe, and Pr). The denominator is fixed, and refers to the number of variables. Note that the variables used in the index were all positively correlated (For all: Spearman correlation test $p < 0.05$). The value of the sociality index increases with the strength of a relationship (Silk et al., 2006a).

We first checked that relationships differed on the basis of their strength. We did so by verifying that in each year, the cumulative distribution of the sociality indices followed a power function and not a linear function, which would indicate that some relationships were stronger than others (Clauset et al., 2009). Then, for each year, we used the 'breakpoint' method (function CE.NB in R package breakpoint v.1.1; Priyadarshana & Sofronov, 2015) to estimate and locate the point, or threshold value, from which the cumulative distribution turned from linear to power, indicating that the strength of relationships changed. This split the cumulative distributions into two parts, allowing to isolate the few stronger relationships located in the tail of the distribution. All dyads located before the breakpoint were then considered as *weak relationships*. For those located after, we distinguished: i) the *primary relationships*, representing the strongest relationships for both partners; ii) and the *secondary relationships*, in case one or both partners were already involved in another stronger relationship.

Characterisation of the relationships

Pattern of interaction

We first investigated whether the relationships were characterised by different mixes of behaviours (i.e. considering the relative proportions of spatial proximities and affiliations), using a generalised mixed model adapted for proportions with a binomial distribution and a logit link function (GLMM; function glmer and cbind in R package lme4 v.1.1-9; Bates et al., 2015). This model allowed us to compare the relative proportions of proximities and affiliations (i.e. both used in the response variable using the function 'cbind' in R package lme4 v.1.1-9), according to the category of relationship (i.e. weak, secondary or primary), the sex of the dyad (i.e. same-sex or mixed-sex), and their interaction as fixed factors. We also included the identity of the dyad nested in year as random factor, as all potential dyads changed from one year to another because of the group composition modifications (i.e. introduction and losses of individuals).

Reciprocity of interactions

We then considered the direction of the spatial proximities and the affiliations (i.e. only available in 2014 and 2015) to compute two indices of reciprocity per dyad and per year as follow (Leinfelder et al., 2001; Seyfarth, 1980):

$$Rij,\ year_{\ proximities} = 2 \times Min(Pij\ , Pji\ )/(Pij + Pji\ ) * 100$$

$$Rij,\ year_{\ affiliations} = 2 \times Min(Aij\ , Aji\ )/(Aij + Aji\ ) * 100$$

With Pij and Pji, the respective frequency of proximities initiated by individual i or j towards j or i, and similarly for the directed frequency of affiliations Aij and Aji. Both reciprocity indices vary from 0 to 100, with 100 indicating that the relationship is perfectly balanced. We used a GLMM with a Poisson distribution and a logit link function to investigate the effect of the relationship category, the sex composition of the dyad and the interaction of these two factors (as fixed factors) on the proximities and the affiliations reciprocity indices (response variable), with the identity of the dyad nested in year as random factor.

Mounting, courtship, co-feeding and aggression

We then used the same model to investigate the effect of the relationship category, the sex composition of the dyad, and the interaction of these two factors (as fixed factors) on the dyadic frequencies of interaction of four variables that were not used in the computation of the sociality index (i.e. response variables; mounting, courtship, co-feeding and aggression). Again, we used the identity of the dyad nested in year as random factor.

Reproductive status

Finally, note that all nesting dyads (i.e. dyads that built and attended a nest, including same-sex dyads that did not have any eggs), were involved in a primary relationship, except one (see results). Thus, following the previous models, for primary relationships only, we investigated whether the reproductive status of the dyad (i.e. fixed factor; nesting, non-nesting) had an impact on various response variables: i) the relative proportion of spatial proximities and affiliations using a GLMM adapted for proportions (see earlier; cbind function in R package lme4 v.1.1-9; Bates et al., 2015); ii) and the reciprocity indices for proximities and affiliations, the sociality indices (i.e. indicating the strength of the relationship) and iii) the dyadic frequencies of mounting, courtship, co-feeding and aggression behaviours; using for ii) and iii) a GLMM with a Poisson distribution and a log link function. For all models we add the identity of the dyad nested in year as random factor.

All statistics were performed in R version 3.1.3 (R Core Team, 2015), with a significance threshold set at α=0.05. We discussed results for each response variable using the estimated values of the parameters provided by the model.

Visualisation of the social structure

Social networks were built for each year on the basis of the sociality indices, using the software Gephi 0.2.8-beta (Bastian et al., 2009). In order to better describe the group structure, we computed two network properties depicting the degree of connectivity of the structure: i) the density, indicating how complete the network is - a complete network has all possible edges (i.e. connections between individuals) and a density equal to 1; ii) and the mean degree, which is the mean number of connections per node (i.e. individual) in the network (Bastian et al., 2009). We also ran a cluster analysis using a modularity-based approach (at a resolution of 1), in order to identify clusters of individuals more strongly associated with each other than with other individuals (Newman, 2004).

Ethical note

This research followed the guidelines of the Association for the Study of Animal Behaviour, and respected European and French legislation. It was approved by the regional ethical committee on animal experimentation under the license n°A67-382.

Results

Identifying and categorizing relationships

Over the three years we recorded the following events: 2331 contact-sits, 4957 perch proximities, 1350 ground proximities, 2470 allofeeding events, 788 allopreening events, and 2034 aggressions.

For each year, the cumulative distribution of sociality indices was best fitted with a power function (2012: $R^2_{power} = 0.78$, $R^2_{linear} = 0.37$; 2014: $R^2_{power} = 0.76$, $R^2_{linear} = 0.37$; 2015: $R^2_{power} = 0.64$, $R^2_{linear} = 0.32$, Figure 1). This shows that relationships were not randomly distributed. It also further indicates that some relationships had a very high level of sociality indices compared to the others, meaning that they concentrated a large proportion of the proximities and affiliations (Figure 1). We identified a total of 170 weak relationships below the breakpoint (2012: 46, 2014: 73, and 2015: 51). After the breakpoint (not included), we identified 16 primary relationships (i.e. the strongest relationship for both partners; 2012: 5, 2014: 6, and 2015: 5) and 26 secondary relationships (2012: 4, 2014: 12, and 2015: 10). Note also that 50% of the primary relationships and 54% and of the secondary relationships involved same-sex partners.

Most individuals were involved in a primary relationship (10 over 11 in 2012, 12 over 14 in 2014 and 10 over 12 in 2015), and a great number of these individuals were simultaneously

Behaviour (2016) DOI: 10.1163/1568539X-00003372

involved in one or several secondary relationships (5 over 10 in 2012, 9 over 12 in 2014 and 8 over 10 in 2015). Primary relationships always represented more than 50% of an individual total sociality index (i.e. the sum of all its sociality indices), whilst secondary relationships represented 5% to 50 %, and weak relationships always less than 5%.

Same-sex dyads occurred, and represented on average: i) 60% of the primary relationships in 2012 (sex-ratio: 9 males and 2 females), 67% in 2014 (sex-ratio: 9 males 5 females) and 20% in 2015 (sex-ratio: 8 males 4 females); ii) 25% of the secondary relationships in 2012, 67% in 2014 and 50% in 2015; and iii) 71% of the weak relationships in 2012, 47% in 2014, and 55% in 2015.

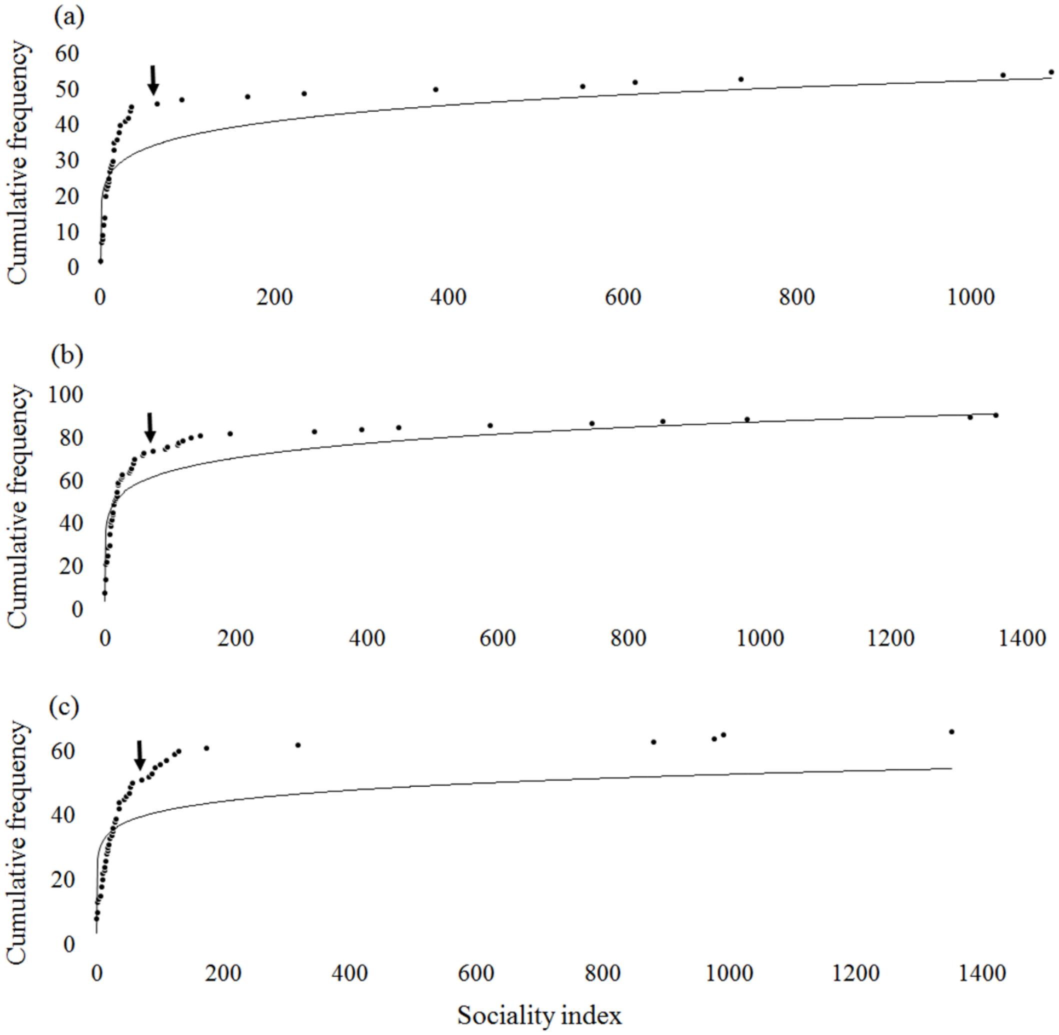


Figure 1. Cumulative distribution of the sociality indices in (a) 2012, (b) 2014, and (c) 2015. Solid lines represent the power function fitted to the distributions. Weak relationships are located before the breakpoint (indicated by an arrow), and primary and secondary relationships after it.

Characterisation of the relationships

Pattern of interaction

Primary and secondary relationships were both characterised by proximities (GP, PP) and affiliations (CS, Fe, Pr). They both significantly displayed a higher proportion of affiliations over proximities compared to weak relationships, which were almost entirely characterised by proximities (GLMMs Table 1; Figure 2). Primary and secondary relationships did not significantly differ for their relative proportion of proximities over affiliations (GLMMs Table 1; Figure 2). The sex composition of the dyad also had an effect on the relative proportions of proximities and affiliations, but this was only true of secondary relationships, in which mixed-sex dyads displayed slightly more affiliations than proximities compared to the same-sex secondary dyads (GLMMs Table 1; Figure 2).

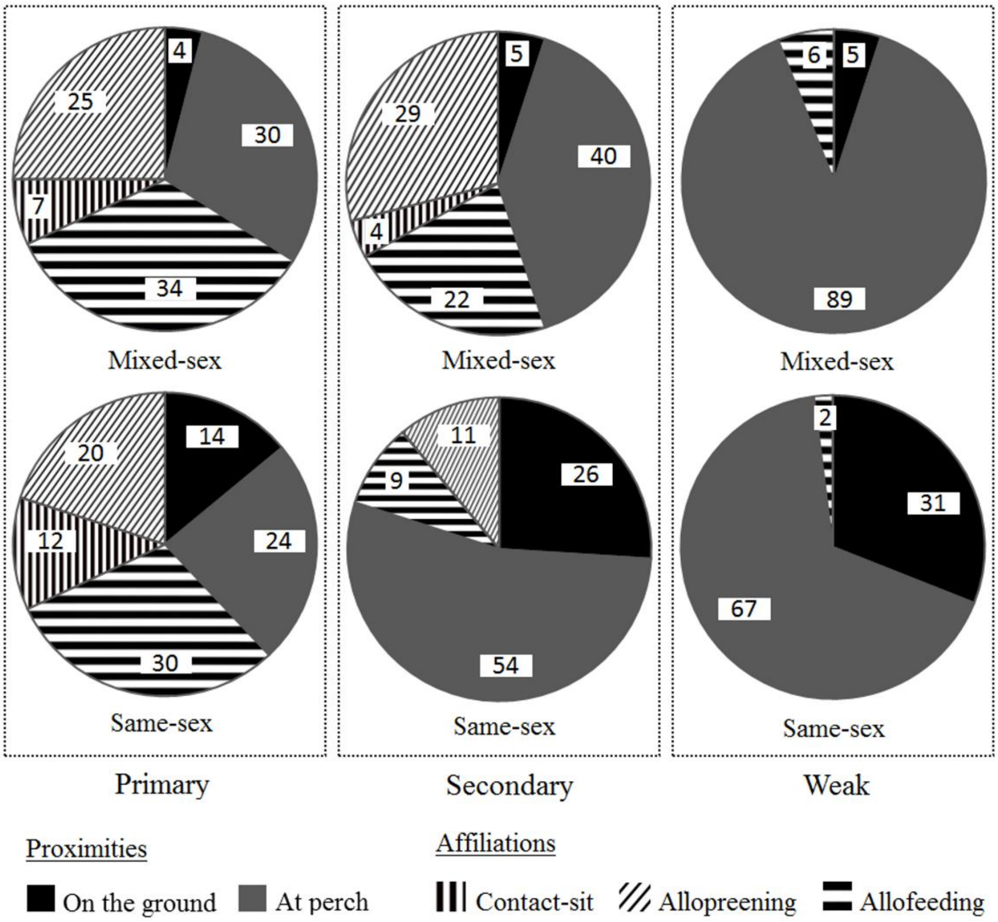


Figure 2. Relative proportions of spatial proximities (i.e. on the ground and at perch) and affiliations (i.e. contact-sit, allopreening, allofeeding) according to the relationship category (i.e. primary, secondary and weak) and the sex composition of dyad (i.e. mixed-sex, same-sex).

Reciprocity

The relationship category had no significant effect on the reciprocity of proximities (GP, PP; GLMMs Table 1). However, primary and secondary relationships showed similar level of reciprocity for affiliations, and both significantly higher compare to weak relationships (GLMMs Table 1). The sex composition of the dyad had a significant effect on the reciprocity of proximities and not affiliations, however this effect was significant when considering all dyads, but non-significant in within each category of relationship (GLMMs Table 1).

Mounting, courtship, co-feeding and aggression

Primary and secondary relationships had similar rates of all positive behaviours (i.e. mounting, courtship, co-feeding) and aggressions (GLMMs Table 2, Figure 3). Compared to weak relationships, they both had higher rates of mounting, co-feeding and aggressions, but similar rates of courtship (GLMMs Table 2, Figure 3). The sex composition of the dyad had a significant effect on the frequencies of mounting and courtship when considering all dyads, but was non-significant within each category of relationship (GLMMs Table 2). Similarly, the sex composition also had a significant effect on the frequencies of aggressions, but this was only true of weak relationships, with higher rates of aggression for same-sex dyads (GLMMs Table 2).

Response variable: Fixed variables	Estimate ± SE	Z value	P value	N	Mean values ± se
Pattern of interaction: ***(proximities, affiliations)***					
Relationship					
Secondary – Weak	-3.55 ± 0.50	-7.04	< **0.001 *****	26 – 170	(68±24, 43±27) – (11±7, 0.4±0.7)
Primary – Weak	-4.14 ± 0.57	-7.23	< **0.001 *****	16 – 170	(167±34, 276±66) – (11±7, 0.4±0.7)
Primary – Secondary	-0.59 ± 0.63	-0.91	0.61	16 – 26	(167±34, 276±66) – (68±24, 43±27)
Sex					
SS – MS	0.95 ± 0.42	2.28	< **0.05 ***	117 - 95	(28±24, 19±33) – (32±28, 36±49)
Relationship : Sex					
Weak : SS– MS	0.95 ± 0.42	2.28	0.20	95 – 75	(11±6, 0.3±0.4) – (11±8, 0.64±0.9)
Secondary : SS– MS	3.23 ± 0.64	5.05	< **0.001 *****	14 – 12	(63±18, 12±8) – (73±31, 79±30)
Primary : SS– MS	0.21 ± 0.70	0.31	0.99	8 - 8	(166±33, 246±48) – (166±37, 305±81)
Reciprocity of proximities:					
Relationship					
Secondary – Weak	1.34 ± 0.92	1.45	0.31	26 – 170	41 ± 13 – 38 ± 18
Primary – Weak	2.50 ± 1.08	2.31	0.05	16 – 170	60 ± 10 – 38 ± 18
Primary – Secondary	1.17 ± 1.33	0.88	0.65	16 – 26	60 ± 10 – 41 ± 13
Sex					
SS– MS	0.99 ± 0.48	2.05	< **0.05** *	117 - 95	47 ± 18 – 33 ± 16
Relationship : Sex					
Weak: SS– MS	0.99 ± 0.45	2.05	0.29	95 – 75	46 ± 19 – 31 ± 17
Secondary: SS– MS	0.93 ± 1.10	0.85	0.95	14 – 12	45 ± 12 – 35 ± 15
Primary: SS– MS	0.36 ± 1.51	0.24	0.99	8 - 8	73 ± 10 – 50 ± 5
Reciprocity of affiliations:					
Relationship					
Secondary – Weak	7.75 ± 1.87	4.16	< **0.001 *****	26 – 170	15 ± 14 – 3 ± 7
Primary – Weak	9.63 ± 2.15	4.48	< **0.001 *****	16 – 170	47 ± 16 – 3 ± 7
Primary – Secondary	1.88 ± 2.45	0.77	0.72	16 – 26	47 ± 16 – 15 ± 14
Sex					
SS– MS	-0.48 ± 1.3	-0.37	0.72	117 – 95	6 ± 10 – 9 ± 12
Relationship : Sex					
Weak: SS– MS	-0.48 ± 1.31	-0.37	0.99	95 - 75	1 ± 4 – 4 ± 9
Secondary: SS– MS	-4.96 ± 2.21	-2.25	0.20	14 – 12	12 ± 14 – 20 ± 14
Primary: SS– MS	-0.12 ± 2.78	-0.05	1.00	8 - 8	49 ± 20 – 46 ± 13
Mounting:					
Relationship					
Secondary – Weak	2.65 ± 0.78	3.40	< **0.01 ****	26 – 170	0.9 ± 0.8 – 0.1 ± 0.2
Primary – Weak	3.92 ± 0.88	4.47	< **0.001** ***	16 – 170	2.9 ± 1.5 – 0.1 ± 0.2
Primary – Secondary	1.26 ± 0.94	1.35	0.36	16 – 26	2.9 ± 1.5 – 0.9 ± 0.8
Sex					
SS– MS	-2.23 ± 1.12	-1.99	< **0.05** *	117 - 95	0.2 ± 0.5 – 0.6 ± 0.7
Relationship : Sex					
Weak: SS– MS	-2.23 ± 1.12	-1.99	0.30	95 – 75	0.0 ± 0.1 – 1.2 ± 0.3
Secondary: SS– MS	-1.42 ± 0.96	-1.45	0.67	14 – 12	0.4 ± 0.5 – 1.4 ± 0.9
Primary: SS– MS	-0.51 ± 0.98	-0.52	0.99	8 - 8	2.5 ± 1.6 – 3.3 ± 1.4

Courtship:					
Relationship					
Secondary – Weak	2.69 ± 1.29	2.08	0.09	26 – 170	2.9 ± 2.5 – 0.7 ± 1.3
Primary – Weak	1.83 ± 1.53	1.20	0.45	16 – 170	3.9 ± 3.3 – 0.7 ± 1.3
Primary – Secondary	-0.86 ± 1.79	-0.48	0.88	16 – 26	3.9 ± 3.3 – 2.9 ± 2.5
Sex					
SS– MS	1.55 ± 0.76	2.03	< **0.05** *	117 – 95	2.1 ± 2.3 – 0.3 ± 0.4
Relationship : Sex					
Weak: SS– MS	1.55 ± 0.76	2.03	0.30	95 - 75	1.3 ± 1.7 – 0.1 ± 0.2
Secondary: SS– MS	1.61 ± 1.53	1.06	0.89	14 – 12	4.6 ± 3.1 – 0.9 ± 0.6
Primary: SS– MS	3.76 ± 1.93	1.95	0.34	8 - 8	7 ± 4.1 – 0.8 ± 0.7
Co-feeding:					
Relationship					
Secondary – Weak	1.51 ± 0.53	2.84	< **0.05** *	26 – 170	4.3 ± 5.5 – 1.1 ± 1.0
Primary – Weak	2.62 ± 0.59	4.45	< **0.001** ***	16 – 170	11.8 ± 7.9 – 1.1 ± 1.0
Primary – Secondary	1.11 ± 0.72	1.55	0.26	16 – 26	11.8 ± 7.9 – 4.3 ± 5.5
Sex					
SS– MS	0.24 ± 0.31	0.80	0.42	117 - 95	2.1 ± 3.3 – 2.6 ± 3.3
Relationship : Sex					
Weak: SS– MS	0.24 ± 0.31	0.80	0.96	95 – 75	0.9 ± 0.7 – 1.4 ± 1.4
Secondary: SS– MS	-0.89 ± 0.63	-1.38	0.72	14 – 12	2.1 ± 1.7 – 6.8 ± 7.8
Primary: SS– MS	0.12 ± 0.79	0.16	1.00	8 - 8	15.6 ± 10.6 – 7.9 ± 3.8
Aggressions:					
Relationship					
Secondary – Weak	1.03 ± 0.27	3.78	< **0.001** ***	26 – 170	22.8 ± 14.9 – 8.5 ± 5.1
Primary – Weak	1.02 ± 0.33	3.06	< **0.01** **	16 – 170	13.3 ± 7 – 8.5 ± 5.1
Primary – Secondary	-0.02 ± 0.4	-0.04	0.99	16 – 26	13.3 ± 7 – 22.8 ± 14.9
Sex					
SS– MS	0.58 ± 0.15	3.91	< **0.001** ***	117 - 95	13 ± 9.1 – 7.6 ± 4.4
Relationship : Sex					
Weak: SS– MS	0.58 ± 0.15	3.91	< **0.01** **	95 – 75	10.7 ± 6 – 5.3 ± 2.8
Secondary: SS– MS	0.63 ± 0.33	1.93	0.36	14 – 12	29.3 ± 19 – 14.5 ± 4.9
Primary: SS– MS	-0.49 ± 0.45	-1.09	0.87	8 - 8	9.6 ± 5.4 – 17 ± 8.3

Table 1. GLMM results investigating the effect of the relationships category (i.e. weak, secondary and primary), the sex composition of the dyad (i.e. same-sex: SS, mixed-sex: MS), and their interaction as fixed factors, on several response variables: i) the pattern of interaction of the dyad (i.e. relative proportions of spatial proximities and affiliations; using the function ‘cbind’ in R package lme4 v.1.1-9); ii) the reciprocity for proximities and affiliations; iii) and the dyadic frequencies of mounting, courtship, co-feeding, and aggressions, variables that were not use to compute the social index. For all models the identity of the dyad nested in year is used as random factor. Significant p-value is shown in bold print. Response variable is in bold, fixed factor is underlined; mean percentages ± SE are also indicated. *** < 0.001, ** < 0.01, * ≤ 0.05

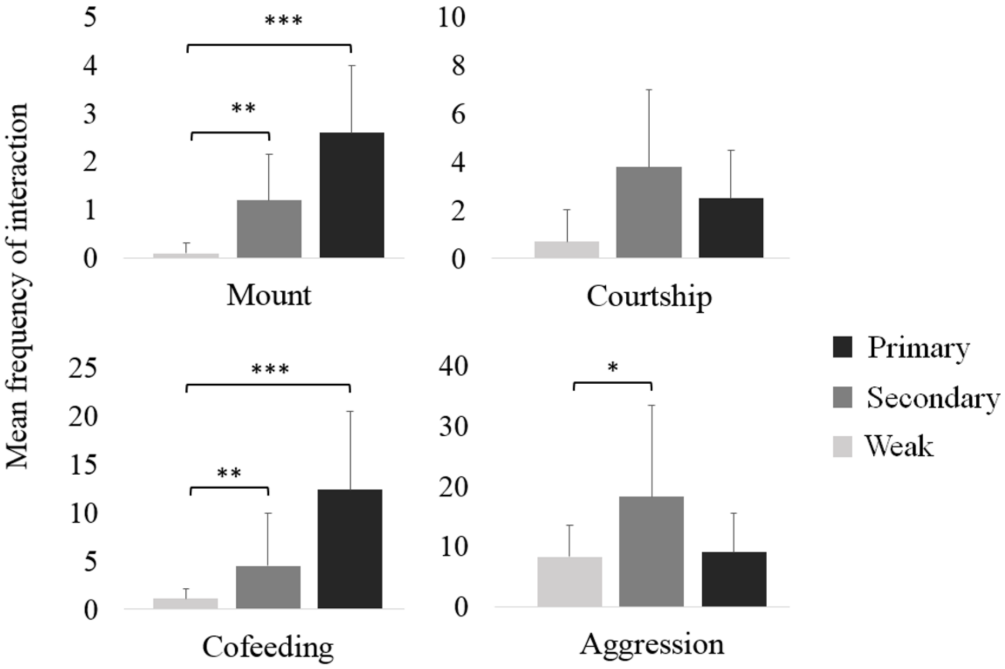


Figure 3. Effects of the relationship category on the mean dyadic frequencies of mounting, courtship, co-feeding and aggression behaviours, according to the relationship category (i.e. primary, secondary and weak) [2]. Statistics are based on the estimates given the best models, and the visual representation is based on the means SE of the data. *** < 0.001, ** < 0.01, * ≤ 0.05.

Reproductive status

All nesting dyads (i.e. dyads that built and attended a nest) were involved in a primary relationship (2012: 3 out of 5, 2014: 2 out of 6, and 2015: 3 out of 5), with the exception of one dyad involved in a secondary relationship in 2014 (k-p, which became a primary nesting dyad in 2015). All nesting dyads were mixed-sex, except one (n-z). Among the individuals involved in a nesting dyads, 4 over 6 (2012), 1 over 4 (2014) and 5 over 6 (2015) were simultaneously involved in a secondary relationship. Note that none of the nesting dyads successfully produced surviving offspring during the study (as commonly observed in captive corvids). Among primary relationships, nesting and non-nesting dyads showed similar proportions of proximities over affiliations (i.e. both with a higher proportion of affiliations compare to proximities), and similar values of sociality index, courtship, co-feeding and

---

[2] Mean frequency per year (i.e. data collected between January and early June in 2012, 2014 and 2015).

aggression (GLMMs Table 2). Nesting dyads only differed from non-nesting dyads by higher rates of mounting behaviour (GLMMs Table 2).

Response variables:	Estimate ± SE	Z value	P value	N	Mean values ± SE
Pattern of interaction: ***(proximities, affiliations)***					
Nesting – Non-nesting	-0.08 ± 0.18	-0.47	0.63	8 – 8	(173±27, 318±63) – (23±37, 13±60)
Reciprocity of proximities:					
Nesting – Non-nesting	-0.42 ± 0.13	-3.14	**< 0.01 ****	8 – 8	40.5 ± 5.6 – 40 ± 8.7
Reciprocity of affiliations:					
Nesting – Non-nesting	-0.02 ± 0.43	-0.04	0.97	8 – 8	36.8 ± 6.9 – 6.3 ± 21.3
Sociality index:					
Nesting – Non-nesting	0.20 ± 0.27	0.73	0.46	8 – 8	880 ± 129 – 835 ± 204
Mounting:					
Nesting – Non-nesting	1.48 ± 0.55	2.69	**< 0.01 ****	8 – 8	4.5 ± 1.3 – 1.3 ± 1.2
Courtship:					
Nesting – Non-nesting	-0.90 ± 1.18	-0.76	0.45	8 – 8	1.8 ± 1.3 – 6 ± 4.4
Co-feeding:					
Nesting – Non-nesting	0.19 ± 1.00	0.19	0.85	8 – 8	11.4 ± 8.3 – 12.1 ± 8.1
Aggression:					
Nesting – Non-nesting	0.04 ± 0.57	0.06	0.95	8 – 8	15.3 ± 9.3 – 11.8 ± 5.2

Table 2. GLMMs results for models on primary relationships only, investigating the effect of the breeding status of the dyad as fixed factor (i.e. nesting, non-nesting) on several response variables: i) the pattern of interaction of the dyad (i.e. relative proportions of spatial proximities and affiliations); ii) the dyadic indices of reciprocity for proximities and affiliations; iii) and the dyadic frequencies of mounting, courtship, co-feeding, and aggressions, variables that were not use to compute the social index. For all models the identity of the dyad nested in year is used as random factor. Significant p-value is shown in bold print. Mean percentages ± SE are also indicated. *** < 0.001, ** < 0.01, * ≤ 0.05

Visualisation of the social structure

The networks were built for primary and secondary relationships only. Without the weak relationships, the network densities were close to 20% (2012: 0.16, 2014: 0.20, and 2015: 0.23; Figure 4), and the mean degree indicated that individuals were on average connected to 15 %, 19 % and 21 % of all potential partners (2012: 1.6, 2014: 2.6 and 2015: 2.5; Figure 4) [3]. Clusters were comprised of a maximum of five individuals more strongly

---

[3] Connected: involved either in a primary or a secondary relationship

associated with each other than with other individuals (in 2015; Figure 4). All clusters contained at least one or two primary relationships, sometimes connected with other individuals. It is noteworthy that pairs tended to be more isolated (i.e. alone in their own cluster) under stable conditions (in 2012, before the addition of new individuals to the group; Figure 4).

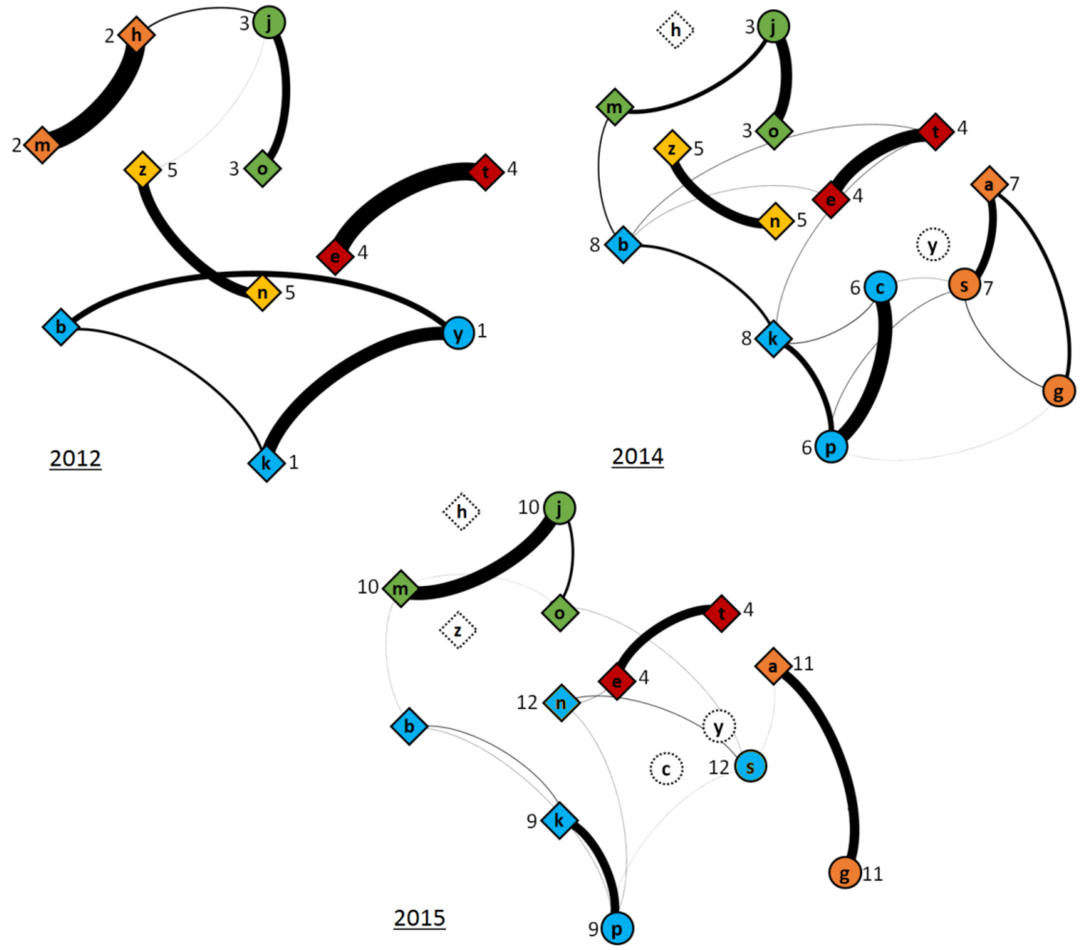


Figure 4. Social networks based on the sociality indices of primary and secondary relationships. Nodes represent individuals, and the thickness of the lines indicates the strength of the relationship (i.e. thicker lines for higher sociality index).

Diamonds indicates males and circles females. Nodes that belong to the same cluster have the same colour, and primary relationships are indicated by identical numbers. Doted nodes indicate lost individuals. In 2012, all primary relationships were established since several years (at least four years; personal observations). Among primary relationships: i) only one lasted throughout the entire study (e-t); ii) three terminated due to the disappearance of a former partner (k-y and h-m in 2012; n-z in 2014); iii) three separated as the consequence of a partner leaving for a new relationship (c-p, -a-s, j-o in 2014, all mixed-sex dyads). Note that three secondary relationships established in 2014 (k-p, a-g, j-m), turned into primary relationship in 2015.

Discussion

In this study, we investigated the social relationships in a group of captive adult rooks, and in particular the possibility of extra-pair and same-sex social relationships. Computing social indices to characterise the strength of all potential relationships, we found that a few were stronger than others. According to the distribution of the social indices, we distinguished three categories of social relationships: primary, secondary, and weak relationships. Crucially, spatial proximities, affiliations, co-feeding and sexual behaviours were not restricted to primary relationships, and secondary relationships were clearly recognizable. In addition, same-sex dyads occurred, even for primary relationships. In all categories, same-sex dyads behaved exactly like mixed-sex dyads, except for a lower rates of affiliations in secondary relationships and a higher rate of aggression in weak relationships. All but one nesting dyads were mixed-sex and were involved in a primary relationship. Primary (core unit) and secondary relationships formed the backbone of the social structure, forming a composite network of pairs and subgroups.

When investigating social bonding in monogamous birds, studies traditionally focus on the mated pair, which is by far the strongest social unit in monogamous birds (Dunbar & Shultz, 2007). In lifelong pair-bonding species like rooks, reproductive partners show complex affiliative interactions throughout the year (Emery et al., 2007). In such species, the mated pair is thus often likened to the longterm alliance seen in complex social species like primates or dolphins (Clayton & Emery, 2007). In this study, the strongest relationships (primary relationships) showed the highest levels of spatial proximities (on the ground, at perch), and affiliations (contact-sit, allofeeding, and allopreening). In addition, nearly all dyads that were building and attending a nest were involved in a primary relationship. Although some primary dyads did not attempt to breed (as may be expected under captive conditions), the reproductive status had no significant impact on the social value of the relationships. With the exception of a lower mounting rate and a decrease reciprocity for spatial proximities, all primary dyads behaved similarly. They interacted more frequently through affiliations than proximities, displayed the same level of reciprocity for affiliations, and showed similar proportions of courtship, co-feeding and aggressions. In addition, both increase of mounting rate and decrease of proximities reciprocity are very consistent with the reproductive status and its inherent constraints (i.e. males initiate most contacts when females incubates the eggs). All primary relationships thus correspond well to dyads commonly characterized as pairs (Jolles et al., 2013; Bird & Emery, 2008; Emery et al., 2007).

Given the strength of the pair bond in rooks, proximities and affiliations could be expected to be exclusive to the mated partners in adults (Jolles et al., 2013; Emery et al., 2007). However, they also occurred outside the pairs. Although individuals interacted primarily within their pair (i.e. primary relationship), they also interact through substantial levels of all proximities and affiliations with secondary partners, outside the pair. Secondary partners also showed similar level of reciprocity for proximities and affiliations to those of pairs, and similar levels of mounting, courtship and co-feeding behaviours. In addition, mixed-sex secondary partners behaved like pairs, interacting slightly more often through affiliations than proximities. Globally, this shows that extra-pair relationships in adult rooks can correspond to strong affiliative bonds. The occurrence of aggression in both pairs and secondary relationships may thus seem surprising, as valuable partners should seek to avoid aggression in order to preserve the relationship and all the resulting advantages (Clayton & Emery, 2007; Fraser & Bugnyar, 2010). Yet aggression between affiliates could be explained by the time the individuals spend in proximity. Frequent associations indeed expose individuals to higher chances of aggression, as noted in other social species (*Macaca fuscata*: Soltis et al., 1997; *Macaca mulatta*: Bernstein et al., 1993).

Most of the paired partners (i.e. involved in a primary relationship) were simultaneously involved in secondary relationships, whether they tried or not to access to reproduction (i.e. nesting or non-nesting). One possible explanation for the occurrence of extra-pair bonds in adults, is that some of them could be pairs in the making. Indeed, the modifications of the group composition resulted in new partner opportunities (due to the introduction and loss of individuals), and as expected, some pairs separated and new ones were formed. After the group modifications, the proportion of secondary relationships increased. More interestingly, some of the mixed-sex secondary relationships became pairs in the following year, resulting in an increase of the proportion of same-sex pairs in 2015. In addition, as indicated earlier, mixed-sex secondary partners behaved like pairs (i.e. more affiliations than proximities), interacting, even, through sexual behaviours. However, in juvenile corvids, affiliations and in particular allofeeding, are considered as essential behaviours for pair bond formation (Emery et al., 2007; Scheid et al., 2008; von Bayern et al., 2007). Similarly, it has been suggested that extra-pair copulation facilitates mate switching (e.g. in cockatiels, *Nymphicus hollandicus*: Spoon et al., 2007). Following this in adult rooks, extra-pair affiliations and sexual behaviours may have facilitated mate switching and the formation of new pair bonds in adults (Emery et al., 2007; Scheid et al., 2008; von Bayern et al., 2007). In adults, extra-pair relationships could then be a strategy to search for and to evaluate potential new partners. Further investigations are now necessary to better understand the mechanisms involved in mate switching in adult rooks.

It should be underlined that the subject of this study are captive birds. It could be argued that the captive set up may have enhanced the probabilities of interactions between birds. If true, almost all birds should have been linked by secondary relationships. However, this was not the case as secondary relationships made up a small part of all the dyadic relationships in the group. This was true in all three years, despite the modifications of the group composition, and despite the addition of wild adult individuals. This highlights that rooks did not randomly associate and interact, but instead actively chose their social partners. This further indicates that the extra-pair bonding did not result from the space limitation inherent to the captive set up. Another limitation due to the captive set up is the unbalanced sex-ratio, which is likely to have facilitated the formation of same-sex social bonds. Indeed same-sex bonds can occur when opposite sex partners are not available (as described in greylag geese, *Anser anser*: Kotrschal et al., 2006). However, in our study, even if they had no hope of successful breeding, same-sex pairs had similar social value compared to mixed-sex pairs. They also behaved similarly (i.e. more affiliations than proximities), and displayed similar levels of mounting, courtship, co-feeding, and aggressions. In addition, male-male pairs did not split up in favour of the newly introduced females. In fact, only one of the 4 established male-male pairs separated (b-k) whilst two mixed-sex pairs did so. Thus, it indicates that the unbalanced sex ratio is not the sole explanation for good relationship between same-sex partners in rooks. These results are consistent with previous findings in juveniles rooks, which form bonds long before the first reproduction attempt (Emery et al., 2007), and not necessarily with opposite sex partners (Emery et al., 2007; Jolles et al., 2013; Scheid et al., 2008). In captive ravens, it was also found that male-male relationships were as compatible and as secure as mixed-sex relationships (Fraser & Bugnyar, 2010). In wild non-breeder ravens, male-male affiliations were also found, even if rare. Similarly in captive zebra finches (*Taeniopygia guttata*), same-sex and mixed-sex pair bonds have equivalent quality and stability (Elie et al., 2011). Besides from reproductive motivations, it suggests that affinity could also play a role in sustaining bonding in monogamous captive species.

Adult rooks ability to form and maintain several social bonds, is not surprising given that they are colonial birds (Benchley, 1986; Swingland, 1977). Coloniality involves dealing with social and environmental challenges such as competition for nest sites or resources. Interactions with nesting neighbours can have major influence on breeding success (Lewis et al., 2007), and conflicts often lead to breeding failure (Jovani & Grimm, 2008). Rooks are depicted as a highly tolerant species regarding nest proximity (Kasprzykowski, 2008). Yet, beyond this tolerance, their additional capacity in forming several strong social bond could provide some advantages: cooperative nest surveillance against predators or non-affiliated individuals (Arroyo et al., 2001; Erwin, 1979), avoidance of theft of nest material or eggs pilfering (Carrascal et al., 1995; Ogilvie, 1951), breeding synchrony with neighbours (Jovani & Grimm, 2008), thermoregulation grouping (Zitterbart et al., 2011), or the reduction of the stress and the prevention of fights (Lewis et al., 2007). By creating a safer breeding environment, multiple bonding may therefore increase individual fitness (Jovani & Grimm, 2008), as suggested in a growing number of studies in a wide range of social species (in mammals: Silk et al., 2010; Cameron et al., 2009; Schülke et al., 2010; and in birds: Oh & Badyaev, 2010; Ryder et al., 2008). More broadly, rooks ability to bond with several social partners suggests that their colonies might be more than just an aggregation of pairs, and should therefore be acknowledged as a multilevel social structure.

In this study, the captive set up allowed us to scrutinise the social interactions of adult rooks, providing focused observations of individual's social patterns. Such detailed observations are virtually impossible in the wild. The results highlight adult ability to bond with several partners, and indicate that a flock of rooks is a complex social unit that goes beyond an aggregation of pairs. Although future studies in wild conditions are now needed to confirm the results, this raises intriguing questions about corvids society. In particular, they underline the importance of considering extra-pair interactions in corvids and more broadly in longterm monogamous species.

Acknowledgements

We would like to thank B. Thierry and V. Viblanc for their valuable help with the manuscript. We are also grateful to E. Rojas and N. Rebout for statistical advices.

References

Altmann, J. (1974). Observational study of behavior: sampling methods. — Behaviour 49: 227-266.

Aplin, L.M., Farine, D.R., Morand-Ferron, J., Cole, E.F., Cockburn, A. & Sheldon, B.C. (2013). Individual personalities predict social behaviour in wild networks of great tits (Parus major). — Ecol. Lett. 16: 1365-1372.

Archie, E.A., Tung, J., Clark, M., Altmann, J. & Alberts, S.C. (2014). Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. — Proc. Roy. Soc. Lond. B: Biol. Sci. 281: 20141261.

Arnold, K.E. (2000). Group mobbing behaviour and nest defence in a cooperatively breeding Australian bird. — Ethology 106: 385-393.

Arroyo, B., Mougeot, F. & Bretagnolle, V. (2001). Colonial breeding and nest defence in Montagu's harrier (Circus pygargus). — Behav. Ecol. Sociobiol. 50: 109-115.

Bastian, M., Heymann, S. & Jacomy, M. (2009). Gephi: an open source software for exploring and manipulating networks. — ICWSM 8: 361-362.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). lme4: linear mixed-effects models using Eigen and S4. R package, version 1(7). — R Foundation for Statistical Computing, Vienna.

Benchley, A. (1986). The breeding distribution and abundance of the rook (Corvus frugile- gus L.) in Great Britain since the 1920's. — J. Zool. Lond. 210: 261-278.

Berghänel, A., Ostner, J., Schröder, U. & Schülke, O. (2011). Social bonds predict future cooperation in male Barbary macaques, Macaca sylvanus. — Anim. Behav. 81: 1109- 1116.

Bernstein, I.S., Judge, P.G. & Ruehlmann, T.E. (1993). Kinship, association, and social rela- tionships in rhesus monkeys (Macaca mulatta). — Am. J. Primatol. 31: 41-53.

Bird, C.D. & Emery, N.J. (2008). Using video playback to investigate the social preferences of rooks, Corvus frugilegus. — Anim. Behav. 76: 679-687.

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

Boeckle, M. & Bugnyar, T. (2012). Long-term memory for affiliates in ravens. — Curr. Biol.

22: 801-806.

Bond, A.B., Kamil, A.C. & Balda, R.P. (2003). Social complexity and transitive inference in corvids. — Anim. Behav. 65: 479-487.

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

Brosset, A. (1978). Social organization and nest-building in the forest weaver birds of the genus Malimbus (Ploceinae). — Ibis 120: 27-37.

Bugnyar, T. & Heinrich, B. (2006). Pilfering ravens, Corvus corax, adjust their behaviour to social context and identity of competitors. — Anim. Cogn. 9: 369-376.

Bugnyar, T., Schwab, C., Schloegl, C., Kotrschal, K. & Heinrich, B. (2007). Ravens judge competitors through experience with play caching. — Curr. Biol. 17: 1804-1808.

Cameron, E.Z., Setsaas, T.H. & Linklater, W.L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. — Proc. Natl. Acad. Sci. USA 106: 13850-13853.

Carlisle, T.R. & Zahavi, A. (1986). Helping at the nest, allofeeding and social status in immature Arabian babblers. — Behav. Ecol. Sociobiol. 18: 339-351.

Carrascal, L.M., Moreno, J. & Amat, J.A. (1995). Nest maintenance and stone theft in the chinstrap penguin (Pygoscelis antarctica). — Polar Biol. 15: 541-545.

Clauset, A., Shalizi, C.R. & Newman, M.E. (2009). Power-law distributions in empirical data.

— SIAM Rev. 51: 661. doi:10.1137/070710111

Clayton, N.S. & Emery, N.J. (2007). The social life of corvids. — Curr. Biol. 17: R652-R656.

Clutton-Brock, T. (1991). The evolution of parental care. — Princeton University Press, Princeton, NJ.

Cockburn, A. (2006). Prevalence of different modes of parental care in birds. — Proc. Roy.

Soc. Lond. B: Biol. Sci. 273: 1375-1383.

Connor, R.C., Heithaus, M.R. & Barre, L.M. (2001). Complex social structure, alliance stabil- ity and mating access in a bottlenose dolphin “super-alliance”. — Proc. Roy. Soc. Lond. B: Biol. Sci. 268: 263-267.

de Kort, S.R., Emery, N.J. & Clayton, N.S. (2006). Food sharing in jackdaws, Corvus mon- edula: what, why and with whom? — Anim. Behav. 72: 297-304.

de Kort, S.R., Emery, N.J. & Clayton, N.S. (2003). Food offering in jackdaws (Corvus mon- edula). — Naturwissenschaften 90: 238-240.

de Villiers, M.S., Richardson, P.R.K. & van Jaarsveld, A.S. (2003). Patterns of coalition formation and spatial association in a social carnivore, the African wild dog (Lycaon pictus). — J. Zool. 260: 377-389.

Dunbar, R.I.M. (2012). Bridging the bonding gap: the transition from primates to humans. — Philos. Trans. Roy. Soc. Lond. B: Biol. Sci. 367: 1837-1846.

Dunbar, R.I.M. (1998). The social brain hypothesis. — Evol. Anthropol. 6: 178-190.

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

DuVal, E.H. (2007a). Adaptive advantages of cooperative courtship for subordinate male lance-tailed manakins. — Am. Nat. 169: 423-432. DOI:10.1086/512137.

DuVal, E.H. (2007b). Social organization and variation in cooperative alliances among male lance-tailed manakins. — Anim. Behav. 73: 391-401.

Elie, J.E., Mathevon, N. & Vignal, C. (2011). Same-sex pair-bonds are equivalent to male– female bonds in a life-long socially monogamous songbird. — Behav. Ecol. Sociobiol. 65: 2197-2208.

Emery, N.J. (2004). Are corvids “feathered apes”? — Comp. Anal. Minds 181: e213.

Emery, N.J. & Clayton, N.S. (2004). The mentality of crows: convergent evolution of intelli- gence in corvids and apes. — Science 306: 1903-1907.

Emery, N.J., Seed, A.M., von Bayern, A.M.P. & Clayton, N.S. (2007). Cognitive adaptations of social bonding in birds. — Philos. Trans. Roy. Soc. Lond. B: Biol. Sci. 362: 489-505.

Erwin, R.M. (1979). Species interactions in a mixed colony of common terns (Sterna hirundo) and black skimmers (Rynchops niger). — Anim. Behav. 27: 1054-1062.

Fraser, O.N. & Bugnyar, T. (2012). Reciprocity of agonistic support in ravens. — Anim.

Behav. 83: 171-177.

Fraser, O.N. & Bugnyar, T. (2010). The quality of social relationships in ravens. — Anim.

Behav. 79: 927-933.

Frère, C.H., Krützen, M., Mann, J., Connor, R.C., Bejder, L. & Sherwin, W.B. (2010). Social and genetic interactions drive fitness variation in a free-living dolphin population. — Proc. Natl. Acad. Sci. USA 107: 19949-19954.

Gaston, A.J. (1977). Social behaviour within groups of jungle babblers (Turdoides striatus). — Anim. Behav. 25: 828-848.

Goodwin, D. (1955). Some observations on the reproductive behaviour of rooks. — Br. Birds 48: 97-107.

Hatchwell, B.J. (2009). The evolution of cooperative breeding in birds: kinship, dispersal and life history. — Philos. Trans. Roy. Soc. Lond. B: Biol. Sci. 364: 3217-3227.

Hinde, R.A. (1976). Interactions, relationships and social structure. — Man 11: 1-17.

Hunt, G.R. & Gray, R.D. (2003). Diversification and cumulative evolution in New Caledonian crow tool manufacture. — Proc. Roy. Soc. Lond. B: Biol. Sci. 270: 867-874.

Jolles, J.W., Ostojic´, L. & Clayton, N.S. (2013). Dominance, pair bonds and boldness deter- mine social-foraging tactics in rooks, Corvus frugilegus. — Anim. Behav. 85: 1261-1269.

Jovani, R. & Grimm, V. (2008). Breeding synchrony in colonial birds: from local stress to global harmony. — Proc. Roy. Soc. Lond. B: Biol. Sci. 275: 1557-1563.

Kasprzykowski, Z. (2008). Nest location within the tree and breeding parameters of rooks Corvus frugilegus. — Bird Stud. 55: 59-65.

Kotrschal, K., Hemetsberger, J. & Weiß, B.M. (2006). Making the best of a bad situation: homosociality in greylag geese. — In: Homosexual behaviour in animals: an evolutionary perspective (Sommer, V. & Vasey, P.L., eds). Cambridge University Press, New York, NY, p. 45-76.

Lehmann, J., Korstjens, A.H. & Dunbar, R.I.M. (2007). Group size, grooming and social cohesion in primates. — Anim. Behav. 74: 1617-1629.

Leinfelder, I., de Vries, H., Deleu, R. & Nelissen, M. (2001). Rank and grooming reciprocity among females in a mixed-sex group of captive hamadryas baboons. — Am. J. Primatol. 55: 25-42.

Lewis, S., Roberts, G., Harris, M.P., Prigmore, C. & Wanless, S. (2007). Fitness increases with partner and neighbour allopreening. — Biol. Lett. 3: 386-389.

Lusseau, D. (2003). The emergent properties of a dolphin social network. — Proc. Roy. Soc. Lond. B: Biol. Sci. 270(Suppl. 2): S186-S188.

Lusseau, D. & Newman, M.E.J. (2004). Identifying the role that animals play in their social networks. — Proc. Roy. Soc. Lond. B: Biol. Sci. 271(Suppl. 6): S477-S481.

Mikolasch, S., Kotrschal, K. & Schloegl, C. (2013). Transitive inference in jackdaws (Corvus monedula). — Behav. Process. 92: 113-117.

Newman, M.E.J. (2004). Analysis of weighted networks. — Phys. Rev. E 70: 056131. Ogilvie, C.M. (1951). The building of a rookery. — Br. Birds 44: 1-5.

Oh, K.P. & Badyaev, A.V. (2010). Structure of social networks in a passerine bird: conse- quences for sexual selection and the evolution of mating strategies. — Am. Nat. 176: E80-E89.

Palagi, E. & Cordoni, G. (2009). Postconflict third-party affiliation in Canis lupus: do wolves share similarities with the great apes? — Anim. Behav. 78: 979-986.

Priyadarshana, W.J.R.M. & Sofronov, G. (2015). Multiple break-points detection in array CGH data via the cross-entropy method. — IEEE/ACM Trans. Comput. Biol. Bioinf. 12: 487-498.

R Core Team (2015). R: a language and environment for statistical computing. — R Founda- tion for Statistical Computing, Vienna, available online at http://www.R-project.org.

Radford, A.N. & Fawcett, T.W. (2014). Conflict between groups promotes later defense of a critical resource in a cooperatively breeding bird. — Curr. Biol. 24: 2935-2939.

Richardson, S.C., Patterson, I.J. & Dunnet, G.M. (1979). Fluctuations in colony size in the rook, Corvus frugilegus. — J. Anim. Ecol. 48: 103-110.

Ridley, A.R., Nelson-Flower, M.J. & Thompson, A.M. (2013). Is sentinel behaviour safe? An experimental investigation. — Anim. Behav. 85: 137-142.

Riehl, C. & Jara, L. (2009). Natural history and reproductive biology of the communally breeding greater ani (Crotophaga major) at Gatún Lake, Panama. — Wilson J. Ornithol. 121: 679-687.

Roell, A. & Bossema, I. (1982). A comparison of nest defence by jackdaws, rooks, magpies and crows. — Behav. Ecol. Sociobiol. 11: 1-6.

Røskaft, E. & Espmark, Y. (1984). Sibling recognition in the rook (Corvus frugilegus). — Behav. Process. 9: 223-230.

Rutz, C., Burns, Z.T., James, R., Ismar, S.M., Burt, J., Otis, B., Bowen, J. & St Clair, J.J. (2012). Automated mapping of social networks in wild birds. — Curr. Biol. 22: R669- R671.

Ryder, T.B., McDonald, D.B., Blake, J.G., Parker, P.G. & Loiselle, B.A. (2008). Social networks in the lek-mating wire-tailed manakin (Pipra filicauda). — Proc. Roy. Soc. Lond. B: Biol. Sci. 275: 1367-1374.

Scheid, C., Schmidt, J. & Noë, R. (2008). Distinct patterns of food offering and co-feeding in rooks. — Anim. Behav. 76: 1701-1707.

Schülke, O., Bhagavatula, J., Vigilant, L. & Ostner, J. (2010). Social bonds enhance repro- ductive success in male macaques. — Curr. Biol. 20: 2207-2210.

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

Seibert, L.M. & Crowell-Davis, S.L. (2001). Gender effects on aggression, dominance rank, and affiliative behaviors in a flock of captive adult cockatiels (Nymphicus hollandicus). — Appl. Anim. Behav. Sci. 71: 155-170.

Seyfarth, R.M. (1980). The distribution of grooming and related behaviours among adult female vervet monkeys. — Anim. Behav. 28: 798-813.

Shultz, S. & Dunbar, R.I.M. (2010a). Bondedness and sociality. — Behaviour 147: 775-803.

Shultz, S. & Dunbar, R.I.M. (2010b). Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment. — Biol. J. Linn. Soc. 100: 111-123.

Silk, J.B. (2007). Social components of fitness in primate groups. — Science 317: 1347-1351.

Silk, J.B., Altmann, J. & Alberts, S.C. (2006a). Social relationships among adult female baboons (Papio cynocephalus) I. Variation in the strength of social bonds. — Behav. Ecol. Sociobiol. 61: 183-195.

Silk, J.B., Alberts, S.C. & Altmann, J. (2006b). Social relationships among adult female baboons (Papio cynocephalus) II. Variation in the quality and stability of social bonds. — Behav. Ecol. Sociobiol. 61: 197-204.

Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M. & Cheney, D.L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. — Curr. Biol. 20: 1359-1361.

Soltis, J., Mitsunaga, F., Shimizu, K., Yanagihara, Y. & Nozaki, M. (1997). Sexual selection in Japanese macaques I: female mate choice or male sexual coercion? — Anim. Behav. 54: 725-736.

Spoon, T.R., Millam, J.R. & Owings, D.H. (2007). Behavioural compatibility, extrapair copulation and mate switching in a socially monogamous parrot. — Anim. Behav. 73: 815-824.

Spoon, T.R., Millam, J.R. & Owings, D.H. (2006). The importance of mate behavioural compatibility in parenting and reproductive success by cockatiels, Nymphicus hollandicus. — Anim. Behav. 71: 315-326.

Stulp, G., Emery, N.J., Verhulst, S. & Clayton, N.S. (2009). Western scrub-jays conceal auditory information when competitors can hear but cannot see. — Biol. Lett. 5: 583- 585.

Sueur, C., Jacobs, A., Amblard, F., Petit, O. & King, A.J. (2011). How can social network analysis improve the study of primate behavior? — Am. J. Primatol. 73: 703-719.

Swingland, I.R. (1977). The social and spatial organization of winter communal roosting in rooks (Corvus frugilegus). — J. Zool. Lond. 182: 509-528.

Thierry, B., Gauthier, C. & Peignot, P. (1990). Social grooming in Tonkean macaques (Macaca tonkeana). — Int. J. Primatol. 11: 357-375.

Tornick, J.K., Gibson, B.M., Kispert, D. & Wilkinson, M. (2011). Clark's nutcrackers (Nu- cifraga columbiana) use gestures to identify the location of hidden food. — Anim. Cogn. 14: 117-125.

Van De Pol, M., Heg, D., Bruinzeel, L.W., Kuijper, B. & Verhulst, S. (2006). Experimental evidence for a causal effect of pair-bond duration on reproductive performance in oyster- catchers (Haematopus ostralegus). — Behav. Ecol. 17: 982-991.

von Bayern, A., de Kort, S., Clayton, N.S. & Emery, N.J. (2007). The role of food- and object- sharing in the development of social bonds in juvenile jackdaws (Corvus monedula). — Behaviour 144: 711-733.

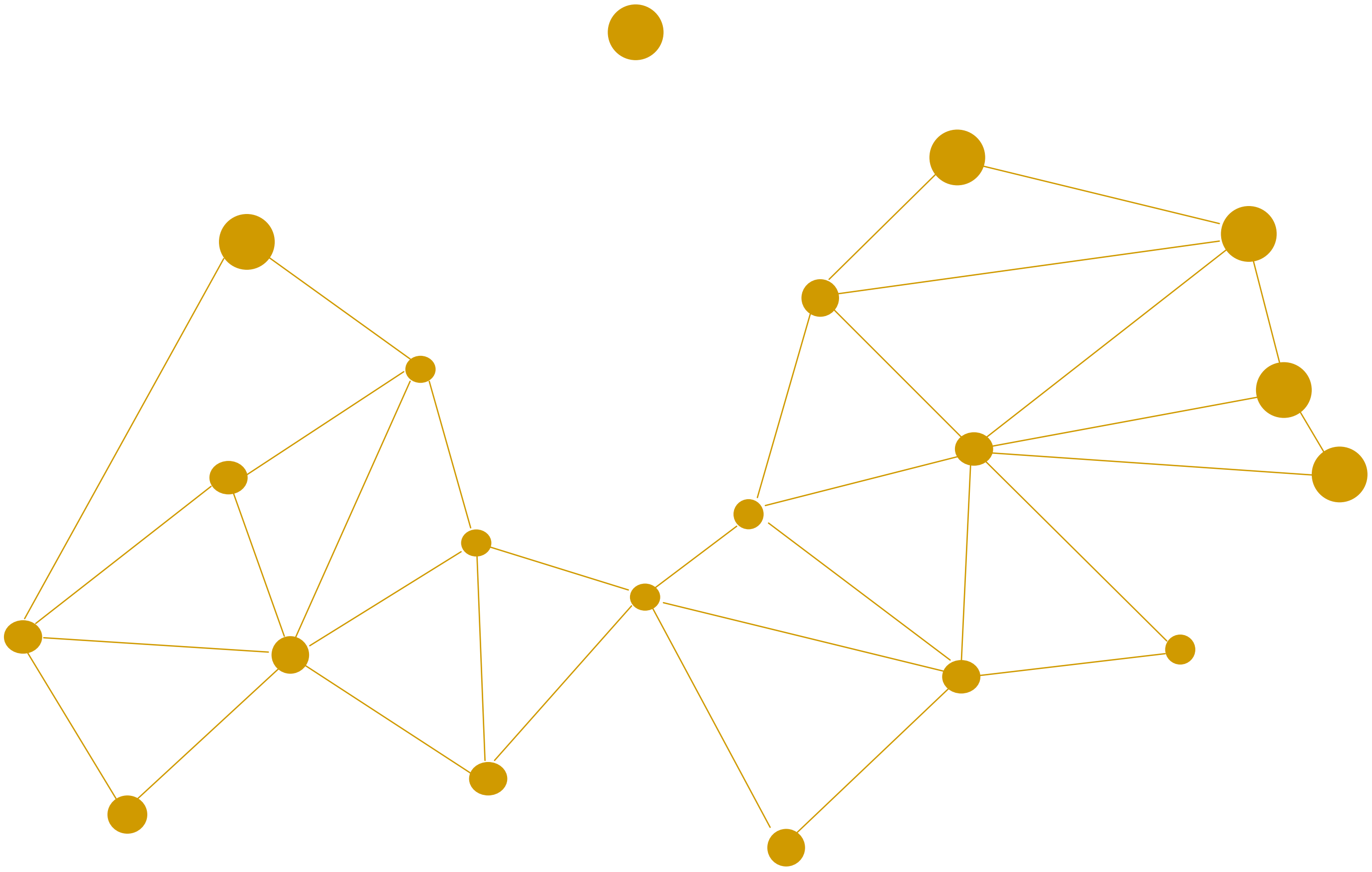
Wascher, C.A., Valdez, J.W., Cebrián, C.N., Baglione, V. & Canestrari, D. (2014). Social factors modulating attention patterns in carrion crows. — Behaviour 151: 555-572.

Wey, T., Blumstein, D.T., Shen, W. & Jordán, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. — Anim. Behav. 75: 333-344.

Zitterbart, D.P., Wienecke, B., Butler, J.P. & Fabry, B. (2011). Coordinated movements pre- vent jamming in an emperor penguin huddle. — PLoS One 6: e20260.

4

Chapter 4



Much ado about something: behavioural mechanisms of pair bond separation and formation in long-term pairing rooks.

Boucherie Palmyre H. [a,b]**, Poulin Nicolas** [c]**, Dufour Valérie** [a,b]

[a] Institut Pluridisciplinaire Hubert Curien, University of Strasbourg, 23 rue Becquerel 67087 Strasbourg, France.

[b] Centre National de la Recherche Scientifique, UMR 7178, 67087 Strasbourg, France.

[c] Institut de Recherche Mathématiques Avancées, UMR 7501, 67200 Strasbourg, France

Corresponding author: Boucherie P. H., palmyre.boucherie@iphc.cnrs.fr

Submitted

Summary

In monogamous avian species, the continuity of the partnership was found to be negatively correlated to the likelihood of divorce. Long-term pairing indeed increases breeding success and in turn secures the relationship. Thus, considering the strength and the intricacy of the pair bonding in long-term monogamous bird species, it would be particularly interesting to study the behavioural mechanisms underlying divorce and new pair formation in such species. Here, we scrutinized the behavioural mechanisms of divorce and new pair formation in a group of captive adult rooks, a long-term monogamous species, following several modifications of the group composition (i.e. losses and addition of individuals). We identified all pair bonds and monitored the strength of these relationships over time. Divorces occurred, all concomitant to the formation of new pairs, with one or both separating partners gradually switching from one valuable relationship to another. Separating pairs only differed from stable ones in terms of higher rates of aggression, and an unequal social investment of partners in the relationship. Food sharing (i.e. allofeeding and co-feeding) played a role in the formation of new pairs, but sexual behaviours did not. Crucially, individuals were found to behave differently during the mate-switching process: solitary individuals actively supplanted paired individuals to form a new relationship, while individuals that were soon to be single (i.e. on the point of being abandoned by their partner) sought to preserve their current relationship. We showed that adult rooks do not necessarily pair for life, but have the ability to strongly re-bond with another partner. This emphasises the social flexibility of this cognitively advanced species, and sheds new light on mate choice strategies in long-term monogamous species.

Keywords: Corvids, divorce, pair bonding, extra-pair relationship, social structure

Choosing the right mate is crucial in most animal species. This is even more true for those that are monogamous, like 85% of bird species (Greenwood 1980). Interestingly, the vast majority of bird species also divorce (more than 92% of the species; Jeschke & Kokko 2008 cited in Culina et al. 2014). Divorce occurs when one or both partners re-pair with a new mate after surviving the breeding season (Ens et al. 1996; Ens et al. 1993; Rowley 1983; Coulson 1972). Divorce often follows breeding failures (Culina et al. 2014; Desrochers & Magrath 1996; Choudhury 1995; Dhondt & Adriaensen 1994; Brooke 1978), and is often correlated with an increase in breeding success when it leads to the formation of a new pair (Culina et al. 2014). As such, divorce can be seen as an adaptive strategy for individuals to deal with sub-optimal reproductive conditions (Culina et al. 2014; Dubois & Cézilly 2002). Several hypotheses have been proposed to explain why and when divorce occurs between monogamous partners. Among the most studied are: i) the 'incompatibility hypothesis', which predicts that incompatible partners (i.e. for behavioural and or morphological traits) will jointly engage in divorce when facing reduced breeding success (Coulson 1972, 1966); i) and the 'better option hypothesis', which argues that divorce can be expected when the benefits of the separation outweigh the costs associated with mate switching and new partner research processes (Ens et al. 1993). Large inter-specific variations are observed in the frequencies of divorce (Jeschke & Kokko 2008). For instance, in the greater flamingo, pairs always separate after the breeding season (*Phoenicopterus roseus*, Cezilly & Johnson 1995), while in the wandering albatross (*Diomedea exulans*), or the great blue heron (*Ardea herodias*), pairs almost never do (Jouventin et al. 1999; Simpson et al. 1987).

Numerous determinants were found to impact the likelihood of divorce, such as the degree of mutual ornamentation, sexual dichromatism, coloniality or part-time partnership (i.e. all positively correlated to the rate of divorce; Choudhury 1995; Jeschke & Kokko 2008). Conversely, the continuity of the partnership was found to limit the risk of divorce (Jeschke & Kokko 2008). When mated partners remain together throughout the year, they are indeed less likely to separate at the end of the breeding season (Ens et al. 1996; Jeschke & Kokko 2008; Rowley 1983). The duration of the partnership positively influences reproductive success, even after controlling for the effects of age or previous breeding (Sánchez-Macouzet & al. 2014; Ens et al. 1996). With time, continuous partners tend to become more like their mate: they increase their behavioural synchronicity (Emery et al. 2007; Ens et al. 1996) and even show similar hormonal levels (Ouyang et al. 2014), increasing their efficiency in providing parental care (Mariette & Griffith 2015, 2012; Davis 1988). Thus with time, their breeding success increases, which in turn secures the relationship. This virtuous circle may be particularly true of long-term pairing species, in which the mated partners stay together over several breeding seasons and possibly for life.

In addition, in long-term pairing species the pair bond can go beyond the reproductive function (e.g. in geese, albatrosses, swans, corvids, parrots Emery et al., 2007; Shultz and Dunbar, 2010), in the sense that its formation and temporal dynamic cannot be solely explained by mating strategies. This is especially true of cognitively advanced species like corvids or parrots, who can develop stable and intricate partnerships, by interacting in a positive manner all year long (i.e. during and outside the breeding context; Emery, 2004, 2006, 2007; Seed et al., 2009, 2007). In these species, the pair bond conveys many other non-reproductive benefits that certainly limit the risk of divorce, independently of breeding success. For instance, being involved in a long term partnership can facilitate the access or the monopolisation of food resources, it ensures a better territory defence, or improves social status (Braun & Bugnyar 2012; Clayton & Emery 2007; Emery et al. 2007; Lamprecht, 1985; Tamm, 1977). In rooks or jackdaws for instance, two social corvids species, the pair bond is akin to long-term alliances that can be found in highly social mammals like primates or dolphins (e.g. jackdaws, *Corvus monedula*; rooks, *Corvus frugilegus*; Emery et al., 2007). In these two species, the mated partners spend a substantial amount of time in association and frequently interact through an array of affiliative behaviours (e.g. preening, food sharing, allofeeding, joint manipulation of objects, support after conflict; de Kort et al., 2006, 2003; Emery et al., 2007; Scheid et al., 2008; Logan et al., 2012; Seed et al., 2007). Therefore, considering the strength and the intricacy of the pair bond in long-term pairing species, when it occurs, we might expect divorce or partner switching to be gradual, and expressed through the modification of partners' pattern of interactions. Yet certainly due to the scarcity of the phenomena, divorce and partner switching are not well documented in rooks or jackdaws, which are often supposed to pair up for life (Clayton and Emery, 2007; Emery et al., 2007). In addition, although numerous studies have focused on the ultimate causes and consequences of divorce in birds (Dhondt 2002), little attention has been paid to the behavioural mechanisms involved (Cezilly et al. 2000).

Still, extra-pair copulations, partner switching, and in particular partner usurpations (i.e. when an individual takes the place of another in a pair), have already been reported in this two species (in rooks: Richards 1976; Røskaft 1983; Boucherie et al., 2016; in jackdaws: Logan et al., 2012, 2013). Furthermore, when juveniles, rooks and jackdaws have the ability to switch from one valuable relationship to another during the process of the pair bond formation (in rooks: Clayton & Emery 2007; Emery et al. 2007; in jackdaws: von Bayern et al. 2007). Early in life, they preferentially bond with their siblings and sometimes with same-sex partners, then, they gradually start interacting with a unique partner to pair up with, most often non-sibling and of opposite sex (i.e. in rooks: Emery et al. 2007; Scheid et al., 2008; in jackdaws: de Kort et al., 2006, 2003; von Bayern et al., 2007). During the partner research process, affiliative behaviours and in particular food sharing (i.e. allofeeding and co-feeding), have been considered as essential behaviour for the establishment and the strengthening of the pair bond (in rooks: allofeeding, Emery et al. 2007; but also co-feeding behaviour, Scheid et al., 2008; in jackdaws: von Bayern et al., 2007). We might therefore expect extra-pair affiliations and/or copulations to facilitate mate switching and possibly trigger divorce in adult rooks and jackdaws.

In this study, we explored the behavioural mechanisms involved in divorce and new pair formation in adult rooks (i.e. resulting from mate switching), a long-term pairing species. To do so, we followed a captive group of adult rooks soon after several modifications of the group composition (i.e. losses and introduction of new individuals). We first identified pairs on the basis of interaction frequencies (i.e. proximities and affiliations). We then monitored how the strength of these relationships evolved over time, to characterise their dynamics (i.e. stable, separating, in formation, newly formed). We predicted that if divorce occurred, separating pairs should be characterised by bonds of lower quality (e.g. lower strength, lower rates of affiliations, higher rates of aggressions, shorter associations). We also predicted that the formation of new pairs should be preceded by extra-pair affiliations and in particular food sharing (i.e. allofeeding and co-feeding), and/or copulations. Finally, whenever separations and new pair formations occurred, we investigated the responsibility of each individual involved in the process (i.e. comparing the proportion of interactions received and emitted by both partners in each relationship). In case divorces were consistent with the incompatibility hypothesis, we expected separating partners to engage similarly in the separation process (i.e. to display similar proportions of interactions received and emitted; Coulson 1966); and in case they best fitted with the best option hypothesis, we expected separations to be concomitant with new pair formations (i.e. with one or both partner switching from one relationship to another).

Methods

Subject and study site

The studied group was composed of 14 adult rooks, housed in the campus of Cronenbourg in Strasbourg, France. Nine birds belonged to an original group, collected from the nest in a wild local colony between 2006 and 2007 (Table 1). Five other birds were added to this group in October 2013 (i.e. one juvenile male and 4 adult females, rescued from hunting traps in southern Alsace; Table 1). Several birds were lost between 2013 and 2014: before the introduction of the new group members, in 2013, two individuals escaped after rodents damaged the aviary (i.e. one male: h, and one female: y); after the introduction of the new group members, in 2014, two other individuals died of natural causes (i.e. one male: z, one female: c; Table 1). Note that at the time of their loss, h, y, and z were all involved in a pair relationship. Birds were housed in a large outdoor aviary (18m x 6 m x 3.5 m) containing wooded perches, platforms, suspended baskets, ropes, vegetation cover and branches, as well as 2 small water pools for enrichment and bathing. Individuals were fed daily with a mixture of pellets and fresh products (eggs, yoghurt, and fruit) and had ad libitum access to water. All birds were easily identified by coloured leg rings.

Period	**2012**	**October 2013 → May 2014**	**August 2014 → September 2014**
Individuals	b	a	a
	e	b	b
	h *	C *	e
	J	e	G
	k	G	J
	m	J	k
	n	k	m
	o	m	n
	t	n	o
	Y *	o	P
	z	P	S
		S	t
		t	
		z *	
Individuals	11	14	12
Sex-ratio	(9 M / 2 F)	(9 M / 5 F)	(8 M / 4 F)

Table 1. Temporal modifications of the group composition from 2012 to 2014. Females are shown in capitals, and males in lowercase letters. Individuals introduced in the group in 2013 are colored in red, original group member in black. Asterisks indicate individuals that were lost before the study in 2012 (i.e. h and y) and in the course of the study in 2014 (i.e. c and z). The columns corresponding to the studied period are grayed out. The number of individual present in the group and the sex ratio are also indicated.

Data collection

Data were collected from January to September 2014, which covered the breeding period (March to early June). We used 10-minutes individual focal sampling to record spatial proximities (i.e. perch proximity, ground proximity), affiliative interactions (i.e. allofeeding, allopreening, and contact-sit), co-feeding events, sexual behaviours (i.e. mounting, courtship) and aggressions (i.e. supplant, avoid, peck, charge, and chase) (Altmann, 1974). In addition, rare behaviours (i.e. allofeeding, co-feeding and sexual behaviours), were also recorded by ad libitum sampling, thus for all individuals during each focal sampling (Altmann 1974). We recorded perch proximity or ground proximity when two individuals were 10 to 50 cm apart when perched, or 0 to 1 m apart on the ground, i.e. the distances at which individuals interact at these locations. Contact-sit was recorded when two individuals were perched less than 10 cm apart. Allofeeding was recorded when one bird actively put a food item into the beak of another (Scheid et al. 2008), co-feeding when two birds fed together at the same food sources (i.e. a round table measuring 1m in diameter), and allopreening when one bird ran its beak through the feathers of another. We performed a total of 83 observation sessions. All observation sessions were performed between 08:00 and 18:00 hours by one observer (PB), and we never performed more than one observation session per day. During each observation session, all individuals were observed in a random order, totalling 13:50 hours of observation per individual (except for z and c, lost in the course of the study).

Temporal monitoring of pairs

Sociality index

Pairs were first identified per week, in order to detect variations in the strength of the pair bonding on a very fine scale. Note that we only considered week composed of more than two observation sessions. Following Boucherie et al. (2016), for each dyad on each week, we computed a sociality index inspired by Silk et al. (2006) using the spatial proximities (ground proximity: GP, perch proximity: PP), and the affiliations (allofeeding: Fe, allopreening: Pr, and contact-sit: Cs):

$$Sij1 = \frac{((GPij1 / GP1) + (PPij1 / PP1) + (Feij1 / Fe1) + (Prij1 / Pr1) + (CSij1 / CS1))}{5} \times 100$$

where $GPij^1$ equals the frequency of ground proximity for the dyad ij on the first week, divided by GP^1, the overall mean of ground proximity for all dyads on the first week (and similarly for all other variables: PP, Fe, Pr, Cs). The numerator refers to the number of variables. The value of the index indicates the strength of the relationship, with high (low) values for strong (weak) relationships. For each individual, we then computed an individual index, summing the sociality indices of all the relationships in which the individual was involved. Based on Boucherie et al. (2016), a pair was then considered as established if the sociality index of the relationship represented more than 50% of both partners' individual indices.

Pair dynamics

To solely focus on fully established pairs on the analysis, we only considered pairs identified on a minimum of two consecutive weeks. Pairs identified on a single week were thus removed from the analysis. Thereafter, all analyses were performed per fortnight, pooling data every two weeks.

We discriminated four different pair dynamics, according to their variation of status (i.e. established or not) fortnight after fortnight. Firstly, we characterised '*stable'* pairs, for pairs that were already established at the beginning of the study and that did not separated throughout the studied period (considering all fortnights of the dataset). Secondly, the '*separating'* pairs, for pairs that separated in the course of the study (considering all fortnights for which the pair is established, until the separation i.e. when the sociality index of the relationship represent less than 50% of both partners individual indices). Finally, for new pairs that established during the course of the study and did not separate afterwards, we distinguished two different temporal stages characterising: i) pairs '*in formation*', for dyads in the process of becoming a pair (considering all fortnights preceding the establishment of the pair and for which the sociality index of the relationship was above 5% of both partners individual indices); and ii) '*newly formed*' pairs (considering all fortnights after the establishment of the pair). Note that stable, separating and newly formed pairs, all corresponded to established pairs (i.e. the sociality index of the relationship represented more than 50% of both partners' individual indices). See Figure 1 for a schematic representation of the different pair dynamics.

Using this procedure, we added a temporal component in the analyses, which were therefore performed on repeated measures for each pair (i.e. one measure corresponding to one fortnight). More precisely, we characterised: (1) two stable pairs, respectively identified on 8 and 12 fortnights; (2) three separating pairs, identified on 5, 6 and 8 fortnights; and four news pairs, respectively identified as (3) pairs in formation on 2, 3, 6 and 8 fortnights; and as (4) newly formed pairs on 4, 4, 6 and 7 fortnights.

Behavioural mechanisms of pair separations and formations

We first investigated whether pairs had different strength according to their dynamic, using a linear mixed model (LMM; function 'lmer' in R package lme4 v.1.1-9; Bates et al., 2015), with the sociality index per fortnight as response variable, and the dynamic of the pair as fixed factor (i.e. stable, separating, in formation, newly formed). We also investigated whether the strength of the pair significantly varied over time (i.e. fortnight after fortnight), according to its dynamic, by testing the interaction between the dynamic of the pair and the cumulative number of fortnight as continuous variable. In this model, we also added the identity of the dyad, and the breeding period (i.e. before or during the breeding period) as random factors.

Then, we used generalized linear mixed models (GLMM; function ‘glmer’ in R package lme4 v.1.1-9; Bates et al., 2015) to investigate whether the dynamic of the pair had an impact on the following response variables: (1) the pattern of interactions, comparing the relative proportions of affiliations (Fe, Pr, Cs) over spatial proximities (PP, GP) per fortnight, using a model adapted for proportions with a binomial distribution and a logit link function (function ‘glmer’ and ‘cbind’ in R package lme4 v.1.1-9; Bates et al., 2014); (2) the ratio between the duration and the frequency of spatial associations per fortnight (i.e. proximities plus contact-sit; higher ratios indicates longer associations); and (3) the frequencies of allofeeding, co-feeding, aggressions and sexual behaviours per fortnight. In all models, we added the identity of the dyad nested in the fortnight, and the breeding period as random factor.

Individual dynamics: responsibility in separation and new pair formation processes

Finally, we investigated individuals’ responsibility within separations and new pair formation processes. Individuals involved in stable pairs are therefore not included in this part of the analysis. To do so, we compared the proportion of interactions (i.e. proximities and affiliations) received and emitted by the different partners for each dynamic of relationship (i.e. separating, in formation, and newly formed pairs). Note that all separations and new pairs formations occurring in the course of the study resulted from mate switching: one pair separates while another (two other) forms, with one (or both) partner(s) shifting from one pair to another. Therefore, we distinguished and compared three different individual dynamics: (1) ‘*intermediate*’, for individuals forming a new pair whilst maintaining their current relationship (i.e. individuals involved simultaneously in a separating pair and in a pair in formation); (2) ‘*soon to be single*’, for paired individuals involved in a separating pair, and whose partner is simultaneously involved in another pair in formation; (3) and ‘*outsider*’, for solitary individuals forming a new pair with an individual already paired to another group member (Figure 1). For each individual, we then computed directed sociality indices per fortnight, for each relationship in which they were involved: (1) two relationships for intermediate individuals (i.e. $S_{\text{intermediate} \rightarrow \text{soon to be single}}$ and $S_{\text{intermediate} \rightarrow \text{outsider}}$); (2) one relationship for individuals soon to be single ($S_{\text{soon to be single} \rightarrow \text{intermediate}}$); and one relationship for outsiders (i.e. $S_{\text{outsider} \rightarrow \text{intermediate}}$).

Then, for each dynamic of relationship separately (i.e. separating, in formation, newly formed), we used a LMM with the individual directed sociality index per fortnight as response variable, and the individual dynamic as fixed factor (i.e. Separating pair: $S_{\text{intermediate}} \rightarrow S_{\text{soon to be single}}$ vs. $S_{\text{soon to be single}} \rightarrow S_{\text{intermediate}}$; Pair in formation: $S_{\text{intermediate}} \rightarrow S_{\text{outsider}}$ vs. $S_{\text{outsider}} \rightarrow S_{\text{intermediate}}$; Newly formed pair: $S_{\text{intermediate}} \rightarrow S_{\text{outsider}}$ vs. $S_{\text{outsider}} \rightarrow S_{\text{intermediate}}$), in order to compare the relative responsibility of each individuals in forming and maintaining their current relationship(s).

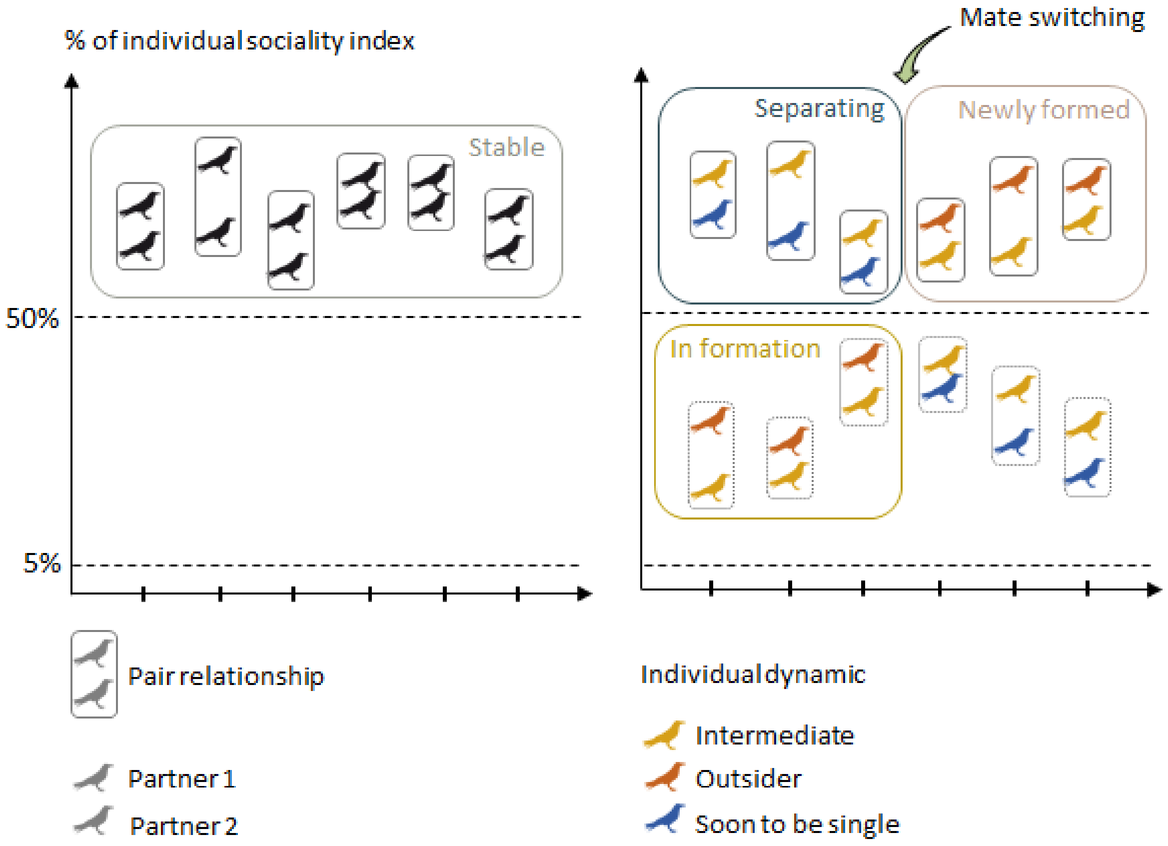


Figure 1. Schematic representation of the four different pair dynamics (i.e. stable, separating, in formation, newly formed), and the three different individual dynamics in case of mate switching (i.e. intermediate, soon to be single, outsider).

Data analysis

For all GLMMs, according to the dispersion of the data, we used a poisson distribution with a log link function. In all models (GLMMs and LMMs) concerned, we scale the sociality indices when it was used as response variable (i.e. for directed or undirected sociality indices). Post-hoc comparisons were performed using Tukey's contrasts procedure for multiple comparisons. All statistics were performed using R 3.1.3 software (R Core Team, 2015), with the significance threshold set at α=0.05.

Ethical note

This research was purely observational, followed the guidelines of the Association for the Study of Animal Behaviour and respected European and French legislation. The study was approved by the regional ethical committee on animal experimentation under license n°A67-382.

Results

Temporal monitoring of pairs

All individuals were involved in a pair in at least one week of the study (Figure 2), but one among 14 has never been involved in a pair for more than one week (b; Figure 2). Regardless of their dynamic or duration, we identified 12 different pairs (three of which were only identified in a single week; b-k, b-m, n-o; Figure 2). Among the pairs that lasted more than one week: two remained stable over the whole studied period (i.e. stable pairs; e-t, n-z), three separated (i.e. separating pairs; a-s, c-p, j-o), and four formed in the course of the study (i.e. pairs in formation turning after their establishment into newly formed pairs; a-g, k-p, j-m, o-s). All four newly formed pairs resulted from a mate switching, following the separation of the three separating pairs (Figure 2). Among the four newly formed pairs, three were still established more than one year later (i.e. in June 2016; a-g, k-p, j-m; Figure 2), but one separated shortly after its formation (o-s; Figure 2). All pairs that separated and formed were mixed-sex except one (i.e. c-p, separating; Figure 2), and the two stable pairs were male-male. In two mate switching over four, the outsider was a male and the intermediate individual a female (i.e. k for c-p → k-p; m for j-o → j-m). In the two others mate switching, the outsider was a female and the intermediate individual a male (i.e. g for a-s → a-g; s for j-o → o-s; Figure 2). Note that all mate switchings occurred during the breeding season (Figure 2).

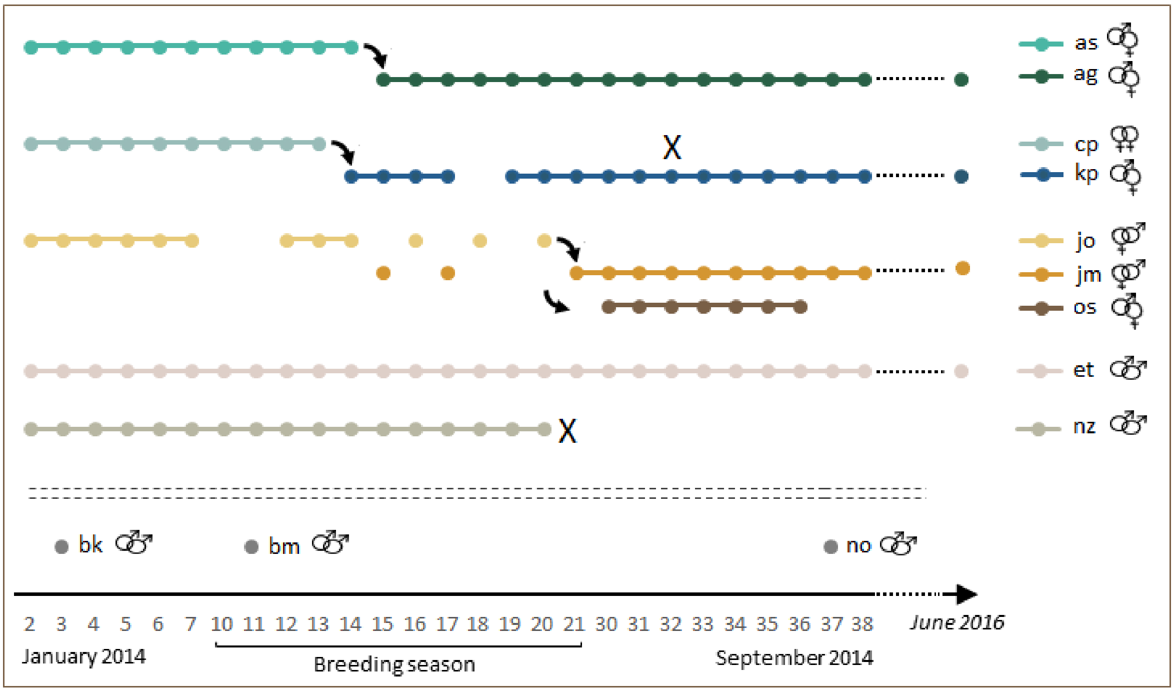


Figure 2. Evolution of pair bonds per week, between January and September 2014. Established pairs are represented by coloured points (i.e. the sociality index of the relationship represent more than 50% of both partners' individual indices). Crosses indicate the loss of the two individuals, z and c, in the course of the study. Mate switching are indicated by arrows (i.e. when one individual separate from its current partner and form a new pair relationship with a new partner). The pairs that were already established at the beginning of the study (a-s, c-p, j-o, n-z, e-t) had existed for at least 5 weeks (i.e. a-s, c-p; following the introduction in the group), and up to six years (j-o, n-z, e-t). Among those pairs, three never build or attempted to build a nest (i.e. a-s, c-p, e-t), and two did so over 6 consecutives breeding seasons but never successfully produced surviving offspring (i.e. j-o, n-z, maximal offspring survival over six breeding seasons: 21 days). Finally, the pairs established at the end of the study (a-g, k-p, j-m, e-t), were still stable more than one year later (i.e. in June 2016), and all but one (e-t, male-male pair), built a nest and attempted to breed in 2015 and 2016.

Behavioural mechanisms of pair separations and formations

Analysis were performed on a total of 1296 proximities (i.e. at perch and on the ground), 2746 affiliations (i.e. allofeeding, allopreening and contact-sit), 227 co-feeding events, 41 sexual behaviours and 128 aggressions (i.e. supplant, avoid, peck, charge and chase). Note that on average, 63% of sexual behaviours were produced by stable pairs (i.e. both male-male pairs; 26 occurrences), and pairs in formation produced less than 5% of sexual behaviours (i.e. 2 occurrences). Due to the limited number of events, we did not investigated the distribution of the sexual behaviours any further.

All established pairs (i.e. stable, newly formed and separating) had similar sociality indices, all significantly higher than pairs in formation (Table 2; Figure 3).

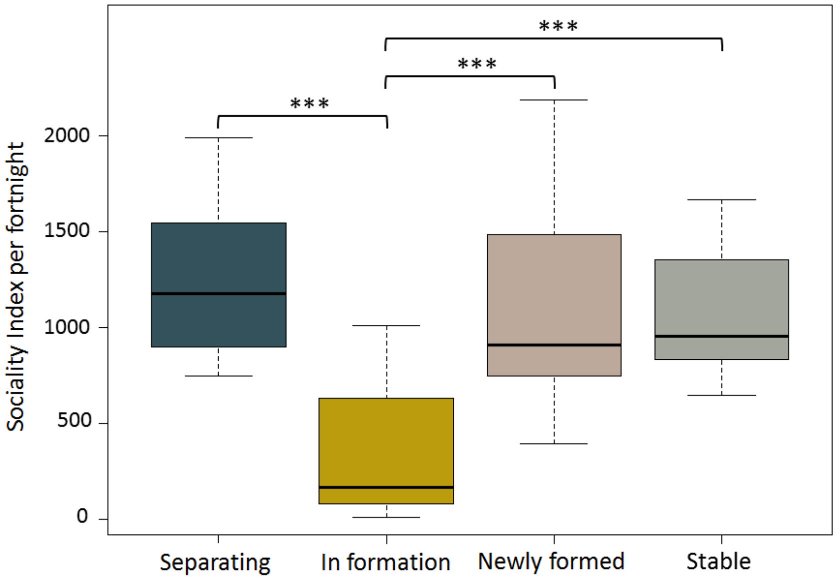


Figure 3. Boxplot showing the distribution of sociality indices per fortnight, according to the dynamic of the pair. Sample size: 3 separating pairs (5, 6 and 8 repeated measures for each), 4 pairs in formation (2, 3, 6 and 8 repeated measures for each), 4 newly formed pairs (4, 4, 6 and 7 repeated measures for each), and 2 stable pairs (8 and 12 repeated measures for each). For all boxplot figures, the bottom of the boxplot represents the first quartile, the top the third quartile, and the thick line across the box indicates the median. Whiskers extend to the highest and lowest values. Statistics are based on the estimates given by the model. *** < 0.001, ** < 0.01, * ≤ 0.05.

The sociality indices of established pairs (i.e. stable, newly formed, and separating) did not significantly vary over time (i.e. fortnight after fortnight; Table 2, Figure 4), whereas the sociality index of pairs in formation significantly increased over time (Table 2; Figure 4). Note that immediately after the mate switching (i.e. when the sociality index of the newly formed pair became stronger than the sociality index of the separating pair), the sociality index of separating pair drastically decreased.

Figure 4. Temporal variations of pairs' sociality index according to their dynamic (i.e. stable, separating, in formation, newly formed), fortnight after fortnight from January 2014 to September 2014. Over the whole dataset: the two stable pairs have been identified on 8 (nz) and 12 (et) fortnights; the three separating pairs on 5 (cp), 6 (as) and 8 (jo) fortnights; and the four news pairs as pairs in formation on 2 (kp), 3 (os), 6 (ag), and 8 (jm) fortnights, and as newly formed pairs on 7 (kp), 4 (os), 6 (ag), and 4 (jm) fortnights. Stable pairs and mate switchings (involving separating, in formation, and newly formed pairs) are represented on separate graphs.

Pairs established at the beginning of the study (i.e. stable and separating pairs) displayed similar proportions of affiliations over proximities, and both displayed significantly higher proportion of affiliations over proximities compared to pairs in formation (Table 2;

Figure 5). However, they both displayed a significantly lower proportion of affiliations over proximities than newly formed pairs. Pairs in formation indeed significantly increased their proportion of affiliation once established (i.e. pair in formation vs. newly formed pair; Table 2; Figure 5).

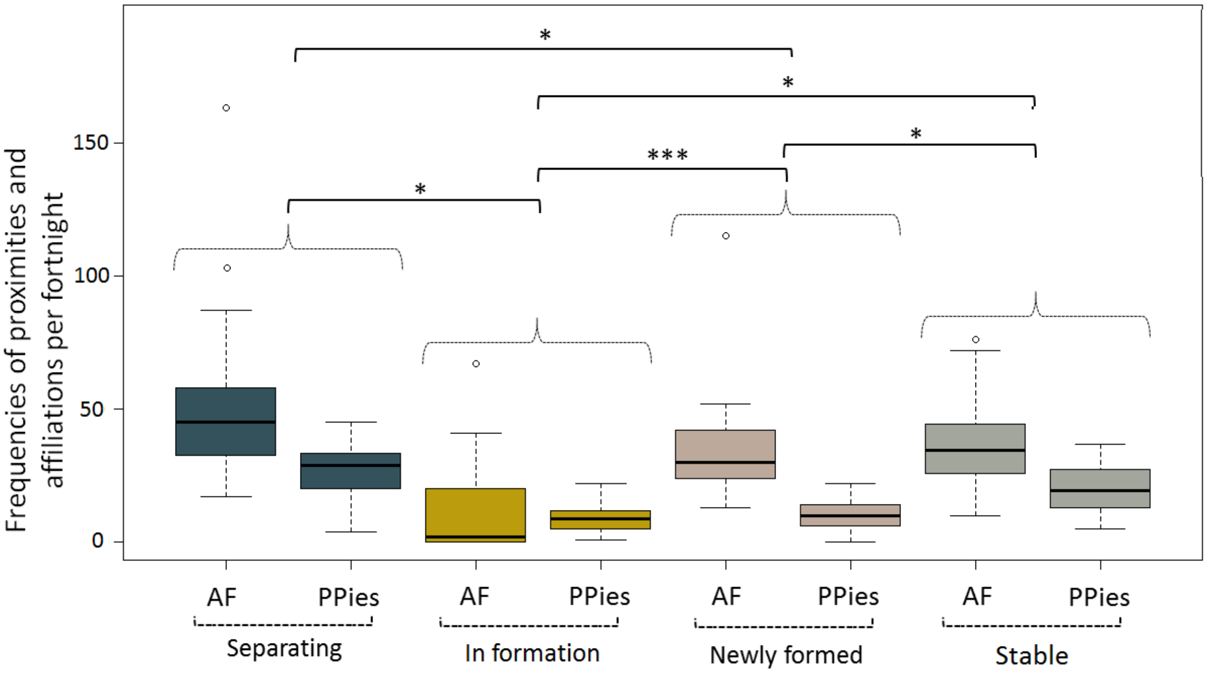


Figure 5. Boxplot showing the distribution of the respective frequencies of proximities (i.e. perch and ground proximity: PPies) and affiliations (i.e. allofeeding, allopreening, and contact-sit: AF) per fortnight, according to the dynamic of the pair. Sample size: 3 separating pairs (5, 6 and 8 repeated measures for each), 4 pairs in formation (2, 3, 6 and 8 repeated measures for each), 4 newly formed pairs (4, 4, 6 and 7 repeated measures for each), and 2 stable pairs (8 and 12 repeated measures for each). Outliers are represented by circles. Statistics are based on the estimates given by the model. *** < 0.001, ** < 0.01, * ≤ 0.05.

Pairs in formation were characterised by significantly shorter spatial associations than all established pairs (i.e. stable, newly formed and separating). Separating pairs displayed an intermediary ratio, between the other established pairs (i.e. newly formed and stable) and pairs in formation (Table 2).

Whatever their dynamic, all pairs displayed similar rates of allofeeding (i.e. 705 allofeeding in total; separating: 20%, in formation: 19%, newly formed: 24%, stable: 36%), except stable pairs that displayed significantly higher rates compared to pairs in formation (Table 2).

Similarly, all pairs displayed similar rates of co-feeding (i.e. 227 co-feeding in total; separating: 12%, in formation: 17%, newly formed: 26%, stable: 45%), except stable pairs that displayed significantly higher rates compared to all other pairs (i.e. separating, in formation, newly formed).

Separating pairs had higher rates of aggressions compared to the other established pairs (i.e. stable and newly formed; Table 2; Figure 6). Pairs in formation had intermediary rate, which remained similar once the pair was further established (i.e. pair in formation vs. newly formed; Table 2; Figure 6). Note that among separating pairs, we recorded on average 3 times more aggressions directed from intermediary individuals toward their partners (i.e. individuals soon to be single) than the contrary (i.e. intermediary → soon to be single: 57 aggressions recorded; soon to be single → intermediary: 18 aggressions).

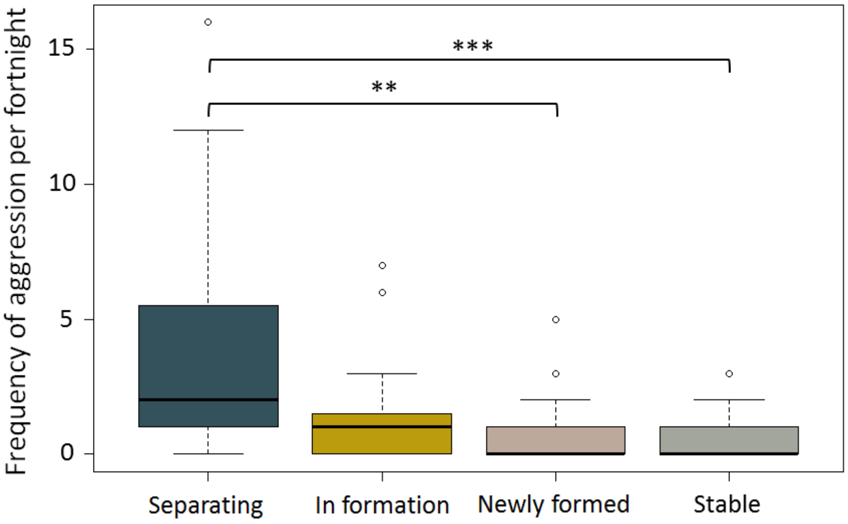


Figure 6. Boxplot showing the distribution of the frequencies of aggressions (i.e. supplant, avoid, peck, charge and chase) per fortnight, according to the dynamic of the pair. Sample size: 3 separating pairs (5, 6 and 8 repeated measures for each), 4 pairs in formation (2, 3, 6 and 8 repeated measures for each), 4 newly formed pairs (4, 4, 6 and 7 repeated measures for each), and 2 stable pairs (8 and 12 repeated measures for each). Statistics are based on the estimates given by the model. *** < 0.001, ** < 0.01, * ≤ 0.05.

Individual dynamics: responsibility in separation and new pair formation processes

Intermediate individuals were significantly less responsible than individuals soon to be single in maintaining their current relationship, and less responsible than outsiders in forming the new relationship (i.e. intermediate individuals had lower directed sociality index compared to their partners: they received more interactions from their partners than they initiated; Table 2; Figure 7). Once the new pair was established, outsider were still more active than intermediate individuals in maintaining the relationship.

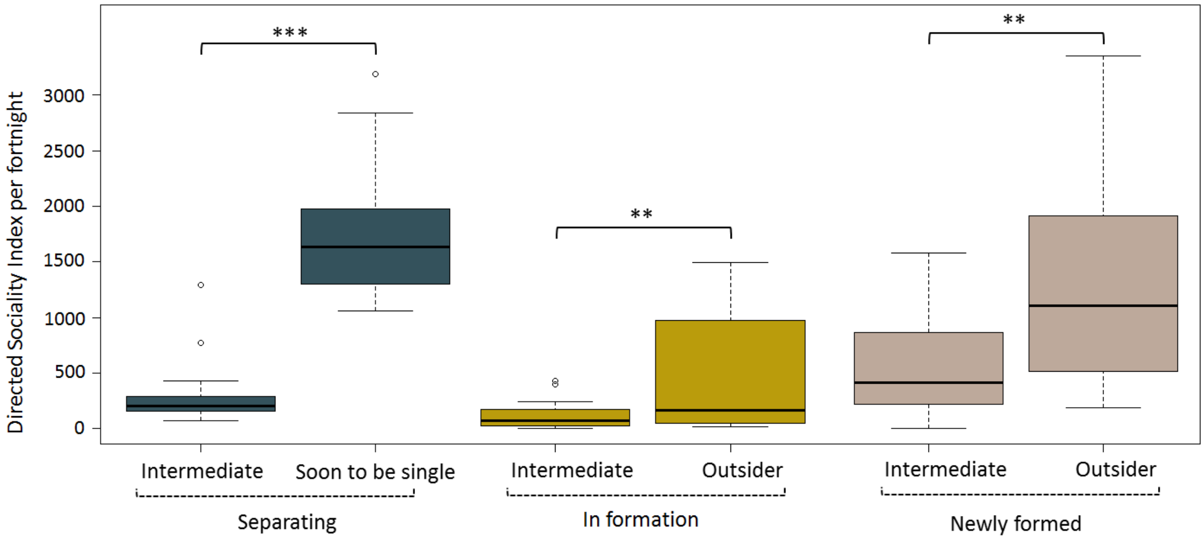


Figure 7. Boxplot showing the distribution of the directed sociality indices per fortnight, according to the dynamic of the pair, and individuals' dynamic. Sample size: 3 separating pairs (5, 6 and 8 repeated measures for each individual in each pair), 4 pairs in formation (2, 3, 6 and 8 repeated measures for each individual in each pair), 4 newly formed pairs (4, 4, 6 and 7 repeated measures for each individual in each pair), and 2 stable pairs (8 and 12 repeated measures for each individual in each pair). Statistics are based on the estimates given by the model. *** < 0.001, ** < 0.01, * ≤ 0.05.

Model 1: Sociality indices	Estimate ± SE	t value	P value
Intercept	1.25 ± 0.68	1.83	0.07
Newly formed : Fortnight	-0.07 ± 0.04	-1.60	0.11
In formation : Fortnight	0.20 ± 0.06	3.33	< **0.001** ***
Separating : Fortnight	-0.01 ± 0.06	-0.21	0.83
Stable : Fortnight	-0.05 ± 0.03	-1.65	0.10
	Estimate ± SE	z value	P value
In formation - Separating	-2.99 ± 0.62	-4.78	< **0.001** ***
Newly formed - Separating	0.59 ± 0.80	0.74	0.88
Stable - Separating	-0.10 ± 0.64	-0.16	0.99
Newly formed – In formation	3.58 ± 0.70	5.09	< **0.001** ***
Stable - In formation	2.89 ± 0.65	4.45	< **0.001** ***
Stable - Newly formed	-0.69 ± 0.82	-0.84	0.83
Model 2: Pattern of interactions (Proximities; Affiliations)	Estimate ± SE	z value	P value
In formation - Separating	0.86 ± 0.30	2.83	< **0.05** *
Newly formed - Separating	-0.77 ± 0.27	-2.81	< **0.05** *
Stable - Separating	-0.03 ± 0.26	-0.12	0.99
Newly formed – In formation	-1.63 ± 0.33	-4.87	< **0.001** ***
Stable - In formation	-0.89 ± 0.31	-2.92	< **0.05** *
Stable - Newly formed	0.74 ± 0.27	2.72	< **0.05** *
Model 3: Ratio between the duration and the frequency of spatial associations			
In formation - Separating	-0.61 ± 0.18	-3.45	< **0.01** **
Newly formed - Separating	0.56 ± 0.22	2.60	< **0.05** *
Stable - Separating	0.26 ± 0.18	1.47	0.45
Newly formed – In formation	1.17 ± 0.22	5.39	< **0.001***
Stable - In formation	0.86 ± 0.18	4.89	< **0.001***
Stable - Newly formed	-0.31 ± 0.19	-1.61	0.37
Model 4: Frequency of allofeeeding			
In formation - Separating	-0.60 ± 0.71	-0.84	0.83
Newly formed - Separating	0.81 ± 0.69	1.17	0.64
Stable - Separating	1.48 ± 0.67	2.21	0.12
Newly formed – In formation	1.42 ± 0.74	1.91	0.22
Stable - In formation	2.08 ± 0.70	2.99	< **0.05** *
Stable - Newly formed	0.67 ± 0.63	1.05	0.72

Model 5: Frequency of co-feeding			
In formation - Separating	0.26 ± 0.56	0.46	0.97
Newly formed - Separating	0.32 ± 0.58	0.55	0.95
Stable - Separating	1.66 ± 0.53	3.15	< **0.01****
Newly formed – In formation	0.06 ± 0.56	0.10	0.99
Stable - In formation	1.40 ± 0.52	2.69	< **0.05 ***
Stable - Newly formed	1.34 ± 0.53	2.54	**0.05**
Model 6: Frequency of aggressions			
In formation - Separating	-1.03 ± 0.44	-2.34	0.09
Newly formed - Separating	-1.74 ± 0.52	-3.37	< **0.01 ****
Stable - Separating	-2.21 ± 0.52	-4.23	< **0.001*****
Newly formed – In formation	-0.71 ± 0.56	-1.26	0.58
Stable - In formation	-1.18 ± 0.55	-2.13	0.14
Stable - Newly formed	-0.47 ± 0.59	-0.79	0.86
Model 7: Individuals responsibility in mate switching			
Separating : Soon to be single vs Intermediate	1.64 ± 0.18	9.05	< **0.001*****
In formation : Outsider vs Intermediate	0.83 ± 0.27	3.01	< **0.01 ****
Newly formed : Outsider vs Intermediate	0.91 ± 0.28	3.28	< **0.01 ****

Table 2. LMMs and GLMMs results investigating the effect of the pair dynamic (i.e. stable, separating, in formation, newly formed) on: (1) the value of the sociality index (i.e. fixed effect), and its temporal variation (i.e. by testing the interaction between the dynamic of the pair and the cumulative number of fortnight); (2) the patterns of interaction (i.e. by comparing the relative frequencies of affiliations and proximities; using a model adapted for proportion, function 'cbind' on R package lme4 v.1.1-9; Bates et al., 2014); (3) the ratio between the duration and the frequency of spatial associations (i.e. contact-sit plus proximities), (4) the frequencies of allofeeding, (5) co-feeding; and (6) aggressions. Finally, are also reported the GLMM results investigating the effect of the individual dynamics (i.e. intermediate, soon to be single, outsider) on the individual directed sociality indices. For all models, we used the breeding period and the identity of the dyad nested in fortnight as random factors (except in model 1, for which the cumulative number of fortnight is used as fixed factor in interaction with the dynamic of the pair). Significant p-values are shown in bold print, *** < 0.001, ** < 0.01, * ≤ 0.05.

Discussion

In this study, we show that rooks can divorce and have the ability to strongly re-pair, forming several pair bonds throughout their life. All separations were concomitant to the establishment of new pairs (three of which were still established more than one year later), and thus corresponded to mate switchings. Once established, the newly formed pairs behaved exactly like all other established pairs (i.e. stable and separating pairs). Separating pairs had as strong and as stable sociality indexes as the other pairs, but also displayed higher rates of aggressions between partners. Food sharing (i.e. allofeeding and co-feeding) played a role in the formation of new pairs, but not the sexual behaviours. Crucially, individuals behaved differently during the mate-switching process: intermediate individuals, switching from one pair to another, were more passive (i.e. they received more interactions from their partners than they initiated), while individuals soon to be single and outsiders were the most active (i.e. they gave more than they received).

Although separating pairs had existed for between several weeks and several years, the separations appeared almost imperceptible. Before the mate switching, separating pairs engaged in affiliations and co-feeding, and had similar strength (i.e. sociality index) and similar pattern of interaction (i.e. proportion of affiliations over proximities) than the other established pairs. In addition, as long as the partner shift was not clearly effective, their sociality index appeared as steady as the one of the other established pairs (i.e. no variation of their sociality index). Indeed, the shift in partner occurred rather suddenly, and was marked by a drastically decrease of separating pairs' sociality index. However, looking into more details, it is interesting to note that separating partners were more aggressive towards each other compared to the other established pairs. In addition, most aggressions were emitted by intermediary individuals (i.e. shifting from one relationship to another) toward their former partner, validating the choice of the new partner over the former. Besides, separating pairs also displayed intermediary duration of spatial associations compared to pairs in formation and other established pairs. This make sense as it may be more risky (i.e. in term of aggressions) to stay close to an individual with whom the relationship is no longer firmly established. Similar increased levels of aggression has been observed prior to mate switching in adult cockatiels (Spoon et al. 2007). Thus, particular attention must be paid to increasing aggression within pairs in long-term pairing species, as it might be the sign that the relationship is deteriorating. Further research should also clarify whether aggression causes or is result from the pair-bond dissolution.

Contrary to established pairs (i.e. stable, newly formed and separating), the sociality index of pairs in formation significantly and gradually increased over time. During this period, future partners displayed food sharing (i.e. allofeeding and co-feeding), which is consistent with previous findings on juveniles rooks, were allofeeding (Emery et al. 2007) and co-feeding (i.e. but not allofeeding; Scheid et al. 2008) had alternatively been found to correlated with familiarity and the formation of new pairs. Besides, like in juveniles (Emery et al. 2007), new pairs were characterised by low rates of aggressions (i.e. in formation and once formed). More strikingly, sexual behaviours were almost never produced during the pair bond formation process; although all four mate switchings occurred during the breeding period. This contrasts with previous findings on numerous birds species, where the non-exclusivity of the sexual partners often precedes mate switching (Jouventin et al. 2007; Cezilly & Nager 1995; Heg et al. 1993; Spoon et al. 2007). It confirms that bonding may overcome the reproductive aspect in rooks, and indicates that the formation of a new pair is neither highly demonstrative nor strongly displayed, and remains a discrete process in this species. After the mate switching, newly formed pairs became as strong and as stable as the other established pairs. Yet new partners were not equally investing in the relationships, indicating that the establishment of a new pair bond is a gradual phenomenon that spread over several weeks. All except one of the pairs that established in the course of the study were still stable more than one year later. Newly formed pairs behaved exactly like stable pairs (i.e. similar sociality index, low rates of aggression and long spatial associations). Furthermore, they engaged more frequently in affiliations than other established pairs, suggesting that the new partners actively invested in their new relationship, certainly to quickly reinforce and secure the bond. This confirms that rooks have the ability to form several strong pair bonds throughout their life. This makes sense, considering that partner death is likely to occur in the wild, which require to be able to re-invest in a long lasting bond to reproduce (Goodwin, 1955; Jennings, 1955).

Among the four pairs that separated, three never attempted to breed (recently formed or same-sex pairs) and one never successfully produced offspring surviving over 3 weeks (j-o). The absence of any attempt to breed, as well as repeated breeding failures, could have weakened these relationships, and possibly favoured divorce (Dhondt 2002; Dubois & Cézilly 2002; Choudhury 1995). All separations were concomitant to the formation of a new pair, with one or both partner(s) switching from one relationship to another. By switching from one pair to another, rooks might actually change partner while preserving all the advantages associated with pair bonding in this species (e.g. support in conflicts, facilitated access to resource, reproduction; Emery et al., 2007). Interestingly, intermediary individuals, who shifted from one pair to another, seemed little involved in the process of mate switching (either in the process of separation or in the new pair formation). As it is, the intermediary individual did not seem to choose its partner, but simply to go with whomever was the most persistent. Compare to intermediary individuals, individual's soon to be single (i.e. on the point of being abandoned by their partner) and outsiders (i.e. supplanting the latters in their relationships), were much more responsible for the maintenance/formation of the pair bond. This suggest that individuals soon be single were actively attempting to rescue or at least maintain the relationship, while outsiders acted like usurpers, actively supplanting paired individuals in their relationships.

The fact that partners on the point of being separated were not equally responsible in the separation process challenges the 'incompatibility hypothesis' (Coulson 1972, 1966), as it requires both partners to actively engage in the separation (Coulson 1966). Besides, the separations and new pair formations occurred a few months after the introduction of new individuals in the group (i.e. mainly females, in October 2013), and after the loss of two original group members, both involved in a pair relationship at that time (i.e. in 2013). Those perturbations likely had two sizeable effects on all birds: (1) pair bond disruptions, and (2) the creation of new partner opportunities (Dhondt 2002; Catry et al. 1997; Ens et al. 1993). More generally, we may also expect captivity to decrease the costs associated with the partner research process compared to the cost in wild populations. Thus, added to the fact that all separations corresponded to mate switchings, taken together, all these elements could favour the 'better option hypothesis' to explain the occurrence of divorces in this study group, as it states that divorce occurs when the benefits of the separation outweigh the cost associated with mate switching and new partner-seeking processes (Ens et al. 1993). Longer term data regarding the breeding success of the newly formed pairs, should now provide elements to support the 'better option hypothesis', and to answer the theoretical notion that divorce might indeed be an adaptive strategy for these birds (Culina et al. 2014).

This study of a captive corvids population is the first to scrutinise the behavioural mechanisms involved in the scarce and discrete processes of divorce and adult pair bond formation in a lifelong monogamous species. The limit of our study possibly lies in the difficulty encountered by these species when they attempt to breed in captivity. However, all the pairs that formed during the study were mixed-sex and attempted to breed in the following breeding seasons. Interestingly, we found that paired individuals can easily accept affiliative solicitations from others. In some cases, it can lead to new pair bond formation and might even trigger divorce. Tolerating and eventually seeking extra-pair relationships could then be a strategy for paired individuals to keep potential future partners close at hand. This makes sense, given that corvids are long-living bird species, and that beside divorce, the death or disappearance of the partner is likely to occur in the wild. This must be particularly true of rooks, often killed to prevent damage to agricultural crops. Overall, this study underlines that adult rooks do not necessarily pair up for ever, and have the ability to establish strong pair bonds with several partners throughout their life. It suggests that the social environment of rooks may be more intricate and variable than expected, made up of multiple social bonds that can flexibly evolve over time. This results also sheds new light on the dynamics of mating strategies in long-term monogamous species, and opens up exciting new perspectives for the study of the socio-cognitive mechanisms underlying mate-choice decisions in cognitively advanced birds.

The authors declare that they have no competing interests.

References

Altmann, J., 1974. Observational Study of Behavior : Sampling Methods. Behaviour 49, 227–267.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. lme4: Linear mixed-effects models using Eigen and S4. R Packag. version 1.1-9 https://CRAN.R–project.org/package=lme4.

Boucherie, P.H., Mariette, M.M., Bret, C., Dufour, V., 2016. Bonding beyond the pair in a monogamous bird: impact on social structure in adult rooks (Corvus frugilegus). Behaviour. doi:10.1163/1568539X-00003372

Braun, A., Bugnyar, T., 2012. Social bonds and rank acquisition in raven nonbreeder aggregations. Anim. Behav. 84, 1507–1515. doi:10.1016/j.anbehav.2012.09.024

Brooke, M.D.L., 1978. Some factors affecting the laying date, incubation and breeding success of the Manx Shearwater, Puffinus puffinus. J. Anim. Ecol. 477–495.

Catry, P., Ratcliffe, N., Furness, R., 1997. Partnerships and mechanisms of divorce in the great skua. Anim. Behav. 54, 1475–1482. doi:10.1006/anbe.1997.0552

Cezilly, F., Johnson, A.R., 1995. Re-mating between and within breeding seasons in the Greater Flamingo Phoenicopterus ruber roseus. Ibis (Lond. 1859). 137, 543–546. doi:10.1111/j.1474-919X.1995.tb03264.x

Cezilly, F., Nager, R.G., 1995. Comparative evidence for a positive association between divorce and extra-pair paternity in birds. Proc. R. Soc. London B Biol. Sci. 262(1363), 7-12.

Cezilly, F., Préault, M., Dubois, F., Faivre, B., Patris, B., 2000. Pair-bonding in birds and the active role of females: A critical review of the empirical evidence. Behav. Processes 51, 83–92. doi:10.1016/S0376-6357(00)00120-0

Choudhury, S., 1995. Divorce in birds: a review of the hypotheses. Anim. Behav. 50, 413–429. doi:10.1006/anbe.1995.0256

Clayton, N.S., Emery, N.J., 2007. The social life of corvids. Curr. Biol. 17, R652–6. doi:10.1016/j.cub.2007.05.070

Coulson, J.C., 1972. The significance of the pair-bond in the kittiwake. Proc. Int. Ornithol. Congr. 15. pp. 424-433

Coulson, J.C., 1966. The influence of the pair-bond and age on the breeding biology of the kittiwake gull Rissa tridactila. J. Anim. Ecol. 269–279.

Culina, A., Radersma, R., Sheldon, B.C., 2014. Trading up: the fitness consequences of divorce in monogamous birds. Biol. Rev. 90(4), 1015–1034. doi:10.1111/brv.12143

Davis, L.S., 1988. Coodination of incubation rourines and mate choice in Adélie penguins (Pygoscelis adeliae). Auk 105, 428–432.

de Kort, S. R., Emery, N. J., & Clayton, N. S. (2003). Food offering in jackdaws (Corvus monedula). Naturwi., 90(5), 238-240.

de Kort, S.R., Emery, N.J., Clayton, N.S., 2006. Food sharing in jackdaws, Corvus monedula: what, why and with whom? Anim. Behav. 72, 297–304. doi:10.1016/j.anbehav.2005.10.016

Desrochers, A., Magrath, R.D., 1996. Divorce in the European blackbird: seeking greener pastures? Oxf. Orni. Ser., 6, 177-191.

Dhondt, A.A.., 2002. Changing mates. Trends Ecol. Evol. 17, 55–56. doi:10.1016/S0169-5347(01)02407-7

Dhondt, A.A., Adriaensen, F., 1994. Causes and effects of divorce in the blue tit Parus caeruleus. J. Anim. Ecol. 63, 979–987. doi:10.2307/5274

Dubois, F., Cézilly, F., 2002. Breeding success and mate retention in birds: A meta-analysis. Behav. Ecol. Sociobiol. 52, 357–364. doi:10.1007/s00265-002-0521-z

Emery, N.J., 2006. Cognitive ornithology: the evolution of avian intelligence. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 361, 23–43. doi:10.1098/rstb.2005.1736

Emery, N.J., Clayton, N.S., 2004. The Mentality of Crows : Convergent Evolution of Intelligence in Corvids and Apes. Science (80). 306, 1903–1907.

Emery, N.J., Seed, A.M., von Bayern, A.M.P., Clayton, N.S., 2007. Cognitive adaptations of social bonding in birds. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 362, 489–505. doi:10.1098/rstb.2006.1991

Ens, B., Choudhury, S., Black, J.M., 1996. Mate fidelity and divorce in monogamous birds, in: Partnerships in Birds: The Study of Monogamy. (Ed. by Black, J.M.). Oxford University Press, UK.

Ens, J.E., Safriel, U.N., Harris, M.P., 1993. Divorce in the long-lived and monogamous oystercatcher, Haematopus ostralegus: Incompatibility or choosing the better option. Anim. Behav. 45, 1199–1217.

Goodwin, D. 1955. Some observations on the reproductive behavior of rooks. British Birds, 48, 97-107.

Greenwood, P., 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 1140–1162.

Heg, D., Ens, B.J., Burke, T., Jenkins, L., Kruijt, J.P., 1993. Why does the typically monogamous Oystercatcher (Haematopus ostralegus) engage in extra-pair copulations? Behaviour 247–289. doi:10.1017/CBO9781107415324.004

Jennings, A. R. 1955. Diseases in wild birds. Bird study, 2(2), 69-72.

Jeschke, J.M., Kokko, H., 2008. Mortality and other determinants of bird divorce rate. Behav. Ecol. Sociobiol. 63, 1–9. doi:10.1007/s00265-008-0646-9

Jouventin, P., Charmantier, A., Dubois, M.P., Jarne, P., Bried, J., 2007. Extra-pair paternity in the strongly monogamous Wandering Albatross Diomedea exulans has no apparent benefits for females. Ibis (Lond. 1859). 149, 67–78. doi:10.1111/j.1474-919X.2006.00597.x

Jouventin, P., Lequette, B., Dobson, F.S., 1999. Age-related mate choice in the wandering albatross. Anim. Behav. 57, 1099–1106. doi:10.1006/anbe.1999.1083

Lamprecht, J.Ü.R.G. (1986). Social dominance and reproductive success in a goose flock (Anser indicus). Behaviour, 97(1), 50-65.

Logan, C.J., Emery, N.J., Clayton, N.S., 2012. Alternative behavioral measures of postconflict affiliation. Behav. Ecol. 24, 98–112. doi:10.1093/beheco/ars140

Logan, C.J., Ostojić, L., Clayton, N.S., 2013. Rook, But Not Jackdaw, Post-Conflict Third-Party Affiliation Reduces Aggression for Aggressors. Ethology 119, 427–435. doi:10.1111/eth.12078

Mariette, M.M., Griffith, S.C., 2015. The adaptive significance of provisioning and foraging coordination between breeding partners. Am. Nat. 185, 270–80. doi:10.1086/679441

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. doi:10.1111/j.1600-048X.2012.05555.x

Ouyang, J.Q., van Oers, K., Quetting, M., Hau, M., 2014. Becoming more like your mate: hormonal similarity reduces divorce rates in a wild songbird. Anim. Behav. 98, 87–93. doi:10.1016/j.anbehav.2014.09.032

R Core Team, 2015. R: A language and environment for statistical computing. Vienna, Austria. URL http//www. R-project. org.

Richards, P.R., 1976. Pair Formation and Pair Bond in Captive Rooks. Bird Study 23(3), 207–211.

Røskaft, E., 1983. Male promiscuity and female adultery by the rook Corvus frugilegus. Ornis Scand. 175–179.

Rowley, I., 1983. Re-mating in birds, in: Mate-Choice (Ed. by P. Bateson). Cambridge University Press, pp. 331–360.

Sánchez-Macouzet, O., Rodríguez, C., Drummond, H., 2014. Better stay together: pair bond duration increases individual fitness independent of age-related variation. Proc. Biol. Sci. 281, 20132843. doi:10.1098/rspb.2013.2843

Scheid, C., Schmidt, J., Noë, R., 2008. Distinct patterns of food offering and co-feeding in rooks. Anim. Behav. 76, 1701–1707. doi:10.1016/j.anbehav.2008.07.023

Shultz, S., & Dunbar, R. I. (2010). Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment. Bio. J. Lin. Soc.,100 (1), 111-123.

Seed, A., Emery, N., Clayton, N., 2009. Intelligence in Corvids and Apes: A Case of Convergent Evolution? Ethology 115, 401–420. doi:10.1111/j.1439-0310.2009.01644.x

Seed, A.M., Clayton, N.S., Emery, N.J., 2007. Postconflict third-party affiliation in rooks, Corvus frugilegus. Curr. Biol. 17, 152–8. doi:10.1016/j.cub.2006.11.025

Silk, J.B., Altmann, J., Alberts, S.C., 2006. Social relationships among adult female baboons (papio cynocephalus) I. Variation in the strength of social bonds. Behav. Ecol. Sociobiol. 61, 183–195. doi:10.1007/s00265-006-0249-2

Simpson, K., Smith, J.N., Kelsall, J.P., 1987. Correlates and consequences of coloniality in great blue herons. Can. J. Zool. 65(3), 572–577.

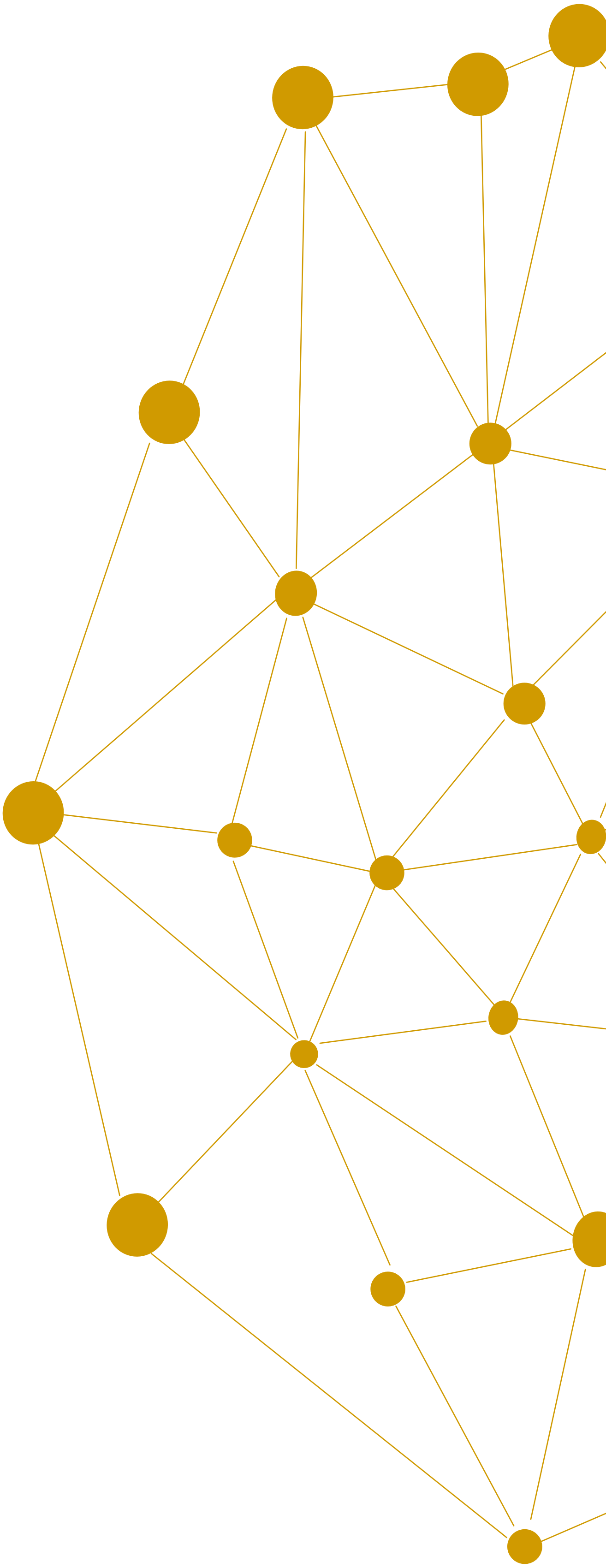
Spoon, T.R., Millam, J.R., Owings, D.H., 2007. Behavioural compatibility, extrapair copulation and mate switching in a socially monogamous parrot. Anim. Behav. 73, 815–824. doi:10.1016/j.anbehav.2006.10.010

Tamm, S., 1977. Social dominance in captive jackdaws (Corvus monedula). Behav. Processes 2(3), 293–299. doi:10.1016/0376-6357(77)90032-8

von Bayern, A.M.., de Kort, S.R., Clayton, N.S., Emery, N.J., 2007. The role of food- and object-sharing in the development of social bonds in juvenile jackdaws (Corvus monedula). Behaviour 144, 711–733. doi:10.1163/156853907781347826

5

Chapter 5



Current zoology (2016) DOI 10.1093/cz/zow083

A longitudinal network analysis of social dynamics in rooks *Corvus frugilegus*: repeated group modifications do not affect social network in captive rooks

Boucherie Palmyre H. [a,b,*], **Sosa Sebastian** [c], **Pasquaretta Cristian** [a,b],
Dufour Valérie [a,b]

[a]Institut Pluridisciplinaire Hubert Curien, University of Strasbourg, 23 rue Becquerel 67087 Strasbourg, France ;
[b]Centre National de la Recherche Scientifique, UMR 7178, 67087 Strasbourg, France ;
[c]Formerly affiliated with Grupo de Conducta Adaptativa e Interacción, Psychology Faculty, University of Barcelona, Spain.
Address correspondence to Boucherie Palmyre. E-mail: palmyre.boucherie@iphc.cnrs.fr.

Accepted 24 June 2016

Abstract

Numerous studies have investigated the remarkable variation of social features and the resulting structures across species. Indeed, relationships are dynamic and vary in time according to various factors such as environmental conditions or individuals attributes. However, few studies have investigated the processes that stabilize the structures within a given species, and the behavioural mechanisms that ensure their coherence and continuity across time. Here, we used a dynamic actor-based model, RSiena, to investigate the consistency of the temporal dynamic of relationships of a group of captive rooks facing recurrent modifications in group composition (i.e. the loss and introduction of individuals). We found that changes in relationships (i.e. formation and removal) followed consistent patterns regardless of group composition and sex-ratio. Rooks preferentially interacted with paired congeners (i.e. unpopular attachment) and were more likely to form relationships with individuals bonded to a current social partner (i.e. “friends of friends”, or triadic closure). The sex of individuals had no effect on the dynamic of relationships. This robust behavioural mechanisms formed the basis of inter-connected networks, composed of sub-structures of individuals emerging from the enmeshment of dyadic and triadic motifs. Overall, the present study reveals crucial aspects of the behavioural mechanisms shaping rooks social structure, suggesting that rooks live in a well-integrated society, going far beyond the unique monogamous pair-bond.

Key words social network analysis, social interactions, temporal dynamics, preferential attachment, triadic closure, corvids.

Numerous species live in groups, which vary widely in forms and complexity, from simple aggregations to more complex form of sociality as found in social mammals or some birds' species like corvids (Sumpter 2006). In social species, the social structure is characterised by the nature, the quality but also the patterning of relationships (Hinde 1976). While the structure tend to be stable in a given species, the relationships that underlie the structure are not static, and they can vary in strength and stability over time (Silk et al. 2006a, 2006b). Numerous factors are expected to modulate the way individuals interact, and thus ultimately the form taken by sociality, such as environmental conditions (e.g. habitat, resource distribution, predation risk; Banks et al. 2007; Henzi et al. 2009; Kluever et al. 2008), individual attributes (e.g. age, sex; Sosa 2016) personality (Aplin et al. 2013; Pike et al. 2008), or group constraints (e.g. size or demography ; Dazey et al. 1977). However, whereas numerous studies have investigated the variability of the social features according to internal and external pressures, very few examined the processes that stabilize the structures. To fully understand the diversity of forms taken by sociality, we must not only consider the processes that challenge social structures, but also those that ensure their coherence and continuity across time, group composition, generations, and environments (Jacobs and Petit, 2011; Thierry, 2007; Sosa, 2014).

In numerous species, the coherence and continuity of grouping patterns can be ensured by general rules of attraction and repulsion among group members, which generally relates to the number of individuals aggregating and to the distance and alignment with closest neighbours (e.g. birds' flocks in flight or fish schools; Couzin et al. 2002; Krause and Ruxton 2002; Sumpter 2006). However, if those rules provide a valuable background for the understanding of grouping patterns, more and more studies also showed that individuals are not identical and interchangeable, and inter-individual differences can significantly influence collective patterns (e.g. physiology, social status; Jolles et al. 2013a; Nagy et al. 2010; Petit and Bon 2010). This may become even more complicated in highly social species, where group structures result from more intricate patterns of interactions among group members. Macaques for instance, show great variations of their social structures from one species to another, but within each species, a remarkable consistency and stability of the social features and interactions patterns is also observed (also referred to as social style, Thierry, 2007; Duboscq et al. 2013a,b). Those social styles are characterised by the co-variation of several social traits (e.g. development of cooperative behaviour, conciliatory tendency, rates and patterning of social play), unduly conserved and consistent across groups, generations and environments (Thierry 2007, Thierry 2013). In highly social species, the structure can thus be partially independent of its components (i.e. individuals), as it persists over time while individuals vary (i.e. temporal variations of individuals attributes, group composition, or sex-ratio) and eventually disappear (e.g. death or migration).

One way to investigate the consistency and the robustness of social patterns, is thus to follow and analyse the temporal dynamics of relationships over time (i.e. the formation and removal of relationships). However, such investigation must be performed at the structure level, in the sense that all changes occurring in the network (i.e. define by the enmeshment of all relationships) must be considered simultaneously. Indeed, in a cohesive structure, changes occurring in one relationship can potentially affect the others (Hinde 1976). Such challenging investigations are now made possible and improved by the use of dynamic actor-based approaches like RSiena (Snijders 2001; Snijders et al. 2010; Pinter-Wollman et al. 2013; Ripley et al. 2015). RSiena was first created to study the dynamic of human social relationships (Mercken et al. 2010; Schaefer et al. 2011; Steglich et al. 2006), but has also recently been successfully applied to explore the dynamic of social interactions in animal species (Ilany et al. 2015; Pasquaretta et al. 2016: Borgeaud et al. 2016). In more details, among the patterns that can be explored, two are susceptible to favour network cohesion: (1) first the growth-preferential attachment, which states that individuals preferentially form relationships with highly connected group members (i.e. generally more central or popular individuals; PA; Barabási & Albert 1999); (2) and secondly, the triadic closure, which states that individual preferably form relationships with common partners, a process also known as "my friends' friends have now become friends of mine" (TC; Banks & Carley 1996). When found in a network, the PA and the TC highlight that nodes (i.e. individuals) do not randomly form new connections, and therefore display heterogeneous levels of connectivity. This heterogeneity probably has two main consequences: firstly, all individuals will contribute differently to the network cohesion, and secondly, it should ensure the assimilation of new individuals within the network without damaging its global cohesion (Barabási and Albert 1999; Lusseau 2003). In addition, such structures are also expected to be highly resilient to the random removal of group members (Lusseau 2003; Manno 2008; Sosa 2014). PA and TC could thus be particularly interesting to investigate in highly social species facing constant perturbations or modifications of the group composition.

Among birds, in which sociality is far less often studied compared to mammals, rooks *Corvus frugilegus* appear to meet all conditions for the emergence of intricate social structures, and robust social patterns. They are indeed well known for their social abilities, notably their ability to collect and use social information (Clayton & Emery 2007; Emery et al. 2007; Scheid et al. 2008). Rooks breed in colonies of tens or hundreds of birds, but also live in groups throughout the year, joining massive winter roosts out of the breeding season, that can sometimes reach thousands of individuals. They form long-term and sophisticated monogamous pair bonds, but can also bond out of the pair with several partners (i.e. in juveniles, Emery et al. 2007; Scheid et al. 2008; but also in adults, Boucherie et al. 2016). In line with this, it was also found that triads make up a significant proportion of rooks flocks in the wild (on average, 14%; Jolles et al. 2013a) and were also reported in captive groups (Richards, 1976). Furthermore, their colonial dynamic is thought to express high level of fission-fusion dynamics (Emery 2004; Clayton & Emery 2007; Mikolasch et al. 2013), which relates to “the extent of variation in spatial cohesion and individuals membership over time” (Aureli et al. 2008). Indeed, in the wild, rooks alternatively merge and split from the main colony, foraging in smaller subgroups during the day and roosting all together at night (Goodwin 1955; Swingland 1977; Roell and Bossema 1982). Thus their social structure faces recurrent modifications of the group composition and membership over time. Altogether, it makes rooks an ideal model to investigate in a non-primate species, if and how consistent and robust patterns can shape the dynamic of relationships, and possibly ensure the permanency of the structure.

In this study, we investigated the consistency of the relationships pattern in a group of captive rooks facing recurrent modifications of group composition (i.e. losses and additions of new individuals). To do so, we used a dynamic actor-based model, RSiena, to examine the temporal dynamic of relationships over three different four-month periods (i.e. in 2012, 2014, and 2015). We first tested whether the temporal dynamic of relationships followed growth-preferential attachment (i.e. relationships are preferentially formed with popular individuals), triadic closure (i.e. my friends’ friends have now become friends of mine), and whether it was influenced by the sex of individuals for each year. Then, we investigated whether the social status (i.e. socially paired or solitary), the sex (i.e. male or female), and the group origin of the individual (i.e. original or newly added member), but also the breeding period (i.e. before or during the breeding period), had an effect on the quantity of relationship in which individuals were involved (i.e. individuals’ degree). We also tested whether the social status and the breeding period had an effect on the directionality of interactions (i.e. identity of preferential partners and responsibility in relationship formation). Finally, we evaluated the resilience of the social structure facing recurrent group modifications, using the network entropy, an indicator of social network disorder.

Materials and Methods

Subject and study site

We studied all the spatial associations and social interactions among a group of captive birds over three non-consecutive years. Captivity reduces the possibility of noise linked to external pressures such as environmental changes, thus providing an ideal opportunity to collect substantial amount of data for a complex modelling approach, and allowing us to focus specifically on group modifications, i.e. losses and introduction of new individuals. All birds were easily identified by coloured leg rings. Birds were housed in a large outdoor aviary (18m x 6 m × 3.5 m) on the Cronenbourg campus in Strasbourg, France. In 2012, the flock was composed of 11 adults birds (9 males and 2 females), collected as nestlings from a wild local colony between 2006 and 2007. This group composition remained stable from 2010 until April 2013. Several major disruptions of the group composition and sex-ratio then occurred between 2013 and 2015: i) six new birds rescued from hunting trap in south Alsace, were added into the group (one male and five females), ii) and five individuals escaped or died (for more information about the modifications of the group composition, see Table 1). The aviary contained wooded perches, platforms, suspended baskets, ropes, vegetation cover and branches, as well as two small water pools for enrichment and bathing. Birds were fed daily with a mixture of pellets and fresh products (eggs, yoghurt and fruit) and had ad libitum access to water.

Individuals	2012	2014	2015
b	◆	◆	◆
e	◆	◆	◆
h	◆		
j	●	●	●
k	◆	◆	◆
m	◆	◆	◆
n	◆	◆	◆
o	◆	◆	◆
t	◆	◆	◆
y	●		
z	◆	◆	
a *		◆	◆
c *		●	
g *		●	●
p *		●	●
s *		●	●
Sex ratio	(9M / 2F)	(9M / 5F)	(8M / 4F)

Table 1. Modifications of the group composition and the sex-ratio over time. Diamonds represent males, and circles females. Asterisks indicate new individuals added into the group. In 2012, the group composition had been stable since 2010. In April and June 2013, two individuals escaped after rodents damaged the aviary (h, male; y female). In October 2013, six new individuals were added to the group (a, juvenile male; c, g, p, s, w, females), one of which escaped a few days afterwards and thus do not appear in the table (w, female). Finally, two other birds died of natural causes in May and August 2014 (z, male; c, female).

Data collection

Data were collected through four-month periods (from January to the end of April) in three non-consecutive years: (1) in 2012, when group composition had been stable since 2010; (2) in 2014 and 2015, following modifications of the group composition (Table 1). Note that all modifications of group composition occurred between collection periods. Half of the data collection period covered a non-breeding period (from January to the end of February), and the other half part of the breeding season (from March to the end of April). For this group, the beginning and the end of the breeding period were respectively defined as the day at which the individuals started building nests, and as the day at which they started dismantling them (usually in the end of May). Spatial proximities (perch proximity, ground proximity) and affiliative interactions (allofeeding, allopreening and contact-sit) were recorded with 10-

minute individual focal sampling (Altmann 1974). Ad libitum sampling was used for rare behaviours (allofeeding and allopreening). Perch or ground proximity events were recorded if two birds were 10 to 50 cm apart when perching or 0 to 1 m apart on the ground, respectively. Contact-sit was recorded when two birds were less than 10 cm apart when perching. Allofeeding was recorded when one bird actively put a food item into the beak of another (Scheid et al. 2008), and allopreening was considered to have occurred when one bird ran its beak through the feathers of another. All observations were conducted between 08:00 and 18:00 hours by a single observer (PB). For each observation session, all individuals were observed in a random order (i.e. same amount of time for all), for a total of 08:40, 07:10, and 06:00 hours per individual and per respective year (2012, 2014 and 2015). The direction of spatial approaches and affiliative interactions was only recorded in 2014 and 2015 and was later used to investigate individual preferences and responsibilities.

Data analysis

Dynamic analysis, RSiena modelling

We ran a dynamic agent-based model with R (version 3.1.3; R Core Team 2015) and the RSiena package (version 1.1-232; Ripley et al. 2015). Siena (Simulation Investigation for Empirical Network Analysis) is a dynamic model based on Markov processes that permits longitudinal network analyses. The RSiena model operates on a series of consecutive matrices. Therefore, we constructed 12, 13 and 12 consecutive matrices for 2012, 2014 and 2015 respectively, summing the data per week (the number of observation sessions per week ranged from two to five). Two consecutive matrices were separated by at least 2 days without observations. We worked with symmetrical binary matrices, where the value of 1 indicated non-random relationships. We used an individual social index based on spatial associations and affiliative interactions to distinguish non-random relationships from others (see Supplementary material 1 for the calculation of the social index). Non-random relationships included social pairs (i.e. relationships representing more than 50% of the summed sociality indices of each partner) and extra-pair affiliations. In addition, individuals were define as ‘solitary’, if they were not involved in a social pair. Note that individuals could not be involved in more than one social pair at a given time. However, both paired and solitary individuals could be involved in several extra-pair affiliations.

As a prerequisite for RSiena, we first computed a Jaccard index for each year (2012, 2014 and 2015) to control that there was sufficient diversity between two consecutive matrices but also sufficient similarity to indicate the successive states of the same network. When the

Jaccard index equals 0, the degree of similarity between two matrices is null. When it equals 1, the matrices are considered to be exactly the same. The Jaccard index has to be higher than 0.2 to allow for the use of RSiena modelling (Ripley et al. 2015).

To explain network changes over time, we ran a dynamic agent-based model for each year and considered four potential structural effects: 1) the growth-preferential attachment (PA); 2) the triadic closure process (TC); 3) the homophily and heterophily of relationships according to the sex of individuals i.e. whether individuals preferentially interact with individuals of their sex, or in the contrary with this opposite sex; 4) and the individuals responsibility on the changes rate in relationships according to their sex. Calculation details of both PA and TC values are described in Table 2 (see also the RSiena manual, Ripley et al. 2015). The effect of density was also included in the model, as required by the creators of RSiena (Ripley et al. 2015). 1000 permutations were performed, and the Wald-type test was used to estimate the explanatory power of each effect. Each model was validated by running a goodness of fit test, which compared the observed values with simulated values for each of the three years.

Model	Formula	Description
Preferential attachment (PA)	$PA(i) = \sum_j x_{ij} \sum_h x_{hj}$	Analyses the popularity of each individual. This effect reflects individual preference for links with popular individuals (*i.e.* individuals with the highest degrees receive more incoming links). *PA(i)* is defined, for individual *i*, as the number of relations received by individual *j*, to whom *i* is linked. Here x_{ij} in {0, 1} denotes a link between i and j.

		Analyses the transitivity of the connection pattern for each individual. This describes the « friends of my friends are my friends » phenomenon.
Triadic closure (TC)	$TC(i) = \sum_{j,h} x_{ij}x_{ih}x_{jh}$	*TC(i)* is the number of transitive patterns including individual *i* in the network, i.e. *i* is linked to *j* and *h*, which are also linked together. Here x_{ij} in {0, 1} denotes a link between *i* and *j*.

Table 2. Calculation details for the growth preferential attachment (PA) and the triadic closure (TC) effects.

Effect of social status on the quantity and directionality of interactions

First, we ran a generalized linear mixed model (GLMM; function ‘glmer’ in R package lme4 v.1.1-9; Bates et al. 2014) using a Poisson distribution and a log link function to test the effect of the individual social status (i.e. socially paired or solitary), the breeding period (i.e. before or during the breeding period), the sex of the individual (i.e. male or female), and the individual group status (i.e. original or newly added member), on the average degree of connectivity of each individual (i.e. the response variable: the total number of social partners an individual is connected to). Individual identity and week nested in year were used as random factors.

The direction of spatial approaches and affiliations (hereafter called directed interactions; only available for 2014 and 2015) was then used to answer two questions. Firstly, do solitary individuals favour individuals with a particular social status (i.e. paired or solitary) for interaction? This was achieved using a generalized linear mixed model that was adapted for proportions with a binomial distribution and logit link function (GLMM; using the ‘cbind’ command in function ‘glmer’ in R package lme4 v.1.1-9; Bates et al. 2014), to compare the proportion of interactions emitted by solitary towards paired or other solitary individuals. Given that the number of solitary and socially paired individuals varied from one matrix to another, we divided the proportions of directed interactions by the proportion of each type of relationships in the networks (i.e. solitary-solitary or solitary-paired relationships). Secondly, which of the paired and solitary individuals were the most active when interacting together? Similarly, we used a GLMM adapted for proportions with a binomial distribution and logit link function to compare the proportion of interactions emitted by paired individuals toward solitary individuals and by the latter towards the former. In the two models, we also added the breeding period (i.e. before or during the breeding period) as fixed factor, and the week number nested in year as random factor.

Entropy

We then investigated whether the modification of the group composition impacted the entropy of the network, used here as a measure of network disorder. Originally established to measure the inconsistency of a source of information, entropy measures the heterogeneity of the individual's degrees in a graph (i.e. total number of social partner an individual is connected to). For an undirected network, the entropy is maximal (i.e. equals to 1) if all individuals have the same degree. The entropy was computed for each matrix in each year, using Matlab software (Matlab version R2015a 8.5.0). We then used a linear model (LM; function 'lm' in R package stats v.3.1.3; R Core Team 2015) to investigate how the year (2012, 2014, and 2015), the week number and the interaction between year and week number affected the network entropy (i.e. response variable). All statistics were performed in R version 3.1.3 (R Core Team 2015), with the significance threshold set at $\alpha = 0.05$. All results are discussed using the estimated parameter values provided by the models. All networks were visualized using R package igraph (i.e. in total 2012: 12, 2014:13, 2015:12 networks; package igraph v.0.701; Csardi and Nepusz 2006; Figure 2).

Ethical note

Research was purely observational, adhered to the guidelines of the Association for the Study of Animal Behaviour, and respected European and French legislation. The study was approved by the regional ethical committee on animal experimentation under the license n°A67-382.

Results

Over the three years, on average in each network, random and non-random relationships (i.e. social pairs and extra-pair relationships) represented less than half of all potential relationships in the group (Figure 1). In addition, on average in each network, more than half of the non-random relationships were extra-pair relationships (Figure 1).

Over all the different networks, we identified 7 (2012), 10 (2014), and 6 (2015) different social pairs (i.e. identified in at least one network), indicating that some social pairs varied from one network to another, especially in 2012 and 2014 (Figure 2). 3 social pairs over 7 (2012, m–h, e–t, n–z), 5 over 10 (2014, c–p, b–m, b–k, e–t, n–z), and 1 over 6 (2015, e–t) were same–sex pairs, and all but one in 2014 and all but two in 2015 were composed of individuals with the same group status (original, or newly added group member; Figure 2). Note that among all social pairs, 3 over 7 (2012, j–o, k–y, n–z), 3 over 10 (2014, j–o, k–p, n–z), and 3 over 6 (2015, a–g, j–m, k–p) built nests and attempted to breed.

However, none of those nesting pairs successfully produced surviving offspring during the study. Besides, over all the different networks, we identified a total of 26 (2012), 44 (2014), and 41 (2015) different extra-pair relationships, of which 73% (2012), 59% (2014), and 54% (2015) were same-sex relationships (Figure 2). In addition, 68% (2014), and 63% (2015) of those extra-pair relationships were composed of individuals with the same group status (original, or newly added group member; Figure 2).

Triads occurred, and we identified a total of 22 (2012), 54 (2014), and 37 (2015) occurrences per year over all the different networks. 91% (2012), 57% (2014), and 49% (2015) of those triads were composed of a social pair with another paired individual or a solitary. Among the triads that did not comprise a social pair, 4.5% (2012), 30% (2014), and 32% (2015) were composed of a majority of solitary individuals, and 4.5% (2012), 13% (2014), and 19% (2015) were composed of a majority of paired individuals (Figure 2; see for example triad b-t-k in the ninth week of 2012).

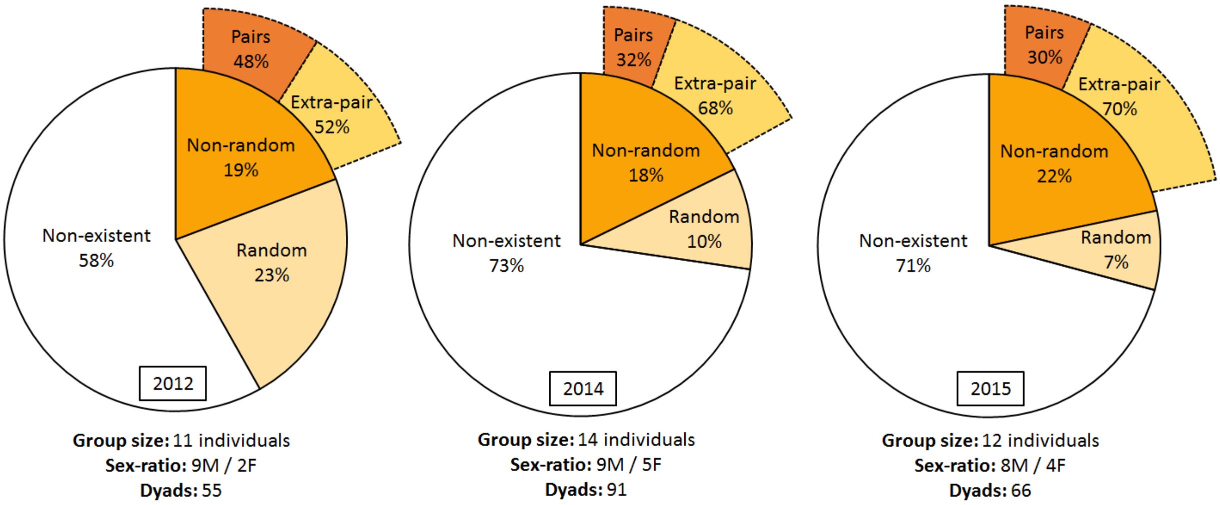


Figure 1. Average proportions of non-existent relationships, random relationships, and non-random relationships (i.e. social pairs and extra-pair relationships) over all potential relationships in the group, per networks and per year. The group size, the sex-ratio, and the maximum number of relationships that can be formed in the group according to group size are indicated below (i.e. Dyads).

Dynamic analysis, RSiena modelling

The Jaccard indices were above 0.2 in 2012, 2014 and 2015, ensuring sufficient changes in consecutives networks to permit the use of RSiena modelling. The density of connection significantly increased in 2012 and 2014, but remained stable in 2015 (Table 3). Note that the following results concern the dynamic of relationships over time in the networks over the three years, and relates indifferently to both social pairs and extra-pairs relationships. The RSiena results show that over time, rooks were more likely to form a relationship with less-connected individuals i.e. individuals with a lower degree (i.e. a reverse effect of preferential attachment, see Table 3). Over time, rooks were also more likely to form relationships with individuals that were already connected to their current social partners (i.e. triadic closure; see Table 3 for statistical results and Supplementary material 2 for theoretical illustration). However, for each year, we found no significant effect of the homophily/heterophily, indicating that over time, rooks did not show any preferences for same/opposite sex partners when forming relationships (Table 3). In addition, the sex of the individuals had no impact on the rate of changes in relationships over time in the network, except in 2015, where males were more responsible than females for changes in relationships (Table 3). See Figure 2 for networks visualisation.

Model	Estimate	Standard error	*t*-ratio	*P*
2012				
Density	4.60	1.85	-0.01	< **0.05** *
Triadic closure	1.71	0.52	0.02	< **0.001** ***
Preferential attachment	-1.82	0.63	0.01	< **0.01** **
Homophily /Heterophily	-1.37	0.66	-0.00	0.06
Sex on rate change : Male	3.53	7.32	-0.02	0.57
Overall maximum convergence ratio: 0.080				
Goodness of fit: 0.106				
2014				
Density	1.75	0.67	0.04	< **0.01** **
Triadic closure	1.33	0.26	0.01	< **0.001** ***
Preferential attachment	-1.07	0.26	0.04	< **0.001** ***
Homophily /Heterophily	-0.11	0.23	0.01	0.61
Sex on rate change : Male	0.03	0.34	-0.06	0.91
Overall maximum convergence ratio: 0.070				
Goodness of fit: 0.068				
2015				
Density	0.37	0.50	0.01	0.44
Triadic closure	0.72	0.23	-0.01	< **0.001** ***
Preferential attachment	-0.49	0.19	0.01	< **0.01** **
Homophily /Heterophily	0.18	0.21	0.01	0.41
Sex on rate change : Male	1.12	0.58	-0.01	**0.04**
Overall maximum convergence ratio: 0.036				
Goodness of fit: 0.664				

Table 3. Dynamic actor-based model according to the year (2012, 2014 and 2015) showing results for the three structural effects: density, triadic closure and preferential attachment. The overall maximum convergence ratio of the model is below 0.25 in all years, indicating a satisfactory convergence of the algorithm. In addition, the goodness of fit is above 0.05 in all years, indicating that the average values are close to the values observed in the data (Ripley et al. 2015). *** < 0.001, ** < 0.01, * ≤ 0.05.

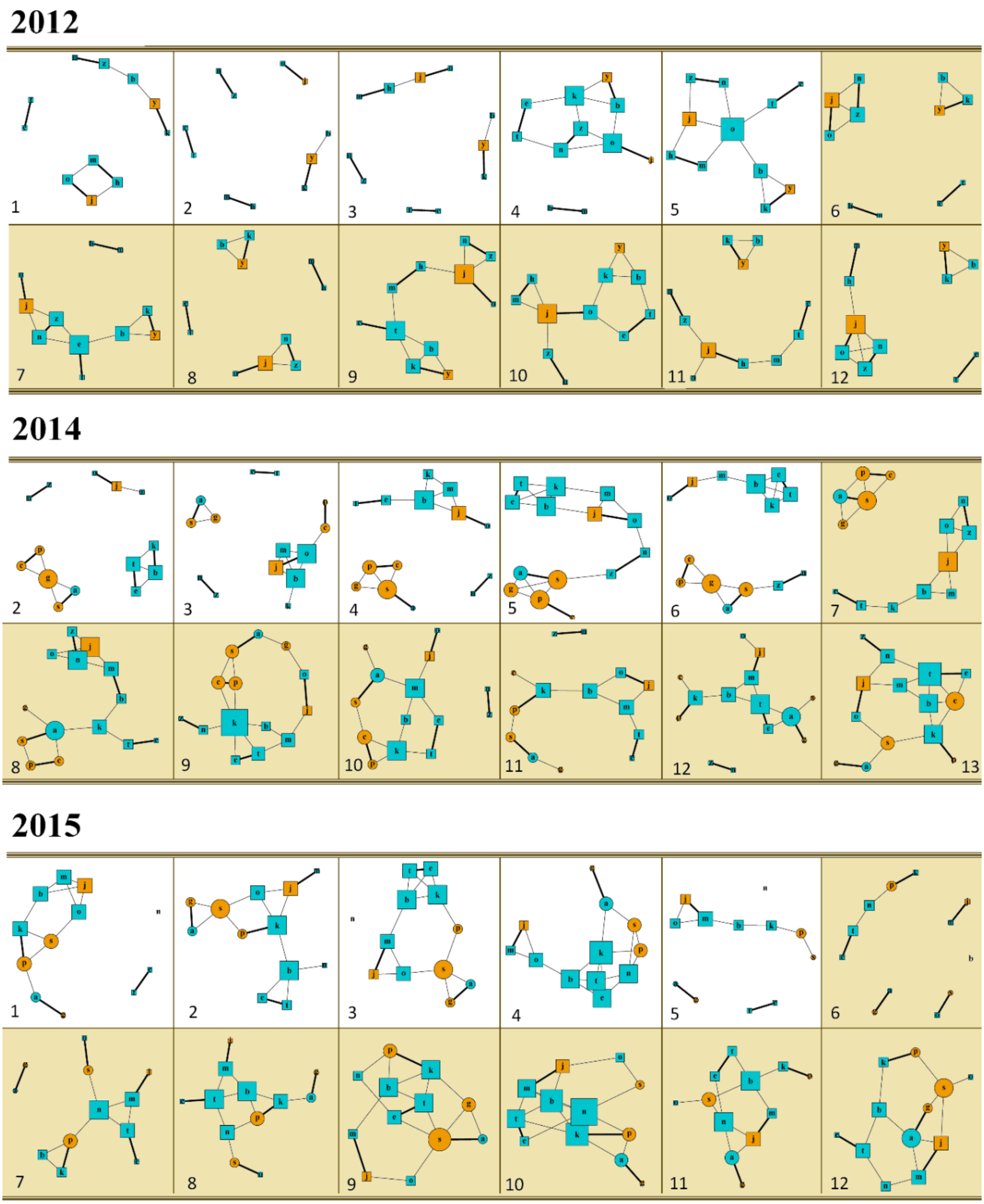


Figure 2. Temporal modifications of the social networks of social pairs and extra-pair affiliations, computed per week between January and the end of April, in 2012, 2014 and 2015. The thicker lines represent the social pairs, and the thinner the extra-pair affiliations. Females are represented in orange and males in blue. Squares represent original group members, and circles newly added members (i.e. present in the group in 2014 and 2015). The size of the nodes (i.e. individuals) is proportional to the degree of the individual in the

network (i.e. total number of social partners an individual is connected to). Finally, networks with coloured background occur during the breeding season (i.e. March to the end of April). Note that to homogenise the visualisation, the first network in 2014 is not reported here, as 13 networks were used in 2014 instead of 12 in 2012 and 2015.

Effect of social status on the quantity and directionality of interactions

For all three years studied, solitary individuals were involved in significantly more relationships than socially paired individuals (i.e. they showed a higher degree than paired individuals; GLMM: solitary vs. paired, estimates = 0.25, standard error = 0.08, $Z = 3.25$, $P < 0.01$). However, neither the group status (GLMM: original vs. newly added member, estimates = -0.01, standard error = 0.13, $Z = -0.12$, $P = 0.91$), the sex of the individual (GLMM: male vs. female, estimates = -0.05, standard error = 0.11, $Z = -0.46$, $P = 0.65$) nor the breeding period (GLMM: before vs. during the breeding period, estimates = -0.07, standard error = 0.07, $Z = -0.96$, $P = 0.34$), had a significant effect on the individual degree (Figure 2).

Considering the direction of interactions for 2014 and 2015 (i.e. associations and affiliations), we found that solitary individuals preferentially interacted with paired individuals than other solitary individuals (GMM: solitary towards paired vs. solitary, estimates = 2.65, standard error = 1.10, $Z = 2.51$, $P < 0.05$), with an increased preference during the breeding period (GMM: before vs. during the breeding period: estimates = -3.06, standard error = 1.45, $Z = -2.12$, $P < 0.05$). Finally, we found that interactions between solitary and paired individuals were initiated significantly more often by the solitary individuals (GLMM: solitary vs. paired, estimates = 1.23, standard error = 0.39, $Z = 3.17$, $P < 0.01$), and this both before and during the breeding season (GLMM: before vs. during the breeding period, estimates = -0.03, standard error = 0.36, $Z = -0.08$, $P = 0.94$).

Entropy

The entropy of the network was similar for all three years and in all weeks (average value of 0.66 in 2012, 0.64 in 2014 and 0.71 in 2015; LM; Year: $F = 1.71$, $P > 0.05$; Week: $F = 2.67$, $P > 0.05$; Year x Week: $F = 0.82$, $P > 0.05$).

Discussion

This study investigated the temporal dynamics of social relationships (i.e. social pairs and extra-pair affiliations), in a social network of captive rooks facing repeated modifications in group composition. Using RSiena, an innovative tool for the study of sociality, we found that the dynamic of rooks relationships was not random, but followed two consistent patterns, namely triadic closure (TC) and 'unpopular attachment' (hereafter referred to as UA; i.e. the reverse effect of preferential attachment). These two patterns intervened in the same way on the dynamics of relationships both before and after the modifications in group composition (i.e. losses and introduction of individuals), which did not affect the level of network entropy. Despite the addition of new females in the group to compensate an initially strongly unbalanced sex-ratio, neither the dynamic of relationships nor the individual degree, were affected by the sex of individuals. In addition, neither the group origin of the individual, nor the breeding period, had an effect on individuals' degree.

More specifically, the temporal dynamics of relationships did not follow preferential attachment in any of the three years considered, but rather a reverse mechanism that could be termed "unpopular attachment" (UA; for PA see also Barabási and Albert, 1999). This indicates that rooks were more likely to form new relationships with individuals who had fewer connections in the network. As it happens, the less connected individuals were found to be, predominantly, the paired individuals. This makes sense as, by definition, socially paired individuals primarily interact with one social partner (i.e. at least 50% of their interactions), which necessarily limits the number of social partners they can interact with. Combined, the UA and the low degree of paired individuals, suggest a general attractor effect of pairs on social interactions. Consistently, we found that solitary individuals also interacted significantly more often with paired individuals, and that they were generally responsible for the establishment of these relationships. This was even more true during the breeding period, which may be due to the fact that solitary individuals cannot attempt to reproduce and may try to have access to females or juveniles. Alternatively, they may just try to interfere in the reproduction of mixed pairs (Goodwin 1955).

Triadic closure – "my friends' friends have now become friends of mine" - significantly increased over time for each year (see also Banks & Carley 1996; Borgeaud et al. 2016). Rooks thus preferentially formed relationships with individuals that were already connected to one of their current social partners, resulting in the formation of triads within the network. Consistently with the attractor effect of the pair, most triads formed in the networks were centred on social pairs. More precisely, most triads resulted from the completion of a pair with either another paired or a solitary individual, or were composed of a majority of paired individuals interacting together, and more rarely of a majority of solitary individuals. Overall, the attractor effect of the pair and the TC, gives the social structure its shape. This shape, an arrangement and overlap of dyadic and triadic motifs, form the basis of an inter-connected network composed of more complex sub-structures of individuals (groups of four individuals, or more).

Major modifications occurred in this group: addition of wild individuals, modification of sex ratio (strongly unbalanced at the beginning of the study). Thus, we could have expected these modifications to damage the social structure and to induce social instability (as shown by Ilany et al. 2013), disturbing the general pattern of interactions of the group. However, all results on relationships dynamics remained consistent over the three years (i.e. UA, TC, individuals' degree, directionality of interactions). In addition, neither the group status, the sex of the individuals, nor the breeding period, affected individuals' degree of connectivity in the network. And, despite important changes in sex-ratio, the sex of the individual had no effect on the dynamic of relationships expected in 2015, where males where slightly more responsible than females for the changes occurring in the network. Finally, group modifications did not altered the level of network disorder (i.e. entropy). Overall, this highlights that the dynamics of relationships are not random in rooks, and follow robust and consistent behavioural patterns. This provides the structure a certain degree of resilience to perturbations, ensuring some continuity and coherence over time. Those results reinforce the hypothesis that rooks social structure is more complex than just an aggregate of isolated pairs (Boucherie et al. 2016). They further suggest that rooks live in a well-integrated society, in which the diversity of relationships (i.e. in terms of stability and quality), may results in numerous feedbacks on individuals patterns of interactions, stabilising the structure (Sumpter 2006; Thierry 2007).

More broadly, the formation and the continuity of a cohesive network of affiliative relationships beyond pairs, might increase some of the advantages associated with group living, while allowing to better deal with its competitive aspect (Dunbar 1989; Krause and Ruxton, 2002). For instance, in rooks, affiliates are more likely to tolerate each other's, especially in the context of food competition (Emery et al. 2007; Jolles et al. 2013b; Seed et al. 2008). Bonding with familiar congeners or closely nesting neighbours, possibly facilitate the emergence of cooperative behaviours (e.g. collective nest vigilance, limitation of nests pilfering; Ogilvie 1951). Bonding with neighbours may also ensure a safer breeding environment, by reducing local stress, due to neighbour agitations and conflicts (Jovani and Grimm 2008; Lewis et al. 2007). This could explain why rook breeding parameters are not negatively affected by the very close proximity of other nests in rookeries (i.e. clutch size, number of hatchlings; Kasprzykowski 2008). Note that structural processes such as triadic closure are also expected to promote reciprocity and cooperative behaviours in networks (Banks & Carley 1996; Walker et al. 1997; Buskens 2002; Lou et al. 2013; Righi & Takács 2014). Furthermore, individuals may become solitary after their partner's death in the wild (Goodwin 1955; Jennings, 1955). By bonding with paired individuals, they may guarantee their continued inclusion within the colony (Goodwin 1955). This inclusion may also help them reform a new pair more quickly.

It is important to bear in mind that the subjects in this study were captive rooks. It could be argued that spatial associations were influenced by captivity, as there is a higher probability that group members encounter each other than in the wild. If true, almost all group members should have been linked by non-random relationships - i.e. social pairs or extra-pair affiliations. However, this was not the case. Non-random and random relationships made up less than half of all potential relationships in the network. Another limitation could be the strongly unbalanced sex ratio at the beginning of the study. Same-sex relationships occurred, both in pairs and extra-pairs relationships, as it is often the case when partners of the opposite sex are lacking (Kotrschal et al. 2006). However, same-sex relationships are also expected in highly social species (Mitani et al. 2000; Sterck et al. 1997). In addition, in this group, individuals showed no tendency to bond preferentially with same sex individuals (i.e. homophily), or on the contrary to avoid same-sex individuals (i.e. heterophily). It shows that social bonding can go beyond the reproductive function in rooks (Emery et al. 2007; Boucherie et al. 2016), and that the dynamic of relationships cannot be solely explained by individuals mating strategies, and the necessity to start or maintain (mated) pair bonds.

This study uses a stochastic agent-based model RSiena to investigate the temporal dynamics of relationships in captive adult rooks. We found that changes in rooks' relationships followed robust and consistent patterns, regardless of the group composition or the sex-ratio, and to a certain extent without being affected by the breeding period. Rooks social structure was flexible enough to allow temporal variations without being dismantled. This makes sense considering that wild populations of rooks exhibit high level of fission-fusion dynamics, requiring individuals to deal with constant modifications of individuals' membership in the different colony parties (Emery 2004; Clayton & Emery 2007; Mikolasch et al. 2013). Further investigations are now needed (1) to confirm the robustness of social patterns in other groups (in particular in wild populations) and across ecological contexts, and (2) to test for the existence of other structural mechanisms in rook. To the best of our knowledge, this is the first study to identify and explore the robustness of the social patterns in social birds. Our findings provide a reliable starting point for a closer examination of social dynamics in corvids, but also for the comparison of the robustness of social processes with other bird species.

The authors declare that they have no competing interests.

Appendix 1

Construction of binary matrices

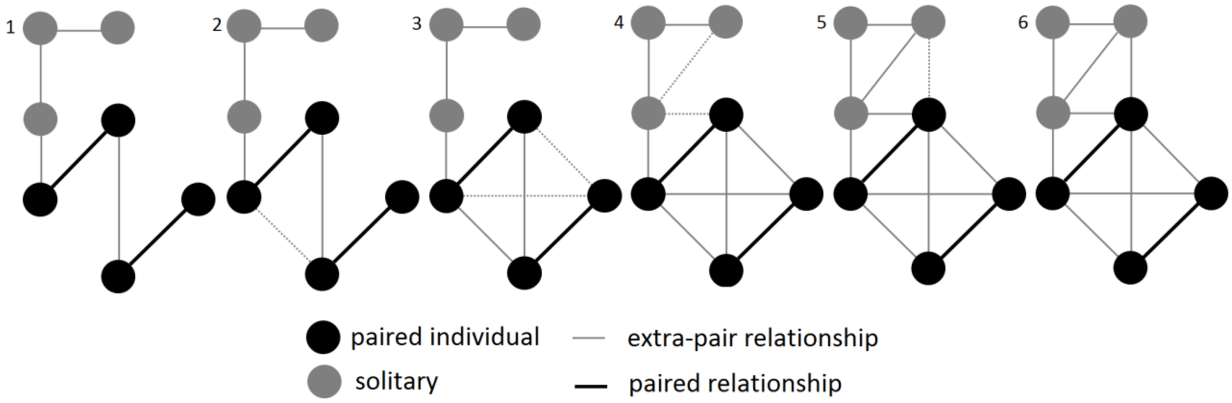
In order to discriminate the non-random relationships (i.e. social pairs and extra-pairs affiliations) from others in each matrix, we used spatial proximities (ground proximity: GP, perch proximity: PP) and affiliations (allofeeding: Fe, allopreening: Pr, and contact-sit: Cs) to compute the sociality indices of all potential relationships (Silk et al., 2006b), as follows:

$$Sij^1 = \frac{((GPij^1 / GP^1) + (PPij^1 / PP^1) + (Feij^1 / Fe^1) + (Prij^1 / Pr^1) + (CSij^1 / CS^1))}{5} \text{ x } 100,$$

where $GPij^1$ equals the frequency of ground proximity for the dyad ij, divided by GP^1 , which equals the overall mean of ground proximity for all dyads for matrix 1. We followed the same procedure for all other variables: PP, Fe, Pr, and Cs. The numerator refers to the number of variables.

Higher (lower) values of the index indicate stronger (weaker) relationships. We then computed the sociality indices of each individual, summing all the sociality indices for the relationships in which each individual was involved. Based on previous data, we considered that individuals were involved in a social pair when the sociality index of the relationship represented more than 50% of each individual's sociality indices, and in an extra-pair affiliation when the sociality index of the relationship represented 5-50% of each individual sociality index, or more than 50% for only one of the two partners. Thus, individuals could only be socially paired with one partner at the same time, but they could be involved in several extra-pair affiliations.

Appendix 2



Appendix 2. Theoretical illustration showing the progressive structural effect of triadic closure (i.e. “my friends’ friends are now friends of mine”), from step 1 to step 6, in a network composed of paired and solitary individuals.

References

Altmann J, 1974. Observational Study of Behavior : sampling Methods. Behaviour 49: 227–267.

Aplin LM, Farine DR, Morand-Ferron J, Cole EF, Cockburn A et al., 2013. Individual personalities predict social behaviour in wild networks of great tits *Parus major*. Ecol. Lett. 16: 1365–1372.

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J et al., 2008. Fission-fusion dynamics: new research frameworks. Curr. Anthropol. 49: 627–654.

Banks DL, Carley KM, 1996. Models for network evolution. J. Math. Sociol. 1995: 1–36.

Banks SC, Piggott MP, Stow AJ, Taylor AC, 2007. Sex and sociality in a disconnected world: a review of the impacts of habitat fragmentation on animal social interactions. Can. J. Zool. 85, 1031–1048.

Barabási A-L, Albert R, 1999. Emergence of scaling in random networks. Science 286: 509–512. doi:10.1126/science.286.5439.509

Bates D, Maechler M, Bolker B, Walker S, 2014. lme4: Linear mixed-effects models using Eigen and S4. R Package version 1.1-9. https://CRAN.R-project.org/package=lme4.

Buskens V, 2002. *Social Networks and Trust*. Boston: MA.Kluwer.

Borgeaud C, SOSA, Sueur C, Bshary R, van de Waal E, 2016. Intergroup variation of social relationships in wild vervet monkeys: a dynamic network approach. Front. Psychol 7: 915.

Boucherie PH, Mariette MM, Bret C, Dufour V, 2016. Bonding beyond the pair in a monogamous bird: impact on social structure in adult rooks *Corvus frugilegus*. Behaviour. doi:10.1163/1568539X-00003372.

Clayton NS, Emery NJ, 2007. The social life of corvids. Curr. Biol. 17: R652–656.

Couzin ID, Krause J, James R, Ruxton GD, Franks NR, 2002. Collective memory and spatial sorting in animal groups. J. Theor. Biol. 218: 1–11.

Csardi G, Nepusz T, 2006. The igraph software package for complex network research. InterJournal. Complex Syst. 1695: 1–9.

Dazey J, Kuyk K, Oswald M, Martenson J, & Erwin J, 1977. Effects of group composition on agonistic behavior of captive pigtail macaques, *Macaca nemestrina*. Am. J. Phys. Anthropol. 46: 73–76.

Duboscq J, Micheletta J, Agil M, Hodges K, Thierry B et al., 2013. Social tolerance in wild female crested macaques *Macaca nigra* in Tangkoko-Batuangus Nature Reserve, Sulawesi, Indonesia. Am. J. Primatol. 75: 361–375.

Dunbar RIM, 1989. Social systems as optimal strategy sets: the costs and benefits of sociality. Comp. Socioecology 73–88.

Emery, N. J. 2004 Are corvids ’feathered apes’? Cognitive evolution in crows, jays, rooks and jackdaws. In Comparative analysis of minds (ed. S. Watanabe), pp. 181–213. Tokyo, Japan: Keio University Press.

Emery NJ, Seed AM, von Bayern AMP, Clayton NS, 2007. Cognitive adaptations of social bonding in birds. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 362, 489–505.

Goodwin D, 1955. Some observations on the reproductive behavior of rooks. Br. Birds 48, 97–107.

Henzi SP, Lusseau D, Weingrill T, Van Schaik C., Barrett L, 2009. Cyclicity in the structure of female baboon social networks. Behav. Ecol. Sociobiol. 63:1015–1021.

Hinde RA, 1976. Interactions, relationships and social structure. Man. 11, 1–17.

Ilany A, Barocas A, Koren L, Kam M, Geffen E, 2013. Structural balance in the social networks of a wild mammal. Anim. Behav. 85:1397–1405.

Ilany A., Booms AS, Holekamp KE, 2015. Topological effects of network structure on long-term social network dynamics in a wild mammal. Ecol. Lett. 8: 687–695.

Jacobs A, Petit O, 2011. Social network modeling: a powerful tool for the study of group scale phenomena in primates. Am. J. Primatol. 73: 741–7.

Jenning, 1955. Diseases in Wild Birds. Bird Study 2: 69–72.

Jolles JW, King AJ, Manica A, Thornton A, 2013a. Heterogeneous structure in mixed-species corvid flocks in flight. Anim. Behav. 85: 743–750.

Jolles JW, Ostojić L, Clayton NS, 2013b. Dominance, pair bonds and boldness determine social-foraging tactics in rooks *Corvus frugilegus*. Anim. Behav. 85: 1261–1269.

Jovani R, Grimm V, 2008. Breeding synchrony in colonial birds: from local stress to global harmony. Proc. Biol. Sci. 275: 1557–1563.

Kasprzykowski Z, 2008. Nest location within the tree and breeding parameters of rooks *Corvus frugilegus*. Bird Study 55: 59–65.

Kluever BM, Breck SW, Howery LD, Krausman PR, Bergman DL, 2008. Vigilance in cattle: the influence of predation, social interactions, and environmental factors. Rangel. Ecol. Manag. 61: 321–328.

Kotrschal K, Hemetsberger J, & Weiss BM, 2006. Making the best of a bad situation: homosociality in male greylag geese. In: *Homosexuality in animals* (Sommer, V. & 567 Vasey, P. L., eds), pp. 45-76. Cambridge University Press, Cambridge.

Krause J, Ruxton GD, 2002. *Living in Groups.* Oxford:Oxford University Press.

Lewis S, Roberts G, Harris MP, Prigmore C, Wanless S, 2007. Fitness increases with partner and neighbour allopreening. Biol. Lett. 3: 386–9.

Lou T, Tang JIE, Hopcroft J, Fang Z, Ding X, 2013. Learning to predict reciprocity and triadic closure in social networks. ACM Trans. Knowl. Discov. Data 7,5.

Lusseau D, 2003. The emergent properties of a dolphin social network. Proc. Biol. Sci. 270(Suppl 2): S186–18

Manno TG, 2008. Social networking in the Columbian ground squirrel *Spermophilus columbianus*. Anim. Behav. 75: 1221–1228. doi:10.1016/j.anbehav.2007.09.025

Mercken L, Snijders TAB, Steglich C, Vartiainen E, de Vries H, 2010. Dynamics of adolescent friendship networks and smoking behavior. Soc. Networks 32: 72–81.

Mikolasch S, Kotrschal K, Schloegl C, 2013. Transitive inference in jackdaws *Corvus monedula*. Behav. Processes 92 : 113–117.

Mitani J, Merriwether D, Zhang C, 2000. Male affiliation, cooperation and kinship in wild chimpanzees. Anim. Behav. 59: 885–

Nagy M, Akos Z, Biro D, Vicsek T, 2010. Hierarchical group dynamics in pigeon flocks. Nature 464: 890–893.

Ogilvie CM, 1951. The building of a rookery The building of a rookery. Br. Birds 44: 1–5.

Pasquaretta C, Klenschi E, Pansanel J, Battesti M, Mery F et al., 2016. Understanding dynamics of information transmission in *Drosophila melanogaster* using a statistical modeling framework for longitudinal network data (the RSiena package). Front. Psychol. 7.

Petit O, Bon R, 2010. Decision-making processes: the case of collective movements. Behav. Processes 84: 635–647.

Pike TW, Samanta M, Lindstrom J, Royle NJ, 2008. Behavioural phenotype affects social interactions in an animal network. Proc. R. Soc. B-Biological Sci. 275: 2515–2520.

Pinter-Wollman N, Hobson EA, Smith JE, Edelman AJ, Shizuka D et al., 2014. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. Behav. Ecol. 25: 242–255.

R Core Team, 2015. *R: A Language and Environment for Statistical Computing*. Vienna, Austria. URL http//www. R-project. org.

Richards PR, 1976. Pair formation and pair bond in captive rooks. Bird Study 23: 207–211.

Righi S, Takács K, 2014. Triadic balance and closure as drivers of the evolution of cooperation. In Social Simulation Conference. Bellaterra, Cerdanyola Del Vallès, 121–124. http://ddd.uab.cat/record/125597.

Ripley RM, Snijders TA, Boda Z, Vörös A, Preciado P, 2015. *Manual for RSiena*: *Tech. Report*. Oxford:, Oxford Univ. Dep. Stat.

Roell A, Bossema I, 1982. A comparison of nest defence by Jackdaws, rooks, magpies and crows. Behav. Ecol. Sociobiol. 11: 1–6.

Schaefer DR, Simpkins SD, Vest AE, Price CD, 2011. The contribution of extracurricular activities to adolescent friendships: new insights through social network analysis. Dev. Psychol. 47: 1141–1152.

Scheid C, Schmidt J, Noë R, 2008. Distinct patterns of food offering and co-feeding in rooks. Anim. Behav. 76: 1701–1707.

Seed AM, Clayton NS, Emery NJ, 2008. Cooperative problem solving in rooks *Corvus frugilegus*. Proc. Biol. Sci. 275: 1421–1429.

Silk JB, Alberts SC, Altmann J, 2006a. Social relationships among adult female baboons *Papio cynocephalus*. II. Variation in the quality and stability of social bonds. Behav. Ecol. Sociobiol. 61: 197–204.

Silk JB, Altmann J, Alberts SC, 2006b. Social relationships among adult female baboons *Papio cynocephalus*. I. Variation in the strength of social bonds. Behav. Ecol. Sociobiol. 61: 183–195.

Snijders TA, 2001. The statistical evaluation of social network dynamics. Sociol. Methodol. 31: 361–395.

Snijders TAB., van de Bunt GG, Steglich CEG, 2010. Introduction to stochastic actor-based models for network dynamics. Soc. Networks 32: 44–60.

Sosa S, 2014. Structural architecture of the social network of a non-human primate *Macaca sylvanus*: a study of its topology in la foret des singes, Rocamadour. Folia Primatol. 85: 154–163.

Sosa S, 2016. The influence of gender, age, matriline and hierarchical rank on individual social position, role and interactional patterns in *Macaca sylvanus* at “La Forêt des singes”: a multilevel social network approach. Front. Psychol. 7.

Steglich C, Snijders TA, West P, 2006. Applying siena. Methodology 2: 48–56.

Sterck EHM, Watts DP, vanSchaik CP, 1997. The evolution of female social relationships in nonhuman primates. Behav. Ecol. Sociobiol. 41: 291–309.

Sumpter DJ, 2006. The principles of collective animal behaviour. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 361: 5–22.

Swingland IR, 1977. The social and spatial organization of winter communal roosting in rooks *Corvus frugilegus*. J. Zool. London 182: 509–528.

Thierry B, 2013. Identifying constraints in the evolution of primate societies. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 368: 20120342.

Thierry B, 2007. Unity in diversity: lessons from macaque societies. Evol. Anthropol. 16: 224–238.

Walker G, Kogut B, Shan W, 1997. Social Capital, Structural Holes and the Formation of an Industry Network. Organ. Sci. 8: 109–125.

6

Chapter 6

Temporal and behavioural dynamics in dominance hierarchies in rooks *Corvus frugilegus*.

Boucherie Palmyre H. [a,b], **Dufour Valérie** [a,b]

[a] Institut Pluridisciplinaire Hubert Curien, University of Strasbourg, 23 rue Becquerel 67087 Strasbourg, France.
[b] Centre National de la Recherche Scientifique, UMR 7178, 67087 Strasbourg, France.

Corresponding author: Boucherie P. H., palmyre.boucherie@iphc.cnrs.fr

Submitted

Summary

When living in groups, individuals face competition for food resources but also for reproduction. In this context, the emergence of dominance relationships and the resulting hierarchies can regulate and limit conflicts. To date, very few studies have examined the behavioural processes underlying the emergence of dominance relationships in birds, especially in species displaying high variation in group composition and group cohesion over time. In this study, we used a dynamical approach to examine the behavioural processes shaping dominance relationships in a group of captive rooks (*Corvus frugilegus*) over two years, a monogamous corvid species expressing high degree of fission-fusion dynamic. We first examined structural characteristics of the hierarchy (i.e. linearity, steepness, directionality of conflicts). Then, we used Elo-rating to examine the dynamic of individuals' dominance strength over time. The hierarchy was mostly linear when compiling long term data, and did not reflect the actual dominance rankings of individuals at any point in time, as dominance relationships were highly variable in time. In addition, we found low individual differences in the propensity to win conflicts. Finally, aggressiveness and pair-bonding determined individuals rating, but not the sex. Overall, our results question the very notion of dominance relationships in rooks, and stress the need for further investigations to conclude on the prevalence of dominance hierarchy in this species.

Key words: Corvids, dominance relationships, hierarchy, linearity, Elo-rating

Living in groups conveys many benefits, such as reduced predation risk or increased foraging success (Dunbar, 1989; Krause and Ruxton, 2002). It also increases competition between individuals, and group members rarely benefit equally from habitat, resources, or the access to reproduction (Robichaud et al., 1996; White and Wood, 2007). In this context, dominance relationships can reduce the cost inherent to constant competition between individuals by regulating and limiting conflicts (Bernstein 1981; de Waal 1986). Dominance hierarchies emerges at the group level from the network of dyadic dominance relationships (Bernstein, 1981; de Waal, 1986; Drews, 1993). They can be found in numerous taxa, from mammals (Frank, 1986; Wittemyer and Getz, 2007; Wittig and Boesch, 2003), to birds (Chiarati et al., 2010; E.-I. Izawa and Watanabe, 2008; Woolfenden and Fitzpatrick, 1977). In numerous species, it is a structural element that formally constrains individual interactions (Bernstein, 1981; Drews, 1993; Thierry et al., 2004). One of the most important consequences of dominance hierarchy is indeed the establishment of a priority of access to coveted resources which often follows individuals' position in the hierarchical rank ladder (Alanärä et al., 2001; Alberts et al., 2003; Amsalem and Hefetz, 2011; Bell et al., 2012; Stahl et al., 2001). Investigate how species manage conflicts is therefore crucial for understanding the dynamic of social organisations. While dominance hierarchies exists in many species, they do not necessarily uncover the same behavioural mechanisms of conflicts management (Preuschoft and & van Schaik, 2000), and do not necessarily constrain the group interactions in the same way. However, so far, the proximate mechanisms that mediate the dynamic of dominance relationships often remain unclear.

Dominance relationships directly result from the outcomes of repeated agonistic interactions, or conflicts, between two individuals, according to which dominants and subordinates can be distinguished if one individual wins conflicts against the other (Bernstein 1981). How dominance hierarchy arise, and what makes an individual dominant over others, vary from species to species. Dominance relationships often depends on dyadic differences in individual attributes (e.g. age, sex, body condition, personality, fighting abilities; (Chase et al., 2002; Dingemanse & De Goede, 2004; Martin, 2005), but also on social attributes (Hinde, & Datta, 1981). For instance, in species forming matrilines, the rank of the individual can be 'inherited' from the mother (e.g. Japanese macaques, Chapais et al., 1991; Kutsukake, 2000; spotted hyneas, Frank, 1986; African elephants; Wittemyer and Getz, 2007). Besides, individual ranks are often achieved or maintained when supportive congeners are present and available to provide support in conflicts (e.g. matriline or clan in primates, Barrett et al., 2007;

Chapais et al., 1991; or canids, de Villiers et al., 2003; Smith et al., 2010; mated partners in corvids, Emery et al., 2007; Fraser and Bugnyar, 2012).

Dominance hierarchies are often characterised by the extent to which their structure adhere to the linearity of individual rankings, which means the degree to which dyadic relationships follow transitive rules (i.e. A dominates B, B dominates C, and in consequence A dominates C; de Vries, 1995; Landau, 1951). In addition to linearity, steepness has been proposed as an additional metric that allows quantification of symmetry of dominance relationships in a group (De Vries et al., 2006). More specifically, the steepness relates to the degree of individual's asymmetry in their propensity to win conflicts (De Vries et al., 2006). Indeed, conflicts do not always follow the prediction based on the current hierarchy and subordinates can protest or even win against more dominant individuals (i.e. dominance reversals; de Waal and & Luttrell, 1985; Massen et al., 2014). In macaques for instance, the proportion of dominance reversals and retaliations vary from one species to another, and reflects the degree of social tolerance of the species (Balasubramaniam et al., 2012; Duboscq et al., 2013; Demaria and Thierry, 2001; Thierry, 2013). Clear linear hierarchies, with marked directional asymmetry in individuals' propensity to win conflicts, are typically found in despotic species, like (e.g. rhesus macaques, *Macaca mulatta*; de Waal and & Luttrell, 1985), while linear but shallow hierarchy are typical of more tolerant species (e.g. tonkean macaques, *Macaca tonkeana*; De Marco et al., 2010).

Investigating the properties and characteristics of hierarchies also requires to take in account the social context in which they are formed and maintained. Indeed, dominance hierarchy result from competition among group members, which is be strongly influenced by the form and the dynamic of social organisations (Krause and Ruxton, 2002). Indeed, non-dispersive forms of conflicts resolution, such as clear and stable hierarchy, are rather expected in gregarious species living in permanent and cohesive social groups, where individuals necessarily have to cope with the cost of group living (Aureli et al., 2002; Drews, 1993; Shultz and Dunbar, 2009). Clear and stable hierarchy can also be found in mammal species expressing high degree of fission-fusion dynamics (i.e. variation in spatio-temporal group cohesion and membership; Aureli et al., 2008), but that are also characterised by well-structured social relationships, like chimpanzees, elephants or hyenas (Archie et al., 2006; Holekamp et al., 2007; Wittemyer et al., 2005; Wittig and Boesch, 2003). However, in species expressing high degree of fission-fusion, dispersive form of conflict resolution can always remain a viable strategy to deal with aggressions (Schino, 2000), and in in some species it could prevent the emergence of more complex form of conflict management. Yet how dominance relationships establish in highly dynamic species, and how they stabilise over time, remains poorly understood. Moreover, studies on dominance hierarchies most often rely on the analysis of social structure snapshots, and more rarely examine the temporal variability of the social patterns.

Indeed, investigating social patterns can become very challenging in highly dynamic systems, where all individuals do not frequently encounter. Numerous methods and indices have been developed to study dominance hierarchies (e.g. Clutton-brock et al.'s index, Clutton-Brock et al. 1979, 1982; David's score, David 1987,1988; see also de Vries 1998; Whitehead 2008; Bayly et al., 2006), but they often lack the flexibility needed to take into account social dynamics or to track dominance status over time. Elo-rating, originally used to rank chess players (Elo, 1978), can circumvent problems arising from these issues (Albers and de Vries, 2001; Neumann et al., 2011). This method calculates individual ratings that reflect individual dominance strength. These ratings are continuously updated after each new agonistic interaction an individual was involved in (Albers and de Vries, 2001; Franz et al., 2015; Neumann et al., 2011). The ordinal ranking based on individual Elo-ratings often closely resembles hierarchies derived from other methods, although an Elo-rating *ranking* does not necessarily reflect an (near-) optimal linear hierarchy (e.g., I&SI, de Vries 1998, see also Neumann et al., 2011). Thus, Elo-rating may be seen as an alternative approach to study dominance status, particularly if the focus is on the dynamics of dominance strength over time.

In birds, rooks (*Corvus frugilegus)*, are interesting candidates to investigate the impact of a species social dynamic on dominance hierarchies structure. Indeed, rooks express high degree of fission-fusion dynamics, characterised by high temporal variation in the spatial cohesion and the membership of the colony (Braun et al., 2012; Goodwin, 1955; Roell and Bossema, 1982; Swingland, 1977). They form long-term monogamous pair bond, but also live in group all year-long, breeding in colonies of tens to tens of hundreds of individuals, and gathering in groups out of the breeding season, which can reach thousands of individuals (Goodwin, 1955; Griffin and Thomas, 2000; Lincoln et al., 1980; Marshall and Coombs, 1957). So far, in rooks, and more broadly in corvids, hierarchies were often found or assumed to be stable and linear (in rooks, Jolles et al., 2013; Scheid et al., 2008; Logan et al., 2012; in corvids, Izawa and Watanabe, 2008; Shaw and Clayton, 2012; Strasser et al., 2006), especially in species forming small cohesive groups (Chiarati et al., 2010; Woolfenden and

Fitzpatrick, 1977). However, to what extent the social structure (i.e. social monogamy) and the colonial dynamic in rooks influence the formation and the maintenance of hierarchies remain so far unexplored. Investigating individuals' strategies regarding the establishment and the maintenance of dominance relationships might thus help to understand how individuals compete and/or avoid competition in this species.

In this study, we analysed the stability and the behavioural processes that shaped dominance relationships in a group of captive rooks over two years. We first investigated the structural characteristics of the hierarchy over short- and long-time scales (i.e. linearity, steepness, conflicts directionality, and individuals ordering), in order to assess the stability of dominance relationships and individuals ranking orders. Then, we used the Elo-rating method (Elo, 1978; Neumann et al., 2011) to investigate the behavioural mechanisms underlying the dynamic of dominance strengths over time. In more details, we tested the effects of various conflicts characteristics and individual and social attributes on: individual ratings, individual aggressiveness and conflict intensity; in order to deepen our understanding of the mechanisms shaping and constraining the establishment and maintenance of dominance order in a fluid system.

Methods

Subjects and study site

All birds were housed in an outdoor aviary on the campus of the Centre National de la Recherche Scientifique of Cronenbourg in Strasbourg, France. The group was composed of 14 adult individuals from January to the end of May 2014 (i.e. 9 males and 5 females). Then two birds died of natural causes the 23th of May and the 1st of August 2014. The group was thus composed of 12 individuals (i.e. 8 males and 4 females) from August 2014 to the end of September 2015 (i.e. end of the studied period). Among the 14 birds, 9 were collected as nestlings from a wild local colony between 2006 and 2007 (i.e. original group members), and 5 from hunting traps in south Alsace in August 2013 (i.e. new group members). See Table 1 for temporal modification of the group composition. All birds could be identified by coloured leg rings. The aviary (18m x 6 m x 3.5 m) was composed of wood perches, platforms, suspended baskets, ropes, vegetation cover and branches, as well as 2 small water pools for enrichment and bathing. Birds were fed daily with a mixture of pellets and fresh products (eggs, yoghurt, and fruits) and had ad libitum access to water.

Period	P1	P2	Group origin	Sex
Individuals	a	a	new	
	b	b	original	
	c *	X	new	
	e	e	original	
	g *	g *	new	
	j *	j *	original	
	k	k	original	
	m	m	original	
	n	n	original	
	o	o	original	
	p *	p *	new	
	s *	s *	new	
	t	t	original	
	z	X	original	
Sex-ratio	(9 M / 5 F)	(8 M / 4 F)		

Table 1. Temporal modifications of the group composition. The first period runs from January to May 2014 (P1), and the second period from August 2014 to September 2015 (P2). The group origin (i.e. original; new group member) is reported as well as the sex of the individuals (i.e. females are indicated by an asterisk). Note that two individuals died of natural causes in the course of the study (i.e. z, male, the 23th of May; c, female, the 1st of August 2014). They are therefore symbolised by a cross in the second study period (P2).

Data collection

Data were collected from January to the end of September, in 2014 and 2015, which covered two breeding periods (from March to the end of May). We used 10-minutes individual focal sampling in order to exhaustively record all agonistic behaviours, and to clearly identify initiators and receivers of interactions (Altmann, 1974). We distinguished high intensity (comprising the following behaviours: peck, charge, and chase) and low intensity (avoid, supplant, and threat) agonistic behaviours (see Table 2 for detailed description of the recorded behaviours). In addition, we recorded spatial proximities (i.e. at perch, on the ground), and affiliations (i.e. allofeeding, allopreening, contact-sit), in order to characterise pairs (Boucherie et al., 2016). Observation sessions were conducted from 08:00

am to 06:00 pm, during which all individuals of the group were successively observed by one observer (PB) (i.e. in a randomised order of observation within the session). In total, 166 observation sessions were conducted (2014: 83, 2015: 83), totalling 13 hours and 50 minutes of observation per individual and per year. We never conducted more than one session of observation per day.

Behaviour	***Definition***
	Agonistic behaviours
High intensity behaviours	
Peck	The subject hits another individual with his beak.
Charge	The subject rushes toward another individual, without contacting him. His body and particularly the head is directed toward the receiver. The covered distance is less than 1m.
Chase	The subject pursues another individual on the ground or by flying.
Low intensity behaviours	
Avoid	The subject moves away from an approaching individual, either walking or running on the ground, or by flying away. The two individuals do no enter in contact.
Supplant	The subject moves away from another individual which enters in contact with him and takes his place (i.e. by walking, running or flying).
Threat	A sudden movement of the upper body, directed toward another individual without touching it (i.e. mimicking the start of a peck or a charge). The signal can be accompanied with vocalizations and puffed feathers.
	Proximities
At perch	Individuals are located from 10cm to 50cm apart on the perch
On the ground	Individuals are located from 0m to 1m apart on the ground

Affiliations	
Allofeeding	One subject actively transfers a food item from its beak to the beak of another subject
Allopreening	One subject runs his beak thought the feathers of another subject cleaning it from dirt or parasites
Contact-sit	Individuals are less than 10cm apart on the perch

Table 2. Definitions of collected behaviours.

Pairs' identification

Following Boucherie et al. (2016), two individuals were considered paired if more than 50% of their respective proximities and affiliations (i.e. in which they were involved) occurred between themselves. Considering that pairs might change over time, we characterise them for every week of the dataset. Over the two years, we identified 15 different pairs, indicating that some changes occurred in the partnership over time. Note that 40% of the pairs were same-sex pairs (i.e. five male-male pairs, one female-female pair). Five pairs among 15 were only detected on a single week and one pair on three non-consecutive weeks. The nine other pairs last over several consecutive week. Among those, one remained stable during the whole study, one terminated because of the loss of one partner (i.e. z in May 2014), and one separated a few week after its formation. Finally three mate switchings occurred: three pairs separated while three new pairs were formed, with one partner shifting from one pair to another.

Conflict definition

We define a conflict as a bout of agonistic interactions involving two individuals: the initator (who displays the first agonistic behaviour) and the receiver. According to the response of the receiver, we distinguished: 1) decided conflicts (i.e. clear outcome), in case the receiver retreated or avoided the initiator; from 2) undecided conflicts (i.e. unclear outcome), in case the receiver i) ignored the agonistic behaviour directed at him/her and stayed in contact or in proximity with the receiver, ii) protested by posturing (i.e. puff or laid flat) or vocalising, or iii) defended him/herself by counter-attacking (i.e. by displaying an agonistic behaviour other than avoidance). For agonistic behaviours to be considered part of the same bout, they had to be separated by less than 30 seconds during which none of the opponents engaged in another activity (e.g. preening, foraging). The intensity of the conflict was defined by the behaviour of highest intensity recorded during the sequence. Note that we did not differentiate between conflicts according to contexts (e.g. competition regarding resources, objects or space).

Classical analysis of the dominance hierarchy

Classical analyses of the dominance hierarchy were performed on decided data only. From all agonistic data, we constructed directed dominance matrices using decided conflicts (i.e. clear outcome). The matrices were filled with the number of initiated conflicts per individuals, according to the receiver identity (i.e. initiators in rows and receivers in columns; Martin and Bateson, 1993). We first computed the linearity of the hierarchy following de Vries (1998) (using R 3.1.3 software; Team, 2015), which evaluates the degree of transitivity of the dominance relationships (i.e. A dominates B, B dominates C, and in consequence A dominates C). 0 indicates complete intransitivity, while 1 indicates complete transitivity. Then, we computed the steepness of the hierarchy (function 'steeptest', based on dyadic dominance indices corrected for chance *Dij*, in steepness R package v.0.2-2; Leiva and de Vries, 2014), which measures the extent to which individuals differ from each other in their success in winning conflicts (De Vries et al., 2006). The steepness (Dij) varies from 0 to 1, where 1 represent despotic relationships among individuals, with strong asymmetry in individuals' propensity to win conflicts, and 0 represents egalitarian relations. We also computed the directional consistency index (DCI), which evaluates the consistency of conflict directionality. The DCI is calculated across all dyads, as the number of conflicts that occurred in their more frequent direction (H), minus the number of conflicts that occurred in their less frequent direction (L), divided by the total number of conflicts in the group (i.e. (H-L)/(H+L); van Hooff, J. A., & Wensing, 1987). The DCI varies from 0, for totally balanced relationships, to 1 for a complete unidirectionality. Finally, we used to David's scores to calculate dominance scores or cardinal ranks for each individual in the group, and then ordered them from the highest to the lowest score (David, 1988; Gammell and de Vries, 2003). David's scores measures the degree of dominance of an individual i over an individual j, based on their relative proportions of winning or losing conflicts (David, 1988). More precisely, we computed normalized dyadic dominance index corrected for chance (function 'getNormDS' in steepness R package v.0.2-2; Leiva and de Vries, 2014; see also de Vries et al. 2006).

In order to assess the stability of those hierarchical features over time, we first performed the analysis over two multi-month periods, delimited according to changes in group composition (i.e. P1, 14 individuals, from January 2014 to the end of May 2014; P2, 12 individuals, from August 2014 to September 2015), and then per month (2014: over 8 months, 2015: over 7 months).

Dynamical analysis of the dominance hierarchy

Elo rating procedure

We used the Elo-rating method (Elo, 1978; Neumann et al., 2011) to estimate and follow individual dominance strength over time, using both decided and undecided data. The integration of undecided conflicts on the rating process is indeed one of the main advantage of the Elo-rating procedure (Neumann et al., 2011). We computed individual ratings per day (i.e. one observations session per day), following the procedure described in Neumann et al. (2011). Elo-ratings are continuously updated by considering the conflicts in which individuals are sequentially involved. Contrary to the classical procedure, it works on a sequence of interactions as opposed to aggregated matrices. All individuals start with an arbitrarily selected value of 1000, which is then updated after each conflict in which an individual is involved. The winner of an interaction gains points whereas the loser loses points. The amount of points gained and lost varies according to the expectation of the conflict outcome (i.e. expected outcome: higher-rated individual wins; unexpected outcome: lower-rated individual wins; Albers and de Vries, 2001; Elo, 1978; Neumann et al., 2011). For the following analyses conducted with Elo ratings, we discarded the first week of data collection to allow ratings to stabilize (i.e. burn-in period, 4 observational sessions totalling 77 decided and undecided conflicts).

Factors influencing the Elo-ratings, the aggressiveness, and conflicts intensity

Factors influencing the Elo-ratings

We investigated if Elo-ratings were related to: (1) the sex (i.e. male/female); (2) the group origin (i.e. original/new); and (3) the pairing status (i.e. paired/ solitary) of the individual; as well as (4) the aggressiveness (i.e. numeric; number of initiated conflicts per day, i.e. per observation session) and (5) the number of received conflicts per day (i.e. numeric). We ran a linear mixed model (LMM; function ‘lmer’ in lme4 R package stats v.3.1.3; Bates et al., 2015), with the date of data collection and individual identity as random factors.

Aggressiveness

We investigated if aggressiveness (i.e. number of initiated conflicts per day, i.e. per observation session) was related to: (1) the sex (i.e. male/female); (2) the group origin (i.e. original/new); and (3) the social status (i.e. paired/solitary) of the individual; as well as (4) the breeding period (i.e. in/out). We used a generalised mixed model (GLMM; function glmer in R package lme4 v.1.1-9; Bates et al., 2015), with the date of data collection and identity of the initiator as random factors, using a poisson distribution with a logit link function.

Intensity of the conflicts

We also investigated which factors were related to the intensity of conflicts (i.e. high or low), considering: (1) the sex (i.e. male/female); (2) the group origin (i.e. original/new); (3) the pairing status (i.e. paired/solitary); (4) and the Elo-rating of the initiator (numeric); (5) the breeding period (i.e. in/out); (6) the conflict outcome (i.e. clear outcome: decided, unclear outcome: undecided); (7) the expectation of the conflict (i.e. the initiator had either a higher or a lower-rating than the receiver; respectively logical or illogical); and (8) the absolute difference between the two opponents' Elo-ratings (numeric). We used a GLMM (function glmer in R package lme4 v.1.1-9; Bates et al., 2015), with the date of data collection, the initiator and the receiver identity as random factors, using a binomial distribution with a logit link function.

Statistical analysis

For each model, we tested a full model against a null model using a likelihood ratio test (function 'lrtest' in R package lmtest; Zeileis and Torsten, 2002). Note that in all models, we scaled the Elo-ratings variable (i.e. mean = 0; SD = 1; Schielzeth, 2010), whether it was used as response variable or as factor. All statistics were performed using R 3.1.3 software with $\alpha=0.05$ (R Core Team, 2015).

Results

Over two years, we recorded a total of 1536 conflicts (i.e. mean number of conflicts per observation session: nine). 41% of all conflicts were of high intensity (i.e. peck, charge, or chase) and 59% of low intensity (i.e. avoid, supplant, or threat). 18% of all conflicts were undecided, because: (1) the receiver stayed in contact or proximity with the initiator (90%); (2) the initiator moved away from the receiver (6%); (3) or the receiver moved away after defending (4%; retaliation or dodging). In the two first cases, the receiver either ignored the agonistic behaviour (1: 59%; 2: 59%), protested by posturing or vocalising (1: 13%; 2: 12%), or counter-attacked (1: 28%; 2: 29%). In addition, 80% of all undecided conflicts were of high intensity.

Classical analysis of the dominance hierarchy

Over the two multi-month periods (i.e. P1: 14 individuals from January 2014 to the end of May 2014, P2: 12 individuals from August 2014 to September 2015), linearity was significant and equals to 0.55 (P1) and 0.75 (P2; Table 3). When computed per month, the linearity reached significance only twice (in April 2014 and May 2015), and took values ranging from 0.22 to 0.55 (Table 3). The steepness of the hierarchy was significant over the two multi-months periods and was equal to 0.40 in P1 and 0.57 in P2 (Table 3). In 12 out of the 15 months of the study, the steepness was significant and ranged from 0.06 to 0.29 (Table 3). Finally, the directional consistency index (i.e. DCI) was equal to 0.79 and 0.74 in P1 and P2 respectively and varied between 0.64 and 1 over the 15 months of the study.

The linearity index increased with lower proportion of unknown relationships (i.e. proportion of dyads of individuals for which no conflicts were recorded; Table 3). However, some of the lowest values of DCI were found in P1 and P2, when the proportion of unknown relationships was markedly lower compared to the monthly periods (Table 3), indicating that the more dyadic relationships within a group are known, the more inconsistencies in agonistic behaviour directionality are accumulated.

Period- - Month	N ID	N conflicts	Unknown relationships	Linearity index	P-value linearity	Steepness	P-value steepness	DCI
Pooled data according to the group composition								
P1	14	696	17%	0.55	< **0.001**	0.40	< **0.001**	0.79
P2	12	760	6%	0.75	< **0.001**	0.57	< **0.001**	0.74
2014								
Jan	14	211	56%	0.32	0.14	0.14	< **0.001**	0.92
Feb	14	80	66%	0.34	0.11	0.10	< **0.01**	0.97
Mar	14	169	54%	0.24	0.36	0.16	< **0.001**	0.85
Apr	14	194	43%	0.45	< **0.05**	0.25	< **0.001**	0.92
May	14	42	77%	0.22	0.43	0.06	< **0.05**	0.95
Jul	13	73	71%	0.22	0.47	0.08	0.17	0.81
Aug	12	47	76%	0.25	0.39	0.06	< **0.05**	0.90
Sep	12	99	42%	0.44	0.06	0.23	< **0.001**	0.95
2015								
Jan	12	54	76%	0.30	0.30	0.06	0.23	0.64
Feb	12	93	58%	0.40	0.11	0.17	< **0.001**	0.77
Mar	12	125	44%	0.42	0.08	0.23	< **0.001**	0.85
Apr	12	121	36%	0.40	0.09	0.29	< **0.001**	0.93
May	12	95	41%	0.55	< **0.01**	0.25	< **0.001**	0.93
Jul	12	50	74%	0.36	0.18	0.07	0.11	1
Sep	12	42	61%	0.37	0.17	0.12	< **0.05**	0.95

Table 3. Results for the linearity index, the steepness of the hierarchy, and the directional consistency index (DCI), computed per period (P1, P2), and per month between January 2014 and September 2015. Months corresponding to the breeding period are coloured in green (i.e. March to the end of May). The number of individuals present in the group (N ID), the number of conflicts recorded (N conflicts), and the proportion of unknown relationships (i.e. the percentage of dyads of individuals within the group for which no conflicts were recorded) are also reported for each period. All analyses were performed on decided data only. Significant p-values are marked in bold.

Regardless of the way data were divided (i.e. multi-months or monthly period), the individual rankings obtained with the David's scores were strongly unstable from period to period, or from month to month (Figure 1, Table 4). David's scores varied from 9.43 (i.e. k), to 1.43 (i.e. s; Table 4). The individuals showing the highest variation in David's scores (i.e. o; Table 4), and the individuals showing the lowest variation (i.e. z, lost in the course of the study; Table 4), had scores comprised between 4.01 and 8.25, scores between 6.60 and 8.42.

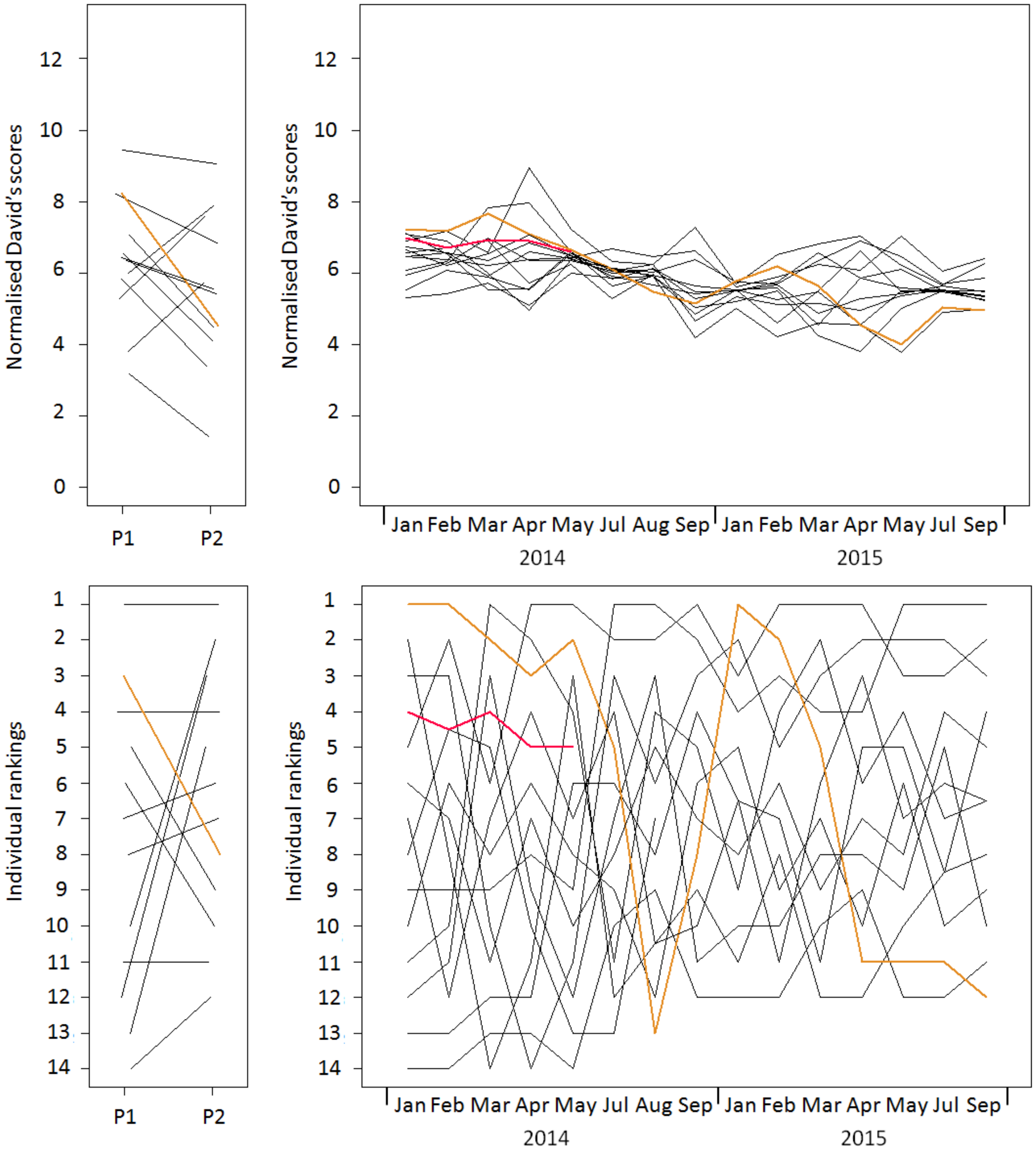


Figure 1. Temporal changes in normalised David's scores and associated individual rankings, a) between P1 and P2; and b) per month, from January 2014 to September 2015. The two individuals which respectively display the highest and the lowest coefficient of variation for the David's scores per month, are respectively coloured in orange and red (i.e. respectively o and z; Table 4. Note that the two individuals that died over the course of the study were not present in P2 (i.e. c & z) and are therefore not reported in the first part of the figure (i.e. P1 vs. P2; 12 individuals represented instead of 14).

ID	Max	Min	Coefficient of variation
a	7.08	4.97	9.03
b	6.99	4.67	11.53
c	6.88	5.30	9.20
e	7.10	3.40	15.40
g	6.62	3.81	8.66
j	8.22	5.37	12.82
k	9.43	5.66	11.90
m	7.88	5.62	5.39
n	6.84	4.11	10.91
o	8.25	4.01	18.34
p	7.07	4.50	11.68
s	5.98	1.43	13.45
t	6.73	4.88	9.57
z	8.42	6.60	2.37
Group	9.43	1.43	13.33

Table 4. Maximum, minimum and coefficient of variation (i.e. sd/mean x 100), for individuals' David's scores per month, from January 2014 to September 2015. The maximum, minimum and the coefficient of variation for all David's scores across the whole group is also reported.

Dynamical analysis of the dominance hierarchy

In 15% of all conflicts, the initiator had a lower Elo-rating than the receiver (11% for decided conflicts; 36% for undecided conflicts). Among those conflicts, 51% were of high intensity against 49% of low intensity.

Individuals Elo-ratings varied from 1542 (i.e. j and k) to 466 (i.e. s, Table 5; Figure 2). Like David's scores, individuals Elo-rating strongly varied over time (i.e. Elo rating are computed per day, 166 ratings per individual; Figure 2, Table 5). The individuals respectively showing the highest (i.e. o), and lowest variation in their Elo-rating over time (i.e. z), were the same than for David's scores. Their ratings varied from 591 to 1352 (i.e. o) and from 1038 to 1206 (i.e. z; Table 5).

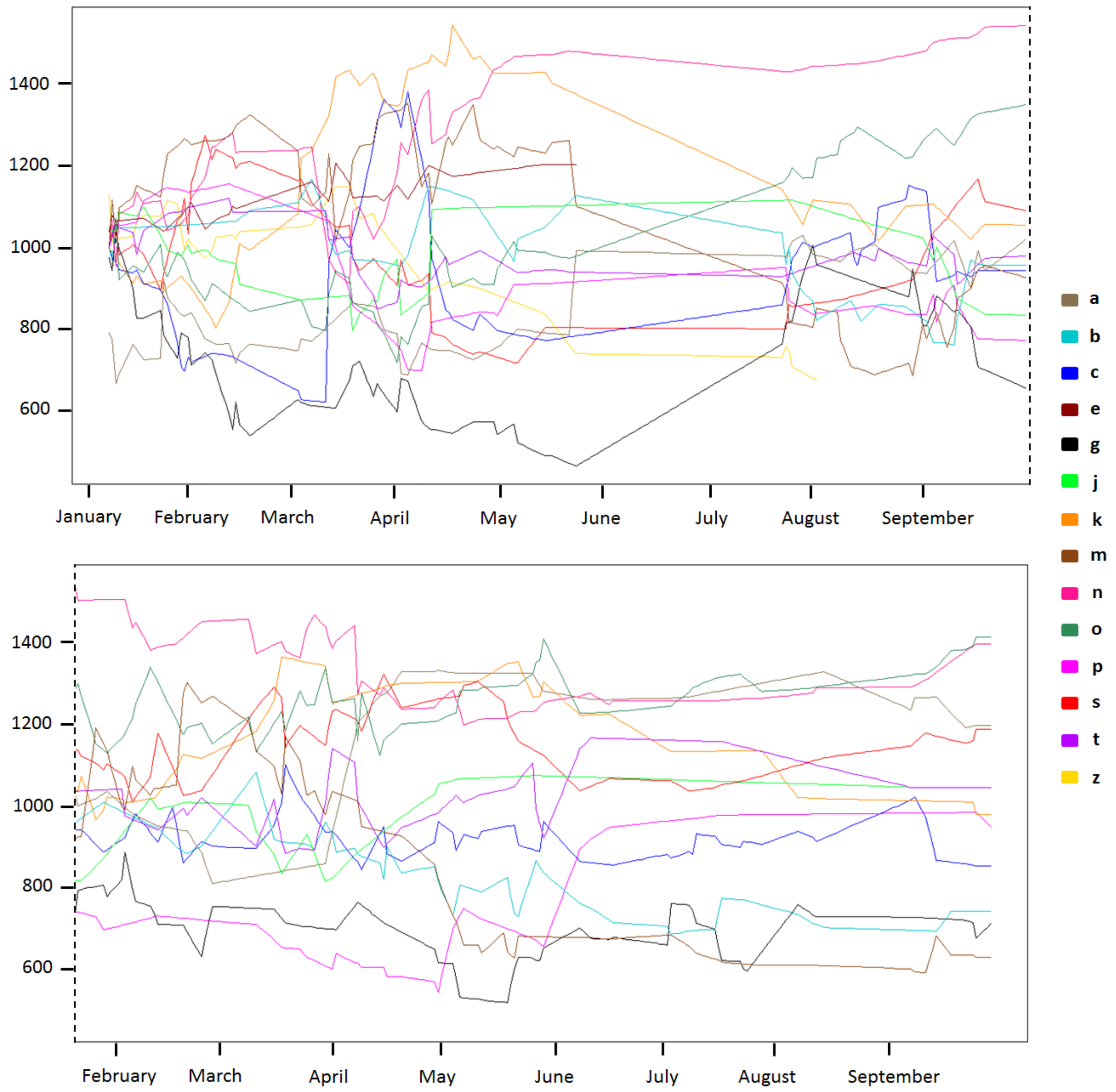


Figure 2. Temporal changes in individual Elo-ratings between January 2014 and September 2015 (166 ratings per individual). The two individuals that died over the course of the study appear on the Elo-plot until their disappearance (i.e. z in May 2014, c in August 2014).

ID	**Max**	**Min**	**Coefficient of variation**
a	1320	719	13,96
b	1379	622	13,93
c	1149	678	13,41
e	1154	542	18,71
g	1328	667	20,94
j	1542	803	14,75
k	1542	912	11,16
m	1410	718	15,38
n	1166	684	14,36
o	1352	591	25,85
p	1115	796	8,94
s	1038	466	17,08
t	1164	849	7,63
z	1206	1038	4,75
Group	1542	466	21.14

Table 5. Maximum, minimum and coefficient of variation (i.e. sd/mean x 100), for individuals' Elo-ratings per month, from January 2014 to September 2015. The maximum, minimum and the coefficient of variation across the whole group is also reported.

Factors influencing the Elo-ratings

Solitary individuals had lower Elo-ratings than paired individuals (LMM: solitary vs. paired, estimates = -0.53, standard error = 0.04, t-value = -13.47, *P* < 0.001; Table 6; Figure 3). In addition, higher-rated individuals were significantly more aggressive than lower-rated individuals (i.e. higher rates of conflict initiation; LMM: aggressiveness, estimates = 0.14, standard error = 0.01, t-value = 12.34, *P* < 0.001; Table 6), and were also significantly less often the receiver in an agonistic interaction (LMM: Number of received conflicts, estimates = -0.13, standard error = 0.01, t-value = -10.52, *P* < 0.001; Table 6). Neither the sex nor the group origin had a significant impact on individual Elo-ratings (Table 6).

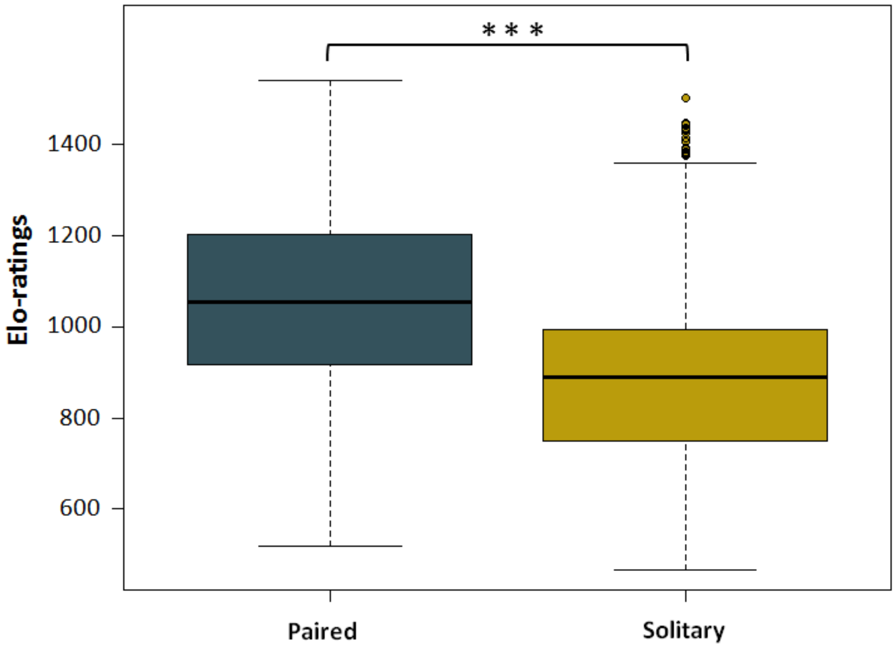


Figure 3. Boxplot showing the distribution of individuals Elo-ratings according to their social status (i.e. paired, solitary). The bottom of the boxplot represents the first quartile, the top the third quartile, and the thick line across the box indicates the median. Whiskers extend to the highest and lowest values. Statistics are based on the estimates given by the model.
*** <0.001, ** < 0.01, * ≤ 0.05.

Aggressiveness

Conflicts were more often initiated by paired individuals than solitary, and were more frequent during the breeding period (GLMM: solitary vs. paired, estimates = -0.47, standard error = 0.07, z-value = -6.59, $P < 0.001$; Breeding period out vs. in, estimates = -0.40, standard error = 0.10, z-value = -4.27, $P < 0.001$; Table 6). Neither the sex, nor the group origin of the individual had an effect on individual aggressiveness (Table 6).

Intensity of the conflicts

Conflicts were more often of lower intensity when initiated by males (GLMM: male vs. female, estimates = -0.57, standard error = 0.23, z-value = -2.47, $P < 0.05$; Table 6). In addition, conflicts were of higher intensity when undecided (i.e. unclear outcome), that is when the receiver ignored the agonistic behaviour, protested by posturing or counter-attacked (GLMM: undecided vs. decided, estimates = 2.06, standard error = 0.20, z-value = 10.40, $P <$ 0.001; Table 6). All other tested variables had no significant effect on the conflict intensity (Table 6).

Model 1: Factors influencing the Elo-ratings	Estimate ± SE	t value	P value
Likelihood ratio test: Model null vs. Model 1, DF = 5, Chisq = 439, P value < **0.001** ***			
Intercept	-0.11 ± 0.27	-0.40	0.69
Sex: male vs. female	-0.06 ± 0.44	-0.14	0.89
Group origin: original vs. new	0.48 ± 0.45	1.09	0.28
Pairing status: solitary vs. paired	-0.53 ± 0.04	-13.47	< **0.001** ***
Aggressiveness	0.14 ± 0.01	12.34	< **0.001** ***
Number of received conflicts	-0.13 ± 0.01	-10.52	< **0.001** ***
Model 2: Aggressiveness	Estimate ± SE	Z value	P value
Likelihood ratio test: Model null vs. Model 2, DF = 4, Chisq = 61.9, P value < **0.001** ***			
Intercept	-0.57 ± 0.34	-1.71	0.87
Sex initiator: male vs. female	0.30 ± 0.53	0.57	0.57
Group origin initiator: original vs. new	0.07 ± 0.53	0.14	0.89
Pairing status initiator: solitary vs. paired	-0.47 ± 0.07	-6.59	< **0.001** ***
Breeding period: out vs. in	-0.40 ± 0.10	-4.27	< **0.001** ***
Model 3: Intensity of the conflicts	Estimate ± SE	Z value	P value
Likelihood ratio test: Model null vs. Model 3, DF = 8, Chisq = 160, P value < **0.001** ***			
Intercept	-0.71 ± 0.30	-2.32	< **0.05** *
Sex initiator: male vs. female	-0.57 ± 0.23	-2.47	< **0.05** *
Group origin initiator: original vs. new	0.26 ± 0.25	1.05	0.30
Pairing status initiator: solitary vs. paired	0.00 ± 0.17	0.01	0.99
Initiator Elo-rating	0.13 ± 0.11	1.28	0.20
Breeding period: out vs. in	-0.05 ± 0.16	-0.33	0.74
Conflict outcome: undecided vs. decided	2.06 ± 0.20	10.40	< **0.001** ***
Expectation of the outcome: logical vs. illogical	0.08 ± 0.21	0.37	0.71
Difference between opponents Elo-ratings	-0.15 ± 0.10	-1.56	0.12

Table 6. LMM and GLMM results for investigations on the factors influencing: 1) individuals’ Elo-rating; 2) aggressiveness; and 3) the intensity of the conflicts (i.e. high or low). Significant p-values are marked in bold *** < 0.001, ** < 0.01, * ≤ 0.05.

Discussion

In this study, we examined the stability of the hierarchical features through time, and the behavioural processes that shaped dominance relationships in a group of captive rooks over two years. We showed that dominance hierarchy can be linear but mostly when data are pooled on a long term basis, which coincides with the risk to mask rank changes. Indeed, computing individuals David's scores, we found high variability in the individual ordering over time. Using the Elo-rating to examine the dynamic of individuals' dominance strength over time, we found that paired individuals were higher-rated than solitary, which mainly related to aggressiveness (i.e. higher rate of conflict initiation). The sex had no significant effect on individuals' ratings, but males displayed more often low intensity aggressions than females.

The hierarchy was non-significantly linear in most months of the study whereas it was found significantly linear when data were pooled over multi-month periods. Our results confirm in rooks, that like in other social species such as primates for instance, the assessment of linearity significance can be very sensitive to data collection efforts and may strongly vary from one period to another (de Vries, 1995; Klass and & Cords, 2011; Shizuka and McDonald, 2015, 2012). This is indeed a well-known phenomenon that relates to the proportion of unknown relationships: the more dyadic relationships within a group are known the more transitive and significant the hierarchy becomes (Klass and & Cords, 2011; Shizuka and McDonald, 2015, 2012). Yet when linear, the hierarchy was found weakly transitive. In addition, the consistency directionality index was lower in multi-months periods compared to monthly periods, which reveals frequent variations in rooks' dominance interactions - and consequently relationships - that accumulate with the increased collection of data over time. Consistently, David's scores rankings and Elo ratings were very unstable, both between years and between months. Thus, we can conclude that multi-months data provided a general picture of the hierarchy, but one that did not necessarily reflect the actual dominance rankings of individuals at any point in time. Furthermore, the steepness of the hierarchy remained low to moderate (i.e. below 0.6) whatever the time period or the quantity of data (i.e. multi-months and monthly periods), indicating low individual differences in the propensity to win conflicts or weak power asymmetries (De Vries et al., 2006). Added to the high variability of dominance relationships, it therefore questions the prevalence and the strength of dominance relationships in rooks. Consequently, if hierarchies may potentially develop in rooks, whether or not they do form and how predominant they are on their social organisation remain to be further investigated.

Considering the instability of rooks dominance relationships in this group, the Elo-rating technique allowed us to investigate into more details the behavioural mechanisms underlying individuals dominance (Elo, 1978; Neumann et al., 2011). We found that aggressiveness and pair-bonding determined individuals' rating, which is consistent with previous findings on numerous avian species (Seibert and Crowell-Davis, 2001), and particularly in corvids (Izawa and Watanabe, 2008). The fact that paired individuals tend to win more than solitary individuals is consistent with expectations about the benefits of pair bonding in corvids, and more broadly in avian species forming long-term monogamous pair bonds (Emery et al., 2007; Lamprecht, 1985; Tamm, 1977). The increase of agonistic success through pairing likely facilitates access to food resources, or the choice of nest sites (Emery et al., 2007; Kasprzykowski, 2008; Swingland, 1977), in a very similar way than long-term alliances in primates or dolphins allow individuals to better access to food resources, or mating partners (Connor, 2007; Cords, 1997). In most avian species, males also usually dominate females and show higher rates of aggression (Wechsler, 1988; Tarvin & Woolfenden, 1997; Seibert & Crowell-Davis, 2001; Izawa & Watanabe, 2008; Chirati et al., 2010; Verhulst et al., 2014). Yet, in this study group, males and females did not differ in their dominance ratings, and show similar aggressiveness. This contrast could result from the use of continuously updated ratings instead of fixed ordinal rankings, capturing a different and more dynamic aspect of the dominance relationship than traditional methods. Females and males only differed by the fact that males initiated more often low intensity conflicts (i.e. threat, avoid, and supplant; more than half of the conflicts), which suggests that to win a conflict, males may not need to be as aggressive as females.

Considering that dominance relationships and hierarchies are supposed to regulate competition and limit the escalation of conflicts (de Waal, 1986), low intensity behaviours could be seen as clearer signs of dominance than direct aggressions. Consistently, in this study group, the receiver of an agonistic interaction was more likely to stay in contact with its opponent, and eventually to protest or retaliate in case of high intensity conflict (i.e. 80% of high intensity conflicts were undecided). Yet, if low intensity behaviours were indeed clearer signs of dominance, we could have expected higher rated individuals (i.e. more dominant) to display more often low intensity conflicts. However, individuals' ratings did not significantly influence the intensity of conflicts. Beside, avoidances and supplantations imply the retreat of the receiver. Thus, although individuals can protest or retaliate both after low and high intensity behaviours, it is by definition more likely to occur after a direct aggression. The intensity of conflicts and the escalation of aggressions (i.e. retaliation) could also be function of the context in which the encounter occurred (i.e. current level of competition for a coveted resources). Indeed, in case of stronger conflicts of interest, both partners may be highly motivated to win the encounter. In tits for instance, dominance is strongly context-dependent, and individuals are more likely to win conflicts when they are close to their territories (Dingemanse & De Goede, 2004). Similarly in rooks, individuals may alternatively win and lose conflicts according to the location and the context during which occurred the encounter. Further investigations are now needed to better conclude on the factors influencing the use of high/low intensity behaviours in conflicts.

Overall, the observed variability of rooks' dominance relationships questions previous findings on rooks hierarchies, which were previously found to be linear (Jolles et al., 2013; Scheid et al., 2008; Logan et al., 2012). However, consistently with our results (i.e. minimum of linearity index = 0.44 maximum = 0.75), if the hierarchy was found strongly linear in juveniles (i.e. in juveniles, linearity index = 0.94, Scheid et al., 2008; in juveniles and young adults, linearity index = 0.88, Logan et al., 2012), it was found weakly linear in adults (i.e. linearity = 0.5; Jolles et al., 2013). Thus, if hierarchies may establish among juveniles, favouring smaller and cohesive sub-groups compare to adults (Henderson, 1991; East, 1988; Dunnet et al., 1969), they may not necessaily establish among adults. This may not be so surprising given that adult rooks live and breed in dense colonies, characterized by a high turn-over rate of individuals, i.e. high level of fission-fusion dynamics (Goodwin, 1955; Roell and Bossema, 1982; Swingland, 1977). Although subgroups of affiliates are likely to emerge in those huge aggregations (Boucherie et al., 2016a, 2016b), the possibility that all individuals frequently encounter is unlikely. In addition the high variability of their grouping patterns (i.e. fission fusion dynamics) may preclude the emergence of stable and pronounced dominance asymmetry between individuals, and thus dominance relationships, which can ultimately preclude the emergence of a significantly linear hierarchy. In avian species, clear hierarchies and stable dominance relationships are most often found in species forming small and cohesive structures, like cooperatively breeding kin-based structure or family groups, where all individuals necessarily have to cope with competition (e.g. in carrion crows, *Corvus corone*, Chiarati et al., 2010; in florida scrub jays, *Aphelocomu c. coerulescens*, Woolfenden and Fitzpatrick, 1977). Beside, to live in a fluid and dynamic social organisation might also increase the opportunity to rely on dispersive strategies to resolve conflicts (e.g. avoidance and spatial separation with opponents), rather than non-dispersive conflicts management mechanisms like hierarchies (Schino, 2000). Finally, it must also be noted that a low risk in conflicts can also preclude the necessity for more complex forms of conflicts management to emerge. In a significant part of the conflicts the victim stayed in contact with the aggressor (i.e. on average 16% of conflicts), and severe conflicts (i.e. leading to injuries) were (almost) never recorded. Daily quarrels in rooks may therefore not be strong enough to require more complex conflict management. Further investigations are now needed to understand if the concept of dominance in its standard form has indeed any sort of meaning in wild corvids and how it may (or not) shape the way rooks interact in various contexts.

Our study, like previous others, involved captive individuals, which limits our evaluation of the effect of competitive pressures found in the wild on hierarchies (e.g. for food, space, reproduction). However, the captive setup allowed us to closely investigate the behavioural and temporal mechanisms underlying rooks' dominance relationships. This is the first time that a temporal rank variation and other hierarchical characteristics other than just linearity are reported in rooks, providing new insights about the dominance in this species. We found that rooks hierarchy was mostly linear when data were polled on long term basis, whereas dominance relationships were found highly variable in time. Therefore, by compiling data we get a picture that did not reflect the actual dominance ranking of individuals. In addition, we found a low directionality in conflicts, and weak power asymmetries. Thus at this stage, whether or not dominance relationships do form in rooks remain unclear. Our results questions the existence and the strength of dominance relationships in this species, and stress that caution is warranted when investigating dominance in species that express great social dynamics. Finally, our results emphasises the benefits of using a dynamic approach to analyse the dynamic of dominance relationships, and stress the need for further investigations to conclude on the prevalence of dominance hierarchy in rooks.

Acknowledgements

We would like to thank C. Neumann and J. Duboscq for their statistical advices and their valuable help with the manuscript.

References

Alanärä, A., Burns, M.D., Metcalfe, N.B., 2001. Intraspecific resource partitioning in brown trout: The temporal distribution of foraging is determined by social rank. J. Anim. Ecol. 70, 980–986. doi:10.1046/j.0021-8790.2001.00550.x

Albers, P.C., de Vries, H., 2001. Elo-rating as a tool in the sequential estimation of dominance strengths. Anim. Behav. 61, 489–495. doi:10.1006/anbe.2000.1571

Alberts, S.C., Watts, H.E., Altmann, J., 2003. Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, Papio cynocephalus. Anim. Behav. 65, 821–840. doi:10.1006/anbe.2003.2106

Altmann, J., 1974. Observational Study of Behavior : Sampling Methods. Behaviour 49, 227–267.

Amsalem, E., Hefetz, A., 2011. The effect of group size on the interplay between dominance and reproduction in Bombus terrestris. PLoS One 6. doi:10.1371/journal.pone.0018238

Archie, E.A., Morrison, T.A., Foley, C.A.H., Moss, C.J., Alberts, S.C., 2006. Dominance rank relationships among wild female African elephants, Loxodonta africana. Anim. Behav. 71, 117–127. doi:10.1016/j.anbehav.2005.03.023

Aureli, F., Cords, M., van Schaik, C.P., 2002. Conflict resolution following aggression in gregarious animals: a predictive framework. Anim. Behav. 64, 325–343. doi:10.1006/anbe.2002.3071

Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., Fiore, A.D., Dunbar, R.I.M., Henzi, S.P., Holekamp, K., Korstjens, A.H., Layton, R., Lee, P., Lehmann, J., Manson, J.H., Ramos-Fernandez, G., Strier, K.B., Schaik, C.P. van, 2008. Fission-Fusion Dynamics: New Research Frameworks. Curr. Anthropol. 49, 627–654. doi:10.1086/586708

Balasubramaniam, K.N., Dittmar, K., Berman, C.M., Butovskaya, M., Cooper, M.A., Majolo, B., Ogawa, H., Schino, G., Thierry, B., De Waal, F.B.M., 2012. Hierarchical Steepness, Counter-Aggression, and Macaque Social Style Scale. Am. J. Primatol. 74, 915–925. doi:10.1002/ajp.22044

Barrett, L., Henzi, P., Rendall, D., 2007. Social brains, simple minds: does social complexity really require cognitive complexity? Philos. Trans. R. Soc. Lond. B. Biol. Sci. 362, 561–75. doi:10.1098/rstb.2006.1995

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. lme4: Linear mixed-effects models using Eigen and S4. R Packag. version 1.1-9 https://CRAN.R–project.org/package=lme4.

Bayly, K.L., Evans, C.S., Taylor, A., 2006. Measuring social structure: A comparison of eight dominance indices. Behav. Processes 73, 1–12. doi:10.1016/j.beproc.2006.01.011

Bekoff, M., Scott, A.C., 1989. Aggression, Dominance, and Social Organization in Evening Grosbeaks. Ethology 83, 177–194. doi:10.1111/j.1439-0310.1989.tb00528.x

Bell, M.B. V., Nichols, H.J., Gilchrist, J.S., Cant, M. a., Hodge, S.J., 2012. The cost of dominance: suppressing subordinate reproduction affects the reproductive success of dominant female banded mongooses. Proc. R. Soc. B Biol. Sci. 279, 619–624. doi:10.1098/rspb.2011.1093

Bergman, T.J., Beehner, J.C., Cheney, D.L., Seyfarth, R.M., 2003. Hierarchical classification by rank and kinship in baboons. Science (80-.). 302(5648), 1234–1236.

Bernstein, I.S., 1981. Dominance: The baby and the bathwater. Behav. Brain Sci. 4, 419–457. doi:10.1017/S0140525X00009614

Bernstein, I.S., Gordon, T.P., 1980. The social component of dominance relationships in rhesus monkeys (Macaca mulatta). Anim. Behav. 28, 1033–1039. doi:10.1016/S0003-3472(80)80092-3

Bird, C.D., Emery, N.J., 2008. Using video playback to investigate the social preferences of rooks, Corvus frugilegus. Anim. Behav. 76, 679–687. doi:10.1016/j.anbehav.2008.04.014

Boucherie, P.H., Mariette, M.M., Bret, C., Dufour, V., 2016a. Bonding beyond the pair in a monogamous bird: impact on social structure in adult rooks (Corvus frugilegus). Behaviour. doi:10.1163/1568539X-00003372

Boucherie, P.H., Sosa, S., Psaquaretta, C., Dufour, V., 2016b. A longitudinal network analysis of social dynamics in rooks Corvus frugilegus: repeated group modifications do not affect social network in captive rooks. Current zoology, Institute of zoology, Chinese academy of sciences, 2016. doi:10.1093/cz/zow083

Braun, A., Walsdorff, T., Fraser, O.N., Bugnyar, T., 2012. Socialized sub-groups in a temporary stable Raven flock? J. Ornithol. 153, 97–104. doi:10.1007/s10336-011-0810-2

Chapais, B., Girard, M., Primi, G., 1991. Non-kin alliances, and the stability of matrilineal dominance relations in Japanese macaques. Anim. Behav. 41, 481–491. doi:10.1016/S0003-3472(05)80851-6

Chase, I. D., 1982. Dynamics of hierarchy formation: the sequential development of dominance relationships. *Behaviour*, *80*(3), 218-239. doi:10.1163/156853982X00364

Chase, I.D., Tovey, C., Spangler-martin, D., Manfredonia, M., 2002. Individual differences versus social dynamics in the formation of animal dominance hierarchies 99, 5744–5749.

Chiarati, E., Canestrari, D., Vera, R., Marcos, J.M., Baglione, V., 2010. Linear and Stable Dominance Hierarchies in Cooperative Carrion Crows. Ethology 116, 346–356. doi:10.1111/j.1439-0310.2010.01741.x

Clotfelter, E.D., Paolino, A. D., 2003. Bystanders to contests between conspecifics are primed for increased aggression in male fighting fish. Anim. Behav. 66, 343–347. doi:10.1006/anbe.2003.2227

Connor, R.C., 2007. Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 362, 587–602. doi:10.1098/rstb.2006.1997

Cords, M., 1997. Friendships, alliances, reciprocity and repair. Machiavellian Intelligence II: Extensions and Evaluations., Cambridge. ed. Cambridge.

David, H.A., 1988. Ranking from unbalanced paired-comparison data. Biometrika 74(2), 432–436.

David, H.A., 1987. Ranking from unbalanced paired-comparison data. Biometrika 74(2), 432–436.

Daws, A.G., Grills, J., Konzen, K., Moore, P. a., 2002. Previous Experiences Alter the Outcome of Aggressive Interactions Between Males in the Crayfish, Procambarus Clarkii. Mar. Freshw. Behav. Physiol. 35, 139–148. doi:10.1080/1023624021000014725

De Marco, A., Cozzolino, R., Dessì-Fulgheri, F., Thierry, B., 2010. Conflicts induce affiliative interactions among bystanders in a tolerant species of macaque (Macaca tonkeana). Anim. Behav. 80, 197–203. doi:10.1016/j.anbehav.2010.04.016

Demaria, C., & Thierry, B. 2001. A comparative study of reconciliation in rhesus and Tonkean macaques. *Behaviour*, *138*(3), 397-410.

de Villiers, M.S., Richardson, P.R.K., van Jaarsveld, A.S., 2003. Patterns of coalition formation and spatial association in a social carnivore, the African wild dog (Lycaon pictus). J. Zool. 260, S0952836903003832. doi:10.1017/S0952836903003832

de Vries, H., 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Anim. Behav. 86, 1097–1105. doi:10.1016/j.anbehav.2013.08.019

de Vries, H., 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Anim. Behav. 50, 1375–1389. doi:10.1016/0003-3472(95)80053-0

De Vries, H., Stevens, J.M.G., Vervaecke, H., 2006. Measuring and testing the steepness of dominance hierarchies. Anim. Behav. 71, 585–592. doi:10.1016/j.anbehav.2005.05.015

de Waal, F., & Luttrell, L.M., 1985. The Formal Hierarchy of Rhesus Macaques : An Investigation of the Bared-Teeth Display. Am. J. Primatol. 9, 73–85.

de Waal, F.B., 1986. The integration of dominance and social bonding in primates. Q. Rev. Biol. 459–479.

Dingemanse, N.J., De Goede, P., 2004. The relation between dominance and exploratory behavior is context-dependent in wild great tits. Behav. Ecol. 15, 1023–1030. doi:10.1093/beheco/arh115

Drews, C., 1993. The Concept and definition of dominance in animal behaviour. Behaviour 125, 283–313. doi:10.1017/CBO9781107415324.004

Duboscq, J., Micheletta, J., Agil, M., Hodges, K., Thierry, B., Engelhardt, A., 2013. Social Tolerance in Wild Female Crested Macaques (Macaca nigra) in Tangkoko-Batuangus Nature Reserve, Sulawesi, Indonesia. Am. J. Primatol. 75, 361–375. doi:10.1002/ajp.22114

Dunbar, R.I.M., 1989. Social systems as optimal strategy sets: the costs and benefits of sociality. Comp. socioecology 73–88.

Elo, A.E., 1978. The Rating of Chess Players, Past and Present. New York Arco.

Emery, N.J., Clayton, N.S., 2004. The Mentality of Crows : Convergent Evolution of Intelligence in Corvids and Apes. Science (80-.). 306, 1903–1907.

Emery, N.J., Seed, A.M., von Bayern, A.M.P., Clayton, N.S., 2007. Cognitive adaptations of social bonding in birds. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 362, 489–505. doi:10.1098/rstb.2006.1991

Frank, L.G., 1986. Social organization of the spotted hyaena Crocuta crocuta. II. Dominance and reproduction. Anim. Behav. 34, 1510–1527. doi:10.1016/S0003-3472(86)80221-4

Franz, M., Mclean, E., Tung, J., Altmann, J., Alberts, S.C., 2015. Self-organizing dominance hierarchies in a wild primate population. Proc. R. Soc. B Biol. Sci. 282, 20151512. doi:10.1098/rspb.2015.1512

Fraser, O.N., & Bugnyar, T., 2012. Reciprocity of agonistic support in ravens. Anim. Behav. 83, 171–177. doi:10.1016/j.anbehav.2011.10.023

Gammell, M.P., de Vries, H., 2003. David’s score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. Anim. Behav. 66, 601–605. doi:10.1006/anbe.2003.2226

Goodwin, D., 1955. Some observations on the reproductive behavior of rooks. Br. Birds 48, 97–107.

Griffin, L.R., Thomas, C.J., 2000. The spatial distribution and size of rook (Corvus frugilegus) breeding colonies is affected by both the distribution of foraging habitat and by intercolony competition. Proc. Biol. Sci. 267, 1463–7. doi:10.1098/rspb.2000.1165

Hinde, R.A. & Datta, S., 1981. Dominance: an intervening variable. Behav. Brain Sci. (4), 442.

Holekamp, K.E., Sakai, S.T., Lundrigan, B.L., 2007. Social intelligence in the spotted hyena (Crocuta crocuta). Philos. Trans. R. Soc. Lond. B. Biol. Sci. 362, 523–38. doi:10.1098/rstb.2006.1993

Izawa, E.I., Watanabe, S., 2008. Formation of linear dominance relationship in captive jungle crows (Corvus macrorhynchos): Implications for individual recognition. Behav. Processes 78, 44–52. doi:10.1016/j.beproc.2007.12.010

Izawa, E.-I., Watanabe, S., 2008. Formation of linear dominance relationship in captive jungle crows (Corvus macrorhynchos): implications for individual recognition. Behav. Processes 78, 44–52. doi:10.1016/j.beproc.2007.12.010

Jackson, W.M., 1991. Why do winners keep winning? Behav. Ecol. Sociobiol. 28(4), 271–276.

Jolles, J.W., Ostojić, L., Clayton, N.S., 2013. Dominance, pair bonds and boldness determine social-foraging tactics in rooks, Corvus frugilegus. Anim. Behav. 85, 1261–1269. doi:10.1016/j.anbehav.2013.03.013

Kasprzykowski, Z., 2008. Nest location within the tree and breeding parameters of Rooks Corvus frugilegus. Bird Study 55, 59–65. doi:10.1080/00063650809461505

Klass, K., & Cords, M., 2011. Effect of unknown relationships on linearity, steepness and rank ordering of dominance hierarchies: simulation studies based on data from wild monkeys. Behav. Processes 88(3), 168–176.

Krause, J., Ruxton, G.D., 2002. Living in groups. Oxford University Press.

Kutsukake, N., 2000. Matrilineal rank Inheritance varies with absolute rank in Japanese macaques. Primates 41, 321–335. doi:10.1007/BF02557601

Lamprecht, J., 1985. Structure and causation of the dominance hierarchy in a flock of bar-headed geese (anser indicus). Behaviour 96, 28–48. doi:10.1163/156853986X00207

Landau, H.G., 1951. On dominance relations and the structure of animal societies: I. Effect of inherent characteristics. Bull. Math. Biophys. 13(1), 1–19.

Leiva, D., de Vries, H., 2014. Testing Steepness of Dominance Hierarchies. R Packag. version 0.2-2.

Lincoln, G.A., Racey, P.A., Sharp, P. J., &, Klandorf, H., 1980. Endocrine changes associated with spring and autumn sexuality of the rook, Corvus frugilegus. J. Zool. 190(2), 137–153.

Logan, C.J., Emery, N.J., Clayton, N.S., 2012. Alternative behavioral measures of postconflict affiliation. Behav. Ecol. 24, 98–112. doi:10.1093/beheco/ars140

Logan, C.J., Ostojić, L., Clayton, N.S., 2013. Rook, But Not Jackdaw, Post-Conflict Third-Party Affiliation Reduces Aggression for Aggressors. Ethology 119, 427–435. doi:10.1111/eth.12078

Loretto, M.-C., Fraser, O.N., Bugnyar, T., 2012. Ontogeny of Social Relations and Coalition Formation in Common Ravens (Corvus corax). Int. J. Comp. Psychol. 25, 180–194.

Marshall, A.J., Coombs, C.J.F., 1956. The interaction of enviromental, internal and behavioral factors in the rooks, Corvus frugilegus.

Martin, J.E., 2005. The influence of rearing on personality ratings of captive chimpanzees (Pan troglodytes). Appl. Anim. Behav. Sci. 90, 167–181. doi:10.1016/j.applanim.2004.08.019

Martin, P., Bateson, P., 1993. Measuring behaviour: an introductory guide. Cambridge University Press. doi:10.1016/0005-7967(94)90179-1

Massen, J.J.M., Pašukonis, A., Schmidt, J., Bugnyar, T., 2014. Ravens notice dominance reversals among conspecifics within and outside their social group. Nat. Commun. 5, 1–7. doi:10.1038/ncomms4679

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., 2011. Assessing dominance hierarchies : validation and advantages of progressive evaluation with Elo-rating. Anim. Behav. 1–11. doi:10.1016/j.anbehav.2011.07.016

Preuschoft, S. & van Schaik, C. P. 2000: Dominance and communication: Conflict management in various social settings. In: Natural Conflict Resolution (Aureli, F. & de Waal, F. B. M., eds). Univ. California Press, Berkeley/Los Angeles, CA, pp. 77—105.

Robichaud, D., Lefebvre, L., Robidoux, L., 1996. Dominance affects resource partitioning in pigeons, but pair bonds do not 840, 833–840.

Roell, A., Bossema, I., 1982. A comparison of nest defence by Jackdaws, rooks, magpies and crows. Behav. Ecol. Sociobiol. 11, 1–6. doi:10.1007/BF00297658

Scheid, C., Schmidt, J., Noë, R., 2008. Distinct patterns of food offering and co-feeding in rooks. Anim. Behav. 76, 1701–1707. doi:10.1016/j.anbehav.2008.07.023

Schielzeth, H., 2010. Simple means to improve the interpretability ofregression coefficients. Methods Ecol. Evol. 1, 103–113. doi:10.1111/j.2041-210X.2010.00012.x

Schino, G., 2000. Beyond the primates: expanding the reconciliation horizon., in: Waal), (Ed. by F. Aureli & F. B. M. de (Ed.), Natural Conflict Resolution. p. 225e242.

Seed, A.M., Clayton, N.S., Emery, N.J., 2008. Cooperative problem solving in rooks (Corvus frugilegus). Proc. Biol. Sci. 275, 1421–9. doi:10.1098/rspb.2008.0111

Seed, A.M., Clayton, N.S., Emery, N.J., 2007. Postconflict third-party affiliation in rooks, Corvus frugilegus. Curr. Biol. 17, 152–8. doi:10.1016/j.cub.2006.11.025

Seibert, L.M., Crowell-Davis, S.L., 2001. Gender effects on aggression, dominance rank, and affiliative behaviors in a flock of captive adult cockatiels (Nymphicus hollandicus). Appl. Anim. Behav. Sci. 71, 155–170. doi:10.1016/S0168-1591(00)00172-6

Shaw, R.C., Clayton, N.S., 2012. Eurasian jays, Garrulus glandarius, flexibly switch caching and pilfering tactics in response to social context. Anim. Behav. 84, 1191–1200. doi:10.1016/j.anbehav.2012.08.023

Shizuka, D., McDonald, D.B., 2015. The network motif architecture of dominance hierarchies. J. R. Soc. Interface 12, 20150080–20150080. doi:10.1098/rsif.2015.0080

Shizuka, D., McDonald, D.B., 2012. A social network perspective on measurements of dominance hierarchies. Anim. Behav. 83, 925–934. doi:10.1016/j.anbehav.2012.01.011

Shultz, S., Dunbar, R.I.M., 2009. Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment - SHULTZ - 2010 - Biological Journal of the Linnean Society - Wiley Online Library 111–123.

Silk, J.B., Alberts, S.C., Altmann, J., 2004. Patterns of coalition formation by adult female baboons in Amboseli, Kenya. Anim. Behav. 67, 573–582. doi:10.1016/j.anbehav.2003.07.001

Smith, J.E., Van Horn, R.C., Powning, K.S., Cole, A.R., Graham, K.E., Memenis, S.K., Holekamp, K.E., 2010. Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. Behav. Ecol. 21, 284–303. doi:10.1093/beheco/arp181

Stahl, J., Tolsma, P.H., Loonen, M.J.J.E., Drent, R.H., 2001. Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks. Anim. Behav. 61, 257–264. doi:10.1006/anbe.2000.1564

Strasser, E.H., Benford, R., Balda, R.P., 2006. Linear Hierarchy Provides Context for Evolution of Social Cognition in Pinyon Jays. 3–5.

Swingland, I.R., 1977. The social and spatial organization of winter communal roosting in Rooks (Corvus frugilegus). J. Zool. London 182, 509–528.

Tamm, S., 1977. Social dominance in captive jackdaws (Corvus monedula). Behav. Processes 2, 293–299. doi:10.1016/0376-6357(77)90032-8

Tarvin, K. a, Woolfenden, G.E., 1997. Patterns of Dominance and Aggressive Behaviour in Blue Jays at a Feeder. Condor 99, 434–444.

Team, R.C., 2015. R: A language and environment for statistical computing. Vienna, Austria. URL http//www. R-project. org.

Thierry, B., 2013. Identifying constraints in the evolution of primate societies. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 368, 20120342. doi:10.1098/rstb.2012.0342

Thierry, B., Singh, M., & Kaumanns, W., 2004. Macaque societies: a model for the study of social organization (Vol. 41)., Cambridge . ed.

van Hooff, J. A., & Wensing, J.A., 1987. Dominance and its behavioral measures in a captive wolf pack., in: Man and Wolf (Frank, H. W., Ed.). Junk Publishers, Dordrecht, The Netherlands, p. 219—252.

Verhulst, S., Geerdink, M., Salomons, H.M., Boonekamp, J.J., 2014. Social life histories: jackdaw dominance increases with age, terminally declines and shortens lifespan. Proc. Biol. Sci. 281. doi:10.1098/rspb.2014.1045

Wechsler, B., 1988. Dominance relationships in jackdaws (Corvus monedula). Behaviour 106(3), 252–264.

White, F.J., Wood, K.D., 2007. Female Feeding Priority in Bonobos, Pan paniscus, and the Question of Female Dominance. Am. J. Primatol. 1222, 1210–1222. doi:10.1002/ajp

Wilson, D.J., 1992. Correlates of agonistic display by great tits parus major. Behaviour 121(3), 168–214. doi:10.1017/CBO9781107415324.004

Wittemyer, G., Douglas-Hamilton, I., Getz, W.M., 2005. The socioecology of elephants: Analysis of the processes creating multitiered social structures. Anim. Behav. 69, 1357–1371. doi:10.1016/j.anbehav.2004.08.018

Wittemyer, G., Getz, W.M., 2007. Hierarchical dominance structure and social organization in African elephants, Loxodonta africana. Anim. Behav. 73, 671–681. doi:10.1016/j.anbehav.2006.10.008

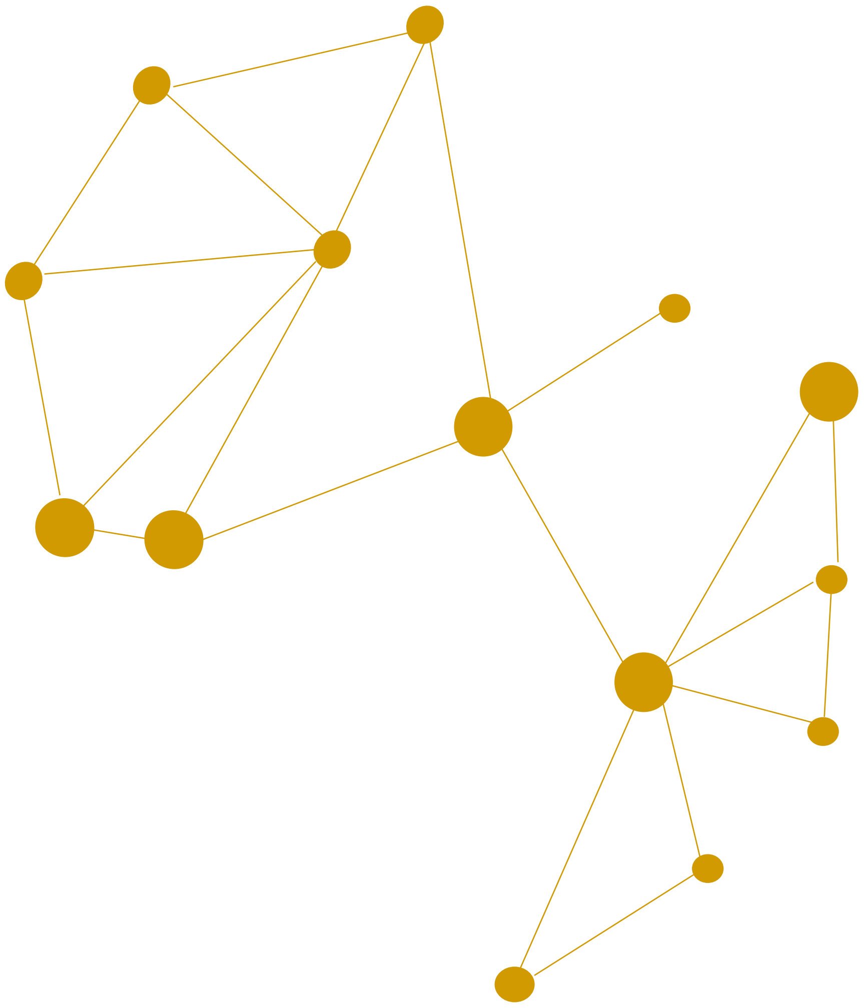
Wittig, R.M., Boesch, C., 2003. Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. Int. J. Primatol. 24, 847–867. doi:10.1023/A:1024632923180

Woolfenden, G.E., Fitzpatrick, J.W., 1977. Dominance in the Florida Scrub-Jay. Condor 79, 1–12. doi:10.1126/science.100.2609.594

Zeileis, A., Torsten, H., 2002. Diagnostic Checking in Regression Relationships. R News 2(3), http://CRAN.R–project.org/doc/Rnews/.

7

DISCUSSION



This thesis constitutes the first in depth study of a group of rooks' social structure, a corvid species forming long-term monogamous pair bonds, but also living in group all year long. This work aimed at providing a close view of the proximate mechanisms that sustain the establishment and the maintenance of relationships in this highly social species. So far rooks sociality remained poorly understood with regard to assumptions made on their social system. This results from the fact that wild populations are difficult to monitor regarding captures and marking. In addition, conducting reliable observations is complicated by the size and the dynamic of wild aggregations. In this thesis, I investigated the diversity of differentiated relationships and the form taken by the social structure in this species, focusing on the quality and temporal dynamic of both pair and extra-pair relationships, and considering both affiliative and dominance relationships.

In chapter 3 I confirmed that extra-pair relationships occur in rooks, and that some of those relationships can be characterized as social bond with regard to the content and quality of their pattern of interaction. In addition, I showed that same-sex relationships may be present in rooks, both in pairs and extra-pair relationships, with similar strength than mixed-sex relationships. In chapter 4, I investigated the impact of extra-pair relationships on the stability and the strength of the pair bonding. I showed that rooks can divorce, and have the ability to strongly re-pair, forming several pair bond throughout their life. More precisely, scrutinizing the behavioural mechanisms underlying separations and new pair formations, I found that outsiders can actively supplant (usurp) paired individuals in their relationships, while other individuals (intermediary) gradually switch from one valuable relationship to another. In chapter 5, I further investigated the way all affiliative relationships organized at the group level, and how they varied in time. I demonstrated that temporal changes in relationships (i.e. formation and removal) follow robust and consistent patterns (i.e. attractor effect of the pair and triadic closure) regardless of group composition and sex-ratio, leading to the emergence of an inter-connected network of affiliates. The consistency of social structural patterns indicates that rooks social structure was flexible enough to allow temporal variations without being dismantled. Finally in chapter 6, I investigated another type of relationship, namely the dominance relationships. More specifically, I investigated the behavioural mechanisms shaping the establishment and maintenance of dominance order in a fluid social system. I showed that rooks may have fairly linear hierarchies at any given point in time, but with quite unstable dominance relationships. In addition, I found a low directionality in conflicts, and weak power asymmetries, suggesting that rooks live in a rather tolerant social structure. Consistently with all previous findings on the strength of the monogamous bond in this species, dominance relationships were mainly determined by the pairing status and the aggressiveness of individuals. Overall, my data confirm that rooks can form non-reproductive social bonds, which results in the formation of a modular social structure composed of both pairs and extra-pair relationships. These results show that rooks social structure can go far beyond a simple aggregation of pairs, and that rooks likely live in a well-integrated and individualised structure. I will now further discuss those findings in the light of the previous literature and rooks socio-ecology, and consider the implications of my results for the understanding of the evolution of sociality.

1. BEING LONG-TERM MONOGAMOUS IN A SOCIAL GROUP

In chapter 3, I investigated the possibility of same-sex and extra-pair bonding in a captive group of rooks over three multi-months periods (i.e. 2012, 2014, and 2015). I used several affiliative and agonistic behaviours to categorize and characterize relationships according to their strength. Three categories of relationships emerged: pairs, secondary affiliations and weak relationships.

1.1. Strength of the monogamous pair bond

First of all, chapter 3 confirms the strength of the monogamous pair bonds in this species. Almost all individuals were involved in a pair (Chapter 3; see also Annex 1). Pairs, as the strongest relationships in the group, combined both the highest frequencies of all positive interactions and associations, and the highest frequencies of affiliations. They were also characterized by a higher proportion of affiliations over spatial proximities, and a high tolerance at the food source. Pairs also corresponded to dyads that build nests and attended to breed in the three years, although not all pairs did so. Nesting and non-nesting pairs had similar strength (i.e. similar sociality index, same behaviours in comparable frequencies, and same patterns of interaction). Nesting pairs only differed from others by higher rates of mounting and the asymmetry of their spatial proximities, which makes sense considering the requirements of reproduction in this species. Indeed, if rooks share parental care, females usually incubates eggs while males fly back and forth to nests to feed females and then chicks (Goodwin, 1955; Lincoln et al., 1980; Ogilvie, 1951).

Overall, my results are partially consistent with what is known on the quality of the pair bonding in this species (e.g. Emery et al., 2007; Jolles et al., 2013b; Scheid et al., 2008), and more broadly in species forming long-term monogamous pair bond like corvids and parrots (e.g. in raven, Fraser and Bugnyar, 2010b; in jackdaws, de Kort et al., 2006a; in New Caledonian crow, Holzhaider et al., 2011; in cockatiels, Spoon et al., 2004; in monk parakeets; Hobson et al., 2014). Emery et al. (2007) notably compared the pair bond in rooks and jackdaws, to the long-term alliances that can be found in some social mammals, like primates or dolphins. In juveniles group, paired individuals have higher dominance ranking than solitary individuals, a phenomena that is stronger as the process of pair bond formation progresses (Emery et al., 2007). Although my results show that adult paired individuals had higher dominance rates than solitary, like in juveniles (Chapter 6), I found also that the very notion of dominance needs to be re-examined in rooks (Chapter 6; see following section on rooks dominance). So far, increased dominance through pairing has been found to facilitate access or monopolisation of food resources (Emery et al., 2007; Jolles et al., 2013b; Kasprzykowski, 2008; Seed et al., 2008; Swingland, 1977; Dally et al., 2008), but also to affect foraging tactic (Jolles et al., 2013b), and to impact the access to nest sites (Swingland, 1977). This is reminiscent of the role of coalitions (i.e. joint aggression of at least two individuals against a common target) in primates or dolphins which allow individuals a better access to food resources or mating partners (Connor, 2007; Cords, 1997). Yet the concrete benefits that may result from an increase in dominance status remains to be further investigated in rooks, in particular in the wild.

In this study group, pairs and affiliates (secondary partners) were characterised by a certain amount of aggression among partners (Chapter 3), which was not previously reported in this species, as conflicts were generally described as rare (i.e. in adults and juveniles; Emery et al., 2007; Logan et al., 2012) or even totally absent in pairs (i.e. in young adults, 3 years old; Seed et al., 2007). In other groups, the sex-ratio was slightly to strongly unbalanced in favour of females (i.e. Cambridge set up; Emery et al., 2007; Jolles et al., 2013b; Logan et al., 2012; Seed et al., 2007). An explanation is that the level of aggression might be group specific. The higher proportion of males compared to females in our captive setup coul have induced a higher propensity to aggress others at the group level, including the paired partner. In addition, in our group several changes occurred in pairs, including separations of former partners, concomitantly to modifications of the group composition (Chapter 4). Separating pairs were characterised by higher rates of aggression compared to other pairs, which could partially explain the level of aggression found between paired partners (Chapter 3). Indeed, analysing data on multi-month periods, pairs identified in 2014 (Chapter 3) were actually pairs that later separated (Chapter 4; see also Annex 1). Yet all results in Chapter 3 were found on three different years and for three different group compositions, controlling for the effect of year in the analyses. Thus changes in pair's composition might not be the sole explanation for the level of aggression found among pairs and affiliates. Indeed, it must be recalled that if aggression rarely occurred among weak partners in rooks, they also also rarely associated (Chapter 3). When computing the ratio between the frequency of aggression and the frequency of association, pairs were actually characterised by lower ratio of aggression compare to affiliates and weak partners[4]. Thus, although aggression occurred among all

---

[4] Additional analyses, GLMM: pairs vs. affiliates, estimates ± SE = -2.74 ± 0.48, z value = -5.68, p value < 0.001; pairs vs. weak, estimates ± SE = -3.30 ± 0.43, z value = -7.88, p value < 0.001; affiliates vs. weak, estimates ± SE = -0.56 ± 0.28, z value = -2.04, p value = 0.10.

partners in the group, weak partners and affiliates more frequently engaged in conflicts than pairs considering the time they spend together, which is consistent with the fact that pairs are by definition the most valuable relationships.

1.2. Secondary affiliations in a socially monogamous species

Beyond the pair, further affiliative relationships emerged (Chapter 3, 4, 5). In the study group, rooks indeed interacted out of the pair. Secondary affiliations; or extra-pair relationships), were characterized like pairs by frequent spatial associations, but also by some affiliations and sexual behaviours (Chapter 3). Pairs and secondary affiliations both displayed affiliations and sexual behaviours and similar patterns of interactions (i.e. in particular mixed-sex secondary affiliations; proportion of affiliations over proximities; Chapter 3). In addition, secondary partners were as tolerant as paired partner at the food sources (i.e. co-feeding; Chapter 3). Thus, some of those secondary affiliations at least, might be acknowledged as social bonds (i.e. dyads that frequently associated but also affiliated; Shultz and Dunbar, 2010a). As discussed earlier, secondary partners were also characterised by higher rates of aggression than pairs (and similar rates to weak partners) when considering the time they spend together. This result could call into question the fact that secondary relationships are indeed social bonds in the strict sense; define notably by high amounts of affiliations and low frequencies of aggression (van Schaik and Aureli 2000; Silk et al., 2013). Yet, apart from the fact that secondary partners engaged in affiliations and tolerate each other at the food source, they did not associated randomly. Indeed, both pairs and secondary affiliations represented a very small part of all potential relationships in the group regardless of the changes in group composition and sex-ratio (i.e. on average 20% all potential relationships in the networks; Chapter 3 & 5). This indicate that although they were hold on a restricted area, rooks actively choose the partner they interacted with. In addition, aggressions between affiliates are also observed in other species where partners spend a significant part of their time together. In macaques for instance, frequent associations can expose individuals to higher chances of (low risk) aggression (e.g. in macaques, *Macaca fuscata*: Soltis et al., 1997; *Macaca mulatta*: Bernstein et al., 1993). Overall, the formation of secondary affiliations indicates that pairs in adult rooks are not as exclusive as expected (Emery et al., 2007). It also demonstrates rooks ability to simultaneously invest in the monogamous pair bond and in other valuable relationships, attesting of a high degree of social flexibility in this species.

The occurrence of secondary affiliations indicates that rooks colonies are more than just an aggregation of pairs. However, in the wild, due to the high density of some rooks' colonies, it seems unlikely that each bird knows every other member in the colony. Yet knowing closely nesting or roosting neighbours would suffice to form sub-groups of affiliated individuals that interact more often and more frequently with each other. Considering rooks socio-ecology, the formation of secondary affiliations could provide a number of advantages. First, the formation of a cohesive network of affiliates should at least ensure the coherence of the group over time, bringing some benefits associated to group living (e.g. predation detection, increased foraging efficiency, transmission of information about habitat quality), while allowing to better deal with its competitive aspect (Dunbar, 1989; Krause and Ruxton, 2002). Indeed, the establishment of close social bonds between group members is believed to promote group cohesion and cooperation (Dunbar 2012; Lehmann et al. 2007a; Lusseau & Newman 2004; Berghänel et al. 2011). In rooks, the degree of tolerance among partners positively correlates with their performance on a collaborative task (Seed et al., 2008).

In the colonial context, the formation of secondary affiliations could decrease the costs associated with the close proximity of nest during reproduction (i.e. nests can sometimes touch each other; personal observations in the wild and in the aviary; see also Ogilvie, 1951). Indeed, the close proximity of nests may favour nest material pilfering and young harassment, both behaviours being frequently reported in wild colonies (Goodwin, 1955; Marshall and Coombs, 1957; Owen, 1959; Swingland, 1977) and also in captivity (personal observations in the aviary; Richards, 1976). In addition, frequent conflicts or harassment can ultimately lead to breeding failure (Jovani & Grimm, 2008). In this context, bonding with neighbours may facilitate the emergence of cooperation, like cooperative nest surveillance (Erwin, 1979; Arroyo et al., 2001), avoidance of nest material or eggs pilfering (Ogilvie, 1951; Carrascal et al., 1995), the increase in breeding synchrony with neighbours (Jovani & Grimm, 2008), or more broadly the reduction of stress and the prevention of fights (Lewis et al., 2007). Moreover, the fact that rooks breeding parameters are not affected by the very close proximity of other nests (i.e. clutch size, number of hatchlings; Kasprzykowski 2008) supports the hypothesis that sub-units of affiliates form in rooks' colonies, resulting in a safer breeding environment (i.e. at least in the close vicinity of the nest). In addition, if we were to extrapolate from our captive data, we may expect the sub-groups of affiliated individuals not only to cooperate in the breeding context, but also to forage and mob predators together. For instance, work on tit for tat strategies in passerine highlighted that unrelated nesting neighbours can reciprocate mobbing by joining neighbours that helped them previously to harass predators (i.e. Pied Flycatchers, *Ficedula hypoleuca*; Krams et al., 2006). Adult rooks ability to form secondary affiliations may also be particularly interesting for individuals who are not yet paired. Groups of sub-adults and unpaired individuals might for instance be better at monopolising food resources against subgroups of paired individuals. Indeed, in ravens, and before sexual maturity, individuals express a tendency to form groups, joined sometimes by unpaired adults (Braun et al., 2012; Marzluff and Heinrich, 1991). Non-breeder ravens can actively recruit partners to feeding sites (Heinrich, 1988b), and by doing so increase their chances to monopolise food resources against territorial pairs (Marzluff and Heinrich, 1991). However, in rooks the level of competition while foraging might not be that high, and it is frequent to see subgroups of individuals with juveniles after fledging, even together with other species (i.e. a gathering of rooks, jackdaws and crows; Jolles et al., 2013a).

The emergence of secondary affiliations between familiar congeners in rooks could ultimately result in direct fitness benefits, as already suggested in a wide range of social species (in mammals: Cameron et al., 2009; Schülke et al., 2010; Silk et al., 2010; and in birds: Ryder et al., 2008; Oh & Badyaev, 2010). Further research is now needed to see if secondary affiliations in fact play a role in the emergence of cooperation among unrelated conspecifics in wild populations (e.g. reciprocity of support in mobbing or alarm calls, cooperative defence at nests, monopolisation of food resources).

1.3. Impact of secondary affiliations on the monogamous pair bond

Among the various secondary affiliations identified in this thesis (Annex 1), some were pairs in the making. Changes in partners in corvid species are not frequently reported (i.e. in jackdaws and jays; Logan et al., 2012), and rooks are often supposed to pair for life. Yet in the course of the thesis I had the opportunity to document in real time several pair separations and formations (Chapter 3 & 4, see also Annex 1). Before the introduction of new individuals, highly stable pairs had existed for several years in this group (up to 9 years, for one still on-going pair bond), confirming that mate switching remains a rare phenomenon. When it occurred, mate-switching resulted in the re-forming of bonds as strong and as valuable with a new partner (Chapter 4). Proportionally, newly formed pairs engaged more frequently in affiliations than other pairs, indicating that individuals actively invested in the new relationship, possibly to quickly reinforce and secure the bond. This makes sense, considering that partner death is likely to occur in the wild (Goodwin, 1955; Jennings, 1955), and that it is necessary for these birds to be able to re-invest in a long-lasting bond.

Separations occurred in 2014, after the introduction of new individuals in the group - mainly females - and the loss of several original group members (Chapter 4; Annex 1). All separations were concomitant with the formation of a new pair. Interestingly, those new pairs formed through extra-pair associations and affiliations, mostly food sharing, which is described as essential in the partner's research process in juvenile corvids (i.e. in rooks, Emery et al., 2007; Scheid et al., 2008; but also in jackdaws, de Kort et al., 2006a, 2003; von Bayern et al., 2007). Sexual behaviours however, did not play a role in mate switching (Chapter 4), despite the fact that extra-pair copulations is known to trigger divorce in numerous avian species (Cezilly and Nager, 1995; Spoon et al., 2007). An interesting result is that the shift in partner occurred rather suddenly. Before the mate switching, the sociality index of both pairs in formation and separating pairs did not vary significantly. Until the very end, except for a higher rate of aggressions, separating pairs were apparently as strong (i.e. same sociality index, same pattern of interactions, frequent associations and affiliations), and as stable as other established pairs (Chapter 4). However, the mate switching process was characterised by a sharp decrease of the sociality index of separating pairs, while the index of newly formed pairs quickly and significantly increased over time (Chapter 4). The fact that individuals did not leave one relationship without having another in formation, emphasises again the importance of the pair bonding in this species. By switching from one partner to another, individuals may actually change partner without losing the benefits of being paired (Emery et al., 2007). Plus, regarding the costs and benefits associated with mate switching (i.e. in terms of becoming paired or solitary), individuals behaved differentially. In fact, intermediary individuals, shifting from one pair to another, seemed rather little involved in the process of separation as all increases of interactions were initiated by the usurpers or the individuals soon to be single (Chapter 4). This is rather surprising as intermediary individuals did not seem to choose their partner, but simply to go with whomever is the most persistent. Yet among separating partners, most aggressions were perfomred by the intermediary individual, validating the choice of a new partner over the former one in the process of mate switching. But whether the newly formed pair could be seen as an alliance against the former partner needs to be further investigated.

The occurrence of mate switching raises questions about the actual competition that can exist among group members for mating partner in wild colonies. Indeed, among the three individuals that lost their partner (i.e. because of natural death or after escape; k, m, n; see Annex 1), two later acted as usurpers to form new pairs (i.e. k and m; Chapter 4). Thus in wild colonies, solitary individuals (at least some) may be potential usurpers to established pairs. Further work should aim at establishing the proportions of solitary individuals in wild colonies, and if possible, the relative proportion of mate switchings occurring among an established pair and a ‘solitary outsider’. Linked to the reproductive success of the separating and newly formed pairs, such investigation could provide very valuable insights on whether solitary individuals can indeed be seen as potential usurpers for established pairs. In addition, it could provide insights on whether secondary affiliations can be seen as a strategy to assess the quality of future partners (for solitary individuals), and to keep potential future partners close at hand (for paired individuals).

It should be noted that secondary affiliations formed in the three years of this study, whereas mate switching only occurred in 2014. In addition, most paired individuals were simultaneously involved in one or several secondary affiliations, including individuals involved in stable pairs. Moreover, secondary affiliations could emerge either between paired individuals with solitary or other paired individuals, or between solitary individuals (Chapter 5; Annex 1). Altogether, it suggests that the emergence of secondary affiliations is not necessarily only sustained by mate-switching strategies and reproduction (Chapter 5).

1.4. Same-sex relationships

Captivity and group sex-ratio probably enhanced the proportion of same-sex relationships - pairs and secondary affiliations -, as partners of the opposite sex were lacking. Indeed, valuable same sex relationships has already been described in numerous avian species (mostly captive), including corvids, as an alternative bonding in case opposite sex partners are unavailable (i.e. in ravens, Fraser and Bugnyar, 2010b; in monk parakeets, *Myiopsitta monachus*, Hobson et al., 2014; in zebra finches, *Taeniopygia guttata*, Elie et al., 2011; in jackdaws, von Bayern et al., 2007; in greylag gander, *Anser anser*, Kotrschal, 2006). By adding females, we therefore expected to observe mate switching with same sex pairs splitting to reform mixed sex pairs.

However, if the proportion of same-sex pairs decreased in 2015 (Annex 1), this was mainly due to the fact that two male-male pairs stopped because of the loss of one partner (i.e. death of escape; h-m and n-z; Annex 1). In fact, same-sex pairs, which occurred in all three years, were as stable and as valuable as mixed-sex pairs. Indeed, male-male pairs were strong enough not to separate when they were given the opportunity to pair up with females.

Moreover, only one same-sex pair (female-female, c-p) separated in order to form a mixed-sex pair (k-p; Chapter 4, Annex 1), while three mixed-sex pairs separated. In addition, affiliations and sexual behaviours were not restricted to opposite sex partners, as expected for a monogamous species, and the sex composition of the dyad had no significant effect on the way partners interacted, for both pairs and secondary affiliations (i.e. reciprocity of proximities and affiliations, frequencies of co-feeding, mounting, courtship and even aggression; Chapter 3). The sex of the dyad only affected the pattern of interaction of secondary affiliations (i.e. mixed-sex secondary affiliations displayed more affiliation over proximities than same-sex secondary affiliations), which may result from the fact that some secondary affiliations were pairs in the making (Chapter 4). Note that the existence of valuable same sex relationships in adult rooks is not that suprising, as juvenile corvids can form social bonds with same-sex partners long before the first reproductive attempt (Emery et al., 2007; Fraser and Bugnyar, 2010b; Scheid et al., 2008; von Bayern et al., 2007).

Considering the strength and the stability of same-sex relationships in this study group, the unbalanced sex-ratio may not be the sole explanation for the occurrence of same-sex relationships. Indeed, same-sex relationships not only occur when opposite sex partners are missing, but they are also expected expected in highly social species (Mitani et al., 2000; Sterck et al., 1997), and assumed to provide various functional benefits to the partners (i.e. social partnership hypothesis, Zuk, 2006). In particular, in long term monogamous bird species, the pair bond is assumed to provide survival advantages that may explain the stability of same-sex pairs (e.g. food or space monopolisation, support in conflicts with conspecifics, or against predators; Black, 1996; Zann, 1996; Emery et al., 2007; Kotrschal et al., 2006; King, 2006). In some monogamous species, like opposite sex partners, the same-sex partners can become exclusive (King 2006; Kotrschal et al. 2006; Vasey and Sommer 2006). In some cases, they may even cooperate to raise young after having performed extra-pair copulations to reproduce (e.g. in gulls, *Larus californicus*, Conover and Hunt 1984; or albatrosses, *Phoebastria immutabilis*, Young et al. 2010). Finally, besides reproductive bonds (i.e. pairs in monogamous species), the formation of valuable relationships with same-sex partners in a group may also more broadly serve to regulate social tensions or to limit conflicts (McGraw and Hill 1999; Mitani et al., 2000; van Schaik and Aureli 2000).

1.5. Variation and stability of pairs and secondary affiliations: comments on the notion of scale

Investigating the characteristics of each category of relationships, pairs always represented more than 50% of both partners individual sociality index (i.e. summed index for all relationships in which an individual is involved), and 5 to 50% for secondary affiliations (Chapter 3). These two criteria were then applied to identify pairs and secondary affiliations on chapter 4, 5 and 6 on a finer time-scale (i.e. per week), and for different collection periods (see Annex 1 for more details on the identification of pairs and secondary affiliations according to time-scale and collection period). Finer time-scale allowed to follow the temporal dynamic of pairs and secondary affiliations, by detecting temporal variations in the strength of the relationships weeks after weeks. It allowed notably to recognize separations and formations of pairs (Chapter 4). Moreover, finer time-scales allowed to detect relationships that did not last for long and were therefore undetected on larger time-scale (Annex 1). Indeed, the number of pairs and secondary affiliations identified strongly increased at the week level compare to multi-month data (i.e. all individuals were involved in a pair or a secondary affiliation in at least one week; Annex 1). Yet most additional pairs found on finer time-scale were only identified temporarily on a single week (Annex 1), and therefore rather related to strong relationships than real mated pairs (Chapter 5). Nevertheless, it emphasizes the fact that the strength of the pair bond may vary in time. Pairs were indeed more or less affiliated according to the period, and could temporarily (rarely), shift from one privileged partner to another. Like pairs, secondary affiliations identified on multi-months periods were more stable in time than additional secondary affiliations identified per week (Annex 1). Actually analyses on finer time-scale reveal that secondary affiliations may not all have the same value. If some secondary affiliations were only detected once in a single week, numerous secondary affiliations lasted over several consecutive weeks or were regularly re-detected on different weeks, reinforcing previous results on the strength and quality of those extra-pair relationships. Note that the proportion of secondary affiliations was lower in 2012 compare to 2014 and 2015, regardless of the time-scale used (Annex 1). Possibly, this resulted from the addition of new individuals in the aviary, and a higher proportion of solitary individuals which were significantly involved in more numerous relationships than paired individuals (Chapter 5).

2. INVESTIGATING ROOKS' SOCIAL STRUCTURE

After having investigated the strength and the stability of extra-pair and same-sex relationships in the group, I further investigated the affiliative structure resulting from the enmeshment of those relationships. In addition, the study of the temporal dynamic of pairs and secondary affiliations confirmed that secondary affiliations led to a superior level of integration and complexity in the social structure (Chapter 5).

1.6. The role of pairs and solitary individuals in rooks' structure

Using a sophisticated dynamic actor-based models, Rsiena, to investigate the temporal changes of relationship, I found that the dynamic of relationships was not random in this group. Instead the temporal changes of relationship followed two consistent patterns, namely the unpopular attachment (i.e. individuals preferentially formed relationships with low degree partners, which were found to be paired individuals) and the triadic closure (i.e. my friend's friends are now becoming friends of mine; Chapter 5). Individuals were more likely to form relationships with paired individuals and with individuals already connected to their current social partners. Those two patterns induced the formation of triads in the networks, mostly centred on pairs (Chapter 5). Consistently, all cluster analysed on large time-scale in chapter 3, were composed of one or two pairs, sometimes completed by solitary individuals. Similarly, the large majority of triads detected in chapter 5 (i.e. weekly networks), were centred on pairs, and more rarely composed of a majority of solitary individuals. The attractor effect of the pair likely resulted from the fact that paired partners mainly interacted with one another (Chapter 3), but not only. Paired individuals also interacted with other pairs, as a significant part of triads in the networks were also composed of a majority of paired individuals (i.e. not involved in pairs together; Chapter 5). Furthermore, solitary individuals interacted significantly more often with paired individuals than other solitary. They were mainly responsible for the emergence of those relationships. This is again probably due to the investment required by the pair bonding, as it leaves little time to paired partners to interact with other individuals. Triads of individuals have already been reported in captive rooks, where on occasions solitary individuals connected mated-pairs (Richards, 1976). In the wild, Jolles also describes that a significant part of rooks, but also jackdaws flocks gather by forming triads (in rooks, on average 14% of the flock is clustered in triads and 46% in dyads; in jackdaws, 16% in triads and 41% in dyads; Jolles et al., 2013a). Triads of individuals were also reported in parrots (i.e. in captive and wild monk parakeet, Hobson et al., 2014;

Eberhard, 1998; in captive cockatiels, *Nymphicus hollandicus*, Spoon et al., 2004), which also form long term monogamous pair bond and live in groups. To find triadic structures in the networks is particularity interesting considering that it is expected to promote network cohesion, but also reciprocity and cooperative behaviours among partners (Banks & Carley 1996; Walker et al. 1997; Buskens 2002; Lou et al. 2013; Righi & Takács 2014). In addition, triads reflect an intermediate level in the network, between the single dyad and higher-order sub-units (Wasserman and & Faust, 1994). Therefore, triads are essential 'local' element of the networks through which dyads interconnect to form overall network structures (Nohria, 1992).

Overall, the dynamic of relationships demonstrates that pairs have a strong attractor effect on social interactions, providing novel insights on how such a strong bond can influence the shape of a social structure. Pairs formed the backbone of the group structure, an inter-connected network of affiliates emerging from the enmeshment of dyadic and triadic motifs (Chapter 5). Note that if pairs positively influenced the structure, the contrary was also true, as in some cases extra-pair relationships disrupted pair bonding (i.e. divorce and mate switching; Chapter 4). Finally, finding unpopular attachment and triadic closure in the networks, reinforces the finding that rooks did not interact randomly, but actively chose their partner.

The pairing status also had a strong impact on the level of social activity. Solitary were indeed significantly more connected than paired individuals in the network (Chapter 5). By interacting with several partners (i.e. both solitary and paired), solitary individuals may actually increase their chances to find a mate and to pair or re-pair. In addition, it may also ensure their integration in the social structure. By forming secondary relationships, solitary may avoid to be isolated from the group, and therefore to lose the benefits associated with group living in this species (e.g. decreased predation risk, increase foraging success, thermoregulation; Goodwin, 1955; Halupka, 2013; Swingland, 1977). Solitary were also particularly attracted by pairs during the breeding season (Chapter 5). One explanation is that they may be 'curious' of others reproduction, and could have tried to access to juveniles. Indeed, during the reproduction males often attempted to come close and to look into the nests, which induced strong reaction of the incubating females (i.e. personal observations in the aviary; high intensity aggressions and frequent vocalisations; see also Chapter 6). Another explanation is that solitary individuals may have tried to interfere in pairs' reproduction or may have tried to mate with females. Some studies indeed report cases of aggression of copulating pairs (Goodwin, 1976, 1955; Marshall and Coombs, 1956; Picture 1). In captivity, mount events were also found to increase group agitation, sometimes resulting in attacks of the mounting pair, either by males or females (i.e. personal observations; see also Richards, 1976). Similar third-party interventions has also been reported in ravens, which regularly intervene in others affiliative interactions (i.e. mostly bonded individuals toward individuals that are currently forming bonds; Massen et al., 2014b). It was notably proposed that those interventions could be used to prevent other from forming alliances (Massen et al., 2014b). Future studies on third-party intervention in other corvid species, and notably rooks, would therefore be particularly interesting to better understand this phenomenon.

Picture 1. Sequence of pictures showing the intervention of a third individual during a copulation. Photos by Heinrich Mallison.

1.7. Robustness of social patterns

We could have expected the change in of the group composition, and in particular the addition of wild females in a strongly biased sex ratio, to disrupt the social structure and induce social instability. The addition of new females indeed created new partners opportunities, and we observed changes in relationships, with an increase in the proportion of mixed-sex pairs (Chapter 4; see section limits for discussion regarding the effect of sex-ratio). Yet despite important variations in partnerships, the dynamic of relationships followed the same structural patterns in the three years (Chapter 5). The attractor effect of the pair and the triadic closure reinforced the social network regardless of group composition and sex-ratio, both before and during the breeding season (Chapter 5). In addition, triads were recurrent and very consistent in all networks. Moreover, despite individuals being added and moved out of the group over four years, the disorder of the network remained similar over this long period, indicating a stable network output despite modifications of the group composition. This confirms that rooks live in a well-integrated structure, where the number and diversity of differentiated relationships result in numerous feedbacks on individuals behaviour, providing to the structure a certain degree of resilience to perturbations (Sumpter, 2006). The robustness of the social patterns might actually participate in ensuring the coherence and the continuity of the social structure over time, which appeared flexible enough to allow temporal variations of relationships, group composition and sex-ratio, without being dismantled. This is particularly interesting considering rooks fission-fusion dynamics, and the fact that in the wild individuals constantly face modifications of group cohesion and composition. Further investigations are now needed to confirm the robustness of the social patterns in other groups and in wild populations, across ecological contexts, to conclude on the role of internal and external constraints in shaping social organisation in this species.

1.8. Integration of new group members

Because it mimicked at least partially the fluctuations of individual's memberships observed in wild colonies, the addition of new individuals in the aviary allowed me to investigate how rooks accepted new members in their existing community. Whatever their origin (i.e. original group member or newly added), all individuals had on average the same number of partners in the network and were involved in both pairs and secondary affiliations (Chapter 3 & 4 & 5). In addition, inter-subgroups relationships formed in the network (i.e. pairs and secondary affiliations), with a slightly increase in 2015 compare to 2014 (Chapter 5, Annex 1). Yet more than two years after their introduction, most pairs and secondary affiliations were still composed of individuals of the same subgroup (Chapter 3 & 5), indicating that the integration of two subgroups in a cohesive and homogeneous structure may take some time (Annex 1). The inertia of new group members' integration reinforces the hypothesis that rooks preferentially interact with familiar individuals, which may contribute to the resilience of the network to perturbation (e.g. constant modification of group composition through fission-fusion). But this, again, likely results from the fact that the pair bonding leaves little time to interact out of the pair and thus to explore new partnerships. In addition, forming social bonds in this species seems to be a gradual and relatively slow process (Chapter 4). A survey of the network structure on long time scale should therefore provide good insight on the completeness and the inertia of new group member integration.

2. WHAT ABOUT DOMINANCE RELATIONSHIPS IN ROOKS?

So far, I identified several emergent properties of rooks' social structure, investigating the strength and the temporal dynamic of affiliative relationships. But in this thesis I also studied another type of relationship known to constrain individuals' interactions in numerous species, namely the dominance relationships (Bernstein, 1981; Drews, 1993; Thierry et al., 2004). As such, they provide elements of stability to the structure, notably by regulating and limiting conflicts, or defining how resources partition in the group (e.g. food ressources or reproduction; Amsalem and Hefetz, 2011; Bell et al., 2012; Stahl et al., 2001; Alberts et al., 2003). In rooks some studies have reported or assumed the linearity of social hierarchies (Emery et al., 2007; Jolles et al., 2013b; Logan et al., 2012; Scheid et al., 2008), but they did not address how dominance emerges, and how it affects in turn social dynamics. Therefore, the stability and the mechanisms that govern the dynamic of dominance relationships in this species needed to be investigated.

2.1. Linearity and dominance relationships

Investigating the structure of dominance relationships, I found that if the hierarchy was fairly linear at some points of the dataset, dominance relationships were highly variable in time, which precluded a reliable assessment of linearity (Chapter 6). The hierarchy was mostly linear when compiling data on a large scale (i.e. multi-month period), which might be an artefact of the temporal window chosen for the analysis, providing a picture that did not reflect the dominance relationships of individuals in the group. My results confirmed that the assessment of linearity significance can be very sensitive to data collection efforts (i.e. proportion of unknown relationships), and may strongly vary from one period to another (de Vries, 1995; Klass and & Cords, 2011; Shizuka and McDonald, 2015, 2012). In addition, when linear, the hierarchy was weakly transitive (Chapter 6). Moreover, I found a low directionality in conflicts and a low steepness, indicating limited individual differences in their propensity to win conflicts and weak power asymmetries (Chapter 6). Added with the instability of dominance relationships, it therefore questions the prevalence and strength of dominance relationships in rooks. Thus, if hierarchies can potentially develop in rooks, whether or not they do form and how predominant they are on their social organisation remain unclear.

Considering the weak linearity of the hierarchy and the high variability of dominance relationships, the next step would be to examine whether or not the concept of dominance relationships is in fact relevant in this species. This could be done for instance by investigating further the stability and directionality of each dominance relationships at the dyadic level, to check if constant winner and loser can be identifed within each dyad on a long time period, and thus if dominance relationships do establish among group members.

2.2. Determinants of dominance relationships

To investigate further the inconsistency of dominance relationships, I studied the dynamics of individuals ratings using the Elo-rating technique (Elo, 1978; Neumann et al., 2011). Like in previous studies, I found that the pairing status increased dominance rating (Emery et al., 2007; see also, Lamprecht, 1985; Tamm, 1977). Given that the hierarchy appears to be moderately linear when considering individuals rankings, alternative dominance structure should be examined. Considering the strength and the impact of the pair on rooks social structure (Chapter 3 and 5), we may expect the structuring of dominance relationships to be function of individuals' partnership. Individuals' propensity to win conflicts would therefore solely depends on the presence of the partner close by. Like in this study group, in most avian species pairs or affiliates most often dominate solitary individuals, but also older individuals dominate younger ones, and males females (e.g. in corvid species: carrion crow, Chiarati et al., 2010; jungle crows, *Corvus macrorhynchos*, Izawa and Watanabe, 2008; florida scrub jays, *Aphelocomu c. coerulescens*, Woolfenden and Fitzpatrick, 1977; blue jays, *Cyanocitta cristuta*, Tarvin and Woolfenden, 1997; jackdaws Verhulst et al., 2014; Wechsler, 1988; but also in other birds species: cockatiels, Seibert and Crowell-Davis, 2001; Goffin's cockatoos, *Cacatua goffiniana*, Szabo et al., 2016; great tits, *Parus major*, Wilson, 1992; ravens, Braun and Bugnyar, 2012). However, in our group males and females did not differ in their dominance ratings, and showed similar aggressiveness (i.e. frequency of initiated conflicts; Chapter 6). Males and females only differed in the intensity of the conflicts they initiated, with a higher frequency of low intensity conflicts for males. This first indicates that contrary to females, males do not necessarily need to use real aggressions (e.g. peck, charge), to win the conflict. Furthermore, a little bit more than half of the conflicts recorded were of low intensity, which means avoidance, supplantation and threat in opposition to aggressions like pecking or charge. In addition, the issue of the conflicts were more often less decided (i.e. unclear) when they were of high intensity: the receiver of an agonistic interaction was more likely to stay in contact with its opponent, and eventually to protest or retaliate (Chapter 6). Considering that the function of dominance relationships and hierarchies is to regulate conflicts (de Waal, 1986), it may suggest that lower intensity behaviours are clearer signals of dominance. But if true, we would have expected higher rated individuals (i.e. more dominant) to display more often low intensity conflicts. However, individuals' ratings did not significantly influenced the intensity of conflicts.

Besides, considering that the very notion of dominance is still unclear in this species, the intensity could simply result from the context in which the encounter occurred (i.e. current level of competition for a coveted resources). The escalation of aggressions in high intensity conflicts (i.e. occurrence of protestations or retaliations) could indicate stronger conflicts of interest, as both partners would be highly motivated to win the encounter. In tits for instance, dominance is strongly context-dependent, and individuals are more likely to win conflicts when they are close to their territories (Dingemanse and De Goede, 2004). Similarly in rooks, individuals may alternatively win and lose conflicts according to the location and the context during which occurred the encounter, resulting in rather balanced dominance relationships. To conclude, it would be interesting to study the effects of both individuals spatial preferences in the aviary, and contexts of encounters (e.g. at the nest, at the food source, out in the reproduction) on the intensity of conflicts and individuals willingness to win the encounter.

2.3. Competition and dominance in rooks: on the necessity to establish a dominance hierarchy

At first sight, my results may appear surprising considering that several studies reported linear hierarchies in rooks. However, to compare these results with previous studies, it is necessary to consider the age of individuals. Rooks hierarchies were found strongly linear in captive juveniles (i.e. in juveniles, linearity = 0.94, Scheid et al., 2008; in juveniles and young adults, linearity = 0.88, Logan et al., 2012), but weakly linear in captive adults (i.e. linearity = 0.5; Jolles et al., 2013b), like in the present study group of adult rooks (i.e. minimum linearity = 0.44 maximum = 0.75; Chapter 6). Thus, if dominance hierarchies may establish in juveniles, which are supposed to favour smaller and cohesive sub-groups of individuals (Henderson, 1991; East, 1988; Dunnet et al., 1969), they are not necessarily maintained in adults.

The high flexibility of rooks grouping pattern may also preclude the emergence of stable and pronounced dominance asymmetry between individuals, and thus ultimately the transitivity of the rankings in this species. Indeed, strategies allowing to reduce the cost of competition are more likely to be selected in species where individuals regularly meet other group members, and have no choice but to cope with the competitive aspect of group living (de Waal, 2000; Schino, 2000; Shultz and Dunbar, 2010a). Linear hierarchies are therefore particularly expected in species forming small and cohesive groups, whereas in larger and highly dynamic groups, inconsistencies are expected to increase (e.g. intransitive rankings; Drew, 1993; Appleby, 1983; Chiarati et al., 2010). However, rooks often roost and breed in large colonies which can sometimes reach several thousands of individuals (Clayton and Emery, 2007; Marshall and Coombs, 1957). In addition, rooks colonies frequently vary in size, cohesion and composition, with individuals alternatively splitting and merging from the colony to forage or explore the habitat. Furthermore, if rooks are supposed to breed in the same colony every year (Bull and Porter, 1975); Swingland, 1973; but see also Richardson et al., 1979), in and out the breeding season rooks usually roost in different sites (Marshall and Coombs, 1957). And so far, we have no empirical data on the permanence of membership between breeding colonies and winter roost. Thus in the wild all individuals may not meet regularly and on a long term basis, which may hamper the establishment of clear and stable dominance relationships. Besides, living in a fluid and dynamic system may promote alternative strategies to deal with the costs of repeated conflicts and competition, like the use of dispersive strategies rather than non-dispersive conflicts resolution mechanisms. When living in a highly dynamic organisation, dispersive strategies (i.e. avoidance and spatial separation with opponents) always remain a sustainable strategy to deal with conflicts (Schino, 2000).

Nevertheless, we could expect dominance relationships to establish primarily in subgroups of familiar individuals, for instance between individuals that are nesting close by. In our captive group, the breeding period had no effect on the linearity of the ranking (Chapter 6). In addition, in wild populations, dominance relationships could be more likely to establish during the breeding season. First, the use of dispersive strategies might be limited as individuals have to remain to the nest until the young are fledged (i.e. at least one partner). Second, this is the period of the year where the colony membership is temporarily stable. The level of competition is thus expected to be at the highest, considering the high density of rooks colonies (e.g. for food supply to juveniles, partners, nest sites; Goodwin, 1955;

Marshall and Coombs, 1956; Owen, 1959; Swingland, 1977; Lockie, 1956). However, rooks are opportunists birds, and thus have access to different food sources in the wild (e.g. crops, cereals, insects, or human food rubbish; Waite, 1948; Feare et al., 1974; Feare, 1961; Kasprzykowski, 2003). Therefore, although the distribution of food resources and inter-colony competition affect colony size (Griffin and Thomas, 2000; Mason and Macdonald, 2004), rooks rely on widely distributed and abundant resources, and may not face strong competitive pressures for food availability (Halupka, 2013). Further investigations in wild populations across groups and ecological contexts are necessary to evaluate the type and degree of competition faced by individuals, both during and outside the breeding season.

Dispersive strategies have yet not been directly investigated in rooks. However, a few studies investigated the emergence of non-dispersive conflicts management strategies, and notably post-conflict affiliations (PCA; Arnold and Aureli, 2007; de Waal and van Roosmalen, 1979). Two types of PCA can be distinguished according to the partners involved: i) reconciliation, when occurring among the former opponents, which is expected in species forming valuable relationships as damaging relationships may jeopardise the probability of future cooperation; and ii) third party affiliation, when occurring between a bystander and a former opponent (Arnold and Aureli, 2007; Cords, M. & Aureli, 2000). However, if third party affiliations do occur among paired partners (Logan et al., 2013; Seed et al., 2007), so far reconciliation does not seems to occur in rooks (Seed et al., 2007). The absence of reconciliation in the later study group could be explained by the fact that individuals did not engage in other valuable relationships than their pair (Seed et al., 2007). In addition, paired partners never engaged in conflicts, preventing the need the repair the relationships (Seed et al., 2007). Post-conflict affiliations were not systematically investigated in the course of this study. Yet, considering that in this study group rooks did form valuable non-reproductive relationships, and that aggressions could occurred among pairs, it would therefore be interesting to re-investigate the occurrence of reconciliation in such a social group. Note that in sub-adult ravens several studies suggested the emergence of PCA but also reconciliations among valuable partners (Fraser and & Bugnyar, 2010a; Fraser and Bugnyar, 2011). The proportion of conflicts followed by reconciliation yet remains low compared to what is reported in primates for instance.

It should be noted that a low risk in conflicts may also preclude the necessity for more complex forms of conflicts management to emerge. One crucial condition for the emergence of reconciliation for instance, is that the conflict actually damages or at least disrupts the relationship (Schaffner et al., 2005). In our study group however, in a significant part of the conflicts the victim stayed in contact with the aggressor (i.e. on average 16% of conflicts; Chapter 6). In addition, severe conflicts (i.e. leading to injuries) were (almost) never recorded. Daily quarrels in rooks may therefore not be strong enough to require more complex conflict management, like clear and pronounced hierarchy or post-conflict management strategies like reconciliation.

So, do rooks have a hierarchy or not? So far my work allowed to question former evidences about hierarchical ranking and linearity in rooks. It raises many points that now require further investigations before concluding on the existence, and the need for a dominance hierarchy to establish in rooks. Thus, at the moment, my results indicate that dominance relationships may not have any long lasting effects on the stabilisation of the social structure.

3. Outlook on the social structure: modular organisation of rooks' colonies

Overall I found that rooks social structure is organised around pairs, which are the fundamental social unit of rooks' colonies. But additional relationships complete this picture by forming a secondary layer in the structure: sub-groups of affiliates emerging above the privileged pair unit through the formation of secondary affiliations. We can expect this secondary level to correlate with nests position. However, whether nest positions result from affiliations or the contrary, is something that still need to be investigated. A third level could eventually be differentiated: i) either when considering a layer added by weak relationships, which still needs to be properly investigated; ii) or from the emergence of preferential association or relationships between members of different sub-group of affiliates, or more simply by the aggregations of several sub-groups. Finally, the last level would be the colony, characterised by the whole set of individuals nesting and sleeping in the same site, and that may more or less randomly meet and possibly interact. However, the prevalence and stability of those sub-structures still need to be tested in wild conditions. Considering the high variability of rooks' colonies in cohesion and membership, we may wonder in fact about the prevalence of affiliative relationship in the wild. Nevertheless, if to date no studies have studied social relationships in wild rooks, some suggest that rooks do not randomly associate in the colony (i.e. like in this captive group; Chapter 3, 4, and 5). As discussed earlier, rooks may not be total strangers to one another, as a significant part of the colony is expected to roost in the same place every year (Swingland, 1973; but see also Richardson et al., 1979), possibly using the same nest site from year to year (Swingland, 1973; Goodwin, 1955). Thus, although the factors that influence the choice of the breeding site is still unclear, rooks' fidelity to their colony should at least provide opportunities for regular encounters between the same subset of group members. Overall, if rooks do express such modular or multi-level social organisation in the wild, it could actually ensure the global cohesion of the colony by local reinforcement, small-scale sub-structures leading to the emergence of a larger interconnected network.

Figure 1. Schematic representation of the different levels of organisation in a wild colony of rooks. Pairs, which are the core reproductive units, are nested in a larger structure characterised by sub-groups of affiliates and cliques, which altogether from the colony. Sub-groups of affiliates are formed by secondary affiliations between nesting neighbours, and cliques by the aggregation of several subgroups. Finally, the colony is characterised by the whole set of individuals nesting and sleeping in the same site.

4. LIMITS

4.1. Captive set-up

One of the most important limitations in this work is that subjects were captive rooks, which may have affected the behaviour of the birds, their level of interaction, and possibly, the resulting relationships and structures we recorded. Thus, it could be argue that this work is not representative of a “normal” colony. Indeed, captivity spatially constraints individuals and thus necessarily impact social patterns. In addition, we can expect the effect of captivity to be particularly strong in avian species, and in particular in the one expressing high degree of fission-fusion dynamics, like rooks. More than half of the individuals were captured at the nest and thus developed their socio-behaviour in captivity, which strongly impacts individuals’ time-budget. Captivity also has an effect on the level of competition among group members, notably for food which is provided *ad libitum*. Furthermore, the number of potential partners is limited in captivity compared to wild populations, which necessarily constrains partner choices. Since in the wild rooks do not live in such small and stable groups, where all individuals can potentially interact, the captive set-up could have increased individuals’ probability to form extra pair relationship.

Finally, captivity also altered individuals’ reproductive success. Since the formation of this captive colony, none of the established pair ever produced surviving offspring. Because of this, the group did not comprise juveniles. If that had been the case, the presence of young could have decreased the amount of interactions directed towards other individuals, and ultimately precluded the emergence of extra-pair relationships. But because of the absence of young, we could not investigate the effect of relatedness on social patterns, hampering the study of the mechanisms underlying the distribution of vertical versus horizontal affiliative interactions in the group (e.g. kinship, mutualism, reciprocal altruism). More broadly, the absence of young individuals also impacted the demographic structure of the group in the sense that most group members had the same age (i.e. original group members). Besides, we had no information regarding the age of the newly introduced group members, hampering any analysis regarding the impact of individuals’ age on their pattern of interaction and the resulting social structure. Regardless of individual’s relatedness, we may have expected younger individuals to be socially more active than the older one. For instance, we may have expected younger individuals to be involved in more relationships and to frequently engage in affiliative interactions (e.g food sharing, allopreening), in particular during the process of the first pair bond formation (Emery et al., 2007).

Nevertheless, the distribution and dynamic of relationships tells us that rooks did not interact randomly in the group (i.e. both pairs and secondary affiliations; Chapter 3 & 5). Indeed, we could have expected captivity to increase the probability of random encounters, but the combined proportion of random (i.e. weak) and non-random relationships (i.e. pairs and secondary affiliations) represented a relatively small part of all potential relationships in the three years, regardless of the changes in group composition and sex-ratio (i.e. on average 20% all potential relationships in the networks; Chapter 3 & 5). Thus, although they were hold on a restricted area, rooks actively choose the partner they interacted with. Furthemore, it must be noted that most studies on corvids or parrots cognition and sociality were so far conducted in captivity. Indeed, such approach remains highly relevant for many reasons when studying social behaviour. In fact, in captive set ups, individuals are available for repeated observations. In addition, the captive set up also allows scrutinising social behaviours, providing focused observations on the long term that are almost virtually impossible in the wild. In this way, studies conducted in captivity provide valuable frameworks to develop and to test clear hypothesis. In particular, by presenting very detailed results about rooks social abilities; notably the fact that they can simultaneously engage in relationships with several partners, and can form valuable and stable non-reproductive relationships; this thesis provides very important insights regarding corvids sociality.

4.2. Impact of the sex-ratio on social and reproductive behaviour

Another important limitation in this work is due to the unbalanced sex-ratio, which may have favoured the formation of same-sex pairs, and jeopardized individuals breeding success. Yet, it should be noted that most subjects appeared to have conserved normal reproductive behaviours. Indeed, the breeding rhythm of our colony was perfectly synchronised with neighbouring wild colonies, whatever the year, and with the description of the reproductive behaviour that typically occur in this species (Goodwin, 1955; Lincoln et al., 1980; Marshall and Coombs, 1957; Ogilvie, 1951). In rooks, the breeding season usually starts at the end of February or early March, and last until the end of May (Lincoln et al., 1980). Between January to the end February, old nests and branches get more and more manipulated (Marshall and Coombs, 1957). In March, the nest building and the first copulations start (Lincoln et al., 1980; Marshall and Coombs, 1957). In our study group, branch collection and manipulation started at the end of February, and the first copulations usually a few days later (personal observations and monitoring of the colony's reproduction over more than 6 years). In addition, as already reported in wild and captive colonies, in our group males were more active for branch collection and nest building than females which themselves were more active for the detailed structure of the nest (Marshall and Coombs, 1957; Richards, 1976). An explanation for such distribution of the building task, is that one of the partner remains in the nest to prevent pilfering of nest material (Ogilvie, 1951), which also often occurred in our aviary. Finally, even if they never successfully produced surviving offspring, all stable mixed-pairs attempted to breed (Chapter 3 & 4). Altogether, it indicates that despite captivity and unbalanced sex-ratio, individuals kept a natural breeding rhythm.

Furthermore, sexual behaviours - mount and courtship - were not restricted to pairs. Extra-pair sexual copulations were already described in rooks including in wild colonies (Røskaft, 1983) including forced copulations, or "rape" of incubating and "non-compliant" females (Goodwin, 1976, 1955; Marshall and Coombs, 1957). Interestingly, in our group sexual behaviours occurred in similar proportions in same-sex and mixed-sex dyads (i.e. especially mixed-sex and male-males dyads; Chapter 3). In addition, they did not play a role in the formation of new pairs (Chapter 4), and occurred among all individuals in the group, including among weak partners which almost never had contacts or exchanged affiliations. Thus they may serve another function that we did not examine. For instance, courtship could be used to signify to a partner the willingness to cooperate, or could signify the strength of an alliance. Further investigation on the use of sexual behaviours and in particular courtship across contexts (notably during conflicts), should help to better understand their function.

Finally, thanks to the introduction of new females in the group, I had the opportunity to examine in more details the impact of the sex-ratio on social patterns, and more precisely relationships formation and disruption (Chapter 5). I found no effect of homophily or heterophily, meaning that individuals were not favouring partners of the same/opposite sex to interact with (Chapter 5). Moreover, males and females were involved in the same proportion of relationships, and were equally responsible for the changes in relationships. Indeed, in the three years, males and females had on average the same number of partners in the network (Chapter 5). In addition, the sex of the individuals had no major influence in the overall dynamic of relationships: in 2012 and 2014, although the sex ratio was strongly unbalanced in favour of males (in particular in 2012), males were not more responsible than females for the temporal changes occurring in the network (Chapter 5).

Overall, this confirms again that in this captive group of rooks relationships were not solely motivated by mating or reproductive strategies. But on the contrary, besides reproductive motivations, affinity appears to play a significant role in sustaining bonding in rooks and more broadly in monogamous species (at least in captive groups).

5. PERSPECTIVES

5.1. A word on social tolerance

Social tolerance is a notion that relates to the co-variation of several various social traits (Duboscq et al., 2013a,b; Thierry, 2013). It usually implies high levels of spatial associations and affiliations among group members, which should not be reserved to the family unit (i.e. reproductive partners, young), weak power asymmetry (i.e. low steepness), frequent protestations or counter-aggressions, low intensity of conflict (i.e. bad injuries are rarely reported), and high conciliatory tendencies (Thierry, 2007). My results on the diversity and the distribution of relationships in the groups (Chapter 3 & 5), and the robustness of the social structural patterns indicate that rooks may be tolerant enough to integrate new individuals, without this dismantling the structure of the group (Chapter 5). I also found weak power asymmetry (i.e. low steepness; Chapter 6), and a significant proportion of undecided conflicts (i.e. unclear outcome). Unclear conflicts mainly resulted from the fact that the receiver ignored the aggression (i.e. on average 2 conflicts over 10), and in some cases protested and even retaliated (41% of the cases; Chapter 6). Thus rooks can exhibit a relatively high degree of social tolerance, which makes sense for a species living and breeding in a dense and dynamic social organisation. However, further investigations on rooks' dominance relationships and conciliatory tendencies, are now needed to better conclude on the level of tolerance expressed in this species.

5.2. Studying wild populations

If my work demonstrates the ability of rooks to form integrated social structure, we still have few insights on the way wild populations are temporally organised. To do so, the extent to which wild populations express fission-fusion dynamics need to be quantified. How permanent is the colony membership? Do individuals actually roost in the same place and same nest year after year? How permanent is the composition of sub-groups emerging from fission-fusion dynamic, across time and context (e.g. nesting, roosting, foraging, or habitat exploration)? How is fission-fusion impacted by individuals' affiliations? Many questions that now need answers. Investigating the emergence of non-reproductive relationships in wild colonies, and their stability over time (i.e. day by day, and season after season) should help getting a more complete view of rooks social structure, and provide insight on the factors that modulate partner choice and mating strategies in this species. Ultimately, in-depth study of the social structure in wild populations should help understanding better how individuals cooperate/compete, and should inform us about the cognitive and social processes that allow individuals to deal with the benefits and costs of group living (e.g. individuals recognition, third-party relationships, dispersive and non-dispersive mechanisms of conflicts resolution).

5.3. Cognitive processes and social organisation

6.3.1. Convergent evolution of avian and mammalian sociality

Because rooks are known for their advanced cognitive skills (Scheid and Noë, 2010; Seed et al., 2006, 2008; Tebbich et al., 2007), a better understanding of their social structure also provides valuable insights for the understanding of the co-evolution of sociality and cognition. The social intelligence hypothesis (independently proposed by: Jolly, 1966; and Humphrey, 1976), posits that the variability and complexity of the social environment promote the emergence of advanced cognitive skills (Dunbar, 1998; Kudo and Dunbar, 2001; Pérez-Barbería et al., 2007). Group living indeed requires individuals to adapt their behaviour to social partners and contexts to deal with the balance of costs and benefits of group living. Thus, considering the current results on rooks' social life, in particular the diversity of differentiated relationships in which they might be involved, rooks advanced cognitive skills might result from the complexity of their social organisation. In fact, it is now more and more often proposed that similarities of avian and mammalians species in cognition and social behaviour result from convergent evolution (Emery, 2006; Emery and Clayton, 2004; Horik et al., 2011; Seed et al., 2009). My data show that rooks, like some other birds (e.g. ravens, Braun et al., 2012; Fraser and Bugnyar, 2010b); parrots, Hobson et al., 2014), and like numerous highly social mammals (e.g. primates, dolphins, elephants or hyenas; Dunbar and Shultz, 2007; Emery et al., 2007), can form valuable relationships with several partners, and live in an individualised and well-integrated society. Nevertheless, caution is needed when comparing avian and mammalians sociality. Indeed, so far, little is known about the evolutionary pressures that have selected and shaped sociality in birds' species. Compared to mammals, there is a huge lack of empirical data on birds' sociality, and the proximate mechanisms that shape their organisations (i.e. behavioural mechanisms underlying the form and the dynamic of social relationships and the resulting structures). Most studies on birds' sociality usually focus on social cognition and experimental studies, and more rarely quantify and qualify the behavioural patterns that delineate social organisations. By providing a focused and very detailed observational study of rooks social abilities, this thesis therefore provides novel insights to better understand bird social organisations, and in particular the behavioural mechanisms that underlie their shape and temporal dynamics.

6.3.2. How do rooks picture the relationship?

Finally, considering the results found in this thesis, we may wonder which knowledge have rooks about the social structure they live in. Considering the size of rooks aggregations, it is likely that individuals know well their close social partners (i.e. mated partners, offspring, close nesting neighbours), and have a more limited knowledge about others individuals that they can observe without necessarily interacting with them. But do individuals see the sum of their interactions as relationships? To identify relationships we add a temporal dimension on the analysis of interactions, which may actually reflect a time-frame meaningless for individuals in their present time (Barrett et al., 2007). Apart from their skills in physical cognition (Seed et al., 2006; Tebbich et al., 2007), rooks are also well known for some of their social abilities (Clayton & Emery 2007; Emery et al. 2007; Scheid et al. 2008; Seed et al. 2007). For instance, they can differentiate congeners, and more precisely discriminate affiliates from non-affiliates (Bird and Emery, 2008). In addition, similar social abilities have also been found in closely related corvid species. In ravens, individuals picture others social relationships without interacting with them (Massen et al., 2014a). In jackdaws or ravens, individuals discriminate conspecifics from others, and in particular parents from neighbours (i.e. in jackdaws, Zandberg et al., 2014), or familiar from unfamiliar individuals, but also affiliates from unaffiliated even three years later (i.e. in ravens, Boeckle and Bugnyar, 2012). More broadly, in numerous corvid species, it is now known that individuals can adjust their behaviour according to the presence of other congeners, but also according to their behaviour, or even their knowledge (Bugnyar et al., 2007; Clayton et al., 2007; Dally, 2006; Emery and Clayton, 2001). Besides, it is likely that highly structured fission-fusion systems promote the emergence of advanced cognitive and social skills (Aureli et al., 2008). Indeed, in such systems individuals need to keep track of individuals and possibly relationships, even if they are not continuously in contact with all social partners. A high degree of fission-fusion is for instance expected to enhance the use of transitive inference and the recognition of third-party relationships (e.g. in hyenas; Engh et al., 2005). Similarly in birds, several studies already suggested that living in large and structured flocks may also promote the use of transitive inference and the ability to track dyadic relationships (e.g. in pinyon jays, *Gymnorhinus cyanocephalus*, Paz-y-Mino et al., 2004; in greylag geese, *Anser anser*, Weiß et al., 2010).

However, if rooks can team up to solve a problem, they do not seem to understand the role that a congener can play in a cooperative task (i.e. string pulling task; Seed et al., 2008). But so far, we lack of empirical data to further conclude on rooks' ability to represent their social environment, and in particular third-party relationships. To possess a mental representation of others relationships would indeed certainly help individuals to live and navigate in such a dense and labile social organisation. To investigate the way individuals negotiate the exchange of goods or services could thus provide valuable insight on this particular point (Annex 3). For instance, it would be interesting to evaluate individuals' ability to assess their partners' willingness to collaborate, and to consequently adjust their behaviour according to their partners' motivations to invest in the relationship (Chapter 4). Indeed, the need for partners to communicate and adapt their investment in relationships can be crucial to deal with social competition, and may be increased when individuals form several valuable bonds susceptible to vary in strength over time (Chapter 4; Annex 1).

5.4.Variations of corvids′ social organisations: comment on internal and external constraints

To compare social organisations across taxa, and more precisely the processes that modulate and stabilise them over time, can provide valuable insights to better understand the different mechanisms sustaining intra- and inter-specific variations of social organisations. Indeed, from one species to another, internal constraints (i.e. phylogenetical constraints) can modulate the impact of ecological pressures on social organisations, stabilising individuals' social behaviour, and the related social structures (Menard, 2004; Thierry, 2013; Thierry et al., 2000). In-depth studies of species' social organisations are therefore needed to better evaluate the relative share of ecological and phylogenical constraints on the evolution of social behavior across species, and ultimately, the function of sociality.

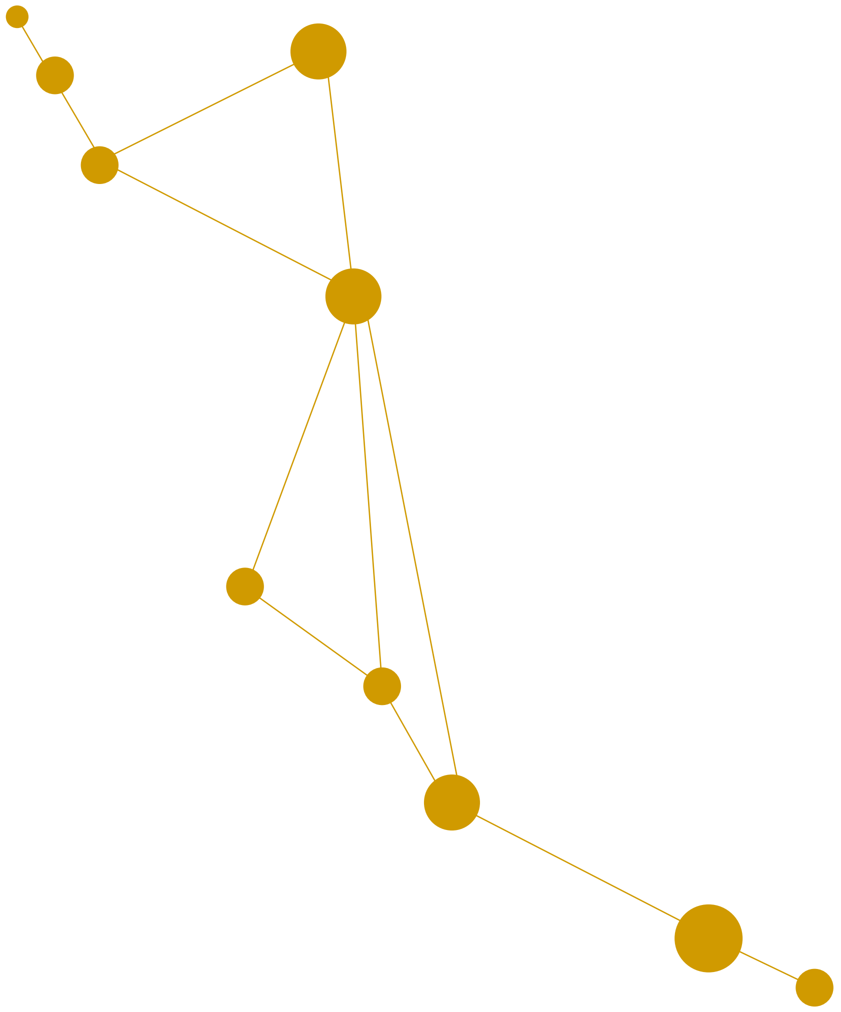
In this respect, my results raise intriguing questions about the differences and similarities observed between corvids social organisations, notably between rooks and ravens. On the one hand, rooks live in groups throughout their life and breed in colonies, where they likely bond with several individuals. On the other hand, ravens display remarkable social complexity as non-breeders individuals, living in structured aggregations of individuals (Braun et al., 2012; Braun and Bugnyar, 2012) and forming valuable relationships with several partners (Fraser and Bugnyar, 2010b). However, they shift from social life to (quasi) solitary life once they become an established territorial pair. Considering the similarities between rooks and ravens social organisations as juveniles (i.e. in rooks, Scheid et al., 2008; Emery et al., 2007; i.e. in ravens, Braun and Bugnyar, 2012; Loretto et al., 2012), we may wonder why their organisations so strongly differ by adulthood. Those differences may relate to variations in the environmental pressures faced by individuals, and/or to differences in the species life-history traits, which likely affect the balance of costs and benefits of sociality, relating to a given set of external factors. It might be that those species face different competitive regimes to raise young (e.g. differences in young nutritional requirements), and therefore not benefit similarly from social life when reproducing. However, it might be also that the variations in corvids social organisations result from different evolutionary pathways, rather than just environmental factors (i.e. see Matsumura, 1999; Menard, 2004; Ossi and Kamilar, 2006; Thierry et al., 2000). Indeed, each species brings a phylogenetic heritage into a particular ecological scene' (Struhsaker, 1969; in Thierry, 2013). As a consequence, species may not answer similarly to same ecological factors (Thierry, 2013, 2007). Thus, we must now pursue the effort to improve our understanding of avian social organisations, in particular in corvid species. Documenting the range of intra and inter-specific variations that can be observed in corvids, across groups and environments should provide a reliable starting point to investigate the processes that modulate and stabilise social organisations, and the relative roles of ecology and phylogeny in the evolution of social behaviour.

6. CONCLUSION / OUTLOOK

My thesis contributes significantly to the understanding of rooks social organisations, and more precisely on the proximate mechanisms that underlie rooks social structure. I uncovered several features of rooks social structural patterns and their dynamics. I demonstrated that rooks interact non-randomly and have the ability to form valuable relationships out of the pair, resulting in the establishment of modular and social structure. Overall, my results highlight a picture of rooks' social life that is partially consistent with the prevalent belief, but also raises a few question about the actual complexity of their social system (e.g. linearity of the hierarchy and stability of dominance relationships). Although future studies in wild populations are now needed to investigate these points in more details, rooks colonies may be more than just a simple aggregation of pairs, and should be acknowledged as a multi-level social organisation. As it is, these findings stress the need to consider more systematically extra-pair interactions in corvids and more broadly in long-term monogamous avian species to better apprehend the diversity of corvids organisations. My contribution to this long term research by identifying target key components of rooks' socials structure could be an important base for future work on wild corvids populations. By providing methods and frameworks, it also provides a reliable starting point for further cross-species comparisons of corvids and avian social organisations.

8

Appendices



1. APPENDIX 1: ADDITIONAL DETAILS ON PAIRS AND SECONDARY AFFILIATIONS HISTORY

In chapter 3, we investigated the possibility of extra-pair bonding in rooks. More specifically, we categorized and characterized relationships according to several affiliative and agonistic behaviours, on three 4-5 months periods of cumulated data (i.e. in 2012, 2014, and 2015). Using a sociality index inspired by Silk et al. (2006), we distinguished three categories of relationships according to their strength (i.e. breakpoint method on the cumulative distribution of sociality indices): pairs, secondary affiliations and weak relationships. We then further investigated the characteristics of each category of relationships, and found that pairs always represented more than 50% of both partners individual sociality index (i.e. sum of the sociality indices of all the relationships in which an individual is involved), and secondary affiliations 5-50%, or more than 50% for only one of the partner.

This criteria was then applied to identify pairs on chapter 4, 5 and 6, on a different time-scale (i.e. per week), and for different collection periods. The use of a finer time-scale (i.e. week), allowed to follow the temporal dynamic of the pairs, by detecting temporal variations in the strength of the bond from week to week.

In this appendix, I summarise all identified pairs and secondary affiliations, according to the time-scale used (i.e. several-month period in chapter 3, and weekly periods on chapter 4, 5 and 6; see Table A1 and A2) and the collection period. I also add a visualisation of the temporal dynamic of the pairs and secondary affiliations per week (see Figure A1 and A2).

Chapter	3	5	3	5	4	6	3	5	6
Year	**2012**		**2014**				**2015**		
Time-scale	**4 Months**	**Week**	**5 Months**	**Week**	**Week**		**5 Months**	**Week**	**Week**
Collection period	January – April	January – April	January – May	January – April	January – September		January – May	January – April	January – September
	et hm jo ky nz	by et hm hj jo ky nz	as bk cp et jo nz	ag as bk bm cp et jm jo kp nz	ag as bk bm cp et jm jo kp no nz os		ag et jm kp ns	ag as et jm kp os	ag as bj bs et jm kp ns os
N pairs	5	7	6	10	12		5	6	9
% same-sex pairs	60%	43%	67%	50%	50%		20%	33%	22%
% same-subgroup pairs			100%	90%	83%		60%	67%	56%
N paired individuals	10 / 11	11 /11	12 / 14	14 /14	14 /14		10 / 12	10 / 12	12 /12

Table A1. All pairs identified in 2012, 2014 and 2015, in the different chapters according to the time-scale used for pairs' identification (i.e. 4-5 months; week), and the collection period. The time-scale used to identify the pair is defined for each chapter, as well as the collection period. The number of different pairs identified, and the number of individuals involved in a pair (i.e. at least in once week), as well as the proportion of same-sex and same-subgroup pairs (i.e. involving two original or two new members), are also reported.

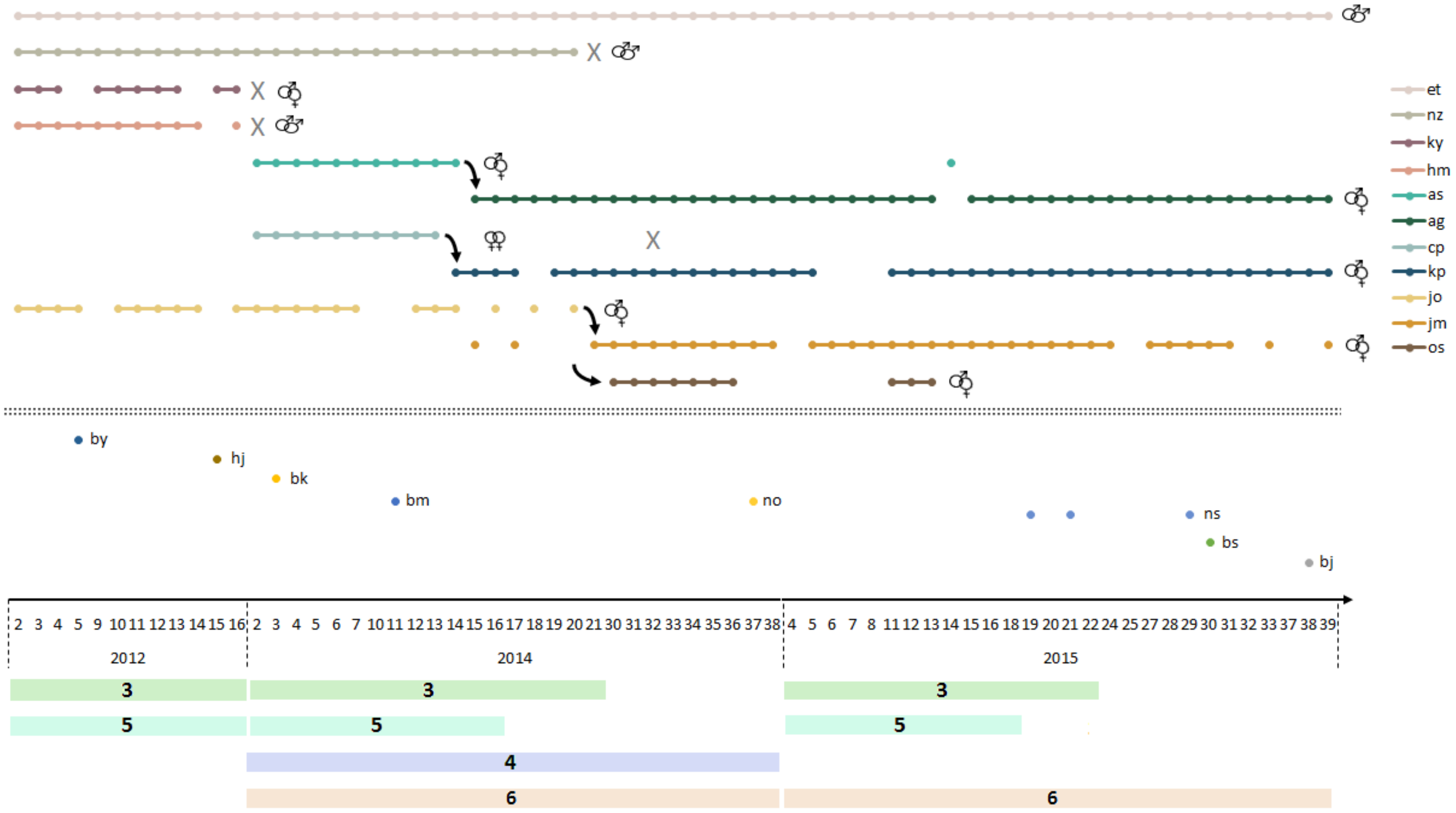


Figure A1. Temporal dynamic of all pair bonds per week, between January 2012 and September 2015. When a pair is identified on a given week, it is represented by a coloured point. Crosses indicate the loss of the two individuals, in the course of the study. Mate switching are indicated by arrows (i.e. when the separation of a pair led to the establishment of one or two newly formed pairs). In total, whatever their duration (i.e. number of weeks), 7, 12 and 9 different pairs were identified in 2012, 2014, and 2015. One pair lasted throughout the entire study period (e–t). Three terminated due to the disappearance of a former partner (n-z, k–y and h–m), three separated as the consequence of a partner leaving for a new relationship (c–p, a–s, j–o in 2014, all mixed-sex dyads). Among the four pairs that formed during the study (in 2014), one separated shortly after its formation (o-s), and the three others lasted until the end of the study period.

Chapter	3	5	3	5	3	5
Year	2012		2014		2015	
Time-scale	**4 Months**	**Week**	**5 Months**	**Week**	**5 Months**	**Week**
Collection period	January – April	January – April	January – May	January – April	January – May	January – April
	bk	be	ag	ac	as	ab
	by	bk	be	ae	bk	ag
	hj	bo	bm	ag	bm	aj
	jz	bt	bt	ak	bp	ak
		by	ck	am	en	am
		bz	cs	ap	jo	an
		ek	gp	as	mo	ap
		en	gs	at	np	as
		eo	jm	ac	os	be
		ez	kp	be	ps	bj
		hj	kt	bj		bk
		hm	ps	bk		bm
		jm		bm		bn
		jn		bo		bo
		jo		bt		bp
		jz		ce		bs
		ko		cg		bt
		kt		ck		ek
		ky		co		en
		kz		cs		es
		mo		ct		gk
		mt		ek		gs
		no		em		jk
		nt		go		jm
		ot		gp		jn
		oz		gs		jo
				jm		js
				jn		kn
				jo		ko
				jz		kp
				km		ks
				kn		kt
				kp		mn
				ks		mo
				kt		mt
				mn		np
				mo		ns
				mt		nt
				no		os
				nt		ps
				os		st
				oz		
				ps		
				sz		
N secondary affiliations	4	26	12	44	10	41
% same-sex	25%	73%	67%	59%	50%	54%
% same-subgroup			83%	68%	70%	63%
N individuals affiliated	6/11	11/11	12/14	14/14	10/12	12/12

Table A2. All secondary affiliations identified in 2012, 2014 and 2015, according to the time-scale and the collection period used (i.e. in chapters 3 and 5). The number of different secondary affiliations identified, the number of individuals involved in a secondary affiliation (i.e. at least in one week), as well as the proportion of same-sex and same-subgroup secondary affiliations (i.e. involving two original or two new members), are also reported.

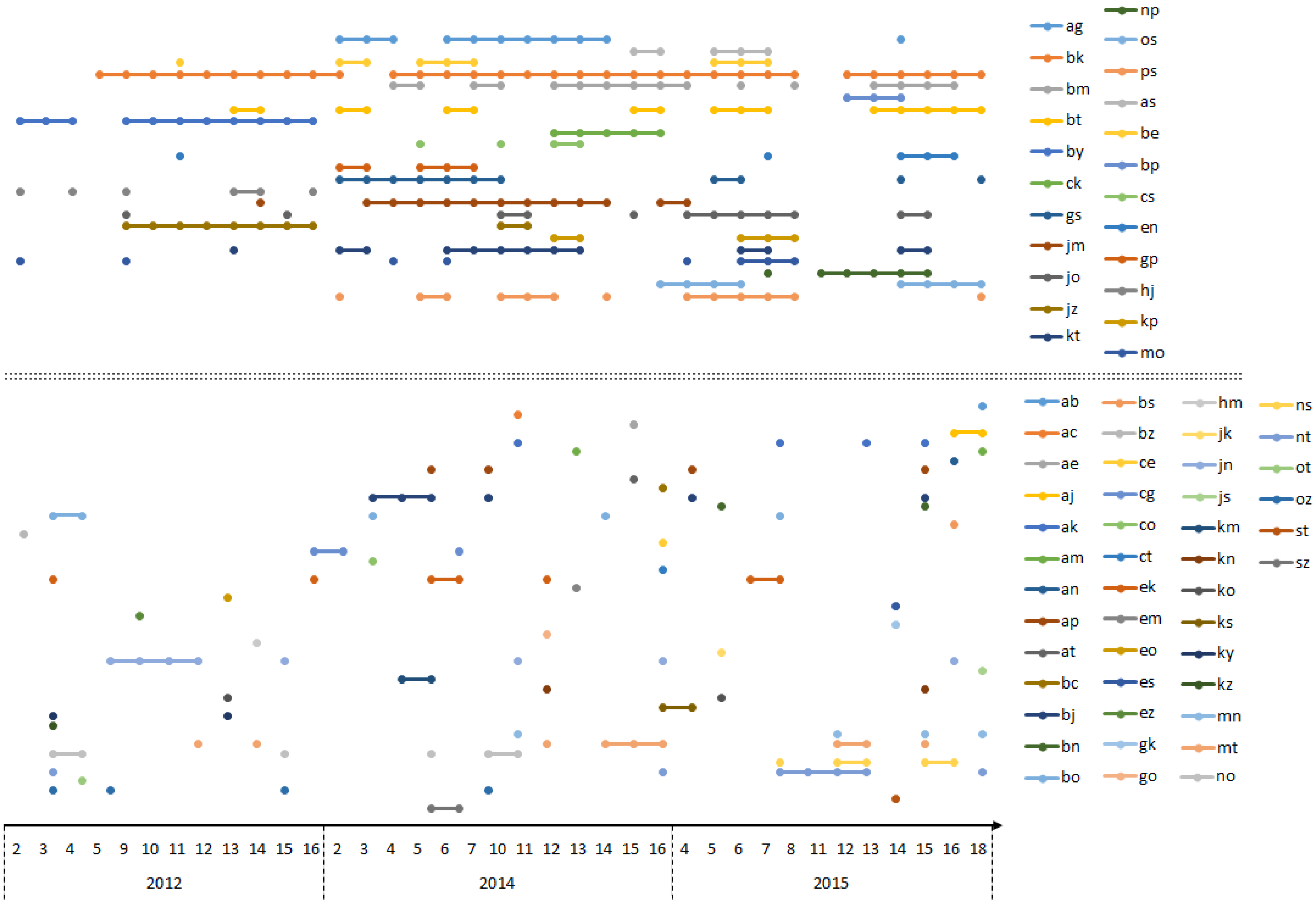


Figure A2. Temporal dynamic of all secondary affiliations identified per week, between January and April 2012, 2014, and 2015 (i.e. dataset used in Chapter 5 for weekly identification of secondary affiliations; see also Table A2). When a secondary affiliation is identified on a given week, it is represented by a coloured point. The first part of the graph represents the dynamic of all the secondary affiliations were identified in chapter 3, and the second part of the graph represents all additional secondary affiliations identified in chapter 5.

References

Boucherie, P.H., Mariette, M.M., Bret, C., Dufour, V., 2016. Bonding beyond the pair in a monogamous bird: impact on social structure in adult rooks (Corvus frugilegus). Behaviour. doi:10.1163/1568539X-00003372

Silk, J.B., Altmann, J., Alberts, S.C., 2006. Social relationships among adult female baboons (papio cynocephalus) I. Variation in the strength of social bonds. Behav. Ecol. Sociobiol. 61, 183–195. doi:10.1007/s00265-006-0249-2

2. APPENDIX 2: PRELIMINARY RESULTS REGARDING THE PATTERNS OF ALLOFEEDING IN ADULT ROOKS

Boucherie Palmyre H. [a,b], Rojas Emilio R. [a,b], Dufour Valérie [a,b]

[a] Institut Pluridisciplinaire Hubert Curien, University of Strasbourg, 23 rue Becquerel 67087 Strasbourg, France.
[b] Centre National de la Recherche Scientifique, UMR 7178, 67087 Strasbourg, France.

Food sharing is well studied in a wide range of mammalian species (i.e. in non human primates, *Cebus apella*, de Waal FB, 2000; *Pan troglodytes*, de Waal, 1997; *Pan paniscus*, Jaeggi et al., 2010; in spotted hyenas, *Crocuta crocuata*, Holekamp and Smale, 1990; in bats, *Desmodus rotundus*, Wilkinson, 1984; in mice, *Acomys cahirinus*, Porter et al., 1981), but also in avian species (i.e. in owls, *Aotus azarai*, Wolovich et al., 2008; in ravens, *Corvus corax*, Heinrich, 1988; in jackdaws, *Corvus monedula*, de Kort et al., 2006b; in Arabian babblers, *Turdoides squamiceps*, Zahavi, 1990). In birds food sharing mainly consists in the active giving of food items (i.e. allofeeding or food offering), which mainly occurs in the context of reproduction to feed offspring and the incubating partners (Eldegard and Sonerud, 2012; Hussell, 1988; Whittingham et al., 2003), or courtship (Lack, 1940; Lifjeld and Slagsvold, 1986; Royama, 1966; Velando, 2004). However, in birds allofeeding can also occur among unrelated individuals, for instance among adult partners that do not reproduce together, like in cooperatively breeding species (Carlisle and Zahavi, 1986; Ligon and Ligon, 1983; Woolfenden and Fitzpatrick, 1977). In addition, allofeeding can serve other functions than partner or juveniles provisioning. In cooperatively breeding species, individuals can feed unrelated offspring as a payment to the breeder to stay in a given territory and access to food resources (Gaston, 1978; Kokko, 2002). In the arabian babblers (*Turdoides squamiceps*). In other context, allofeeding can also increase the social status of the donor (degree of dominance; (Kalishov et al., 2005; Zahavi, 1990). Allofeeding can also be used promote the formation of social bonds among partners (Connor and Curry, 1995; Emery et al., 2007).

In corvids, food sharing (i.e. allofeeding and co-feeding) are often displayed by juveniles, long before the first reproductive attempt (in jackdaws, de Kort et al., 2006b, 2003; von Bayern et al., 2007; in rooks, Emery et al., 2007; Scheid et al., 2008). In the first months after fledging, juveniles rooks and jackdaws gather in group where they interacting with several partners, and later, they choose one partner, most always of opposite sex and non-sibling, to pair up with (in jackdaws, de Kort et al., 2006b, 2003; von Bayern et al., 2007; in rooks, Emery et al., 2007; Scheid et al., 2008). In those aggregations, food sharing is frequently reported. Given its apparent altruistic nature, it provides an interesting window on the pro-social or reciprocal interactions in corvids (Emery et al., 2007; von Bayern et al., 2007). Allofeeding in juveniles could be linked to i) kinship, when occurring among related partners; but also ii) reciprocity; iii) the avoidance of harassment; or iv) the emission of a costly signal of social status (in jackdaws, de Kort et al., 2006a). If the reciprocity and the avoidance of harassment could partially explain the distribution of allofeeding in juveniles' groups (in jackdaws, de Kort et al., 2006a), allofeeding could also be used by juveniles to explore their social environment i.e to evaluate the quality of potential future partners (von Bayern et al., 2007). In both rooks and jackdaws, allofeeding indeed appears as an essential behaviour for the formation of social bonds, and in particular the choice of the mated partner (in jackdaws, von Bayern et al., 2007; in rooks: Emery et al., 2007). Allofeeding could notably advertise the ability to provide food to the future incubating partner and to the chicks (Emery et al., 2007; von Bayern et al., 2007). Yet it must be noted that in another study in juveniles rooks, co-feeding but not allofeeding appeared to play a role in pair bond formation (Scheid et al., 2008). In this study, Scheid et al. (2008) instead proposed that allofeeding could be a signal directed not only to the partner, but to the whole group to signify the quality of the donor (Scheid et al., 2008).

In both rooks and jackdaws, the frequency of allofeeding is supposed to decrease in adults. Once the pair bond is formed, food sharing (mostly allofeeding) is expected to be exclusive to the pair, and to occur primarily in the reproductive and courtship context (Emery et al., 2007; Scheid et al., 2008). Indeed, those two species are not cooperatively breeding, so we did not expect them to allofeed outside of the pair. However, in rooks, we now have evidence that allofeeding is not restricted to the breeding season nor to the pair only (Chapter 3 & 4). By adulthood in rooks, if allofeeding and co-feeding events mainly occur among paired partners (Chapter 3), they can also be occasionally emitted out of the pair (Chapter 3 & 4), sometimes concomitantly to the formation of a new pair (Chapter 4). In this annex, I report preliminary results relating to the distribution of allofeeding in the group. I first investigated this distribution according to the affiliative statuses of the partners (i.e. paired, affiliates). Then I tested whether the distribution of allofeeding could relate to the hypothesis of the avoidance of harassment, could be used to strengthen the bond or could be used to signal the strength of the bond to other group members. To do so, I investigated: i) which one of the two donor/receiver vocalised before and/or during the feeding; ii) which one of the donor/receiver was responsible for the initiation and the breaking of the spatial associations during which occurred the feeding; iii) the occurrence of affiliations and aggressions among the donor and the receiver before and after the allofeeding event.

Methods

Subjects and study site

All birds were housed in an outdoor aviary on the campus of the CNRS of Strasbourg, France. In 2012, the group was composed of 11 individuals (9 males, 2 females), taken from the nest in a wild local colony in 2006 and 2007. Two dyads of those individuals were nest-mates, and all other individuals were singletons (i.e. with no nest-mates; Table 1). In addition, among the five singletons, two were add in the same box of one of the two dyads of nest-mates, and two others singletons were put together in the same nest box, the three others were alone in their boxes (Table 1). Following the escape of two birds in early 2013 (h, male; p, female), in October 2013, six new birds all rescued from hunting traps in southern Alsace, were added to the original group (i.e. 1 juvenile males and 5 females, Table 1 & 2). Finally, two other birds died of natural causes in the end of May and in early August 2014 (z, male c; female). The evolution of the group composition and sex-ratio over time is resumed in Table 2. All birds could be identified by unique combinations of coloured leg rings. The aviary (18 m x 6 m x 3.5 m) was composed of wood perches, platforms, suspended baskets, ropes, vegetation cover and branches, as well as 2 small water pools for enrichment and bathing. Birds were fed daily with a mixture of pellets and fresh products (eggs, yoghurt, and fruits) and had *ad libitum* access to water.

Individuals	Sex	Date of capture	Nest origin	Nest box
a	♂	08/2013	X	X
b	♂	05/2006	1	1
c	♀	08/2013	X	X
e	♂	05/2006	2	2
g	♀	08/2013	X	X
h	♂	05/2006	3	3
j	♀	05/2006	2	2
k	♂	05/2006	4	1
m	♂	05/2006	5	4
n	♂	05/2006	6	1
o	♂	05/2006	7	4
p	♀	08/2013	X	X
s	♀	08/2013	X	X
t	♂	05/2006	8	5
y	♀	05/2006	1	1
z	♂	04/2007	9	6

Table A1. Individuals' sex, date of capture, nest origin and nest-box number during the hand-rearing period. Original group members are colored in green and newly introduced members in orange. The nest origin and nest box are only reported for original group members, which were collected from the nest. Newly introduced individuals were captured as adults.

Period	**2012**	**January → May 2014**	**August 2014 → September 2015**	**Sex**
Group composition	X	**a**	**a**	♂
	b	**b**	**b**	♂
	X	**c ***	X	♀
	e	**e**	**e**	♂
	X	**g**	**g**	♀
	h *	X	X	♂
	j	**j**	**j**	♀
	k	**k**	**k**	♂
	m	**m**	**m**	♂
	n	**n**	**n**	♂
	o	**o**	**o**	♂
	X	**p**	**p**	♀
	X	**s**	**s**	♀
	t	**t**	**t**	♂
	y *	X	X	♀
	z *	**z ***	X	♂
Individuals	11	14	12	
Sex-ratio	(9 M / 2 F)	(9 M / 5 F)	(8 M / 4 F)	

Table A2. Modifications of group composition and sex-ratio over time. Original group members are colored in green and newly introduced members in orange. Asterisks indicate individuals that were lost in the course of the study, and the cross indicate that the individual is no longer in the group. The sex of the individuals is also reported.

Data collection

Data used in this analysis were collected from January to the end of April in 2012 (i.e. 55 observation sessions), and from January to the end of September in 2014 and 2015 (i.e. 83 observations sessions). Part of the data collection period covered the breeding period (i.e. from March to the end of May). The beginning and the end of the breeding period were respectively defined by the day at which the individuals started building nests, and the day at which they started dismantling them. All observations were conducted between 08:00 and

18:00 hours by a single observer (PB). For each observation session, all individuals were observed in a random order (i.e. same amount of time for all), for a total of 9:10, 13:50, and 13:50 hours per individual and per year. Allofeeding were recorded using 10-minutes individual focal sampling (Altmann 1974) in order to monitor all behaviour occurring before and after each allofeeding event, added with *ad libitum* sampling to record all other occurrences of allofeeding among other group members during each focal observations (Altmann 1974). In addition, during the 10-minutes individual focal sampling, we also recorded spatial proximities (i.e. perch proximity, ground proximity), affiliative interactions (i.e. allofeeding, allopreening and contact-sit) and aggressions (i.e. peck, charge, chase, avoid, supplant, threat). Perch or ground proximity were recorded if two birds were 10 to 50 cm apart when perching or 0 to 1 m apart on the ground, respectively. Contact-sit was recorded when two birds were less than 10 cm apart when perching. Allofeeding was recorded when one bird actively put a food item into the beak of another (Scheid et al. 2008), and allopreening was considered to have occurred when one bird ran its beak through the feathers of another.

Pairs' identification

Following Boucherie et al. (2016), we used an individual social index inspired by Silk et al. (2006b), based on spatial proximities and affiliative interactions to identify pairs and extra-pairs affiliations. Two individuals were considered paired if their relationship represented more than 50% both partner individuals sociality index (i.e. the sum of the sociality indices for all relationships in which an individual is involved).

Data analysis

Allofeeding events were analysed using Generalized Linear Mixed Models (GLMMs, with Poisson distribution and log link), for 5 different models, depending on the factors tested on the number of allofeeding events. Note that according to the factor tested, each model was performed on a subset of the total dataset. We first tested the effect of the social status of the dyad (i.e. paired, affiliates) on the number of allofeeding events (model 1). In the second model, in case vocalisations occurred or could be recorded, we investigated their effect on the number of allofeeding, testing in particular the effect of identity of the individual emitting the vocalisation (i.e. emitter or receiver), and when he produced it: before the food transfert (i.e. 10 to 1 second befor) or during (model 2). Note that no particular device was used record the vocalisations during the food transfert. Vocalisations were directly recorded by the observer, who was located approximately 2 meters away from the mesh of the aviary. Model 1 and 2 were performed on allofeeding recorded through focal sampling and *ad libitum* sampling in the three years. More precisely, model 1 was performed on a total of 2743 allofeeding events (i.e. all allofeeding recorded during the data collection period), and model 2 on a total of 1656 events, for which vocalisations occurred or could be recorded.

The next models (i.e. 3 – 5), were performed on focal sampling data recorded in 2014 and 2015 (i.e. in total 470 events), to monitor all behaviour occurring before and after allofeedings during the term of the focal observation (duration of a focal observation: 10 minutes), and the directionality of those behaviours (i.e. not available in 2012). First, in model 3 we tested who initiated the association (i.e. contact-sit or ground proximity) during which occurred the allofeeding, and who broke the association after the allofeeding had occurred (i.e. either the donor, the receiver, or both of them). Model 3 was performed on a subset of 371 events, for which the identities of the initiator and the breaker of the association have been recorded. Then, for models 4 and 5, we considered all affiliations, proximities and aggressions that occurred before and after the allofeeding during the term of the focal observation. More precisely, to insure that behaviours preceding and following the allofeeding events could be recorded (i.e. affiliations, proximities and aggressions), I only considered allofeedings occurring at least two minutes after the start of the focal, and at least two minutes before the end. Models 4 and 5 were performed on a subset of 356 events. In those models we respectively tested whether the number of allofeeding was impacted by the occurrence of affiliations and proximities (model 4) or aggressions (model 5) between the donor and the receiver, before or after the allofeeding event. Note that we only recorded spatial associations (i.e. contact-sit and proximities) that differed from the one during which occured the allofeeding (i.e. the partners had to be spatially separated before re-entering in contact or proximity).

In all models, we also tested the effect of the breeding period (i.e. during or out the breeding season) as a fixed effect. In models 1 – 3, we also tested the effect of the sex composition of the dyad (i.e. mixed/same-sex) as a fixed effect. Finally, for all models, we used the year and the identity of the dyad as random variables. Post-hoc comparisons were performed using Tukey tests for simple and interactions effects. All statistical tests were performed with R 3.2.4 (Team, 2015). GLMMs were tested through the package ‘lme4’ (Bates et al., 2015).

Results

The number of allofeeding significantly increased during the breeding season (64% during the breeding period; GLMMs: Table 3: models 1 – 5, for all p value < 0.01). However, the sex composition of the dyad had no significant effect on the number of allofeeding displayed in the group (GLMMs: Table 3: models 1 - 3, for all p value > 0.05). Over all allofeeding recorded (i.e. 2743 in total), 67% occurred among mixed-sex dyads. In more details, 95% of allofeeding were initiated by males (i.e. 65% toward a female and 35% toward a male), and 5% by females (i.e. 1% toward a female and 99% toward a male).

Allofeeding mainly occurred among paired partners (77% on a total of 2743 events), and then among affiliates (20%) and almost never among unaffiliated partners (3%; GLMM: model 1: paired vs affiliates, estimates = 1.58, z value = 2.62, p value < 0.05; unaffiliates vs affiliates, estimates = -2.06, z value = -3.36, p value < 0.001; unaffiliates vs pairs, estimates = -3.64, z value = -5.80, p value < 0.001; Table 3).

Vocalisations were emitted in 60% of the allofeeding (i.e. over 2743). In 11% of the cases no vocalisations were emitted, and in 28% the emission of vocalisations could not be reliably recorded. Vocalisations were emitted significantly more often by both partners (i.e. the donor and the receiver), then by the donor only, and then but less often by the receiver only (GLMM: model 2: donor vs both, estimates = -3.40, z value = -10.02, p value < 0.001; receiver vs both, estimates = -0.78, z value = -7.19, p value < 0.001; receiver vs donor, estimates = -2.06, z value = 1.63, p value < 0.001; Table 3; Figure 1). Vocalisations occurred significantly more often both “before and during” the allofeeding, and less often “before only” or “during only” (GLMM: model 2: before vs both, estimates = -0.65, z value = -6.26, p value < 0.001; during vs both, estimates = -0.68, z value = -6.42, p value < 0.001; during vs before, estimates = -0.02, z value = -0.19, p value = 0.98; Table 3; Figure 1). In addition, donor vocalised significantly more often “before only” the allofeeding while the receiver vocalised significantly more often “during only” (GLMM: model 2, Table 3; Figure 1). Finally when both the donors and receivers vocalised, they did so significantly more often “during only” and “before only” the allofeeding (GLMM: model 2, Table 3; Figure 1).

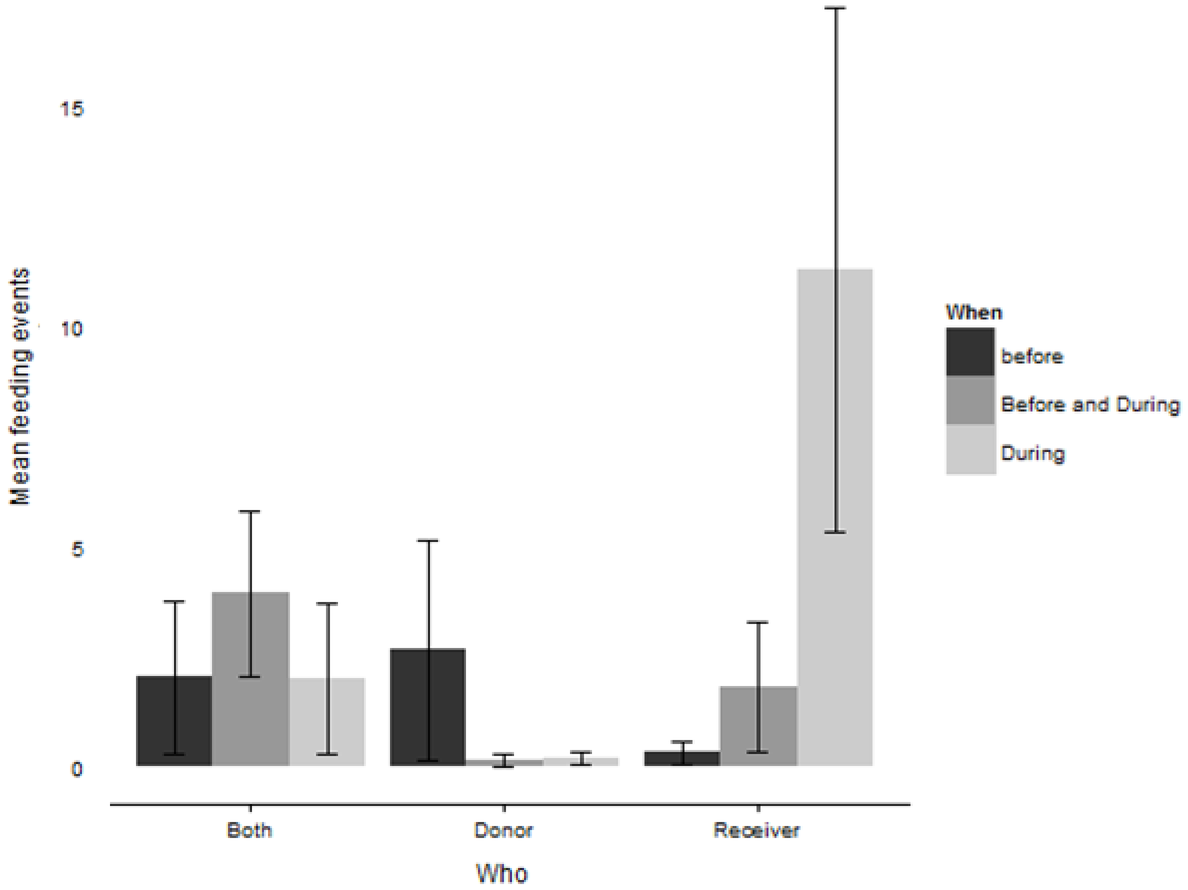


Figure A1. Mean number of allofeeding according to the identity of the individual vocalising (i.e. the donor, the receiver, or both) either: before, during or before and during the allofeeding. Visual representation is based on the means SE of the data.

In 94% of the cases, the association between the two partners (i.e. either in ground proximity or contact-sit) occurred just before the allofeeding (i.e. less than 5 seconds before). The donor initiated significantly more often the spatial association during which the allofeeding occurred (74%), than the receiver (19%), or both partners simultaneously (6%; GLMM: model 3: donor vs both, estimates = 1.79, z value = 3.74, p value < 0.001; receiver vs both, estimates = 0.87, z value = 1.66, p value = 0.22; receiver vs donor, estimates = -0.59, z value = -2.70, p value < 0.05; Table 3; Figure 2). The identity of the breaker had no effect on the number of allofeeding recorded (GLMM: model 3, Table 3; Figure 2). However, when the donor or the receiver initiated the association, they were also significantly more often responsible for the breaking of the association (i.e. left the partner; GLMM: model 3, Table 3; Figure 2).

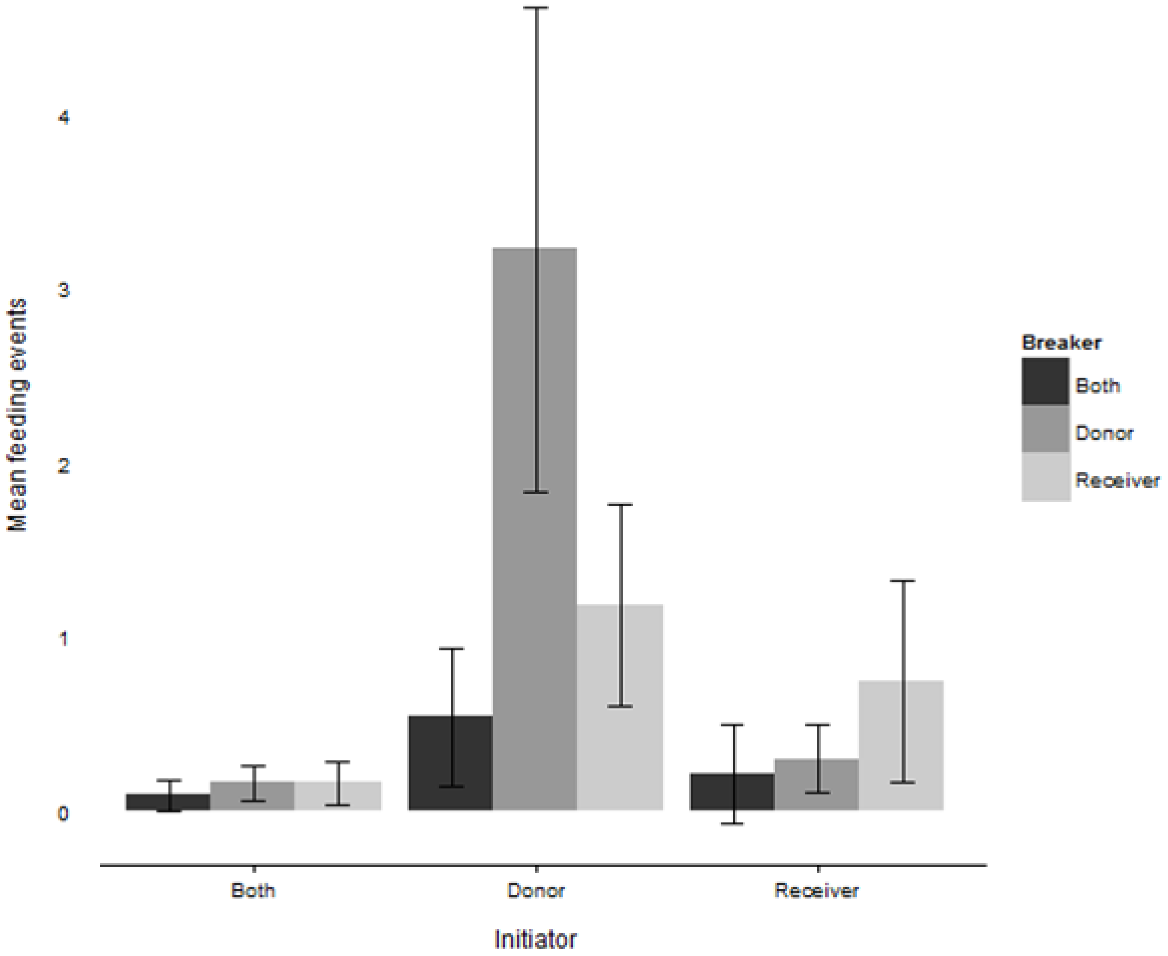


Figure A2. Mean number of allofeeding according to the identity of the individual initating the spatial association during which occured the allofeeding (i.e. initiator), and according to the identity of the individual who broke the association after the allofeeding (i.e. breaker). In both cases, the association can be initatied and/or break by the donor, the receiver, or both of them. Visual representation is based on the means SE of the data.

Allofeeding occurred significantly more often when affiliations or proximities occurred among the partners (i.e. both before and after, GLMM: model 4, before: yes x after: yes vs. no, estimates = 1.44, z value = 1.59, p value < 0.001; Table 3; Figure 3). In addition, allofeeding were more rarely recorded before or after an aggression between the partner, than when no aggression occurred (GLMM: model 5, before: yes vs. no, estimates = -3.22, z value = -11.49, p value < 0.001; after: yes vs. no, estimates = -3.08, z value = -11.76, p value < 0.001; Table 3; Figure 3).

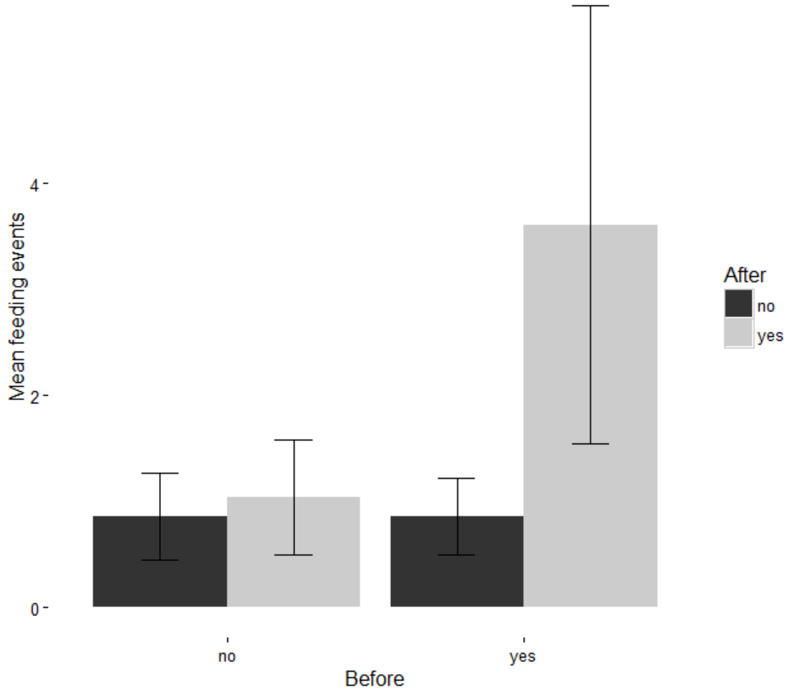


Figure A3. Mean number of allofeeding according to the occurrence of affiliations or proximities occurring between the two partners (i.e. the donor and the receiver), either before or after that the allofeeding occurred, during the term of the focal. In total, they are four possible combinaisons (from the left to the right of the figure): 1) no – no, affiliations or proximities did not occurred between the two partners either before or after the allofeeding; 2) no – yes, affiliations or proximities did not occurred before the allofeeding between the two partners, but after; 3) yes – no, affiliations or proximities occurred before the allofeeding between the two partners, but not after; and finally 4) yes – yes, affiliations or proximities occurred before and after the allofeeding between the two partners. Visual representation is based on the means SE of the data.

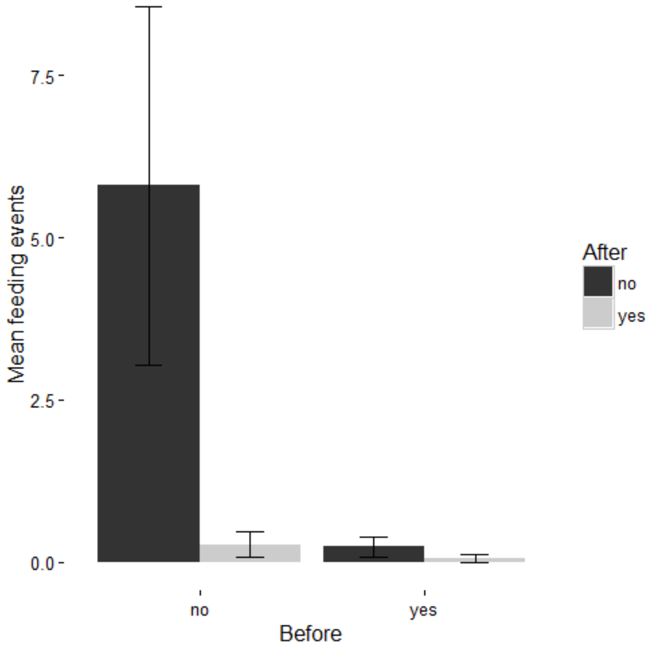


Figure A4. Mean number of allofeeding according to the occurrence of aggressions between the two partners (i.e. the donor and the receiver), either before or after the allofeeding.

Model 1: Affiliative status (N = 2743)	Estimate ± SE	z value	P value
Intercept	2.18 ± 0.53	4.13	0.07
Breeding season: out vs. in	-1.06 ± 0.51	-2.08	< **0.001** ***
Sex: same sex vs. mixed	-0.45 ± 0.52	-0.87	0.55
Affiliative status:			
paired vs. affiliated	1.36 ± 0.05	28.42	< **0.001** ***
unaffiliated vs. affiliated	-1.98 ± 0.12	-16.10	< **0.001** ***
unaffiliated vs. paired	-3.34 ± 0.12	-28.51	< **0.001** ***
Model 2: Vocalisations (N = 1656)	Estimate ± SE	z value	P value
Intercept	0.05 ± 0.95	0.06	0.95
Breeding season: out vs. in	-0.65 ± 0.05	-12.63	< **0.001** ***
Sex: same sex vs. mixed	-2.06 ± 1.63	-1.26	0.21
Who:			
donor vs. both	-3.40 ± 0.34	-10.02	< **0.001** ***
receiver vs. both	-0.78 ± 0.11	-7.19	< **0.001** ***
receiver vs. donor	-2.06 ± 1.63	7.56	< **0.001** ***
When:			
before vs. both	-0.65 ± 0.10	-6.26	< **0.001** ***
during vs. both	-0.68 ± 0.11	-6.42	< **0.001** ***
during vs. before	-0.02 ± 0.12	-0.19	0.98
Who x When:			
donor: before vs. both	3.00 ± 0.34	8.81	< **0.001** ***
donor: during vs. both	0.37 ± 0.43	0.85	0.99
donor: during vs. before	-2.63 ± 0.29	-9.19	< **0.001** ***
receiver: before vs. both	-1.76 ± 0.24	-7.47	< **0.001** ***
receiver: during vs. both	1.84 ± 0.10	18.92	< **0.001** ***
receiver: during vs. before	3.60 ± 0.22	16.31	< **0.001** ***
both: before vs. both	-0.65 ± 0.10	-6.26	< **0.001** ***
both: during vs. both	-0.67 ± 0.11	-6.42	< **0.001** ***
both: during vs. before	-0.02 ± 0.12	0.18	1
Model 3: Initiation and breaking association (N= 371)	Estimate ± SE	z value	P value
Intercept	-2.80 ± 0.69	-4.03	< **0.001** ***
Breeding season: out vs. in	-0.54 ± 0.11	-5.02	< **0.001** ***
Sex: same sex vs. mixed	-0.59 ± 0.88	-0.67	0.50
Initiation:			
donor vs. both	1.79 ± 0.48	3.74	< **0.001** ***
receiver vs. both	0.87 ± 0.53	1.66	0.22
receiver vs. donor	-0.59 ± 0.88	-2.70	< **0.05** *
Breaking:			
donor vs. both	0.58 ± 0.55	1.06	0.54
receiver vs. both	0.58 ± 0.55	1.06	0.54
receiver vs. donor	0.00 ± 0.47	0.00	1
Initiation x Breaking :			

donor: donor vs. both	1.80 ± 0.19	9.20	< **0.001 *****
donor: receiver vs. both	0.79 ± 0.22	3.61	< **0.01 ****
donor: receiver vs. donor	-1.00 ± 0.14	-7.08	< **0.001 *****
receiver: donor vs. both	0.35 ± 0.37	0.93	0.99
receiver: receiver vs. both	1.25 ± 0.32	3.86	< **0.01 ****
receiver: receiver vs. donor	0.90 ± 0.28	3.17	< **0.05 ***
both: donor vs. both	0.59 ± 0.55	1.06	0.97
both: receiver vs. both	0.59 ± 0.55	1.06	0.97
both: receiver vs. donor	0.00 ± 0.47	0.00	1
Model 4: Before & after affiliations (N= 356)	Estimate ± SE	z value	P value
Intercept	-0.10 ± 0.55	-1.84	0.07
Breeding season: out vs. in	-0.28 ± 0.11	-2.66	< **0.01 ****
Before: yes vs. no	-0.00 ± 0.20	0.00	1
After: yes vs. no	0.19 ± 0.19	0.97	0.33
Before x After			
yes : yes vs. no	1.44 ± 1.59	9.03	< **0.001 *****
no : yes vs. no	0.19 ± 0.19	0.98	0.76
Model 5: Before & after aggressions (N= 356)	Estimate ± SE	z value	P value
Intercept	0.91 ± 0.54	1.71	0.09
Breeding season: out vs. in	-0.28 ± 0.11	-2.67	< **0.01 ****
Before: yes vs. no	-3.22 ± 0.28	-11.49	< **0.001 *****
After: yes vs. no	-3.08 ± 0.26	-11.76	< **0.001 *****
Before x After			
yes : yes vs. no	-1.47 ± 0.63	-2.31	0.08
no : yes vs. no	-3.08 ± 0.26	-11.76	< **0.001 *****

Table A3. GLMM results for investigations on the factors influencing the number of allofeeding according to: 1) the social status of the dyad (i.e. paired, affiliates, unaffiliates); 2) the emission of vocalisations either by the donor or the receiver, before or after of the allofeeding; 3) the identity of the initiator and breaker of the spatial association during which occurred the allofeeding (i.e. donor or receiver); 4) the occurrence of affiliations; or 5) aggressions between the donor and the receiver, before or after the allofeeding. The number of allofeeding events on which are performed the analysis is indicated before the model results (N). Significant p-values are marked in bold. *** < 0.001, ** < 0.01, * ≤ 0.05.

Discussion

More than half of the allofeeding recorded occurred during the breeding period although most of the data were collected outside it. This is consistent with the primarily function of allofeeding, which serves to feed offspring and incubating partners. Like in juveniles, allofeeding could occur among males in adults (Scheid et al., 2008). Moreover, we found no significant effect of the sex of the dyad (i.e. mixed or same-sex), reinforcing the hypothesis that valuable and stable same-sex relationships can emerge in captive corvids (in rooks: Emery et al., 2007; Scheid et al., 2008; Jolles et al., 2013a,b; in jackdaws: von Bayern et al., 2007; in ravens: Fraser and Bugnyar, 2010), including when adults (in rooks: Chapter 4). However, allofeeding were mostly initiated by males, and when females did so, they also fed males, which is also consistent with previous results on juveniles (Scheid et al., 2008). In addition, allofeeding mostly occurred among valuable partners (i.e. paired or affiliated), confirming previous results on the role of this behaviour in the formation and the maintenance of positive relationships among partners (Chapter 4 & 5). It also reaffirms that allofeeding can be produced out of the pair in adult rooks, and that valuable bond can emerge out of this privileged social unit.

Vocalisations were rarely emitted by the receiver of the allofeeding. In addition, vocalisations emitted before the allofeeding, were more often emitted by the donor than the receiver, who most frequently vocalised during the feeding. This result suggests that in this group, vocalisations rarely corresponded to begging behaviour. In addition, the donor approached more often the receiver than the opposite. Plus, he/she almost always initiated the association just before the allofeeding, suggesting that the donor actually approached its partner to feed her/him. Overall, all these results indicate that allofeeding may not result from the avoidance of harassment. Furthermore, allofeeding were almost never recorded before or after aggressions, but more often in a bout of affiliative interactions or proximities between the two partners. This reinforce previous results on the correlation between the degree of familiarity and affiliation of the two partners, and the occurrence of allofeeding. Moreover, in most cases, both partners vocalised, before and during the allofeeding. Thus, if allofeeding certainly serves the reinforcement of the strength of a given relationship, those results also suggest that aside from its reproductive function, it may also be used as a signal directed to all group members, to signify the quality and the strength of the relationships. Further analyses need now to be conducted to investigate the dynamic of this behaviour and notably regarding the potential for reciprocity in those food transfers.

References

Altmann, J., 1974. Observational Study of Behavior : Sampling Methods. Behaviour 49, 227–267.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. lme4: Linear mixed-effects models using Eigen and S4. R Packag. version 1.1-9 https://CRAN.R–project.org/package=lme4.

Boucherie, P.H., Mariette, M.M., Bret, C., Dufour, V., 2016. Bonding beyond the pair in a monogamous bird: impact on social structure in adult rooks (Corvus frugilegus). Behaviour. doi:10.1163/1568539X-00003372

Carlisle, T.R., Zahavi, A., 1986. Helping at the nest, allofeeding and social status in immature arabian babblers. Behav. Ecol. Sociobiol. 18, 339–351. doi:10.1007/BF00299665

Connor, R.C., Curry, R.L., 1995. Helping non-relatives: a role for deceit? Anim. Behav. 49, 389–393. doi:10.1006/anbe.1995.0051

de Kort, S.R., Emery, N.J., Clayton, N.S., 2006. Food sharing in jackdaws, Corvus monedula: what, why and with whom? Anim. Behav. 72, 297–304. doi:10.1016/j.anbehav.2005.10.016

de Kort, S.R., Emery, N.J., Clayton, N.S., 2003. Food offering in jackdaws (Corvus monedula). Naturwissenschaften 90, 238–40. doi:10.1007/s00114-003-0419-2

de Waal FB, 2000. Attitudinal reciprocity in food sharing among brown capuchin monkeys. Anim. Behav. 60, 253–261. doi:10.1006/anbe.2000.1471

de Waal, F.B.., 1997. The Chimpanzee’s service economy: Food for grooming. Evol. Hum. Behav. 18, 375–386. doi:10.1016/S1090-5138(97)00085-8

Eldegard, K., Sonerud, G. a., 2012. Sex roles during post-fledging care in birds: female Tengmalm’s Owls contribute little to food provisioning. J. Ornithol. 153, 385–398. doi:10.1007/s10336-011-0753-7

Emery, N.J., Seed, A.M., von Bayern, A.M.P., Clayton, N.S., 2007. Cognitive adaptations of social bonding in birds. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 362, 489–505. doi:10.1098/rstb.2006.1991

Fraser, O.N., Bugnyar, T., 2010. The quality of social relationships in ravens. Anim. Behav. 79, 927–933. doi:10.1016/j.anbehav.2010.01.008

Gaston, A.J., 1978. The Evolution of Group Territorial Behavior and Cooperative Breeding. Am. Nat. 112, 1091. doi:10.1086/283348

Heinrich, B., 1988. Food sharing in the raven, Corvus corax., in: Slobodchikoff, C.N. (Ed.), The Ecology of Social Behavior. pp. 285–311.

Holekamp, K.E., Smale, L., 1990. Provisioning and Food Sharing by Lactating Spotted Hyenas, Crocuta crocuta (Mammalia: Hyaenidae). Ethology 86, 191–202. doi:10.1111/j.1439-0310.1990.tb00429.x

Hussell, D.J., 1988. Supply and demand in tree swallow broods: a model of parent-offspring food-provisioning interactions in birds. Am. Nat. 175–202.

Jaeggi, A. V, Stevens, J.M.G., Van Schaik, C.P., 2010. Tolerant food sharing and reciprocity is precluded by despotism among bonobos but not chimpanzees. Am. J. Phys. Anthropol. 143, 41–51. doi:10.1002/ajpa.21288

Jolles, J.W., Ostojić, L., Clayton, N.S., 2013. Dominance, pair bonds and boldness determine social-foraging tactics in rooks, Corvus frugilegus. Anim. Behav. 85, 1261–1269. doi:10.1016/j.anbehav.2013.03.013

Kalishov, A., Zahavi, A., Zahavi, A., 2005. Allofeeding in Arabian Babblers (Turdoides squamiceps). J. Ornithol. 146, 141–150. doi:10.1007/s10336-005-0073-x

Kokko, H., 2002. The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? Behav. Ecol. 13, 291–300. doi:10.1093/beheco/13.3.291

Lack, D., 1940. Courtship feeding in birds. Auk 57, 169–178.

Lifjeld, J.T., Slagsvold, T., 1986. The function of courtship feeding during incubation in the pied flycatcher Ficedula hypoleuca. Anim. Behav. 34, 1441–1453. doi:10.1016/S0003-3472(86)80215-9

Ligon, J.D., Ligon, S.H., 1983. Reciprocity in the green woodhoopoe (Phoeniculus purpureus). Anim. Behav. 31, 480–489. doi:10.1016/S0003-3472(83)80069-4

Porter, R.H., Moore, J.D., White, D.M., 1981. Food sharing by sibling vs nonsibling spiny mice (Acomys cahirinus). Behav. Ecol. Sociobiol. 8, 207–212. doi:10.1007/BF00299832

Royama, T., 1966. A re-interpretation of courtship feeding. Bird Study 13, 116–129. doi:10.1080/00063656609476115

Scheid, C., Schmidt, J., Noë, R., 2008. Distinct patterns of food offering and co-feeding in rooks. Anim. Behav. 76, 1701–1707. doi:10.1016/j.anbehav.2008.07.023

Team, R.C., 2015. R: A language and environment for statistical computing. Vienna, Austria. URL http//www. R-project. org.

Velando, A., 2004. Female control in yellow-legged gulls: Trading paternity assurance for food. Anim. Behav. 67, 899–907. doi:10.1016/j.anbehav.2003.08.019

von Bayern, A.M.., de Kort, S.R., Clayton, N.S., Emery, N.J., 2007. The role of food- and object-sharing in the development of social bonds in juvenile jackdaws (Corvus monedula). Behaviour 144, 711–733. doi:10.1163/156853907781347826

Whittingham, L.A., Dunn, P.O., Clotfelter, E.D., 2003. Parental allocation of food to nestling tree swallows: the influence of nestling behaviour, sex and paternity. Anim. Behav. 65, 1203–1210. doi:10.1006/anbe.2003.2178

Wilkinson, G.S., 1984. Reciprocal food sharing in the vampire bat. Nature 308(5955), 181–184.

Wolovich, C.K., Perea-Rodriguez, J.P., Fernandez-Duque, E., 2008. Food transfers to young and mates in wild owl monkeys (Aotus azarai). Am. J. Primatol. 70, 211–221. doi:10.1002/ajp.20477

Woolfenden, G.E., Fitzpatrick, J.W., 1977. Dominance in the Florida Scrub-Jay. Condor 79, 1–12. doi:10.1126/science.100.2609.594

Zahavi, A., 1990. Arabian babblers: the quest for social status in a co- operative breeder., in: Stacey, P.B., & Koenig, W.D. (Eds.), Cooperative Breeding in Birds: Long-Term Studies of Ecology and Behavior. pp. 103–130.

3. APPENDIX 3: APPLICATION DE L'ANALYSE DES RÉSEAUX SOCIAUX CHEZ LES OISEAUX

Extracted from

Boucherie P.H. [a,b], Mariette M.M. [c], Rat M. [d], Heeb P. [e], Doutrelant C. [f], Bousquet C. [g] (2014) Application de l'analyse des réseaux sociaux chez les oiseaux. In *Analyse des réseaux sociaux appliquée à l'éthologie et l'écologie*. (Ed. Matériologiques.) pp. 161-204 DOI: 10.13140/RG.2.1.4100.5601

[a] Institut Pluridisciplinaire Hubert Curien, University of Strasbourg, 23 rue Becquerel, 67087 Strasbourg, France

[b] Centre National de la Recherche Scientifique, UMR 7178, 23 rue Becquerel, 67087 Strasbourg, France

[c] Centre for Integrative Ecology, School of Life & Environmental Sciences, Deakin University, Melbourne, VIC 3216, Australia

[d] University of Cape Tow, Cape Town. Department Biological Sciences

[e] Laboratoire Évolution et Diversité Biologique (EDB), UMR 5174 Centre National de la Recherche Scientifique (CNRS), Université Paul Sabatier

[f] Centre d'Ecologie Fonctionnelle et Evolutive CEFE, UMR 5175, Université de Montpellier, Université Paul-Valéry Montpellier, EPHE, Montpellier Cedex 5, France

[g] Institute for Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

*Corresponding author's e-mail address: palmyre.boucherie@iphc.cnrs.fr

Résumé

Les oiseaux ont longtemps été considérés comme socialement moins complexes que certaines espèces d'insectes et de mammifères. Une explication est liée à la prépondérance du système d'appariement monogame chez la plupart des espèces aviaires. Mais depuis peu, l'analyse des réseaux sociaux offre un nouvel outil pour observer plus en détail les structures sociales, et donc mieux conceptualiser l'environnement social d'un individu. De par sa richesse et sa souplesse, elle apporte des éléments de réponse originaux à une série de questionnements, aussi bien anciens que récents. Chez les oiseaux, il est désormais par exemple possible de savoir comment une paire reproductrice se forme au sein d'un réseau social plus large ou comment la stabilité des hiérarchies est progressivement établie. Les facteurs influençant les réseaux sont souvent constants et incluent la personnalité des individus, leur condition, leur âge, ou encore l'historique de leurs relations. Les positions occupées par les individus dans le réseau influencent à la fois leur valeur sélective et leur poids dans les prises de décisions collectives. Il est ainsi probable qu'au moins certaines espèces utilisent des stratégies individuelles et/ou sociales pour déterminer ces positions. Une fois établis, les réseaux sociaux peuvent prédire les directions de propagation d'information ou de parasites dans et entre groupes. D'une façon plus générale, l'analyse des réseaux sociaux en ornithologie n'en est qu'à ses débuts mais a déjà considérablement amélioré notre compréhension des divers modes d'organisation de la socialité aviaire.

La technique des réseaux sociaux propose une approche à la fois graphique et analytique, constituant une représentation cartographique d'entités reliées entre elles. « De la même manière qu'une carte est une version simplifiée du paysage, un réseau décrit la topologie d'un système réel, en se concentrant sur les modes de connexion entre ses composants individuels » (Psorakis, Roberts, Rezek, & Sheldon, 2012). L'utilisation des réseaux repose sur une méthodologie qui simplifie l'analyse des données sociales, notamment pour les groupes à grands effectifs, tout en offrant un maximum de précision sur la qualité et la distribution des connexions (Whitehead, 2009). Appliquée aux sociétés animales, elle permet de mieux comprendre la fonction et l'évolution des comportements sociaux (Sih, Hanser, & McHugh, 2009; Wey, Blumstein, Shen, & Jordán, 2008). Utilisée au sein de différents taxons, elle peut devenir un outil d'analyse puissant, autorisant les études comparatives, comme par exemple entre humains, primates, mammifères et oiseaux, par l'utilisation d'une méthodologie commune (Faust & Skvoretz, 2002).

Comme nous avons pu le voir dans les chapitres précédents, cet outil a déjà largement contribué à l'étude des sociétés « complexes », comme chez les primates et autres espèces de mammifères sociaux (primates : Sueur, Jacobs, Amblard, Petit, & King, 2011; Henzi, Lusseau, Weingrill, van Schaik, & Barrett, 2009; cétacés : Connor, Heithaus, & Barre, 2001; Lusseau, 2007; Wiszniewski, Allen, & Möller, 2009; éléphants : Wittemyer, Hamilton, & Getz, 2005). Pour ces espèces, la structure sociale est fondée sur l'établissement de multiples relations au sein de groupes. Ces relations sont définies par l'ensemble des interactions qu'entretiennent les membres du groupe entre eux et par leurs associations spatiales (Hinde, 1976). De fait, ces associations spatiales sont généralement non aléatoires et corrélées aux interactions positives (c'est-à-dire aux comportements affiliatifs ou coopératifs, primates : Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987; cétacés : Mann, 2000; éléphants McComb, Moss, Durant, Baker, & Sayialel, 2001), ce qui permet d'estimer la force des relations entre individus.

Sur le gradient de complexité sociale, la plupart des espèces d'oiseaux ont longtemps été considérés comme peu complexes. En effet, chez les oiseaux, les relations de forte intensité se résument bien souvent au couple reproducteur et à ses jeunes (Dunbar & Shultz, 2007). Au contraire, chez les primates, Shultz et Dunbar (2007) proposent que la relation privilégiée existant entre partenaires reproducteurs se soit généralisée à l'ensemble des partenaires sociaux en dehors du couple. Néanmoins, de nombreuses espèces d'oiseaux vivent en groupe durant l'hiver, la saison de reproduction, ou tout au long de l'année (Krause & Ruxton, 2002). Il est donc possible que les oiseaux entretiennent aussi des relations avec d’autres membres du groupe que leur partenaire de reproduction, mais que ces relations, en apparence plus discrètes et labiles que chez les primates, aient été négligées. En effet, même si les comportements affiliatifs entre membres du groupe sont peu répandus, certaines espèces d´oiseaux présentent des comportements collectifs complexes au sein de leur groupe social. En particulier, le harcèlement collectif des prédateurs (Arnold, 2000), la présence de sentinelles qui signalent un danger au groupe (Ridley, Nelson-Flower, & Thompson, 2013), la construction et l’utilisation collective du nid (Brosset, 1978), la reproduction communautaire (Arnold & Owens, 1998), la parade collective entre plusieurs mâles pour l’accès aux femelles (DuVal, 2007a) ou la formation de crèches (Le Bohec, Gauthier-Clerc, & Le Maho, 2005) sont autant d’indices qui témoignent de la capacité des oiseaux à établir des interactions sociales en groupe. Les systèmes sociaux aviaires méritent donc d’être étudiés plus en profondeur, et l’application de la technique des réseaux sociaux à ces systèmes a d’ailleurs commencé à révéler une complexité jusqu’alors insoupçonnée (Aplin et al., 2013; Oh & Badyaev, 2010; Royle, Pike, Heeb, Richner, & Kölliker, 2012).

D’autre part, bien que la grande majorité des espèces d’oiseaux soit socialement monogame (Cockburn, 2006; au moins 81% des espèces : Greenwood, 1980), cela ne se traduit pas par une uniformité des sociétés aviaires. En effet, la monogamie peut impliquer des interactions très différentes entre individus selon la durée du lien du couple (annuelle, pluriannuelle ou à vie), l’exclusivité des accouplements (la paternité hors-couple varie de 0 à 72% : Griffith, Owens, & Thuman, 2002) et le type de soins parentaux (monoparental mâle ou femelle, ou biparental pendant l’élevage des jeunes et parfois pendant la couvaison : Clutton-Brock, 1991). De plus, d’autres systèmes d’appariement tels que la polygynie ou la promiscuité (par exemple les leks) sont également représentés chez les oiseaux, y compris au sein d’une même espèce. Enfin, la reproduction peut également s’effectuer en groupes coopératifs (9% des espèces aviaires : Cockburn, 2006), dont la composition (individus apparentés ou non) et la stabilité temporelle varient entre espèces. Le système d’accouplement et de soins parentaux définit donc le contexte dans lequel les interactions sociales ont lieu sur la période de reproduction mais aussi, indirectement, en dehors de la période de reproduction (Riehl, 2013). Au-delà du système de reproduction, l’utilisation de l’espace et des ressources en système territorial ou colonial peut aussi influencer les interactions sociales en dehors du couple reproducteur. Enfin, selon que l’espèce soit sédentaire, nomade ou migratrice, les interactions sociales en dehors de la saison de reproduction seront radicalement différentes. Les multiples possibilités de combinaisons de ces trois critères (système de reproduction, territorialité, sédentarité), ainsi que leur diversité propre, forment la base de la très grande diversité d'organisations sociales observée chez les oiseaux (Ekman, 2006). Les exemples utilisés tout au long de ce chapitre reflèteront la diversité de ces sociétés aviaires.

Le recours aux méthodes statistiques et de visualisation proposées par l'analyse des réseaux est particulièrement nécessaire chez les oiseaux pour plusieurs raisons. Premièrement, les comportements affiliatifs sont parfois moins élaborés ou moins facilement décelables que chez certains mammifères, et par conséquent plus difficiles à quantifier. Les données d'association spatiale peuvent alors enrichir la compréhension des comportements, pourvu qu'elles puissent être analysées correctement. Deuxièmement, de nombreuses espèces d'oiseaux présentent des relations sociales étagées, c'est-à-dire à plusieurs niveaux (définis par l'intensité de la relation) imbriqués les uns dans les autres. Ce type de structure est particulièrement bien adapté au système de filtrage qui permet de sélectionner et de visualiser les relations selon la force des liens dans le réseau (Psorakis et al., 2012). Par exemple, un individu peut avoir de fortes relations au sein du groupe familial, des interactions plus discrètes (voire uniquement vocales et à distance) avec ses voisins familiers (Godard, 1991; McGregor, 1993), et faire partie d'une colonie de reproduction ou d'un groupe de migration où les individus ne sont pas tous familiers. Troisièmement, ces groupements coloniaux ou migrateurs pouvant compter jusqu'à plusieurs dizaines voire milliers d'individus (Brown, Stutchbury, & Walsh, 1990), l'analyse des réseaux sociaux semble aussi toute indiquée pour distinguer et quantifier les associations entre individus qui diffèrent du hasard. Ceci afin de vérifier l'existence d'éventuelles structures et d'évaluer la stabilité temporelle dans ses assemblages qui n'étaient pas décelables auparavant (Shizuka et al., 2014). D'autre part, en fournissant une unité de mesure unique des liens sociaux, l'analyse des réseaux sociaux permet de suivre l'évolution de ces liens et donc la position sociale des individus dans les différents contextes qu'ils rencontrent au fil de la journée ou des saisons (par exemple passage de l'utilisation de dortoirs communs pendant la nuit à la dispersion en petits groupes pendant la journée ou encore passage d'un système monogame avec territoires pendant la reproduction à un système de groupes mobiles et parfois composés de plusieurs espèces en hiver).

Enfin, la méthode de l'analyse des réseaux peut être associée à diverses caractéristiques individuelles telles que la personnalité, le statut de dominance, l'expression des caractères sexuels secondaires, l'âge, ou encore la condition physique. Ainsi, le profil social de l'individu pourra par exemple être mis en relation avec son succès reproducteur, une autre façon d'approcher les coûts et bénéfices associés à la vie en groupe, et à terme d'apporter des éléments de réponse sur l'évolution des sociétés animales.

Ce chapitre a donc pour but de synthétiser les résultats récents concernant l'étude des mécanismes sociaux et des phénomènes collectifs chez les oiseaux à l'aide de l'analyse des réseaux sociaux. Nous y découvrirons que cette méthodologie permet non seulement de définir le système social d'une espèce (première partie), mais aussi de mesurer le niveau de socialité des individus au sein de ce système (deuxième partie). Enfin, nous discuterons en troisième partie de la fonctionnalité du réseau dans son ensemble, qui selon ses spécificités (topologie) et les caractéristiques des agents qui le composent, va varier en termes de transfert d'information, de flux de pathogènes ou encore de gènes. En permettant de suivre et d'analyser des liens sociaux bien au-delà de la relation entre appariés, la technique des réseaux devrait occasionner une mise à jour de la notion de socialité chez les oiseaux.

I. Couples et jeunes : caractérisation de l'organisation sociale de l'espèce

A. Soins parentaux et reproduction communautaire

Contrairement aux mammifères, les oiseaux ont en très grande majorité un système de soins biparentaux, où les deux parents participent à l'élevage des jeunes (81% des espèces : Cockburn, 2006). Les espèces varient sur le niveau d'équité des soins entre les deux parents, allant du partage complet de chaque étape de la reproduction à l'absence totale de soins par l'un des deux partenaires (Clutton-Brock, 1991). Les soins biparentaux sont une énigme évolutive car les théories disponibles prédisent que chaque parent devrait essayer de minimiser ses propres coûts liés à la reproduction et par conséquent laisser son partenaire fournir la majorité des soins, voire même leurs totalité (Trivers, 1972). Notamment chez certaines espèces comme le gravelot à collier interrompu (*Charadrius alexandrinus*), il est courant que l'un des deux parents déserte le nid, et laisse la progéniture aux seuls soins de son partenaire (Clutton-Brock, 1991; Székely & Cuthill, 2000). De nombreux modèles théoriques développés depuis les années 1970 prédisent que les partenaires devraient négocier leurs efforts (McNamara, Gasson, & Houston, 1999; Trivers, 1972), et pourraient parfois utiliser l'effort parental de leur partenaire comme source d'information sur les besoins ou valeur de la nichée (Johnstone & Hinde, 2006).

Les interactions sociales au sein du couple sont donc soutenues et souvent complexes, non seulement pour négocier le partage des tâches, mais peut-être aussi pour augmenter l'efficacité des soins parentaux. En effet, il a longtemps été observé que le succès reproducteur d'un couple augmente avec la durée du lien, au-delà de l'effet de l'âge ou de l'expérience individuelle (Black, 1996; Sánchez-Macouzet, Rodríguez, & Drummond, 2014). Cet effet, attribué à l'augmentation de la familiarité entre partenaires, pourrait opérer par le biais d'une meilleure coordination comportementale. Ainsi, chez le diamant mandarin sauvage (*Taeniopygia guttata*), les partenaires synchronisent les soins parentaux en visitant le nid ensemble plutôt qu'indépendamment (Mariette & Griffith, 2012). Lorsque le nombre de poussins à élever est expérimentalement manipulé, les couples augmentent leur synchronisation avec la taille des nichées, et les poussins dont les parents sont plus fortement associés entre eux pendant la recherche de nourriture ont une meilleure croissance (Mariette & Griffith, in press). La coordination des soins parentaux pourrait donc être une stratégie pour augmenter l'efficacité d'approvisionnement des jeunes, particulièrement lorsque la demande est élevée (Mariette & Griffith, in press). La méthode des réseaux permet de quantifier, à partir de données d'association entre partenaires, la force de leur lien dans différents contextes, par exemple au nid ou pendant la recherche de nourriture. Chez les oiseaux coloniaux, cette méthode pourrait aussi permettre d'établir si la force du lien du couple est positivement ou négativement corrélée aux relations en dehors du couple (Mariette et al., in prep). En effet, il est possible que certains individus plus sociaux, le soit aussi avec leur partenaire. Au contraire, les individus qui ont un lien plus faible avec leur partenaire de couple pourraient compenser par de plus fortes relations avec d'autres associés (Mariette et al., in prep). En effet, le couple peut avoir une fonction sociale au-delà de sa fonction reproductive. Plus particulièrement, les partenaires peuvent montrer des comportements de sentinelle (Krams, Krama, & Igaune, 2006), défendre ensemble le territoire (Hall & Peters, 2008), et s'associer pour rechercher de la nourriture (Mariette & Griffith, in press). Cette fonction sociale du couple pourrait alors expliquer la formation de couples homosexuels lorsque la proportion de mâles et femelles est déséquilibrée (Sommer & Vasey, 2006).

Même s'il semble trivial, le lien de couple est souvent le lien social qui a l'effet le plus direct sur la valeur sélective, en déterminant la qualité et la quantité de la descendance, le coût associé à leur production, et enfin les bénéfices de groupe que le couple confère. Le couple est aussi l'unité de base des sociétés grégaires. Une meilleure compréhension de ces sociétés peut émerger de l'application des méthodes d'analyse de réseaux pour explorer comment ce lien se forme (Section I.A), et comment il varie en fonction des autres liens et propriétés du réseau (y compris pas le biais des copulations hors-couple : Section I.B).

La coopération entre deux parents peut parfois s'étendre à d'autres individus, passant ainsi d'un système à soins biparentaux à un système à reproduction communautaire. Ce système coopératif particulier est trouvé chez plusieurs classes d'animaux, tels qu'insectes, mammifères, poissons et oiseaux. Chez ces derniers, environ 9% des espèces retarderaient ainsi leur reproduction pour entrer dans un système de soins alloparentaux (Cockburn, 2006).

Dans les systèmes à reproduction communautaire, une partie de la nourriture apportée aux jeunes est donnée par des individus sexuellement matures qui ne sont pas les parents. Ainsi, des individus – les « helpers » ou assistants – nourrissent des jeunes qui ne sont pas les leurs. Expliquer ce type d'aide a fait l'objet de nombreux débats scientifiques dans les années 1950. Aujourd'hui, un large consensus existe sur le fait qu'il s'agit d'un altruisme apparent qui évoluerait principalement en raison des bénéfices indirects liés à l'augmentation de la valeur sélective inclusive via l'aide fournie à des individus apparentés (Hamilton, 1964a, 1964b). Une autre explication non-exclusive est que la coopération donne des bénéfices directs aux individus qui aident. Actuellement, l'importance relative de ces bénéfices directs et indirects reste à déterminer. Les bénéfices directs peuvent être obtenus par de la réciprocité directe ou bien de la réciprocité indirecte si le comportement coopératif induit une réponse coopérative des individus qui observent l'interaction. Tout comme dans l'exemple des corbeaux, le fait d'aider peut aussi être un signal permettant d'être accepté dans le groupe ou d'obtenir un partenaire (Doutrelant & Covas, 2007). Réaliser des réseaux de cooccurrence à des mangeoires ou à des zones de reproduction ou nidification en association avec des données d'apparentement, de dominance et des mesures de coopérativité pourrait permettre d'évaluer l'importance relative des bénéfices directs/indirects liés à la coopération, mais aussi de tester l'importance potentielle du népotisme. A ce jour, de telles mesures n'ont guère été réalisées chez les oiseaux mais sont particulièrement prometteuses dans d'autres taxons. Chez les mammifères (Madden, Drewe, Pearce, & Clutton-Brock, 2009) ou les poissons (Schürch, Rothenberger, & Heg, 2010), l'utilisation des réseaux sociaux a permis récemment de mettre en évidence de tels liens montrant par exemple des conflits au sein des dominants pour la reproduction chez des cichlidés à reproduction communautaire (*Neolamprologus pulcher* : Dey, Reddon, O'Connor, & Balshine, 2013). Chez les républicains sociaux (*Philetairus socius*), une étude récente a aussi regardé le comportement de construction du nid communautaire et a pu montrer que l'existence de sous-structures au sein de ces colonies est liée à l'apparentement et que les individus investissant plus dans le maintien de la structure communale sont plus centraux (van Dijk et al., 2014). De telles données pourraient aussi être obtenues en relation avec la reproduction communautaire des oiseaux et constituent des perspectives intéressantes à l'utilisation des réseaux sociaux.

B. Apport des réseaux sociaux pour l'étude du choix du partenaire : où et comment ?

A la vue du fort investissement parental que nécessite la reproduction, la formation d'une relation sociale entre les partenaires du couple au-delà de la fonction reproductrice n'est guère étonnante. Le choix du partenaire est donc crucial, d'autant plus pour les espèces longévives qui peuvent rester pendant plusieurs saisons de reproduction avec le même partenaire (Jeschke & Kokko, 2008). Pour les espèces où les couples tendent à se reformer chaque année, l'analyse des réseaux sociaux permet d'examiner si les associations observées entre individus voisins sur un même territoire en début de saison, jouent un rôle dans le choix du partenaire reproducteur. Chez la mésange charbonnière (*Parus major*), une étude de grande ampleur a permis de déterminer les réseaux d'associations de 750 individus, pendant deux hivers consécutifs (Psorakis et al., 2012). L'étude propose un outil méthodologique permettant le suivi des associations en milieu naturel. Les oiseaux sont équipés de puces RFID dont les récepteurs sont localisés dans des zones supplémentées en nourriture. Les résultats montrent que les individus se retrouvent de manière ponctuelle, lors d'événements de « rassemblement alimentaire ». La cooccurrence des individus aux zones alimentaires permet ensuite d'établir le réseau social d'associations. Les données de proximité obtenues autorisent l'identification des couples reproducteurs et montrent l'existence d'associations hors-couple privilégiées, même si ces dernières ont un poids faible dans le réseau. De plus, il a pu être montré que le choix du partenaire se fait au sein des clusters, donc dans un cercle restreint d'individus connectés, déjà familiers. Ainsi, les relations hors-couple peuvent représenter un enjeu particulier pour le choix du futur partenaire d'une saison à l'autre.

L'analyse temporelle des réseaux sociaux permet par ailleurs d'obtenir de nouvelles connaissances quant à la dynamique de formation des nouveaux couples. Dans l'analyse des réseaux de cooccurrence aux mangeoires mentionnée ci-dessus, les couples déjà établis l'année précédente sont retrouvés presque chaque jour au sein du même cluster. En revanche, en début d'hiver, les membres d'une future paire se comportent comme des individus indifférents l'un à l'autre : leur degré d'appartenance à un même cluster n'est pas supérieur à celui d'oiseaux non appariés pris au hasard dans la population. Progressivement, les membres de la future paire vont être de plus en plus souvent associés, pour finalement avoir le même degré d'attachement qu'un couple plus ancien (Psorakis et al., 2012). Une analyse plus fine des interactions interindividuelles devrait permettre de faire ressortir les caractéristiques des partenaires potentiels, et de suivre les étapes impliquées lors de la formation d'un couple.

Chez les corvidés sociaux, espèces longévives et fidèles à un partenaire (à vie ou pour plusieurs saisons de reproduction), les interactions sociales produites entre individus sont particulièrement riches en comparaison d'autres espèces d'oiseaux sociaux (Bond, Kamil, & Balda, 2003; Fraser & Bugnyar, 2011). Ceci peut en partie s'expliquer par le degré de développement de leurs capacités cognitives, qui ont déjà été très largement décrites dans la littérature (corvidés : Emery & Clayton, 2004; corbeaux freux, *Corvus frugilegus* : Seed, Tebbich, Emery, & Clayton, 2006; corbeaux calédoniens, *Corvus moneduloides* Bluff, Weir, Rutz, Wimpenny, & Kacelnik, 2007). Pour ces espèces, le choix du partenaire s'effectue lors de la période juvénile. En effet, les groupes sont particulièrement actifs socialement durant cette période précédant l'appariement. Les juvéniles sont à ce stade associés à plusieurs individus, avec lesquels ils interagissent à travers le toilettage social ou le transfert de nourriture (Clayton & Emery, 2007; Fraser & Bugnyar, 2010). L'analyse de la structure sociale d'un groupe de 12 corbeaux freux juvéniles tenus captifs montre que des paires se forment progressivement, mais que ces relations ne sont pas exclusives. Des interactions affiliatives, principalement toilettage et transfert de nourriture, sont produites entre individus non appariés de même sexe et de sexe opposé (Emery, Seed, von Bayern, & Clayton, 2007). De largement distribué au sein du réseau chez les juvéniles, le comportement de transfert alimentaire tend à devenir exclusif à la relation de couple chez l'adulte, relation qui se consolide également au fil des saisons au travers d'autres interactions affiliatives telles que le toilettage (Emery & Clayton, 2009). Outre les interactions affiliatives, la distribution des interactions agonistiques dans le réseau est également informative. Bien que très fréquentes, les agressions chez les jeunes ne se produisent pas entre partenaires sociaux, ce qui permet sans doute le renforcement de relations privilégiées, menant à la formation des couples reproducteurs (Emery et al., 2007). L'utilisation des réseaux permet ici de visualiser la complexité et l'évolution de la distribution des interactions entre plusieurs partenaires d'un même groupe.

C. Copulations hors-couple et séparations : ce que les réseaux sociaux pourraient nous apprendre

Depuis l'utilisation massive de marqueurs génétiques permettant l'identification individuelle, il a été montré à plusieurs reprises que monogamie sociale ne rime pas forcément avec monogamie génétique (Mock & Fujioka, 1990; Wan, Chang, & Yin, 2013). Par exemple, chez les passereaux, environ 86% des espèces peuvent présenter au moins un jeune issu de copulations hors-couple (Griffith et al., 2002). Ainsi, la formation d'un couple stable pour une ou plusieurs saisons n'implique pas nécessairement l'exclusivité des accouplements entre les deux partenaires. Les paternités hors-couple complèteraient alors les observations directes pour construire le réseau d'interactions des individus en dehors du couple. En effet, du fait que le partenaire mâle est susceptible de diminuer son effort parental lorsqu'il n'est pas le père génétique de toute la nichée (Matysioková & Remeš, 2013), les interactions des femelles avec leur partenaire hors-couple sont typiquement discrètes et échappent pour la plupart aux observateurs humains. Or, la production d'oisillons de pères différents dans la même nichée signifie obligatoirement que les individus interagissent en dehors du couple, et souvent de façon suffisante pour être capable d'estimer la qualité phénotypique de potentiels partenaires. Ainsi, la prévalence des fertilisations hors-couple varie selon le contexte social défini par le ratio de mâles et femelles ou la taille de la population (Liker, Freckleton, & Székely, 2014). Intégrer de telles données dans la construction de réseaux sociaux pourrait considérablement modifier notre perception du système social de certaines espèces où les paternités hors-couple représentent plus de la moitié des copulations. D'autre part, l'utilisation de l'analyse des réseaux sociaux permettrait de suivre les associations interindividuelles avant, pendant et après la reproduction, et d'examiner si elles prédisent entre quels individus auront lieu les copulations hors-couple.

De plus, chez de nombreuses espèces d'oiseaux, la monogamie ne dure pas toute la vie adulte et plus de 92% des espèces monogames présentent un taux de séparation non nul (Jeschke & Kokko, 2008). Une étude conduite sur un groupe de corbeaux freux adultes captifs montre que la structure sociale du groupe peut avoir un impact sur la force des couples et que des séparations peuvent avoir lieu, quelle que soit l'ancienneté du couple (Boucherie et al., in prep). Après l'introduction de nouveaux membres dans un groupe stable (6 nouveaux membres pour 9 anciens), l'analyse des réseaux a permis de suivre les mécanismes de formation de 6 nouvelles paires et la séparation de 3 paires (1 couple « ancien » et 2 couples « récents » formés après introduction). Ces séparations pourraient s'expliquer par la modification du réseau résultant de l'introduction de nouveaux membres, par le stress social associé, ou par l'introduction d'une nouvelle « offre » de partenaires qui aurait fragilisé les couples existants et influencé la formation de nouvelles paires. Enfin, comme chez les mésanges (Psorakis et al., 2012), les résultats montrent que les couples se forment progressivement, et que les partenaires sont choisis parmi des individus familiers, appartenant au même cluster (4 couples sur 6, Boucherie et al., in prep). L'analyse des réseaux sociaux permet donc le suivi des relations dans le temps, les séparations comme les formations de couples pouvant se produire à n'importe quel moment de la vie d'un individu.

II. Relations hors-couple : stratégies individuelles au sein des systèmes sociaux

A. Relations sociales hors-couple

Comme vu précédemment (Section I.B.), les analyses des réseaux sociaux conduites chez les corvidés montrent que des relations peuvent exister en dehors des couples (Emery et al., 2007; Boucherie et al., in prep). Une étude récente effectuée en milieu naturel chez le corbeau calédonien démontre également l'existence d'associations fortes entre individus non appariés (Rutz et al., 2012). Bien que le poids de toutes les associations ne soit pas équivalent, cette étude suggère que le nombre de partenaires sociaux pour l'espèce serait de 10 en moyenne. Un nombre plus élevé que le nombre habituellement reconnu pour l'espèce (3,22 en moyenne, à savoir les membres du couple et leur progéniture : Holzhaider et al., 2011). Donc bien que le couple soit le cœur de la structure sociale, ceci suggère une richesse inattendue de relations sociales hors-couple. Par ailleurs, cette étude ouvre de nouvelles perspectives techniques pour la collecte de données. Les auteurs ont développé un système d'émetteurs-récepteurs numériques sans fil permettant l'enregistrement automatique de données spatio-temporelles de haute qualité pour l'analyse des réseaux sociaux. Ces balises miniatures fixées sur l'animal enregistrent directement la proximité d'une autre balise ainsi que la durée de la « rencontre ». Ce dispositif a permis de relever plus de 28 000 rencontres pour 34 individus équipés pendant 7 jours. Contrairement aux études plus classiquement basées sur la cooccurrence de 2 individus sur un même site (Psorakis et al., 2012), ce procédé permet de relever la totalité des « rencontres » entre les individus équipés. Il permet de compenser les difficultés inhérentes à la collecte de données en milieu naturel. Il serait intéressant de comparer pour la même espèce la quantité de données obtenues avec une méthode plus « classique » d'observation pour évaluer la proportion d'information qui échappe à l'analyse mais aussi la nature des interactions observées : affiliatives, sexuelles, coopératives, agonistiques… Ceci rappelle la nécessité de rester prudent quant aux conclusions tirées de l’analyse des réseaux sociaux, qui ne donne bien souvent qu’un bref aperçu de la réalité sociale de l’espèce.

B. Structure sociale chez les espèces coloniales : analyse de la diversité des associations

Nombre d’espèces aviaires sont grégaires au moins à un moment de leur cycle de vie, notamment les espèces coloniales (13% des espèces aviaires, dont 95% sont des espèces marines : Danchin & Wagner, 1997; Rolland, Danchin, & de Fraipont, 1998) dans lesquelles les individus se regroupent en grand nombre sur un espace restreint (Hoogland & Sherman, 1976). A la vue de cette forte densité, se pose la question de l’existence d’une organisation, voire d’une structure sociale, reposant sur des associations particulières et les interactions entre individus, dans et en dehors des couples. Il a déjà pu être montré au sein de ces regroupements que les associations entre individus peuvent être aléatoires, donc non différentes du hasard (Myers, 1983) mais aussi préférentielles (Harrington & Leddy, 1982). Récemment, l’utilisation de nouvelles techniques (par exemple les Systèmes d’Information Géographique) a relancé l’intérêt scientifique pour l’analyse des relations spatiales entre individus au sein des colonies aviaires (Conklin & Colwell, 2007, 2008). Combinée à l’analyse des réseaux sociaux, cette approche est particulièrement intéressante puisqu’elle devrait permettre de révéler, si elles existent, les structures sociales qui charpentent ces regroupements.

Dans une étude récente menée chez les bécasseaux variables (*Calidris alpina*), l’analyse des associations spatiales d’un groupement de juvéniles montre que la cooccurrence d’individus au sein d’un même groupe, à marée haute, est aléatoire. Les auteurs concluent à l’absence d’une quelconque structure sociale dans les colonies de repos (Conklin & Colwell, 2008). Pour cette espèce, les associations entre individus de la colonie, définies comme la présence de deux individus sur le même site, sont donc ponctuelles. Pourtant, pour les espèces grégaires, la nécessité de maintenir une certaine cohésion de groupe lors d’activités collectives (déplacement, vigilance contre la prédation…) aurait pu se traduire par la formation d’associations non aléatoires entre individus. Dans le cas des bécasseaux variables, il est possible que la cohésion du groupe soit plutôt maintenue indirectement par la fidélité de chaque individu aux sites de repos et d’alimentation (Leyrer, Spaans, Camara, & Piersma, 2006). Ces résultats confirment ceux obtenus par des études antérieures sur le bécasseau sanderling, *Calidris alba*, une autre espèce limicole du même genre pour laquelle les associations interindividuelles sont également aléatoires (Myers, 1983; Roberts & Evans, 1993). Néanmoins, le fait que les juvéniles forment des groupes aléatoires ne veut pas nécessairement dire qu'il n'existe pas de structure sociale entre adultes. De plus, il est possible que la stabilité des associations soit différente pour les colonies de reproduction et celles de repos. D'autres travaux suggèrent d'ailleurs, pour des espèces de la même famille, que les associations entre individus au sein des colonies sont non aléatoires (chevalier gambette, *Tringa totanus* : Furness & Galbraith, 1980; bécasseau maubèche, *Calidris canutus* : Harrington & Leddy, 1982), et les auteurs de ces études concluent pour ces espèces à l'existence d'une « certaine organisation sociale ». Par ailleurs, la diversité des résultats et conclusions obtenus pour des espèces parfois très proches phylogénétiquement souligne l'importance de l'utilisation de méthodes et de techniques standardisées permettant la comparaison des résultats entre espèces.

Chez les bernaches nonettes (*Branta leucopsis*), les associations spatiales entre individus sont également significativement différentes du hasard (Kurvers et al., 2013). En utilisant une technique de permutation des nœuds, les auteurs montrent que certaines associations apparaissent préférentielles, et que les partenaires diffèrent selon les contextes. Durant la recherche alimentaire, les partenaires sont préférentiellement issus du cercle des individus familiers et des apparentés. Au contraire, pour la reproduction, les partenaires sexuels sont choisis parmi les non apparentés. Ces résultats mettent en évidence que les préférences sociales au sein d'un groupe d'individus peuvent différer selon les contextes écologiques et sociaux. Ils soulignent également le fait que des relations particulières peuvent se tisser entre individus en dehors du contexte reproducteur. De la même manière, l'analyse du réseau d'associations d'une population naturelle de roselins familiers (*Haemorhous mexicanus*) en dehors de la période de reproduction montre l'existence d'un réseau structuré, fortement fragmenté et composé d'une vingtaine de clusters d'environ 30 individus (Oh & Badyaev, 2010). Bien que les résultats mettent particulièrement en évidence les couples reproducteurs, ils suggèrent, encore une fois, l'existence de relations sociales particulières en dehors des couples.

Enfin, une étude récente révèle une organisation sociale surprenante sur les zones d'hivernage chez une espèce migratrice, le bruant à couronne doré (*Zonotrichia atricapilla* : Shizuka et al., 2014). Le réseau d'associations observé a une modularité significativement plus élevée que celle non seulement d'un réseau aléatoire mais également d'un réseau construit à partir de l'utilisation de l'espace par les individus. Il suggère donc une préférence sociale au-delà de l'utilisation commune d'un site. De plus, ces associations préférentielles ne sont pas simplement dues au fait que les individus se regroupent pour la journée, mais correspondent à des associations de longue durée maintenues d'une année sur l'autre, et ce, malgré une mortalité élevée (35 à 72%) affectant la composition des communautés entre années (Shizuka et al., 2014). Cette étude illustre parfaitement l'hypothèse que les sociétés aviaires pourraient être beaucoup plus complexes que ne le suggèrent les méthodes d'analyse traditionnelles.

C. Relations intra-sexe et succès d'appariement des individus

Chez les oiseaux, le contexte dans lequel les individus interagissent peut avoir une forte influence sur la structuration des liens sociaux. Certaines études montrent que dans le contexte de l'accès à la reproduction, les mâles peuvent établir des relations particulières entre eux qui facilitent l'accès aux femelles (McDonald, 2007; Oh & Badyaev, 2010; Ryder, Blake, Parker, & Loiselle, 2011). Ceci démontre une fois encore l'importance et le rôle que peuvent jouer les relations sociales hors-couple chez les oiseaux.

Oh et Badyaev (2010) ont examiné les liens entre degré d'élaboration d'ornements sexuels (liés au succès reproducteur) et les types d'associations entre mâles chez le roselin familier. Chez cette espèce, la coloration du plumage des mâles varie du jaune pâle au rouge, et influence significativement le choix des femelles (Hill, 1990). Les résultats montrent que les mâles ayant un ornement sexuel moins élaboré (petit et/ou moins coloré) entretiennent des relations moins stables au sein du réseau d'association observé en hiver, et changent ainsi davantage de groupe. Au contraire, les mâles dont l'ornement est plus élaboré entretiennent des relations plus stables et plus exclusives au sein de leur cluster. Dans l'analyse du réseau, ce résultat est reflété par le coefficient de *betweeness*, qui est donc beaucoup plus élevé pour les mâles dont les ornements sont moins développés. Les auteurs montrent ensuite que parmi les mâles peu colorés, ceux qui ont changé de groupe ont un succès d'appariement plus fort que ceux qui n'ont pas changé de groupe. Ce succès plus fort est dû au fait que les changements de groupe leur ont permis d'arriver dans un groupe où leur niveau d'ornementation est plus élevé que celui des autres membres du groupe. L'analyse des réseaux permet ici d'établir un lien entre le succès d'appariement des mâles et la structure sociale d'une population naturelle d'oiseaux en situation de compétition.

Un autre cas de figure intéressant pour analyser ce lien entre succès reproducteur et structure sociale est celui des leks ou aires de parades, où la compétition est particulièrement intense et prend une forme ritualisée (Kirkpatrick & Ryan, 1991). Les mâles se regroupent dans une zone restreinte appelée arène dans laquelle les individus s'affrontent par le biais de chants et/ou de postures ritualisés afin de gagner et/ou maintenir un petit territoire et ainsi exposer leur qualité auprès des femelles. Ces rassemblements sont à l'origine de nombreuses et complexes interactions sociales entre mâles. L'ensemble de ces interactions est majoritairement agonistique et à l'origine d'une hiérarchie temporaire. Les mâles les plus dominants obtiennent les territoires centraux, zones les plus visitées par les femelles lors de la saison des accouplements. Outre la dominance pure, des coalitions mâles-mâles peuvent faciliter l'acquisition de positions centrales. Chez le manakin filifère (*Pipra filicauda*), des coalitions se forment lors des parades nuptiales et ont comme résultat d'attirer l'attention des femelles, la présence d'un autre mâle stimulant le rythme ou l'intensité des parades par effet d'émulation sociale (Ryder et al., 2011). Le rang hiérarchique des individus semble important dans la formation de ces partenariats (DuVal, 2007b; Whitehead & Connor, 2005). Ainsi, chez le manakin fastueux (*Chiroxiphia linearis*), les coalitions se forment entre un mâle plus dominant et un plus dominé (McDonald, 2007). Outre ces éléments importants, l'analyse du réseau d'association montre que la position des individus dans le réseau peut également avoir une influence sur le statut reproducteur. Chez le manakin filifère, le degré de connectivité d'un individu est corrélé à l'augmentation de son statut social (possession d'un territoire) et donc au succès reproducteur (McDonald, 2007). Ce qui est cependant surprenant est la temporalité avec laquelle la connectivité impacte le statut social. En effet, il semble que ce soit le degré de connectivité dans le réseau 5 ans auparavant qui prédit le mieux l'augmentation de statut social de l'individu, particulièrement chez les jeunes mâles (McDonald, 2007). Une autre étude montre plus précisément que les meilleurs prédicteurs de l'augmentation du statut social et donc du succès reproducteur sont : le *degré*, soit le nombre de mâles avec lequel l'individu focal est connecté ; le *reach*, soit la proportion de nœuds connectés en deux liens ou moins ; et la *betweeness*, mesurant le nombre de plus courts chemins passant par le nœud focal (Ryder, McDonald, Blake, Parker, & Loiselle, 2008). Enfin, en plus des relations directes (degré), ces mesures de réseau mettent en avant l'importance des relations indirectes (*betweeness*, *reach*), donc composées d'intermédiaires, pour l'accès à la reproduction. Ces relations intermédiaires ne pouvaient être visualisées et étaient difficilement quantifiables avant l'émergence de la théorie des graphes.

L'étude de Ryder et al. (2008) établit également que le réseau chez les manakins filifères est caractérisé par une faible valeur moyenne et une forte variance de degré, deux caractéristiques typiques des réseaux dits *scale-free* et qui témoignent d'une forte disparité de la distribution des associations. Selon plusieurs études récentes, cette topologie de réseau favoriserait l'évolution de la coopération, des comportements altruistes ou encore de la réciprocité indirecte (Greiner & Levati, 2005; Nowak & Sigmund, 2005; Santos & Pacheco, 2005). Il a d’ailleurs été proposé une règle simple pour évaluer la dimension coopérative du réseau : « *la sélection naturelle favorise la coopération dans le cas où le bénéfice de l’acte altruiste,* b, *divisé par le coût,* c*, n’est pas supérieur au nombre moyen de nœuds voisins,* k » (Ohtsuki, Hauert, Lieberman, & Nowak, 2006). Appliqué aux systèmes complexes, l’analyse des réseaux pourrait donc apporter des éléments de réponse sur l’évolution des comportements sociaux dits altruistes, notamment dans le cas où de précédentes théories n’avaient pu l’expliquer.

D. Apport des réseaux sociaux pour l’étude des hiérarchies de dominance

L’établissement d’une hiérarchie passe par les relations de dominance qui lient les individus d’un groupe social. Les hiérarchies sont souvent observées chez les espèces d’oiseaux vivant en groupe et plus encore chez celles présentant un système social complexe comme les espèces à reproduction communautaire (Cockburn, 1998). En effet, chez ces espèces, les individus sont fortement interdépendants (Roberts, 2005) et doivent faire face au dilemme entre coopération et compétition pour le partage des ressources. En définissant un ordre de priorité pour l’accès aux ressources, comme le territoire, la nourriture ou encore le partenaire sexuel, les hiérarchies permettent d’éviter les combats couteux en énergie et les agressions (Rowell, 1974). L’ordre de priorité est généralement basé sur les asymétries entre individus en termes d’agressivité ou de capacité à combattre. L’évolution d’un système social hiérarchique favorise la modulation des conflits et facilite ainsi la cohésion du groupe (Chiarati, Canestrari, Vera, Marcos, & Baglione, 2010; Preuschoft & van Schaik, 2000).

La cohésion et la stabilité d’un groupe sont d’autant plus fortes lorsque les hiérarchies sont dites ordonnées ou linéaires (Senar, Copete, & Metcalfe, 1990). Une hiérarchie est linéaire ou ordonnée quand un individu de rang supérieur domine tous les individus de rang inférieur. Cette structure existe quand les relations de dominance entre trois individus sont transitives et non cycliques (Figure 1). Les relations cycliques caractérisent alors les inconsistances dans la hiérarchie.

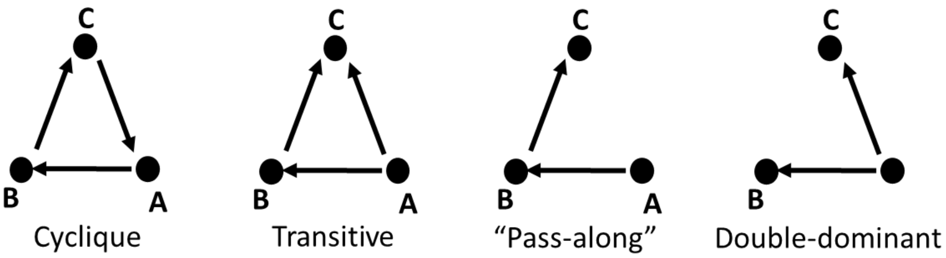


Figure A1. Exemples de configurations triangulaires possibles au sein d'un groupe de 3 individus (adaptée de Shizuka & McDonald, 2012).

Récemment, l'analyse des réseaux sociaux a permis le développement d'un nouvel outil analytique afin de caractériser le niveau d'ordre de la hiérarchie : l'indice de transitivité triangulaire (T_{tri}), développé par Shizuka et McDonald (2012). Cet indice T_{tri} est basé sur la fréquence des différentes configurations de triade observées dans le réseau social ou « *triad census* ». Les auteurs ont démontré que dans un réseau aléatoire, la proportion de triades transitives attendues parmi toutes les configurations possibles est de 0,75 indépendamment du nombre d'individus et d'interactions observées. En se basant sur cette règle, il est possible d'établir une distribution du nombre de triades transitives attendues pour des réseaux comprenant le même nombre d'individus et de victoires que le réseau observé et de déduire la significativité de l'indice T_{tri} observé grâce à cette distribution. Une hiérarchie est alors d'autant plus ordonnée que l'indice T_{tri} se rapproche de la valeur 1 et d'autant plus égalitaire quand T_{tri} tend vers 0. Qui plus est, les auteurs argumentent que cette nouvelle méthode analytique est plus fiable que les outils précédemment développés comme les indices de linéarité (de Vries, 1995; Landau, 1951a, 1951b). En effet, l'indice T_{tri} est moins sensible aux biais engendrés par de fortes proportions de dyades qui n'ont pas été observées en interaction (voir Shizuka & McDonald, 2012 pour plus de détails sur la procédure analytique).

Chez les oiseaux, l'indice T_{tri} a été utilisé pour la première fois afin de qualifier la structure de la dominance chez le républicain social, une espèce coloniale à reproduction communautaire (Rat, Covas, van Dijk, & Doutrelant, in rev) qui vit à l'année dans un nid massif construit coopérativement de génération en génération (Maclean, 1973). Cet outil a permis aux auteurs (Rat et al., in rev) de montrer que les colonies de républicains sociaux forment des hiérarchies très ordonnées (T_{tri} moyen ± ET observé sur 8 colonies : 0.875 ± 0.136). La structure de dominance chez cette espèce est ainsi loin d'être égalitaire comme on aurait pu le penser dû au fait qu'il y ait plusieurs paires reproductrices au sein d'une même colonie et donc potentiellement peu de biais de reproduction (Rat et al., in rev). Les dominants sont donc susceptibles de tirer des bénéfices intrinsèques à leur rang de dominance, comme un accès favorisé à la nourriture ou encore une probabilité plus grande d'être reproducteur.

Les individus dominants ont souvent un rôle particulier au sein du groupe social. Par exemple, chez les cichlidés (*Pulcher spp.*), il a été montré que les individus dominants exerçaient un rôle de renforcement social en punissant les individus peu coopératifs (Bruintjes & Taborsky, 2008). On peut donc imaginer que ces individus dominants occupent des positions centrales dans le réseau. Le nœud d'un dominant dans un réseau devrait ainsi avoir des métriques de centralité élevées. Cette tendance a été montrée chez des deux espèces de macaques (*Macaca mulatta* et *Macaca fuscata*) caractérisés par des groupes à forte hiérarchie (Sueur, Petit, et al., 2011). A l'inverse, chez d'autres espèces de macaques plus tolérantes (c'est-à-dire hiérarchie souple, selon de Vries, Stevens, & Vervaecke, 2006), les individus dominants plus agressifs restent à l'écart du cœur du groupe social (Sueur, Petit, et al., 2011), une caractéristique reflétée par des valeurs de centralité peu élevées. Peu d'études se sont concentrées sur les relations entre la dominance et la position dans le réseau social chez les oiseaux. Cet aspect a pourtant d'importantes implications pour comprendre le rôle de la dominance dans l'organisation sociale, dans la cohésion des groupes mais aussi dans le maintien de la coopération.

Enfin, superposer les réseaux basés sur les interactions agressives ou positives au réseau d'apparentement permet de tester la présence de népotisme. Le népotisme s'exprime par l'obtention de bénéfices pour un individu grâce au fait qu'il soit apparenté à des individus dominants (Barnaby & Griesser, 2010). Par exemple, chez la corneille noire (*Corvus corone*), les mâles reproducteurs dominants s'associent plus fréquemment avec leur progéniture aux stations de nourrissage qu'avec des immigrants, et agressent plus fréquemment et violemment ces derniers que leur progéniture (Chiarati, Canestrari, Vila, Vera, & Baglione, 2011). Dans de tels systèmes sociaux, la matrice d'interactions agonistiques se veut, par conséquent, corrélée négativement à la matrice d'apparentement (Madden, Nielsen, & Clutton-Brock, 2012). L'existence de népotisme chez des oiseaux sociaux dont le groupe social contient des apparentés a été mise en évidence par plusieurs travaux de recherche (Chiarati et al., 2011; Tóth et al., 2009). Pourtant l'utilisation appropriée de l'analyse des réseaux sociaux afin de tester la présence de népotisme chez les oiseaux reste rare dans la littérature. Cette utilisation permettrait de mieux comprendre le rôle de la dominance dans le fonctionnement social des structures familiales.

E. Influence de la personnalité sur le réseau

La personnalité, définie comme la persistance des différences comportementales interindividuelles dans différents contextes et au cours du temps (Capitanio, 1999; Groothuis & Carere, 2005; Sih, Bell, Johnson, & Ziemba, 2004), a été récemment décrite chez de nombreuses espèces animales, notamment les oiseaux (David, Auclair, & Cézilly, 2011; Bousquet et al., in prep; Dingemanse, Both, van Noordwijk, Rutten, & Drent, 2003; Guillette, Reddon, Hurd, & Sturdy, 2009; Herborn, Coffey, Larcombe, Alexander, & Arnold, 2011; Kurvers et al., 2009). Les traits de personnalité les plus souvent étudiés chez les oiseaux sont liés au niveau d'activité en situation routinière : la propension à explorer un environnement nouveau, ou encore la réaction à un objet nouveau ou à une perturbation. Ces traits sont habituellement évalués à partir d'une batterie de tests standards passée par un individu le plus souvent en isolation sociale (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013). Si les tests de personnalité sont généralement effectués en dehors du contexte social, il est toutefois probable que de telles caractéristiques individuelles aient une influence sur le fonctionnement d'un groupe social et donc sur les réseaux qui lui sont associés (Webster & Ward, 2011).

L'étude de la personnalité animale et l'analyse des réseaux sociaux constituent deux développements nouveaux de la biologie animale. L'interaction entre ces deux domaines n'en est donc encore qu'à son commencement (Webster & Ward, 2011). Néanmoins, il a déjà été montré chez la mésange charbonnière que des oiseaux explorateurs possèdent des positions plus centrales dans un réseau d'associations spatio-temporelles que des oiseaux prospectant moins (Aplin et al., 2013). En revanche, les individus ayant un haut niveau d'exploration tissent des connections sociales de plus faible intensité. Autrement dit, connaître la personnalité d'une mésange charbonnière permet d'anticiper sa centralité dans le réseau, ici son niveau de *betweeness*, dans le réseau d'associations spatio-temporelles (Aplin et al., 2013). Des individus plus explorateurs connecteront davantage les différents clusters du réseau. L'analyse de la temporalité de ce réseau révèle que les individus les plus explorateurs ont une moindre propension à se réassocier une fois le contact perdu, particulièrement si la dissociation concernait un partenaire lui-même explorateur (Aplin et al., 2013). La personnalité des individus peut donc avoir une influence directe sur les dynamiques de diffusion d'informations ou de parasites. Cependant, il n'est pas encore possible de prédire quel facteur (un nombre élevé de connections, caractéristique des individus explorateurs, ou une intensité forte des connections, caractéristique des individus peu explorateurs) joue le plus grand rôle (Aplin et al., 2013). A terme, la multiplication de travaux liant détermination de la personnalité des individus et l'analyse des réseaux sociaux devrait permettre d'affirmer si l’association préférentielle selon le type de personnalité est un phénomène actif ou passif de la part des individus impliqués (Webster & Ward, 2011).

F. Relations interspécifiques

Comme vu précédemment, les nœuds d’un réseau social ne sont pas tenus d’être d’une nature particulière. Ils ne sont notamment pas restreints par la barrière spécifique et peuvent parfaitement symboliser des individus d’espèces différentes. L’analyse des réseaux sociaux est donc un outil adapté pour l’étude des interactions interspécifiques, une aire de recherche peu abordée avant l’essor de cette technique (Greig-Smith, 1978; mais voir par exemple : Morse, 1970). Or, chez les oiseaux, les rassemblements multi-spécifiques sont fréquents et généralement de longue durée. Ils représentent ainsi une partie non négligeable de l’environnement social d’un individu. Entre autres, ces rassemblements permettent à un individu de s’associer à des membres d’une autre espèce afin d’augmenter son nombre de partenaires sociaux (notamment si l’individu est subordonné : Farine, Garroway, & Sheldon, 2012) ou de bénéficier d’informations supplémentaires, parfois inaccessibles aux individus de sa propre espèce (Martínez & Zenil, 2012).

Une des questions soulevée par l’existence de ces groupes multi-spécifiques est de savoir si des individus d’espèces différentes peuvent avoir des associations sociales non aléatoires. Pour répondre à cette question, une étude s’est récemment intéressée aux associations entre cinq espèces d’oiseaux (Farine et al., 2012) : la sittelle torchepot (*Sitta europaea*), la mésange charbonnière, la mésange bleue (*Cyanistes caeruleus*), la mésange nonnette (*Poecile palustris*) et la mésange noire (*Periparus ater*). Les auteurs ont construit un réseau social à partir des indices de présence simultanée à un site d’observation. Ils ont dans un premier temps considéré toutes les paires potentielles d’individus constituant le groupe multi-spécifique, sans se soucier de l’appartenance spécifique. Les résultats montrent que pour chaque espèce, les individus ayant les ailes les plus grandes (une caractéristique associée à un statut de dominant) sont les individus ayant le plus de liens homospécifiques. Parallèlement, les individus subordonnés (aux ailes plus petites) ont le plus de liens hétérospécifiques, confirmant l’importance des groupes multi-spécifiques pour ces individus. Un autre résultat pour le moins inattendu est que les liens hétérospécifiques sont généralement plus nombreux que les liens homospécifiques dans le réseau. Cette particularité a pour conséquence de limiter l’effet de la dominance sur la position d’un individu au sein du réseau global (Farine et al., 2012). On aurait en effet pu s’attendre à ce que les plus dominants soient les plus centraux, ce qui n’est pas le cas au vu de la richesse des liens hétérospécifiques.

D’autres travaux s’intéressent également à l’effet des relations hétérospécifiques sur la stratégie de choix des sites d’alimentation. Les acanthizes, oiseaux d’Australie, représentent de bons modèles d’étude à cet égard puisqu’ils appartiennent à un genre (*Acanthiza*) présentant en majorité un mode de reproduction communautaire. D’autre part, les territoires des individus de ces espèces proches se recouvrent fortement (Farine & Milburn, 2013). L’acanthize à croupion beige (*A. reguloides*), l’acanthize à croupion jaune (*A. chrysorrhoa*) et l’acanthize ridé (*A. lineata*) forment souvent des groupes multi-spécifiques (avec d’autres espèces mais moins pertinentes pour l’étude). La mixité de ces groupes est telle que la force des liens hétérospécifiques est seulement légèrement inférieure à celle des liens homospécifiques (Farine & Milburn, 2013). L’analyse détaillée de ces liens montre que les acanthizes à croupion beige changent de niche d’alimentation une fois associés avec l’une ou l’autre espèce. Plus précisément, ils descendent vers le sol pour s’associer avec l’acanthize à croupion jaune, alors qu’ils rejoignent l’acanthize ridé près de la canopée. De même, l’acanthize ridé descend de la canopée où il vit habituellement pour s’associer avec l’acanthize à croupion jaune (Farine & Milburn, 2013). En comparant la betweeness de tous les individus participant aux groupes multi-spécifiques, deux stratégies sociales peuvent être détectées en ce qui concerne les femelles acanthizes à croupion beige. La première consiste pour certaines femelles à changer fréquemment de groupe (la *betweeness* de ces femelles est donc élevée). Au contraire, d’autres femelles restent très fidèles au même sous-groupe, et ont de fait une *betweeness* plus faible. Même si l’âge des femelles n’a pu être établi avec certitude durant l’étude, certains indices semblent montrer que les femelles choisissant la première stratégie soient des juvéniles (Farine & Milburn, 2013).

L’analyse des groupes multi-spécifiques peut également se faire grâce à l’utilisation de réseaux dans lesquels les nœuds représentent les espèces et non plus les individus (Sridhar, Jordán, & Shanker, 2013). Cette représentation est utile quand le nombre d’espèces qui s’associent est élevé. Dans le sud-ouest de l’Inde, une étude a démontré que jusqu’à cinquante-deux espèces appartenant à des genres très différents peuvent interagir de façon plus ou moins pérenne (Sridhar et al., 2013). L’analyse des réseaux sociaux permet alors d’identifier les espèces les plus centrales dans ces associations interspécifiques. Ainsi, six espèces centrales ont pu être identifiées et sont identiques d’une année sur l’autre : le pouillot couronné (*Phylloscopus occipitalis*), l’alcippe à joues brunes (*Alcippe poioicephala*), le drongo à raquettes (*Dicrurus paradiseus*), le grand minivet (*Pericrocotus flammeus*), le tchitrec azuré (*Hypothymis azurea*) et le bulbul à sourcils noirs (*Iole indica*). Les auteurs suggèrent que ce cortège particulier favorise la coexistence d’espèces grégaires (souvent responsables des mouvements de groupe : Sridhar, Beauchamp, & Shanker, 2009), ici le pouillot couronné, l'alcippe à joues brunes et le grand minivet, avec des espèces émettant des alarmes face aux prédateurs (Goodale & Kotagama, 2005), ici le drongo à raquettes et le tchitrec azuré.

Si les interactions interspécifiques sont le résultat de la cohabitation (ou du voisinage) de plusieurs espèces sur une même aire de répartition, la modification de ces aires devrait alors avoir un impact important sur ces interactions. A l'heure du changement climatique, déterminer la réponse des populations animales est complexe, surtout lorsque les effets sur une espèce se répercutent sur d'autres. Les plus récents travaux sur le sujet ont utilisé l'analyse des réseaux pour modéliser les effets respectifs et/ou combinés des interactions entre espèces et du changement climatique sur les différentes aires de répartition de ces espèces au cours du prochain demi-siècle (Araújo, Rozenfeld, Rahbek, & Marquet, 2011). Dans cette approche, les nœuds correspondent à une espèce et les liens illustrent la fréquence de cooccurrence géographique entre chaque paire d'espèces. Ces liens sont confirmés par comparaison avec un réseau issu d'un modèle nul dans lequel les chevauchements entre les aires de répartition sont générés par un processus aléatoire. Les liens du réseau observé qui ne diffèrent pas de ces liens aléatoires sont éliminés avant de poursuivre l'analyse. Différentes mesures de la robustesse du réseau final peuvent être dégagées à partir de ces données. D'abord, il est possible de quantifier la contribution d'une espèce (autrement dit d'un nœud du réseau) à la robustesse du réseau global. L'approche la plus usuelle est le calcul du degré de chaque espèce : plus une espèce a un degré élevé, plus elle contribue à la robustesse du réseau. Une autre mesure plus fine est aussi utilisée : la force d'un nœud du réseau (Barrat, Barthélemy, Pastor-Satorras, & Vespignani, 2004). Dans le cas présent, la force entrante d'une espèce (autrement dit d'un nœud du réseau) est définie comme la somme pondérée de la proportion des distributions géographiques des autres espèces recoupant l'aire de répartition de l'espèce focale. En d'autres termes, une force entrante élevée signifie que les aires de répartition des espèces associées sont quasiment toutes englobées dans l'aire de répartition de l'espèce focale. A l'opposé, les zones de chevauchement d'une espèce focale à faible force entrante ne représentent qu'une faible proportion des aires de répartition de ses espèces associées (Araújo et al., 2011). Par ailleurs, l'analyse nécessite de suivre au moins un des scénarios d'évolution du climat, puisqu'il laisse présager de l'impact des effets climatiques sur les populations dans le futur. Pour son étude, l'équipe d'Araújo (2011) a retenu le scénario A1FI proposé par le Groupe d'experts Intergouvernemental sur l'Évolution du Climat (GIEC), l'un des scénarios dans lequel le climat est le plus impacté (Nakicenovic & Swart, 2000).

Avec un jeu de données incluant 233 espèces d'oiseaux, les auteurs ont pu montrer que les espèces les plus vulnérables au changement climatique (celles dont l'aire de répartition changera le plus) sont celles possédant une force entrante faible et/ou un degré faible. Ce type de résultat pourrait aider à la mise en place de politiques de conservation ciblées pour ces espèces. D'autant plus que le résultat reste assez général, puisqu'il est également valable pour les amphibiens, les reptiles et les mammifères (Araújo et al., 2011). Cependant, cette étude a confirmé que, pour la plupart des espèces, leur réaction au changement climatique n'est pas fortement influencée par la présence ou l'absence d'autres espèces. Ceci peut être en partie expliqué par le fait que la cooccurrence d'espèces sur une même aire de répartition ne signifie pas nécessairement interactions entre les espèces considérées (Araújo et al., 2011).

III. Fonctionnalité des réseaux chez les oiseaux

A. Influence du réseau sur les mouvements collectifs

L'influence sociale de certains individus sur les déplacements collectifs a été étudiée dans plusieurs taxons (les femelles dominantes ont par exemple un impact prépondérant sur la trajectoire du groupe chez les vaches en pâture : Šárová, Špinka, Panamá, & Šimeček, 2010). Toutefois, cet effet de l'individu est souvent limité par l'environnement physique dans lesquels les animaux évoluent (Perna & Latty, 2014). En effet, chez les oiseaux, à l´échelle locale ou continentale, les individus suivent souvent une trajectoire précise, déterminée par la géographie (par exemple : suivi des alignements d'arbres pour suivre le couvert végétal, autoroutes pour s'orienter, évitement de la Méditerranée pendant la migration…). Néanmoins, le vol leur permet tout de même de s'affranchir de la plupart des barrières physiques limitant le mouvement des animaux terrestres. Le déplacement collectif d'oiseaux apparait ainsi être un phénomène actif de la part des individus plutôt qu'une contrainte due à la géographie. Les influences sociales sur le mouvement global et individuel devraient donc avoir un effet marqué chez les oiseaux (Nagy, Ákos, Biro, & Vicsek, 2010).

Théoriquement, la position d'un individu au sein d'un réseau de préférence sociale influe grandement sur sa capacité à attirer les autres membres du groupe lors d'un déplacement (Bode, Franks, & Wood, 2012), même dans le cas où cet individu ne détient pas plus d'information que n'importe quel autre membre du groupe (Bode, Wood, & Franks, 2012). Grâce au développement de techniques de géolocalisation de plus en plus précises et légères, il est désormais possible d'enregistrer les trajectoires individuelles d'oiseaux appartenant à un même groupe (Dell'Ariccia, Dell'Omo, Wolfer, & Lipp, 2008; Nagy et al., 2010). Ainsi, des pigeons voyageurs (*Columba livia domestica*) ont pu être suivis au cours de plusieurs vols (Nagy et al., 2010). Les individus les plus influents quant aux directions de vol sont ceux dont la trajectoire est systématiquement suivie par d'autres individus après un délai d'environ 0,3 s en moyenne. Leurs mouvements sont ensuite modélisés par un réseau social dont les nœuds représentent les membres du groupe en déplacement et les liens expriment les délais de corrélation directionnelle entre deux individus. Les réseaux révélés pour chaque vol ont une structure similaire, indiquant la stabilité des relations d'influence entre les individus pour le choix des trajectoires en vol (Nagy et al., 2010). Cette stabilité est toujours présente, même après une augmentation de l'expérience de navigation personnelle de quelques individus. En effet, ces derniers ne changent pas pour autant leur position dans le réseau social une fois remis en groupe (Flack, Ákos, Nagy, Vicsek, & Biro, 2013).

Lors d'un déplacement collectif, les positions topologiques et/ou métriques entre les individus peuvent soudainement changer (Ballerini, Cabibbo, Candelier, Cavagna, Cisbani, Giardina, Lecomte, et al., 2008; Ballerini, Cabibbo, Candelier, Cavagna, Cisbani, Giardina, Orlandi, et al., 2008). Cela peut avoir une conséquence immédiate sur la perception visuelle et/ou auditive des individus entre eux. Certains oiseaux peuvent par exemple rapidement perdre ou gagner le contact visuel avec d'autres membres du groupe. Une perte de contact qui peut s'avérer dramatique dans certains cas, puisqu'elle peut s'accompagner d'une perte d'information, notamment pour localiser de la nourriture. Ainsi, les vautours du genre *Gyps* qui perdent le contact visuel avec leurs congénères ne trouvent plus aussi efficacement les carcasses d'animaux morts. Ce qui peut avoir un impact considérable sur la survie de ces espèces menacées (Jackson, Ruxton, & Houston, 2008). Idéalement, les études sur les influences sociales en vol devraient donc lier analyse des réseaux d'affinité et analyse des réseaux de perception interindividuelle afin d'appréhender dans leur ensemble les phénomènes de déplacements collectifs (Bode, Faria, Franks, Krause, & Wood, 2010). A l'inverse des réseaux d'affinité souvent stables dans le temps (Oh & Badyaev, 2010; Rutz et al., 2012), les réseaux de perception ont par nature une dynamique temporelle très élevée et doivent donc être analysés par des méthodes appropriées (Blonder, Wey, Dornhaus, James, & Sih, 2012; Pinter-Wollman et al., 2013). Toutefois, la position d'un individu dans son réseau social n'est pas le seul déterminant du leadership lors de mouvements collectifs. D'autres facteurs tels que l'information (Bousquet & Manser, 2011; Couzin, Krause, Franks, & Levin, 2005) ou la personnalité (Johnstone & Manica, 2011; Kurvers et al., 2009) sont aussi à prendre en compte dans les futures études de déplacements animaux (Bousquet et al., in prep).

B. Influence du réseau sur la transmission d'information et de parasites

Le degré de connexion d'un individu dans son réseau peut (entre autres choses) être déterminé par le compromis entre la facilité de transmission d'information utile et la transmission de parasites ou d'éléments contagieux (Danon et al., 2011; Guimarães et al., 2007; Hoppitt, Boogert, & Laland, 2010). Les associations interindividuelles sont définies par la proximité spatiale de deux individus (Hinde, 1976). Ainsi, les individus les plus associés sont les plus susceptibles de se transmettre des maladies. Plus le degré d'un individu va être fort, plus la probabilité d'être contaminé est augmentée. Mais d'autres mesures de réseaux peuvent également permettre d'évaluer cette probabilité. Par exemple, les mesures de centralité comme la *betweeness* déterminent les individus clés dans les phénomènes de contamination et de transmission de pathogènes. L'étude des phénomènes de contamination en lien avec la théorie des réseaux a donc très largement été étudiée (Bell, Atkinson, & Carlson, 1999; Keeling & Eames, 2005; Krause, Croft, & James, 2007). Il a notamment pu être démontré que les modes de transmission sont dépendants du type de réseau, de sa topologie, et de ses caractéristiques (Danon et al., 2011). Par exemple, un réseau très centralisé n'aura pas la même dynamique de transmission qu'un réseau fortement fragmenté. Ce champ d'étude à l'interface entre écologie des populations, études comportementales et épidémiologie se développe également chez les oiseaux (Gaidet et al., 2012). L'analyse des dynamiques de transmission de pathogènes est en effet extrêmement utile pour prévenir et contrôler les phénomènes infectieux touchant les élevages ou les populations sauvages, particulièrement celles en danger d'extinction. De plus, les populations aviaires peuvent constituer des réservoirs de pathogènes dangereux pour d'autres espèces comme l'homme (par exemple le virus H1N1). Le développement d'un outil efficace et précis pour surveiller et prévoir l'évolution de ces phénomènes infectieux est donc particulièrement intéressant.

Dans le cas de la transmission de pathogènes, il est peut être désavantageux d'être hautement connecté au réseau, mais cette position confère également des avantages, comme la richesse et la rapidité d'obtention d'informations. La transmission d'information est par ailleurs essentielle au fonctionnement de nombreux phénomènes collectifs comme les déplacements, le choix de sites alimentaires, la sélection des habitats ou encore le choix des partenaires sociaux (Cortés-Avizanda, Jovani, Donázar, & Grimm, 2014). En effet pour de nombreuses espèces d'oiseaux, les individus recherchent leur nourriture en utilisant l'information fournie par des congénères. Ainsi, au sein des colonies et dortoirs d'oiseaux, certains individus peuvent fournir de l'information et agir en tant que « recruteurs » vers des patchs de nourriture (Richner & Heeb, 1996). Des analyses de ces réseaux d’approvisionnement devraient permettre de déterminer si les individus qui agissent comme recruteurs ou « informateurs » conservent ce rôle, et s’il existe une relation entre le transfert d’information et certaines caractéristiques sociales des individus. Par exemple, chez le diamant mandarin sauvage, les individus qui nichent de façon solitaire trouvent les patches de nourriture plus rapidement que les individus coloniaux (Mariette & Griffith, 2013). Il est possible que les individus capables de trouver de la nourriture par eux-mêmes n’aient pas la nécessité de nicher en colonie, alors que ceux qui dépendent plus fortement des découvertes des « informateurs » préfèrent nicher en colonie pour accéder plus facilement à l’information publique (Mariette & Griffith, 2013). On peut effectivement s’attendre à ce qu’un individu occupant une position centrale dans un réseau bénéficie de plus grandes chances d’obtenir de l’information publique de la part des autres membres du réseau. Alternativement, les individus fournissant de l’information pourraient changer de façon aléatoire d’une interaction à l’autre (l’informateur d’un jour serait potentiellement le récepteur lors d’une interaction future), ce qui correspond à une situation favorisant l’évolution de la réciprocité au sein des groupes (Trivers, 1971). Les analyses en réseau pourraient permettre de différentier entre les deux hypothèses.

Une autre étude, menée sur un groupement grégaire multi-espèces de mésanges, montre ainsi que la probabilité pour un individu de découvrir une nouvelle ressource alimentaire est liée à son degré de connectivité dans le réseau d’association observé au site de fourragement (Aplin, Farine, Morand-Ferron, & Sheldon, 2012). Les auteurs ont ensuite mis en place deux nouveaux sites d’alimentation inconnus de la population afin d’étudier la diffusion de l’information entre le premier individu à découvrir la zone et le reste de la population. Si la découverte d’une nouvelle zone peut être effectuée par n’importe quel individu du réseau, la transmission de l’information va quant à elle suivre les connections propres à cet individu (caractéristiques sociale du nœud). Pour les deux sites, les résultats montrent que la centralité des individus est la caractéristique de réseau déterminante dans la transmission de l’information. Mais selon le site, le type de centralité diffère entre *betweeness* pour l’un et *eigenvector* pour l’autre. Une explication possible est que la topologie des sites permet des mouvements différents et donc des modes de connexions différents entre les individus (Aplin et al., 2012).

Si une information peut circuler par contact visuel et éventuellement physique, comme c’est le cas dans l’apprentissage social (Rahwan, Krasnoshtan, Shariff, & Bonnefon, 2014), elle peut aussi être véhiculée par contact sonore. Ce qui enrichit considérablement les modes de transmission et n’implique pas nécessairement que deux individus soit directement connectés, ou spatialement proches pour échanger des informations. De la même manière, selon le type de vecteur, une maladie peut se propager entre individus connectés par le réseau mais déconnectés spatialement. Ainsi, en rendant visibles des processus initialement imperceptibles, ainsi que les acteurs clés et le chemin parcouru par une information ou une maladie, la théorie des réseaux permet d'approfondir la compréhension des phénomènes épidémiques chez les populations aviaires, ou encore de l'utilisation de l'espace (zones d'alimentation ou de nidification) et des mouvements de populations (localisation de prédateurs, mouvements collectifs).

C. Dynamiques de fission-fusion

Nous avons vu que la plupart des structures sociales et des relations qui les composent sont dynamiques et qu'elles évoluent dans le temps. L'analyse des réseaux doit donc prendre en compte l'impact des saisons, des changements démographiques, ou encore des besoins physiologiques de chaque membre du groupe (Aureli et al., 2008; Henzi et al., 2009). Une bonne illustration de l'aspect dynamique des systèmes sociaux est le phénomène de fission-fusion. Les sociétés concernées par ce processus sont caractérisées par un éclatement temporaire du groupe en sous-groupes, phénomène généralement dû à des motivations individuelles différentes (McFarland Symington, 1990; van Schaik, 1999). Ce processus est le résultat de l'interaction entre la structure sociale, l'environnement écologique et les besoins individuels (Ramos-Fernández, Boyer, & Gómez, 2006). Il impacte à la fois l'individu et la population, puisqu'il modifie la topologie du réseau, qui influence elle-même les phénomènes de transmission (maladies, informations). A la vue de l'extrême mobilité des espèces aviaires et de leurs comportements migratoires, on peut s'attendre à ce que ce processus présente une grande diversité de forme chez les oiseaux. Mais comme pour la plupart des phénomènes sociaux, les dynamiques de fission-fusion n'ont que très peu été documentées chez les oiseaux jusqu'à ce jour (Silk, Croft, Tregenza, & Bearhop, 2014). Pourtant, l'analyse de ce processus chez différents taxons devrait permettre de mieux comprendre comment la structure du groupe et le poids des relations influence la manière dont le réseau se fractionne.

D. Application de la théorie des réseaux à l'étude des chants

Les réseaux représentent un outil idéal pour établir des relations entre entités, quelle que soit leur nature. Ainsi, une nouvelle utilisation des réseaux pour la compréhension de la biologie des oiseaux a récemment vu le jour et elle concerne l'étude des chants.

Lors de la période de reproduction, les oiseaux mâles de la plupart des espèces de Passereaux émettent des chants pour attirer les femelles et repousser les mâles (Catchpole & Slater, 2008). Ces chants peuvent être extrêmement élaborés et même être organisés selon une syntaxe particulière dont l'acquisition présente des similitudes avec celle du langage humain par les jeunes enfants (Lipkind et al., 2013). Chez certaines espèces, les mâles possèdent jusqu'à quelques dizaines de types de chant différents, parfois très dissemblables au niveau de leur structure (Hiebert, Stoddard, & Arcese, 1989; Sandoval, Méndez, & Mennill, 2014; Weiss, Hultsch, Adam, Scharff, & Kipper, 2014). La plupart des chants d'oiseaux peuvent être classés hiérarchiquement. L'unité de base est la note qui est définie comme tout élément individualisable émis par un individu. Plusieurs notes sont souvent combinées en syllabes, elles-mêmes arrangées en motifs. Plusieurs motifs rapidement associés dans le temps forment un type de chant (Berwick, Okanoya, Beckers, & Bolhuis, 2011). Dans la pratique, les types de chant présentant un grand nombre de similarités sont jugés identiques (Hultsch & Todt, 1981). Enfin, l'enchaînement de tous les types de chant constitue la séquence de chants d'un individu (Weiss et al., 2014).

Analyser ces chants à l'aide de l'analyse des réseaux autorise la détection de règles de transition entre types de chant. Les chercheurs travaillant sur ce sujet élaborent un réseau par séquence de chant. Chaque nœud du réseau représente un type de chant, et chaque lien représente les transitions entre tous les types de chant durant la séquence (Sasahara, Cody, Cohen, & Taylor, 2012; Weiss et al., 2014). Les liens du réseau peuvent être pondérés (pour déterminer la fréquence d'association entre deux types de chant) et/ou dirigés (caractérisant ainsi quel type de chant précède tel autre). Chez le moqueur de Californie (*Toxostoma redivivum* : Sasahara et al., 2012) comme chez le rossignol philomèle (*Luscinia megarhynchos* : Weiss et al., 2014), le rapport degré entrant/degré sortant de tous les types de chant permet de les classifier en quatre catégories dont deux sont particulièrement intéressantes : les « branches » et les « goulots d'étranglement ». Un chant de type « branche » possède un faible degré entrant et un degré sortant élevé. Les chants de ce type sont donc souvent situés en début de séquence. A l'inverse, un chant de type « goulot d'étranglement » se caractérise par un degré entrant élevé et un faible degré sortant. Ils sont donc souvent situés en fin de séquence. Les chercheurs ont ensuite testé la fonction de ces transitions en faisant écouter des chants artificiels précis à certains oiseaux (Weiss et al., 2014). Les rossignols philomèles semblent porter une attention particulière aux types de chant qu'ils entendent. Lorsqu'il s'agit d'un chant de type « branche », ils répondent préférentiellement par un chant de type « goulot d'étranglement », et vice versa. Cette influence réciproque entre types de chant d'oiseaux différents permettrait d'augmenter la capacité d'échange d'information (Weiss et al., 2014). Comme toujours avec l'analyse de réseaux, l'étude de ces chants d'oiseaux ne prend tout son sens que si elle compare les réseaux empiriques à des réseaux aléatoires adéquats (Sasahara et al., 2012; Weiss et al., 2014).

Conclusion

Au travers de ce chapitre, nous avons pu voir que les structures sociales existantes chez les oiseaux sont beaucoup plus variées que classiquement reconnu. Les études présentées démontrent la richesse des associations et des interactions sociales chez les oiseaux, y compris en dehors du couple et des relations aux jeunes. Au sein d'une même espèce, les différentes étapes menant à l'établissement d'un couple reproducteur, d'alliances entre mâles pour favoriser l'accès à la reproduction, ou encore d'une hiérarchie stable, ont ainsi été mises en évidence. De plus, il a pu être montré que les individus les plus fortement connectés aux autres membres de leur réseau occupent des rôles primordiaux dans les décisions collectives, les transferts d'informations ou de services. Par ailleurs, la compréhension de l'environnement social des espèces a largement été enrichie par les études de groupes multi-spécifiques.

L'analyse des réseaux offre quatre avantages majeurs pour améliorer la compréhension des sociétés aviaires. D'une part, elle fournit un accès inédit aux relations indirectes, en permettant d'analyser les influences respectives d'individus séparés les uns des autres par plus d'un nœud. D'autre part, l'approche en réseau autorise une analyse temporelle, donc dynamique, des relations entre agents, une perspective de recherche qui enrichit plus encore la compréhension de ces systèmes. En effet, elle permet de concevoir comment différents comportements sociaux rétroagissent sur le devenir du réseau. Troisièmement, l'usage de métriques communes quelle que soit la structure sociale promettent des avancées considérables pour les études comparatives sur l'évolution de la socialité. Finalement, la souplesse d'utilisation des réseaux permet de concevoir de nouveaux champs d'application, comme par exemple l'étude des chants et leurs conséquences sur la communication sociale.

Ainsi, si l'étude des systèmes aviaires au moyen de l’analyse des réseaux n’en est qu’à ses débuts, elle a déjà prouvé son utilité en apportant une nouvelle approche et des éléments de réponse originaux à des problématiques anciennes (choix du partenaire, coopération…) mais aussi à des problématiques nouvelles (personnalité animale…). Cependant, afin de mieux faire le lien entre la biologie d’un organisme et ses conséquences sur le fonctionnement social du groupe (intra ou interspécifique) ou de la population auquel il appartient, il est nécessaire de développer des études transversales, entre structure sociale, physiologie (du stress notamment), cognition et valeur sélective. Pour les espèces les plus complexes socialement, l’analyse des réseaux devrait apporter de nouvelles réponses sur les stratégies sociales mises en place par les individus pour pallier aux effets de la compétition et des modifications environnementales. Enfin, à un niveau plus global, son application devrait améliorer la compréhension de l’agencement des espèces au sein des habitats et de leur dynamique face à un environnement en perpétuel changement.

Bibliographie

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A., & Sheldon, B. C. (2013). Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). *Ecology Letters*, *16*(11), 1365–1372. doi:10.1111/ele.12181

Aplin, L. M., Farine, D. R., Morand-Ferron, J., & Sheldon, B. C. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings of the Royal Society of London B*, *279*(1745), 4199–4205. doi:10.1098/rspb.2012.1591

Araújo, M. B., Rozenfeld, A., Rahbek, C., & Marquet, P. A. (2011). Using species co-occurrence networks to assess the impacts of climate change. *Ecography*, *34*(6), 897–908. doi:10.1111/j.1600-0587.2011.06919.x

Arnold, K. E. (2000). Group mobbing behaviour and nest defence in a cooperatively breeding Australian bird. *Ethology*, *106*(5), 385–393. doi:10.1046/j.1439-0310.2000.00545.x

Arnold, K. E., & Owens, I. P. F. (1998). Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proceedings of the Royal Society of London B*, *265*(1398), 739–745. doi:10.1098/rspb.1998.0355

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., … van Schaik, C. P. (2008). Fission-fusion dynamics: new research frameworks. *Current Anthropology*, *49*(4), 627–654. doi:10.1086/586708

Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., … Zdravkovic, V. (2008). Empirical investigation of starling flocks: a benchmark study in collective animal behaviour. *Animal Behaviour*, *76*(1), 201–215. doi:10.1016/j.anbehav.2008.02.004

Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., … Zdravkovic, V. (2008). Interaction ruling animal collective behavior depends on topological rather than metric distance: evidence from a field study. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(4), 1232–1237. doi:10.1073/pnas.0711437105

Barnaby, J., & Griesser, M. (2010). *The role of nepotism, cooperation, and competition in the avian families*. New York, NY: Nova Science Publishers.

Barrat, A., Barthélemy, M., Pastor-Satorras, R., & Vespignani, A. (2004). The architecture of complex weighted networks. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(11), 3747–3752. doi:10.1073/pnas.0400087101

Beauchamp, G., & Heeb, P. (2001). Social foraging and the evolution of white plumage. *Evolutionary Ecology Research*, *3*(6), 703–720.

Bell, D. C., Atkinson, J. S., & Carlson, J. W. (1999). Centrality measures for disease transmission networks. *Social Networks*, *21*(1), 1–21. doi:10.1016/S0378-8733(98)00010-0

Berwick, R. C., Okanoya, K., Beckers, G. J. L., & Bolhuis, J. J. (2011). Songs to syntax: the linguistics of birdsong. *Trends in Cognitive Sciences*, *15*(3), 113–121. doi:10.1016/j.tics.2011.01.002

Black, J. M. (Ed.). (1996). *Partnerships in birds - The study of monogamy*. Oxford University Press.

Blonder, B., Wey, T. W., Dornhaus, A., James, R., & Sih, A. (2012). Temporal dynamics and network analysis. *Methods in Ecology and Evolution*, *3*(6), 958–972. doi:10.1111/j.2041-210X.2012.00236.x

Bluff, L. A., Weir, A. A. S., Rutz, C., Wimpenny, J. H., & Kacelnik, A. (2007). Tool-related cognition in New Caledonian crows. *Comparative Cognition & Behavior Reviews*, *2*, 1–25. doi:10.3819/ccbr.2008.20001

Bode, N. W. F., Faria, J. J., Franks, D. W., Krause, J., & Wood, A. J. (2010). How perceived threat increases synchronization in collectively moving animal groups. *Proceedings of the Royal Society of London B*, *277*(1697), 3065–3070. doi:10.1098/rspb.2010.0855

Bode, N. W. F., Franks, D. W., & Wood, A. J. (2012). Leading from the front? Social networks in navigating groups. *Behavioral Ecology and Sociobiology*, *66*(6), 835–843. doi:10.1007/s00265-012-1331-6

Bode, N. W. F., Wood, A. J., & Franks, D. W. (2012). Social networks improve leaderless group navigation by facilitating long-distance communication. *Current Zoology*, *58*(2), 329–341.

Bond, A. B., Kamil, A. C., & Balda, R. P. (2003). Social complexity and transitive inference in corvids. *Animal Behaviour*, *65*(3), 479–487. doi:10.1006/anbe.2003.2101

Bousquet, C. A. H., & Manser, M. B. (2011). Resolution of experimentally induced symmetrical conflicts of interest in meerkats. *Animal Behaviour*, *81*(6), 1101–1107. doi:10.1016/j.anbehav.2011.02.030

Brosset, A. (1978). Social organization and nest-building in the forest weaver birds of the genus *Malimbus* (Ploceinae). *Ibis*, *120*(1), 27–37. doi:10.1111/j.1474-919X.1978.tb04996.x

Brown, C. R., Stutchbury, B. J., & Walsh, P. D. (1990). Choice of colony size in birds. *Trends in Ecology & Evolution*, *5*(12), 398–403. doi:10.1016/0169-5347(90)90023-7

Bruintjes, R., & Taborsky, M. (2008). Helpers in a cooperative breeder pay a high price to stay: effects of demand, helper size and sex. *Animal Behaviour*, *75*(6), 1843–1850. doi:10.1016/j.anbehav.2007.12.004

Capitanio, J. P. (1999). Personality dimensions in adult male rhesus macaques: prediction of behaviors across time and situation. *American Journal of Primatology*, *47*(4), 299–320. doi:10.1002/(SICI)1098-2345(1999)47:4<299::AID-AJP3>3.0.CO;2-P

Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G., & Heinsohn, R. (2013). Animal personality: what are behavioural ecologists measuring? *Biological Reviews*, *88*(2), 465–475. doi:10.1111/brv.12007

Catchpole, C. K., & Slater, P. J. B. (2008). *Bird song: biological themes and variations* (Second edition.). Cambridge University Press.

Chiarati, E., Canestrari, D., Vera, R., Marcos, J. M., & Baglione, V. (2010). Linear and stable dominance hierarchies in cooperative carrion crows. *Ethology*, *116*(4), 346–356. doi:10.1111/j.1439-0310.2010.01741.x

Chiarati, E., Canestrari, D., Vila, M., Vera, R., & Baglione, V. (2011). Nepotistic access to food resources in cooperatively breeding carrion crows. *Behavioral Ecology and Sociobiology*, *65*(9), 1791–1800. doi:10.1007/s00265-011-1187-1

Clayton, N. S., & Emery, N. J. (2007). The social life of corvids. *Current Biology*, *17*(16), R652–R656. doi:10.1016/j.cub.2007.05.070

Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton University Press.

Cockburn, A. (1998). Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics*, *29*, 141–177.

Cockburn, A. (2006). Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society of London B*, *273*(1592), 1375–1383. doi:10.1098/rspb.2005.3458

Conklin, J. R., & Colwell, M. A. (2007). Diurnal and nocturnal roost site fidelity of Dunlin (*Calidris alpina pacifica*) at Humbold Bay, California. *The Auk*, *124*(2), 677–689. doi:10.1642/0004-8038(2007)124[677:DANRSF]2.0.CO;2

Conklin, J. R., & Colwell, M. A. (2008). Individual associations in a wintering shorebird population: do Dunlin have friends? *Journal of Field Ornithology*, *79*(1), 32–40. doi:10.1111/j.1557-9263.2008.00143.x

Connor, R. C., Heithaus, M. R., & Barre, L. M. (2001). Complex social structure, alliance stability and mating access in a bottlenose dolphin “super-alliance.” *Proceedings of the Royal Society of London B*, *268*(1464), 263–267. doi:10.1098/rspb.2000.1357

Cortés-Avizanda, A., Jovani, R., Donázar, J. A., & Grimm, V. (2014). Bird sky networks: how do avian scavengers use social information to find carrion? *Ecology*, *95*(7), 1799–1808. doi:10.1890/13-0574.1

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature*, *433*, 513–516. doi:10.1038/nature03236

Danchin, É., & Wagner, R. H. (1997). The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology & Evolution*, *12*(9), 342–347. doi:10.1016/S0169-5347(97)01124-5

Danon, L., Ford, A. P., House, T., Jewell, C. P., Keeling, M. J., Roberts, G. O., … Vernon, M. C. (2011). Networks and the epidemiology of infectious disease. *Interdisciplinary Perspectives on Infectious Diseases*, *2011*, 284909. doi:10.1155/2011/284909

David, M., Auclair, Y., & Cézilly, F. (2011). Personality predicts social dominance in female zebra finches, *Taeniopygia guttata*, in a feeding context. *Animal Behaviour*, *81*(1), 219–224. doi:10.1016/j.anbehav.2010.10.008

Dell’Ariccia, G., Dell’Omo, G., Wolfer, D. P., & Lipp, H.-P. (2008). Flock flying improves pigeons’ homing: GPS track analysis of individual flyers versus small groups. *Animal Behaviour*, *76*(4), 1165–1172. doi:10.1016/j.anbehav.2008.05.022

De Vries, H. (1995). An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour*, *50*(5), 1375–1389. doi:10.1016/0003-3472(95)80053-0

De Vries, H., Stevens, J. M. G., & Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour*, *71*(3), 585–592. doi:10.1016/j.anbehav.2005.05.015

Dey, C. J., Reddon, A. R., O’Connor, C. M., & Balshine, S. (2013). Network structure is related to social conflict in a cooperatively breeding fish. *Animal Behaviour*, *85*(2), 395–402. doi:10.1016/j.anbehav.2012.11.012

Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L., & Drent, P. J. (2003). Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society of London B*, *270*(1516), 741–747. doi:10.1098/rspb.2002.2300

Doutrelant, C., & Covas, R. (2007). Helping has signalling characteristics in a cooperatively breeding bird. *Animal Behaviour*, *74*(4), 739–747. doi:10.1016/j.anbehav.2006.11.033

Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the social brain. *Science, 317*(5843), 1344–1347. doi:10.1126/science.1145463

DuVal, E. H. (2007a). Adaptive advantages of cooperative courtship for subordinate male lance-tailed manakins. *The American Naturalist, 169*(4), 423–432. doi:10.1086/512137

DuVal, E. H. (2007b). Social organization and variation in cooperative alliances among male lance-tailed manakins. *Animal Behaviour*, *73*(3), 391–401. doi:10.1016/j.anbehav.2006.05.017

Ekman, J. (2006). Family living among birds. *Journal of Avian Biology*, *37*(4), 289–298. doi:10.1111/j.2006.0908-8857.03666.x

Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, *306*(5703), 1903–1907. doi:10.1126/science.1098410

Emery, N. J., & Clayton, N. S. (2009). Comparative social cognition. *Annual Review of Psychology*, *60*, 87–113. doi:10.1146/annurev.psych.60.110707.163526

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: Biological Sciences*, *362*(1480), 489–505. doi:10.1098/rstb.2006.1991

Farine, D. R., Garroway, C. J., & Sheldon, B. C. (2012). Social network analysis of mixed-species flocks: exploring the structure and evolution of interspecific social behaviour. *Animal Behaviour*, *84*(5), 1271–1277. doi:10.1016/j.anbehav.2012.08.008

Farine, D. R., & Milburn, P. J. (2013). Social organisation of thornbill-dominated mixed-species flocks using social network analysis. *Behavioral Ecology and Sociobiology*, *67*(2), 321–330. doi:10.1007/s00265-012-1452-y

Faust, K., & Skvoretz, J. (2002). Comparing networks across space and time, size and species. *Sociological Methodology*, *32*(1), 267–299. doi:10.1111/1467-9531.00118

Flack, A., Ákos, Z., Nagy, M., Vicsek, T., & Biro, D. (2013). Robustness of flight leadership relations in pigeons. *Animal Behaviour*, *86*(4), 723–732. doi:10.1016/j.anbehav.2013.07.005

Fraser, O. N., & Bugnyar, T. (2010). The quality of social relationships in ravens. *Animal Behaviour*, *79*(4), 927–933. doi:10.1016/j.anbehav.2010.01.008

Fraser, O. N., & Bugnyar, T. (2011). Ravens reconcile after aggressive conflicts with valuable partners. *PLoS ONE*, *6*(3), e18118. doi:10.1371/journal.pone.0018118

Furness, R. W., & Galbraith, H. (1980). Non-random distribution in roosting flocks of waders marked in a cannon net catch. *Wader Study Group Bulletin*, *29*, 22–23.

Gaidet, N., Caron, A., Cappelle, J., Cumming, G. S., Balança, G., Hammoumi, S., … Dodman, T. (2012). Understanding the ecological drivers of avian influenza virus infection in wildfowl: a continental-scale study across Africa. *Proceedings of the Royal Society of London B*, *279*(1731), 1131–1141. doi:10.1098/rspb.2011.1417

Godard, R. (1991). Long-term memory of individual neighbours in a migratory songbird. *Nature*, *350*, 228–229. doi:10.1038/350228a0

Goodale, E., & Kotagama, S. W. (2005). Testing the roles of species in mixed-species bird flocks of a Sri Lankan rain forest. *Journal of Tropical Ecology*, *21*(6), 669–676. doi:10.1017/S0266467405002609

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, *28*(4), 1140–1162. doi:10.1016/S0003-3472(80)80103-5

Greig-Smith, P. W. (1978). The formation, structure and function of mixed-species insectivorous bird flocks in West African savanna woodland. *Ibis*, *120*(3), 284–297. doi:10.1111/j.1474-919X.1978.tb06789.x

Greiner, B., & Levati, M. V. (2005). Indirect reciprocity in cyclical networks: an experimental study. *Journal of Economic Psychology*, *26*(5), 711–731. doi:10.1016/j.joep.2004.04.003

Griffith, S. C., Owens, I. P. F., & Thuman, K. A. (2002). Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology*, *11*(11), 2195–2212. doi:10.1046/j.1365-294X.2002.01613.x

Groothuis, T. G. G., & Carere, C. (2005). Avian personalities: characterization and epigenesis. *Neuroscience and Biobehavioral Reviews*, *29*(1), 137–150. doi:10.1016/j.neubiorev.2004.06.010

Guillette, L. M., Reddon, A. R., Hurd, P. L., & Sturdy, C. B. (2009). Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, *Poecile atricapillus*. *Behavioural Processes*, *82*(3), 265–270. doi:10.1016/j.beproc.2009.07.005

Guimarães, P. R. J., Argollo de Menezes, M., Baird, R. W., Lusseau, D., Guimarães, P., & dos Reis, S. F. (2007). Vulnerability of a killer whale social network to disease outbreaks. *Physical Review E*, *76*, 042901. doi:10.1103/PhysRevE.76.042901

Hall, M. L., & Peters, A. (2008). Coordination between the sexes for territorial defence in a duetting fairy-wren. *Animal Behaviour*, *76*(1), 65–73. doi:10.1016/j.anbehav.2008.01.010

Hamilton, W. D. (1964a). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, *7*(1), 1–16. doi:10.1016/0022-5193(64)90038-4

Hamilton, W. D. (1964b). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, *7*(1), 17–52. doi:10.1016/0022-5193(64)90039-6

Harrington, B. A., & Leddy, L. E. (1982). Are wader flocks random groupings? - a knotty problem. *Wader Study Group Bulletin*, *36*, 20–21.

Henzi, S. P., Lusseau, D., Weingrill, T., van Schaik, C. P., & Barrett, L. (2009). Cyclicity in the structure of female baboon social networks. *Behavioral Ecology and Sociobiology*, *63*(7), 1015–1021. doi:10.1007/s00265-009-0720-y

Herborn, K. A., Coffey, J., Larcombe, S. D., Alexander, L., & Arnold, K. E. (2011). Oxidative profile varies with personality in European greenfinches. *The Journal of Experimental Biology*, *214*, 1732–1739. doi:10.1242/jeb.051383

Hiebert, S. M., Stoddard, P. K., & Arcese, P. (1989). Repertoire size, territory acquisition and reproductive success in the song sparrow. *Animal Behaviour*, *37*(2), 266–273. doi:10.1016/0003-3472(89)90115-2

Hill, G. E. (1990). Female house finches prefer colourful males: sexual selection for a condition-dependent trait. *Animal Behaviour*, *40*(3), 563–572. doi:10.1016/S0003-3472(05)80537-8

Hinde, R. A. (1976). Interactions, relationships and social structure. *Man*, *11*(1), 1–17.

Holzhaider, J. C., Sibley, M. D., Taylor, A. H., Singh, P. J., Gray, R. D., & Hunt, G. R. (2011). The social structure of New Caledonian crows. *Animal Behaviour*, *81*(1), 83–92. doi:10.1016/j.anbehav.2010.09.015

Hoogland, J. L., & Sherman, P. W. (1976). Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecological Monographs*, *46*(1), 33–58.

Hoppitt, W., Boogert, N. J., & Laland, K. N. (2010). Detecting social transmission in networks. *Journal of Theoretical Biology*, *263*(4), 544–555. doi:10.1016/j.jtbi.2010.01.004

Hultsch, H., & Todt, D. (1981). Repertoire sharing and song-post distance in nightingales (*Luscinia megarhynchos* B.). *Behavioral Ecology and Sociobiology*, *8*(3), 183–188. doi:10.1007/BF00299828

Jackson, A. L., Ruxton, G. D., & Houston, D. C. (2008). The effect of social facilitation on foraging success in vultures: a modelling study. *Biology Letters*, *4*(3), 311–313. doi:10.1098/rsbl.2008.0038

Jeschke, J. M., & Kokko, H. (2008). Mortality and other determinants of bird divorce rate. *Behavioral Ecology and Sociobiology*, *63*(1), 1–9. doi:10.1007/s00265-008-0646-9

Johnstone, R. A., & Hinde, C. A. (2006). Negotiation over offspring care—how should parents respond to each other's efforts? *Behavioral Ecology*, *17*(5), 818–827. doi:10.1093/beheco/arl009

Johnstone, R. A., & Manica, A. (2011). Evolution of personality differences in leadership. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(20), 8373–8378. doi:10.1073/pnas.1102191108

Keeling, M. J., & Eames, K. T. D. (2005). Networks and epidemic models. *Journal of the Royal Society Interface*, *2*(4), 295–307. doi:10.1098/rsif.2005.0051

Kirkpatrick, M., & Ryan, M. J. (1991). The evolution of mating preferences and the paradox of the lek. *Nature*, *350*, 33–38. doi:10.1038/350033a0

Krams, I., Krama, T., & Igaune, K. (2006). Alarm calls of wintering great tits *Parus major*: warning of mate, reciprocal altruism or a message to the predator? *Journal of Avian Biology*, *37*(2), 131–136. doi:10.1111/j.0908-8857.2006.03632.x

Krause, J., Croft, D. P., & James, R. (2007). Social network theory in the behavioural sciences: potential applications. *Behavioral Ecology and Sociobiology*, *62*(1), 15–27. doi:10.1007/s00265-007-0445-8

Krause, J., & Ruxton, G. D. (2002). *Living in groups*. (P. H. Harvey, Ed.). New York: Oxford University Press.

Kurvers, R. H. J. M., Adamczyk, V. M. A. P., Kraus, R. H. S., Hoffman, J. I., van Wieren, S. E., van der Jeugd, H. P., … Jonker, R. M. (2013). Contrasting context dependence of familiarity and kinship in animal social networks. *Animal Behaviour*, *86*(5), 993–1001. doi:10.1016/j.anbehav.2013.09.001

Kurvers, R. H. J. M., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S. E., Ydenberg, R. C., & Prins, H. H. T. (2009). Personality differences explain leadership in barnacle geese. *Animal Behaviour*, *78*(2), 447–453. doi:10.1016/j.anbehav.2009.06.002

Landau, H. G. (1951a). On dominance relations and the structure of animal societies: I. Effect of inherent characteristics. *The Bulletin of Mathematical Biophysics*, *13*(1), 1–19. doi:10.1007/BF02478336

Landau, H. G. (1951b). On dominance relations and the structure of animal societies: II. Some effects of possible social factors. *The Bulletin of Mathematical Biophysics*, *13*(4), 245–262. doi:10.1007/BF02477920

Le Bohec, C., Gauthier-Clerc, M., & Le Maho, Y. (2005). The adaptive significance of crèches in the king penguin. *Animal Behaviour*, *70*(3), 527–538. doi:10.1016/j.anbehav.2004.11.012

Leyrer, J., Spaans, B., Camara, M., & Piersma, T. (2006). Small home ranges and high site fidelity in red knots (*Calidris c. canutus*) wintering on the Banc d’Arguin, Mauritania. *Journal of Ornithology*, *147*(2), 376–384. doi:10.1007/s10336-005-0030-8

Liker, A., Freckleton, R. P., & Székely, T. (2014). Divorce and infidelity are associated with skewed adult sex ratios in birds. *Current Biology*, *24*(8), 880–884. doi:10.1016/j.cub.2014.02.059

Lipkind, D., Marcus, G. F., Bemis, D. K., Sasahara, K., Jacoby, N., Takahasi, M., … Tchernichovski, O. (2013). Stepwise acquisition of vocal combinatorial capacity in songbirds and human infants. *Nature*, *498*, 104–108. doi:10.1038/nature12173

Lusseau, D. (2007). Evidence for social role in a dolphin social network. *Evolutionary Ecology*, *21*(3), 357–366. doi:10.1007/s10682-006-9105-0

Maclean, G. L. (1973). The sociable weaver, part 2: nest architecture and social organization. *Ostrich: Journal of African Ornithology*, *44*(3-4), 191–218. doi:10.1080/00306525.1973.9639159

Madden, J. R., Drewe, J. A., Pearce, G. P., & Clutton-Brock, T. H. (2009). The social network structure of a wild meerkat population: 2. Intragroup interactions. *Behavioral Ecology and Sociobiology*, *64*(1), 81–95. doi:10.1007/s00265-009-0820-8

Madden, J. R., Nielsen, J. F., & Clutton-Brock, T. H. (2012). Do networks of social interactions reflect patterns of kinship? *Current Zoology*, *58*(2), 319–328.

Mann, J. (Ed.). (2000). *Cetacean societies: field studies of dolphins and whales*. University of Chicago Press.

Mariette, M. M., & Griffith, S. C. (in press). The adaptive significance of provisioning and foraging coordination between breeding partners. *The American Naturalist*.

Mariette, M. M., & Griffith, S. C. (2012). Nest visit synchrony is high and correlates with reproductive success in the wild zebra finch *Taeniopygia guttata*. *Journal of Avian Biology*, *43*(2), 131–140. doi:10.1111/j.1600-048X.2012.05555.x

Mariette, M. M., & Griffith, S. C. (2013). Does coloniality improve foraging efficiency and nestling provisioning? A field experiment in the wild zebra finch. *Ecology*, *94*(2), 325–335. doi:10.1890/12-0572.1

Martínez, A. E., & Zenil, R. T. (2012). Foraging guild influences dependence on heterospecific alarm calls in Amazonian bird flocks. *Behavioral Ecology*, *23*(3), 544–550. doi:10.1093/beheco/arr222

Matysioková, B., & Remeš, V. (2013). Faithful females receive more help: the extent of male parental care during incubation in relation to extra-pair paternity in songbirds. *Journal of Evolutionary Biology*, *26*(1), 155–162. doi:10.1111/jeb.12039

Maynard Smith, J. (1977). Parental investment: a prospective analysis. *Animal Behaviour*, *25*(1), 1–9. doi:10.1016/0003-3472(77)90062-8

McComb, K., Moss, C., Durant, S. M., Baker, L., & Sayialel, S. (2001). Matriarchs as repositories of social knowledge in African elephants. *Science*, *292*(5516), 491–494. doi:10.1126/science.1057895

McDonald, D. B. (2007). Predicting fate from early connectivity in a social network. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(26), 10910–10914. doi:10.1073/pnas.0701159104

McFarland Symington, M. (1990). Fission-fusion social organization in *Ateles* and *Pan*. *International Journal of Primatology*, *11*(1), 47–61. doi:10.1007/BF02193695

McGregor, P. K. (1993). Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *340*(1292), 237–244. doi:10.1098/rstb.1993.0063

McNamara, J. M., Gasson, C. E., & Houston, A. I. (1999). Incorporating rules for responding into evolutionary games. *Nature*, *401*, 368–371. doi:10.1038/43869

Mock, D. W., & Fujioka, M. (1990). Monogamy and long-term pair bonding in vertebrates. *Trends in Ecology & Evolution*, *5*(2), 39–43. doi:10.1016/0169-5347(90)90045-F

Morse, D. H. (1970). Ecological aspects of some mixed-species foraging flocks of birds. *Ecological Monographs*, *40*(1), 119–168.

Myers, J. P. (1983). Space, time and the pattern of individual associations in a group-living species: Sanderlings have no friends. *Behavioral Ecology and Sociobiology*, *12*(2), 129–134. doi:10.1007/BF00343203

Nagy, M., Ákos, Z., Biro, D., & Vicsek, T. (2010). Hierarchical group dynamics in pigeon flocks. *Nature*, *464*, 890–893. doi:10.1038/nature08891

Nakicenovic, N., & Swart, R. (Eds.). (2000). *Emissions scenarios: a special report of working group III of the Intergovernmental Panel on Climate Change*. Cambridge University Press.

Nowak, M. A., & Sigmund, K. (2005). Evolution of indirect reciprocity. *Nature*, *437*, 1291–1298. doi:10.1038/nature04131

Oh, K. P., & Badyaev, A. V. (2010). Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. *The American Naturalist*, *176*(3), E80–E89. doi:10.1086/655216

Ohtsuki, H., Hauert, C., Lieberman, E., & Nowak, M. A. (2006). A simple rule for the evolution of cooperation on graphs and social networks. *Nature*, *441*, 502–505. doi:10.1038/nature04605

Perna, A., & Latty, T. (2014). Animal transportation networks. *Journal of the Royal Society Interface*, *11*(100), 20140334. doi:10.1098/rsif.2014.0334

Pinter-Wollman, N., Hobson, E. A., Smith, J. E., Edelman, A. J., Shizuka, D., de Silva, S., … McDonald, D. B. (2013). The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behavioral Ecology*, *25*(2), 242–255. doi:10.1093/beheco/art047

Preuschoft, S., & van Schaik, C. P. (2000). Dominance and communication: conflict management in various social settings. In F. Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution*. University of California Press.

Psorakis, I., Roberts, S. J., Rezek, I., & Sheldon, B. C. (2012). Inferring social network structure in ecological systems from spatio-temporal data streams. *Journal of the Royal Society Interface*, *9*(76), 3055–3066. doi:10.1098/rsif.2012.0223

Rahwan, I., Krasnoshtan, D., Shariff, A., & Bonnefon, J.-F. (2014). Analytical reasoning task reveals limits of social learning in networks. *Journal of the Royal Society Interface*, *11*(93), 20131211. doi:10.1098/rsif.2013.1211

Ramos-Fernández, G., Boyer, D., & Gómez, V. P. (2006). A complex social structure with fission-fusion properties can emerge from a simple foraging model. *Behavioral Ecology and Sociobiology*, *60*(4), 536–549. doi:10.1007/s00265-006-0197-x

Rat, M., Covas, R., van Dijk, R. E., & Doutrelant, C. (in rev). Dominance hierarchies and associated signalling in a cooperative passerine. *Behavioral Ecology and Sociobiology*.

Richner, H., & Heeb, P. (1996). Communal life: honest signalling and the recruitment center hypothesis. *Behavioral Ecology*, *7*(1), 115–118. doi:10.1093/beheco/7.1.115

Ridley, A. R., Nelson-Flower, M. J., & Thompson, A. M. (2013). Is sentinel behaviour safe? An experimental investigation. *Animal Behaviour*, *85*(1), 137–142. doi:10.1016/j.anbehav.2012.10.017

Riehl, C. (2013). Evolutionary routes to non-kin cooperative breeding in birds. *Proceedings of the Royal Society of London B*, *280*(1772), 20132245. doi:10.1098/rspb.2013.2245

Roberts, G. (2005). Cooperation through interdependence. *Animal Behaviour*, *70*(4), 901–908. doi:10.1016/j.anbehav.2005.02.006

Roberts, G., & Evans, P. R. (1993). A method for the detection of non-random associations among flocking birds and its application to sanderlings *Calidris alba* wintering in N.E. England. *Behavioral Ecology and Sociobiology*, *32*(5), 349–354. doi:10.1007/BF00183791

Rolland, C., Danchin, É., & de Fraipont, M. (1998). The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. *The American Naturalist*, *151*(6), 514–529. doi:10.1086/286137

Rowell, T. E. (1974). The concept of social dominance. *Behavioral Biology*, *11*(2), 131–154. doi:10.1016/S0091-6773(74)90289-2

Royle, N. J., Pike, T. W., Heeb, P., Richner, H., & Kölliker, M. (2012). Offspring social network structure predicts fitness in families. *Proceedings of the Royal Society of London B*, *279*(1749), 4914–4922. doi:10.1098/rspb.2012.1701

Rutz, C., Burns, Z. T., James, R., Ismar, S. M. H., Burt, J., Otis, B., … St Clair, J. J. H. (2012). Automated mapping of social networks in wild birds. *Current Biology*, *22*(17), R669–R671. doi:10.1016/j.cub.2012.06.037

Ryder, T. B., Blake, J. G., Parker, P. G., & Loiselle, B. A. (2011). The composition, stability, and kinship of reproductive coalitions in a lekking bird. *Behavioral Ecology*, *22*(2), 282–290. doi:10.1093/beheco/arq213

Ryder, T. B., McDonald, D. B., Blake, J. G., Parker, P. G., & Loiselle, B. A. (2008). Social networks in the lek-mating wire-tailed manakin (*Pipra filicauda*). *Proceedings of the Royal Society of London B*, *275*(1641), 1367–1374. doi:10.1098/rspb.2008.0205

Sánchez-Macouzet, O., Rodríguez, C., & Drummond, H. (2014). Better stay together: pair bond duration increases individual fitness independent of age-related variation. *Proceedings of the Royal Society of London B*, *281*(1786), 20132843. doi:10.1098/rspb.2013.2843

Sandoval, L., Méndez, C., & Mennill, D. J. (2014). Individual distinctiveness in the fine structural features and repertoire characteristics of the songs of white-eared ground-sparrows. *Ethology*, *120*(3), 275–286. doi:10.1111/eth.12206

Santos, F. C., & Pacheco, J. M. (2005). Scale-free networks provide a unifying framework for the emergence of cooperation. *Physical Review Letters*, *95*, 098104. doi:10.1103/PhysRevLett.95.098104

Šárová, R., Špinka, M., Panamá, J. L. A., & Šimeček, P. (2010). Graded leadership by dominant animals in a herd of female beef cattle on pasture. *Animal Behaviour*, *79*(5), 1037–1045. doi:10.1016/j.anbehav.2010.01.019

Sasahara, K., Cody, M. L., Cohen, D., & Taylor, C. E. (2012). Structural design principles of complex bird songs: a network-based approach. *PLoS ONE*, *7*(9), e44436. doi:10.1371/journal.pone.0044436

Schürch, R., Rothenberger, S., & Heg, D. (2010). The building-up of social relationships: behavioural types, social networks and cooperative breeding in a cichlid. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 4089–4098. doi:10.1098/rstb.2010.0177

Seed, A. M., Tebbich, S., Emery, N. J., & Clayton, N. S. (2006). Investigating physical cognition in rooks, *Corvus frugilegus*. *Current Biology*, *16*(7), 697–701. doi:10.1016/j.cub.2006.02.066

Senar, J. C., Copete, J. L., & Metcalfe, N. B. (1990). Dominance relationships between resident and transient wintering siskins. *Ornis Scandinavica*, *21*(2), 129–132.

Shizuka, D., Chaine, A. S., Anderson, J., Johnson, O., Laursen, I. M., & Lyon, B. E. (2014). Across-year social stability shapes network structure in wintering migrant sparrows. *Ecology Letters*, *17*(8), 998–1007. doi:10.1111/ele.12304

Shizuka, D., & McDonald, D. B. (2012). A social network perspective on measurements of dominance hierarchies. *Animal Behaviour*, *83*(4), 925–934. doi:10.1016/j.anbehav.2012.01.011

Shultz, S., & Dunbar, R. I. M. (2007). The evolution of the social brain: anthropoid primates contrast with other vertebrates. *Proceedings of the Royal Society of London B*, *274*(1624), 2429–2436. doi:10.1098/rspb.2007.0693

Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: an integrative overview. *The Quarterly Review of Biology*, *79*(3), 241–277.

Sih, A., Hanser, S. F., & McHugh, K. A. (2009). Social network theory: new insights and issues for behavioral ecologists. *Behavioral Ecology and Sociobiology*, *63*(7), 975–988. doi:10.1007/s00265-009-0725-6

Silk, M. J., Croft, D. P., Tregenza, T., & Bearhop, S. (2014). The importance of fission-fusion social group dynamics in birds. *Ibis*, *156*(4), 701–715. doi:10.1111/ibi.12191

Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., & Struhsaker, T. T. (1987). *Primate societies*. University of Chicago Press.

Sommer, V., & Vasey (Eds.). (2006). *Homosexual behaviour in animals - An evolutionary perspective*. Cambridge University Press.

Sridhar, H., Beauchamp, G., & Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour*, *78*(2), 337–347. doi:10.1016/j.anbehav.2009.05.008

Sridhar, H., Jordán, F., & Shanker, K. (2013). Species importance in a heterospecific foraging association network. *Oikos*, *122*(9), 1325–1334. doi:10.1111/j.1600-0706.2013.00101.x

Sueur, C., Jacobs, A., Amblard, F., Petit, O., & King, A. J. (2011). How can social network analysis improve the study of primate behavior? *American Journal of Primatology*, *73*(8), 703–719. doi:10.1002/ajp.20915

Sueur, C., Petit, O., De Marco, A., Jacobs, A. T., Watanabe, K., & Thierry, B. (2011). A comparative network analysis of social style in macaques. *Animal Behaviour*, *82*(4), 845–852. doi:10.1016/j.anbehav.2011.07.020

Székely, T., & Cuthill, I. C. (2000). Trade-off between mating opportunities and parental care: brood desertion by female Kentish plovers. *Proceedings of the Royal Society of London B*, *267*(1457), 2087–2092. doi:10.1098/rspb.2000.1253

Tóth, Z., Bókony, V., Lendvai, Á. Z., Szabó, K., Pénzes, Z., & Liker, A. (2009). Whom do the sparrows follow? The effect of kinship on social preference in house sparrow flocks. *Behavioural Processes*, *82*(2), 173–177. doi:10.1016/j.beproc.2009.06.003

Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*, *46*(1), 35–57.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man, 1871-1971* (pp. 136–179).

Van Dijk, R. E., Kaden, J. C., Argüelles-Ticó, A., Dawson, D. A., Burke, T., & Hatchwell, B. J. (2014). Cooperative investment in public goods is kin directed in communal nests of social birds. *Ecology Letters*, *17*(9), 1141–1148. doi:10.1111/ele.12320

Van Schaik, C. P. (1999). The socioecology of fission-fusion sociality in Orangutans. *Primates*, *40*(1), 69–86. doi:10.1007/BF02557703

Wan, D., Chang, P., & Yin, J. (2013). Causes of extra-pair paternity and its inter-specific variation in socially monogamous birds. *Acta Ecologica Sinica*, *33*(3), 158–166. doi:10.1016/j.chnaes.2013.03.006

Webster, M. M., & Ward, A. J. W. (2011). Personality and social context. *Biological Reviews*, *86*(4), 759–773. doi:10.1111/j.1469-185X.2010.00169.x

Weiss, M., Hultsch, H., Adam, I., Scharff, C., & Kipper, S. (2014). The use of network analysis to study complex animal communication systems: a study on nightingale song. *Proceedings of the Royal Society of London B*, *281*(1785), 20140460. doi:10.1098/rspb.2014.0460

Wey, T. W., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour*, *75*(2), 333–344. doi:10.1016/j.anbehav.2007.06.020

Whitehead, H. A. L. (2009). SOCPROG programs: analysing animal social structures. *Behavioral Ecology and Sociobiology*, *63*(5), 765–778. doi:10.1007/s00265-008-0697-y

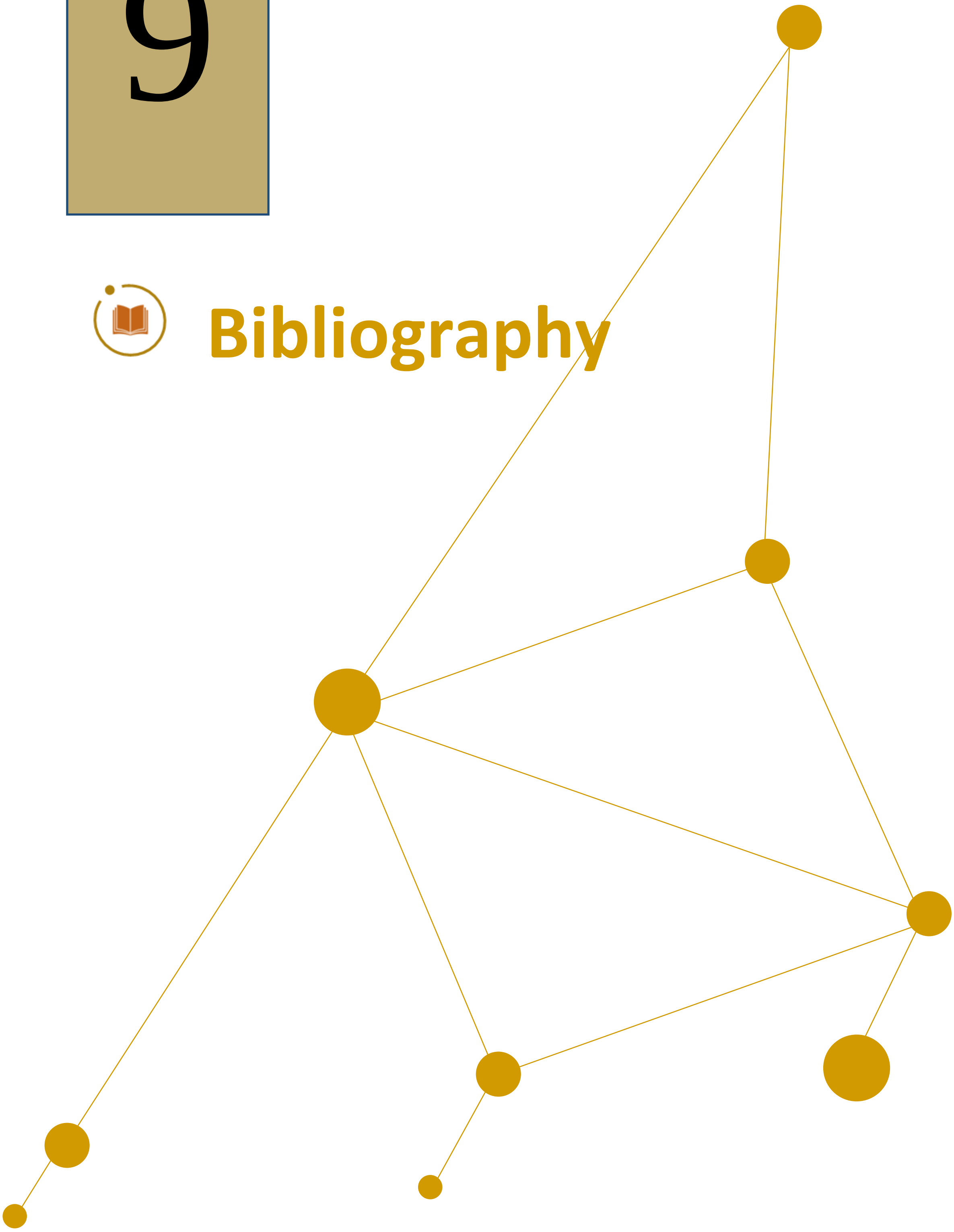
Whitehead, H. A. L., & Connor, R. C. (2005). Alliances I. How large should alliances be? *Animal Behaviour*, *69*(1), 117–126. doi:10.1016/j.anbehav.2004.02.021

Wiszniewski, J., Allen, S. J., & Möller, L. M. (2009). Social cohesion in a hierarchically structured embayment population of Indo-Pacific bottlenose dolphins. *Animal Behaviour*, *77*(6), 1449–1457. doi:10.1016/j.anbehav.2009.02.025

Wittemyer, G., Hamilton, I. D., & Getz, W. M. (2005). The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour*, *69*(6), 1357–1371. doi:10.1016/j.anbehav.2004.08.018

9

Bibliography



A

Alanärä, A., Burns, M.D., Metcalfe, N.B., 2001. Intraspecific resource partitioning in brown trout: The temporal distribution of foraging is determined by social rank. J. Anim. Ecol. 70, 980–986. doi:10.1046/j.0021-8790.2001.00550.x

Alberts, S.C., Watts, H.E., Altmann, J., 2003. Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, Papio cynocephalus. Anim. Behav. 65, 821–840. doi:10.1006/anbe.2003.2106

Alexander, R.D., 1974. The Evolution of Social Behavior. Annu. Rev. Ecol. Syst. 5, 325–383.

Altmann, J., 1974. Observational Study of Behavior : Sampling Methods. Behaviour 49, 227–267.

Ame, J.M., Rivault, C., Deneubourg, J.L., 2004. Cockroach aggregation based on strain odour recognition. Anim. Behav. 68, 793–801. doi:10.1016/j.anbehav.2004.01.009

Amsalem, E., Hefetz, A., 2011. The effect of group size on the interplay between dominance and reproduction in Bombus terrestris. PLoS One 6. doi:10.1371/journal.pone.0018238

Aplin, L.M., Farine, D.R., Morand-Ferron, J., Cole, E.F., Cockburn, A., Sheldon, B.C., 2013. Individual personalities predict social behaviour in wild networks of great tits (Parus major). Ecol. Lett. 16, 1365–72. doi:10.1111/ele.12181

Aplin, L.M., Farine, D.R., Morand-Ferron, J., Sheldon, B.C., 2012. Social networks predict patch discovery in a wild population of songbirds. Proc. Biol. Sci. 279, 4199–205. doi:10.1098/rspb.2012.1591

Appleby, M.C., 1983. The probability of linearity in hierarchies. Anim. Behav. 31, 600–608. doi:10.1016/S0003-3472(83)80084-0

Archie, E.A., Morrison, T.A., Foley, C.A.H., Moss, C.J., Alberts, S.C., 2006. Dominance rank relationships among wild female African elephants, Loxodonta africana. Anim. Behav. 71, 117–127. doi:10.1016/j.anbehav.2005.03.023

Archie, E.A., Tung, J., Clark, M., Altmann, J., Alberts, S.C., 2014. Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. Proc. R. Soc. London B Biol. Sci. 281, 20141261. doi:10.1098/rspb.2014.1261

Arnold, K., Aureli, F., 2007. Post conflict reconciliation. In Primates in Perspective (Campbell, C. J., Fuentes, A., MacKinnon, K. C., Panger, M. & Bearder, S. K., Eds). Oxford Univ. Press, Oxford, p. 592—608. doi:10.1111/j.1540-4560.2008.00563.x

Arnold, K.E., 2000. Group Mobbing Behaviour and Nest Defence in a Cooperatively Breeding Australian Bird. Ethology 106(5), 385–393.

Arroyo, B., Mougeot, F., Bretagnolle, V., 2001. Colonial breeding and nest defence in Montagu’s harrier (Circus pygargus). Behav. Ecol. Sociobiol. 50, 109–115. doi:10.1007/s002650100342

Aureli, F., Cords, M., van Schaik, C.P., 2002. Conflict resolution following aggression in gregarious animals: a predictive framework. Anim. Behav. 64, 325–343. doi:10.1006/anbe.2002.3071

Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., Fiore, A.D., Dunbar, R.I.M., Henzi, S.P., Holekamp, K., Korstjens, A.H., Layton, R., Lee, P., Lehmann, J., Manson, J.H., Ramos-Fernandez, G., Strier, K.B., Schaik, C.P. van, 2008. Fission-Fusion Dynamics: New Research Frameworks. Curr. Anthropol. 49, 627–654. doi:10.1086/586708

B

Baglione, V., Canestrari, D., Marcos, J.M., Ekman, J., 2006. Experimentally increased food resources in the natal territory promote offspring philopatry and helping in cooperatively breeding carrion crows. Proc. Biol. Sci. 273, 1529–1535. doi:10.1098/rspb.2006.3481

Baglione, V., Canestrari, D., Marcos, J.M., Ekman, J., 2003. Kin selection in cooperative alliances of carrion crows. Science 300, 1947–9. doi:10.1126/science.1082429

Baglione, V., Marcos, J.M., Canestrari, D., 2002a. Cooperatively breeding groups of carrion crow (Corvus corone corone) in northern Spain. Auk 119, 790–799. doi:10.1642/0004-8038(2002)119[0790:CBGOCC]2.0.CO;2

Baglione, V., Marcos, M., Canestrari, D., Ekman, J.A.N., 2002b. Direct fitness benefits of group living in a complex cooperative society of carrion crows Corvus corone corone 1–7. doi:10.1006/anbe.2002.0000

Baird, R.W., Whitehead, H., 2000. Social organization of mammal-eating killer whales: group stability and dispersal patterns. Can. J. Zool. 78, 2096–2105. doi:10.1139/cjz-78-12-2096

Balasubramaniam, K.N., Dittmar, K., Berman, C.M., Butovskaya, M., Cooper, M.A., Majolo, B., Ogawa, H., Schino, G., Thierry, B., De Waal, F.B.M., 2012. Hierarchical Steepness, Counter-Aggression, and Macaque Social Style Scale. Am. J. Primatol. 74, 915–925. doi:10.1002/ajp.22044

Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., Orlandi, A., Parisi, G., Procaccini, A., Viale, M., Zdravkovic, V., 2008. Empirical investigation of starling flocks: a benchmark study in collective animal behaviour. Anim. Behav. 76, 201–215. doi:10.1016/j.anbehav.2008.02.004

Banks, D.L., Carley, K.M., 1996. Models for network evolution. J. Math. Sociol. 1995, 1–36. doi:10.1016/j.ehb.2012.05.003

Barrett, L., & Henzi, S.P., 2002. Constraints on relationship formation among female primates. Behaviour 139(2), 263–289.

Barrett, L., Henzi, P., Rendall, D., 2007. Social brains, simple minds: does social complexity really require cognitive complexity? Philos. Trans. R. Soc. Lond. B. Biol. Sci. 362, 561–75. doi:10.1098/rstb.2006.1995

Barrett, L., Henzi, S.P., Weingrill, T., Lycett, J.E., Hill, R.A., 1999. Market forces predict grooming reciprocity in female baboons. Proc. R. Soc. B Biol. Sci. 266, 665. doi:10.1098/rspb.1999.0687

Beauchamp, G., Fernández-Juricic, E., 2004. Is there a relationship between forebrain size and group size in birds? Evol. Ecol. Res. 6, 833–842.

Beisner, B. A., Jackson, M.E., Cameron, A., McCowan, B., 2011. Effects of natal male alliances on aggression and power dynamics in rhesus macaques. Am. J. Primatol. 73, 790–801. doi:10.1002/ajp.20907

Bekoff, M., 1995. Play signals as punctuation: the structure of social play in canids. Behaviour 1, 419–429. doi:10.1017/CBO9781107415324.004

Bekoff, M., 1974. Social play in coyotes, wolves, and dogs. Bioscience. 24(4), 225–230.

Bell, M.B. V., Nichols, H.J., Gilchrist, J.S., Cant, M. a., Hodge, S.J., 2012. The cost of dominance: suppressing subordinate reproduction affects the reproductive success of dominant female banded mongooses. Proc. R. Soc. B Biol. Sci. 279, 619–624. doi:10.1098/rspb.2011.1093

Benchley, A., 1986. The breeding distribution and abundance of the rook (Corvus frugilegus L.) in Great Britain since the 1920's. J. Zool. London 210(2), 261–278.

Berger, J., 1979. " Predator Harassment" as a Defensive Strategy in Ungulates. Am. Midl. Nat. 197–199.

Berghänel, A., Ostner, J., Schröder, U., Schülke, O., 2011. Social bonds predict future cooperation in male Barbary macaques, Macaca sylvanus. Anim. Behav. 81, 1109–1116. doi:10.1016/j.anbehav.2011.02.009

Bergman, T.J., Beehner, J.C., 2015. Measuring social complexity. Anim. Behav. 103, 203–209. doi:10.1016/j.anbehav.2015.02.018

Bernstein, I.S., 1981. Dominance: The baby and the bathwater. Behav. Brain Sci. 4, 419–457. doi:10.1017/S0140525X00009614

Bernstein, I.S., Judge, P.G., Ruehlmann, T.E., 1993. Kinship, association, and social relationships in rhesus monkeys (Macaca mulatta). Am. J. Primatol. 31, 41–53. doi:10.1002/ajp.1350310105

Bird, C.D., Emery, N.J., 2009a. Rooks use stones to raise the water level to reach a floating worm. Curr. Biol. 19, 1410–4. doi:10.1016/j.cub.2009.07.033

Bird, C.D., Emery, N.J., 2009b. Insightful problem solving and creative tool modification by captive nontool-using rooks. Proc. Natl. Acad. Sci. U. S. A. 106, 10370–5. doi:10.1073/pnas.0901008106

Bird, C.D., Emery, N.J., 2008. Using video playback to investigate the social preferences of rooks, Corvus frugilegus. Anim. Behav. 76, 679–687. doi:10.1016/j.anbehav.2008.04.014

Black J.M., 1996. Pair bonds and partnerships. In: Black JM (ed) Partnerships in birds. The study of monogamy. Oxford University Press, New York, pp 3–20

Black, J.M., 2001. Fitness consequences of long-term pair bonds in barnacle geese: monogamy in the extreme. Behav. Ecol. 12, 640–645. doi:10.1093/beheco/12.5.640

Bloomsmith, M.A., Pazol, K.A., Alford, P.L., 1994. Juvenile and adolescent chimpanzee behavioral development in complex groups. Appl. Anim. Behav. Sci. 39, 73–87. doi:10.1016/0168-1591(94)90017-5

Bluff, L.A., Weir, A.A.S., Rutz, C., Wimpenny, J.H., Kacelnik, A., 2007. Tool-related Cognition in New Caledonian Crows 2, 1–25.

Boeckle, M., Bugnyar, T., 2012. Long-term memory for affiliates in ravens. Curr. Biol. 22, 801–6. doi:10.1016/j.cub.2012.03.023

Boesch, C., 2002. Cooperative hunting roles among Tai chimpanzees. Hum. Nat. 13(1), 27–46. doi:10.1007/s12110-002-1013-6

Boesch, C., 1994. Cooperative hunting in wild chimpanzees. Anim. Behav. doi:10.1006/anbe.1994.1285

Bonabeau, E., Theraulaz, G., Deneubourg, J.-L., 1998. Fixed Response Thresholds and the Regulation of Division of Labor in Insect Societies. Bull. Math. Biol. 60, 753–807. doi:10.1006/bulm.1998.0041

Borgeaud, C., van de Waal, E., Bshary, R., 2013. Third-Party Ranks Knowledge in Wild Vervet Monkeys (Chlorocebus aethiops pygerythrus). PLoS One 8, 8–11. doi:10.1371/journal.pone.0058562

Boucherie, P.H., Mariette, M.M., Bret, C., Dufour, V., 2016. Bonding beyond the pair in a monogamous bird: impact on social structure in adult rooks (Corvus frugilegus). Behaviour. doi:10.1163/1568539X-00003372

Boucherie, P.H., Sosa, S., Psaquaretta, C., Dufour, V., 2016. A longitudinal network analysis of social dynamics in rooks Corvus frugilegus: repeated group modifications do not affect social network in captive rooks. Current zoology, Institute of zoology, Chinese academy of sciences, 2016. doi:10.1093/cz/zow083

Boulinier, T., Danchin, E., Monnat, J., Doutrelant, C., Cadiou, B., 2014. Timing of Prospecting and the Value of Information in a Colonial Breeding Bird. J. Avian Biol, 252–256. doi:10.2307/3677230

Bourke, A.. F.G., 1999. Colony size, social complexity and reproductive conflict in social insects. J. Evol. Biol. 12, 245–257. doi:10.1046/j.1420-9101.1999.00028.x

Braun, A., Bugnyar, T., 2012. Social bonds and rank acquisition in raven nonbreeder aggregations. Anim. Behav. 84, 1507–1515. doi:10.1016/j.anbehav.2012.09.024

Braun, A., Walsdorff, T., Fraser, O.N., Bugnyar, T., 2012. Socialized sub-groups in a temporary stable Raven flock? J. Ornithol. 153, 97–104. doi:10.1007/s10336-011-0810-2

Brosnan, S.F., Waal, F.B.M., 2002. A proximate perspective on reciprocal altruism. Hum. Nat. 13, 129–152. doi:10.1007/s12110-002-1017-2

Brosset, A., 1978. Social organization and nest-building in the forest weaver birds of the genus Malimbus (Ploceinae). Ibis (Lond. 1859). 120, 27–37.

Brown, C.R., 1986. Cliff swallow colonies as information centers. Science 234, 83–85. doi:10.1126/science.234.4772.83

Bugnyar, T., 2011. Knower-guesser differentiation in ravens: others' viewpoints matter. Proc. Biol. Sci. 278, 634–40. doi:10.1098/rspb.2010.1514

Bugnyar, T., Schwab, C., Schloegl, C., Kotrschal, K., Heinrich, B., 2007. Ravens judge competitors through experience with play caching. Curr. Biol. 17, 1804–8. doi:10.1016/j.cub.2007.09.048

Bull, P. C., & Porter, R. E. R. 1975. Distribution and numbers of the rook (Corvus frugilegus L.) in the North Island of New Zealand. New Zealand journal of zoology, *2*(1), 63-92.

Bulger, J.B., 1993. Dominance rank and access to estrous females in male savanna baboons. Behaviour 127(1), 67–103.

Burish, M.J., Kueh, H.Y., Wang, S.S.-H., 2004. Brain Architecture and Social Complexity in Modern and Ancient Birds. Brain. Behav. Evol. 63, 107–124. doi:10.1159/000075674

Buskens, V., 2002. Social networks and trust, Springer Science & Business Media.

C

Cameron, E.Z., Setsaas, T.H., Linklater, W.L., 2009. Social bonds between unrelated females increase reproductive success in feral horses. Proc. Natl. Acad. Sci. U. S. A. 106, 13850–13853. doi:10.1073/pnas.0900639106

Carlisle, T.R., Zahavi, A., 1986. Helping at the nest, allofeeding and social status in immature arabian babblers. Behav. Ecol. Sociobiol. 18, 339–351. doi:10.1007/BF00299665

Carrascal, L.M., Moreno, J., Amat, J. A., 1995. Nest maintenance and stone theft in the Chinstrap penguin (Pygoscelis antarctica). Polar Biol. 15, 541–545. doi:10.1007/BF00239645

Cezilly, F., Nager, R.G., 1995. Comparative evidence for a positive association between divorce and extra-pair paternity in birds. Proc. R. Soc. London B Biol. Sci. 262(1363), 7-12.

Chantrey, D. F. 1982. Foraging strategies of Rooks (Corvus frugilegus): A simulation. Zeitschrift für Tierpsychologie, 59(2), 157-171.

Chapais, B., Girard, M., Primi, G., 1991. Non-kin alliances, and the stability of matrilineal dominance relations in Japanese macaques. Anim. Behav. 41, 481–491. doi:10.1016/S0003-3472(05)80851-6

Chapman, C. a., Wrangham, R.W., Chapman, L.J., 1995. Ecological constraints on group size: An analysis of spider monkey and chimpanzee subgroups. Behav. Ecol. Sociobiol. doi:10.1007/s002650050125

Chappell, J., Kacelnik, A., 2004. Selection of tool diameter by New Caledonian crows Corvus moneduloides. Anim. Cogn. 7, 121–7. doi:10.1007/s10071-003-0202-y

Charif, R.A., Ramey, R.R., Langbauer, W.R., Payne, K.B., Martin, R.B., Brown, L.M., 2005. Spatial relationships and matrilineal kinship in African savanna elephant (Loxodonta africana) clans. Behav. Ecol. Sociobiol. 57, 327–338. doi:10.1007/s00265-004-0867-5

Charnov, E.L., 1978. Sex-ratio selection in eusocial Hymenoptera. Am. Nat. 317–326.

Chase, I. D., 1982. Dynamics of hierarchy formation: the sequential development of dominance relationships. Behaviour, 80(3), 218-239. doi:10.1163/156853982X00364

Chase, I.D., Tovey, C., Spangler-martin, D., Manfredonia, M., 2002. Individual differences versus social dynamics in the formation of animal dominance hierarchies 99, 5744–5749.

Cheney, D., Seyfarth, R., 1999. Recognition of other individuals’ social relationships by female baboons. Anim. Behav. 58, 67–75. doi:10.1006/anbe.1999.1131

Cheney, D.L., Seyfarth, R.M., Silk, J.B., 1995. The responses of female baboons (Papio cynocephalus ursinus) to anomalous social interactions: Evidence for causal reasoning? J. Comp. Psychol. 109, 134–141. doi:http://dx.doi.org/10.1037/0735-7036.109.2.134

Chiarati, E., Canestrari, D., Vera, R., Marcos, J.M., Baglione, V., 2010. Linear and Stable Dominance Hierarchies in Cooperative Carrion Crows. Ethology 116, 346–356. doi:10.1111/j.1439-0310.2010.01741.x

Clayton, N.S., Dally, J.M., Emery, N.J., 2007. Social cognition by food-caching corvids. The western scrub-jay as a natural psychologist. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 362, 507–22. doi:10.1098/rstb.2006.1992

Clayton, N.S., Emery, N.J., 2007. The social life of corvids. Curr. Biol. 17, R652–6. doi:10.1016/j.cub.2007.05.070

Clutton-Brock, T.H., & Harvey, P.H., 1977. Primate ecology and social organization. J. Zool. 183(1), 1–39.

Clutton-Brock, T., 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. Science 296, 69–72. doi:10.1126/science.296.5565.69

Clutton-Brock, T., 1991. The evolution of parental care. Princeton University Press.

Clutton-Brock, T.H., 1989. Review lecture: mammalian mating systems. Proc. R. Soc. London B Biol. Sci. 236, 339–372. doi:10.1098/rspb.1979.0086

Clutton-Brock, T.H., Brotherton, P.N.M., O'Riain, M.J., Griffin, a. S., Gaynor, D., Kansky, R., Sharpe, L., McIlrath, G.M., 2001. Contributions to cooperative rearing in meerkats. Anim. Behav. 61, 705–710. doi:10.1006/anbe.2000.1631

Clutton-Brock, T.H., Guinness, F.E., & Albon, S.D., 1982. Red deer: behavior and ecology of two sexes. Chicago.

Clutton-Brock, T.H., Huchard, E., 2013. Social competition and selection in males and females. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 368, 20130074. doi:10.1098/rstb.2013.0074

Cockburn, A., 2006. Prevalence of different modes of parental care in birds. Proc. Biol. Sci. 273, 1375–83. doi:10.1098/rspb.2005.3458

Cockburn, A., 1998. Evolution of Helping Behavior in Cooperatively Breeding Birds. Annu. Rev. Ecol. Syst. 29, 141–177. doi:10.1146/annurev.ecolsys.29.1.141

Connor, R.C., 2007. Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 362, 587–602. doi:10.1098/rstb.2006.1997

Conover M.R., Hunt G.L. Jr, 1984. Experimental evidence that female– female pairs in gulls result from a shortage of breeding males. Condor 86:472–476

Cordoni, G., 2009. Social play in captive wolves (Canis lupus): not only an immature affair. Behaviour 146, 1363–1385. doi:10.1163/156853909X427722

Cords, M. & Aureli, F., 2000. Reconciliation and relationship qualities. In: Aureli, F., & de Waal, Natural Conflict Resolution, Berkeley, pp. 177–198.

Cords, M., 1997. Friendships, alliances, reciprocity and repair. Machiavellian Intelligence II: Extensions and Evaluations. Cambridge University Press, Cambridge, 24-49.

Correia, S.P.C., Dickinson, A., Clayton, N.S., 2007. Western scrub-jays anticipate future needs independently of their current motivational state. Curr. Biol. 17, 856–61. doi:10.1016/j.cub.2007.03.063

Couzin, I.D., Krause, J., 2003. Self-Organization and Collective Behavior in Vertebrates. Adv. Study Behav. 32, 1–75. doi:10.1016/S0065-3454(03)01001-5

Couzin, I.D., Krause, J., James, R., Ruxton, G.D., Franks, N.R., 2002. Collective memory and spatial sorting in animal groups. J. Theor. Biol. 218, 1–11. doi:10.1006/yjtbi.3065

Couzin, I.D., Laidre, M.E., 2009. Fission-fusion populations. Curr. Biol. 19, 633–635. doi:10.1016/j.cub.2009.05.034

Creel, S., & Creel, N.M., 1995. Communal hunting and pack size in African wild dogs, Lycaon pictus. Anim. Behav. 50(5), 1325–1339.

Crook, J.H., 1972. Sexual selection, dimorphism and social organization in the primates, Selection and the Descent of Man, vol. 18711971. Aldine Publ. Co., Chicago. pp. 231–281.

Czirok, A., Vicsek, T., 2000. Collective behavior of interacting self-propelled particles. Phys. A Stat. Mech. its Appl. 281, 17–29. doi:10.1016/S0378-4371(00)00013-3

D

Dally, J.M., 2006. Food-Caching Western Scrub-Jays Keep Track of Who Was Watching When. Science, 312(5780), 1662–1665. doi:10.1126/science.1126539

Dally, J. M., Clayton, N. S., & Emery, N. J. 2008. Social influences on foraging by rooks (Corvus frugilegus). Behaviour, 145(8), 1101-1124.

Danchin, E., Wagner, R.H., 1997. The evolution of coloniality: the emergence of new perspectives. Trends Ecol. Evol. 12, 342–7.

Davis, L.S., 1988. Coodination of incubation rourines and mate choice in Adélie penguins (Pygoscelis adeliae). Auk 105, 428–432.

de Kort, S.R., Emery, N.J., Clayton, N.S., 2006. Food sharing in jackdaws, Corvus monedula: what, why and with whom? Anim. Behav. 72, 297–304.

de Kort, S.R., Emery, N.J., Clayton, N.S., 2003. Food offering in jackdaws (Corvus monedula). Naturwissenschaften 90, 238–40. doi:10.1007/s00114-003-0419-2

de Marco, A., Cozzolino, R., Dessì-Fulgheri, F., Thierry, B., 2010. Conflicts induce affiliative interactions among bystanders in a tolerant species of macaque (Macaca tonkeana). Anim. Behav. 80, 197–203. doi:10.1016/j.anbehav.2010.04.016

de Silva, S., Ranjeewa, A.D., & Kryazhimskiy, S., 2011. The dynamics of social networks among female Asian elephants. BMC Ecology, 11(1), 1.

Demaria, C., & Thierry, B. 2001. A comparative study of reconciliation in rhesus and Tonkean macaques. *Behaviour*, *138*(3), 397-410.

de Villiers, M.S., Richardson, P.R.K., van Jaarsveld, A.S., 2003. Patterns of coalition formation and spatial association in a social carnivore, the African wild dog (Lycaon pictus). J. Zool. 260, S0952836903003832. doi:10.1017/S0952836903003832

de Vries, H., 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Anim. Behav. 50, 1375–1389. doi:10.1016/0003-3472(95)80053-0

de Vries, H., Stevens, J.M.G., Vervaecke, H., 2006. Measuring and testing the steepness of dominance hierarchies. Anim. Behav. 71, 585–592. doi:10.1016/j.anbehav.2005.05.015

de Waal FB, 2000. Attitudinal reciprocity in food sharing among brown capuchin monkeys. Anim. Behav. 60, 253–261. doi:10.1006/anbe.2000.1471

de Waal, F., & Luttrell, L.M., 1985. The Formal Hierarchy of Rhesus Macaques : An Investigation of the Bared-Teeth Display. Am. J. Primatol. 9, 73–85.

de Waal, F. B., & Luttrell, L. M., 1988. Mechanisms of social reciprocity in three primate species: symmetrical relationship characteristics or cognition?. Ethology and Sociobiology, 9(2-4), 101-118.

de Waal, F.B., 2000. Primates--a natural heritage of conflict resolution. Science 289, 586–90. doi:10.1126/science.289.5479.586

de Waal, F.B., 1986. The integration of dominance and social bonding in primates. Q. Rev. Biol. 459–479.

de Waal, F.B.M., van Roosmalen, A., 1979. Reconciliation and consolation among chimpanzees. Behav. Ecol. Sociobiol. 5, 55–66. doi:10.1007/BF00302695

Dehn, M.M., 1990. Vigilance for predators: detection and dilution effects. Behav. Ecol. Sociobiol. 26(5), 337–342.

Despland, E., Collett, M., Simpson, S.J., 2000. Small-scale processes in desert locust swarm formation: how vegetation patterns influence gregarization. Oikos 88, 652–662. doi:10.1034/j.1600-0706.2000.880322.x

Dingemanse, N.J., De Goede, P., 2004. The relation between dominance and exploratory behavior is context-dependent in wild great tits. Behav. Ecol. 15, 1023–1030. doi:10.1093/beheco/arh115

Doligez, B., Cadet, C., Danchin, E., Boulinier, T., 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. Anim. Behav. 66, 973–988. doi:10.1006/anbe.2002.2270

Doligez, B., Danchin, E., Clobert, J., 2002. Public information and breeding habitat selection in a wild bird population. Science 297, 1168–1170. doi:10.1126/science.1072838

Drea, C.M., Carter, A.N., 2009. Cooperative problem solving in a social carnivore. Anim. Behav. 78, 967–977. doi:10.1016/j.anbehav.2009.06.030

Drews, C., 1993. The Concept and definition of dominance in animal behaviour. Behaviour 125, 283–313. doi:10.1017/CBO9781107415324.004

Duboscq, J., Agil, M., Engelhardt, A., Thierry, B., 2013a. The function of postconflict interactions: new prospects from the study of a tolerant species of primate. Anim. Behav. doi:10.1016/j.anbehav.2013.10.018

Duboscq, J., Micheletta, J., Agil, M., Hodges, K., Thierry, B., Engelhardt, A., 2013b. Social Tolerance in Wild Female Crested Macaques (Macaca nigra) in Tangkoko-Batuangus Nature Reserve, Sulawesi, Indonesia. Am. J. Primatol. 75, 361–375. doi:10.1002/ajp.22114

Duboscq, J., Romano, V., Sueur, C., MacIntosh, A.J.J., 2016. Network centrality and seasonality interact to predict lice load in a social primate. Sci. Rep. 6, 22095. doi:10.1038/srep22095

Dufour, V., Wascher, C. A F., Braun, A., Miller, R., Bugnyar, T., 2011. Corvids can decide if a future exchange is worth waiting for. Biol. Lett. 8, 201–4. doi:10.1098/rsbl.2011.0726

Dunbar, R.I.M., 2012. Bridging the bonding gap: the transition from primates to humans. Philos. Trans. R. Soc. B Biol. Sci. 367, 1837–1846. doi:10.1098/rstb.2011.0217

Dunbar, R.I.M., 1998. The social brain hypothesis. Brain, 9(10) 178–190. doi:10.1002/(SICI)1520-6505(1998)

Dunbar, R.I.M., 1992. Neocortex size as a constraint on group size in primates. J. Hum. Evol. 22, 469–493. doi:10.1016/0047-2484(92)90081-J

Dunbar, R.I.M., 1989. Social systems as optimal strategy sets: the costs and benefits of sociality. Comp. socioecology 73–88.

Dunbar, R.I.M., Dunbar, J.B., Bever, R.I.M.&, Dunbar, R., 1998. Neocortex Size Predicts Group Size in Carnivores and Some Insectivores. Ethology 104, 695–708. doi:10.1111/j.1439-0310.1998.tb00103.x

Dunbar, R.I.M., Shultz, S., 2007. Evolution in the social brain. Science 317, 1344–7. doi:10.1126/science.1145463

Dunnet, G. M., Fordham, R. A., & Patterson, I. J. 1969. Ecological studies of the rook (Corvus frugilegus L.) in North-east Scotland. Proportion and distribution of young in the population. Journal of Applied Ecology, 459-473.

E

East, M. 1988. Crop selection, feeding skills and risks taken by adult and juvenile rooks Corvus frugilegus. Ibis, 130(2), 294-299.

Eberhard, J.R., 1998. Breeding biology of the monk parakeet. Wilson Bull. 110, 463–473.

Eberle, M., Kappeler, P.M., 2006. Family insurance: Kin selection and cooperative breeding in a solitary primate (Microcebus murinus). Behav. Ecol. Sociobiol. 60, 582–588. doi:10.1007/s00265-006-0203-3

Ekman, J., 2006. Family living among birds. J. Avian Biol. 37, 289–298. doi:10.1111/j.2006.0908-8857.03666.x

Elgar, M., 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. Biol. Rev. 64, 13–33. doi:10.1111/j.1469-185X.1989.tb00636.x

Elgar, M.A., Catterall, C.P., 1981. Flocking and predator surveillance in house sparrows: Test of an hypothesis. Anim. Behav. 29, 868–872. doi:10.1016/S0003-3472(81)80022-X

Elie, J.E., Mathevon, N., Vignal, C., 2011b. Same-sex pair-bonds are equivalent to male–female bonds in a life-long socially monogamous songbird. Behav. Ecol. Sociobiol. 65, 2197–2208. doi:10.1007/s00265-011-1228-9

Elo, A.E., 1978. The Rating of Chess Players, Past and Present. Arco Pub.

Emery, N.J., 2006. Cognitive ornithology: the evolution of avian intelligence. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 361, 23–43. doi:10.1098/rstb.2005.1736

Emery, N.J., 2004. Are corvids “feathered apes”? Cognitive evolution in crows, jays, rooks and jackdaws. In Comparative Analysis of Minds (Ed. S. Watanabe). Tokyo, Japan: Keio University Press, pp. 181–213.

Emery, N.J., Clayton, N.S., 2004. The Mentality of Crows : Convergent Evolution of Intelligence in Corvids and Apes. Science 306(5703), 1903–1907.

Emery, N.J., Clayton, N.S., 2001. Effects of experience and social context on prospective caching strategies by scrub jays. Nature 414, 443–6. doi:10.1038/35106560

Emery, N.J., Seed, A.M., von Bayern, A.M.P., Clayton, N.S., 2007. Cognitive adaptations of social bonding in birds. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 362, 489–505. doi:10.1098/rstb.2006.1991

Emlen, S.T., 1997. Predicting family dynamics in social vertebrates. Behavioural ecology: an evolutionary approach, 4, 228–253.

Engh, A.L., Siebert, E.R., Greenberg, D.A., Holekamp, K.E., 2005. Patterns of alliance formation and postconflict aggression indicate spotted hyaenas recognize third-party relationships. Anim. Behav. 69, 209–217. doi:10.1016/j.anbehav.2004.04.013

Ens, B. J., & Choudhury, S. 1996. Mate fidelity and divorce in monogamous birds. In ‘Partnerships in Birds: The Study of Monogamy’.(Ed. JM Black.) pp. 344–401. Erwin, R.M., 1979. Species interactions in a mixed colony of common terns (Sterna hirundo) and black skimmers (Rynchops niger). Anim. Behav. 27, 1054–1062. doi:10.1016/0003-3472(79)90053-8

Erwin, R.M., 1979. Species interactions in a mixed colony of common terns (Sterna hirundo) and black skimmers (Rynchops niger). Anim. Behav. 27, 1054–1062. doi:10.1016/0003-3472(79)90053-8

F

Feare, C. J., Dunnet, G. M. & Patterson, I. J. 1974. Ecological studies of the rook (Corvus frugilegus L.) in north-east Scotland: food intake and feeding behaviour. J. Appl. Ecol. 11, 867-896

Feare, C. J. 1978. The ecology of damage by rooks (Corvusfrugilegus). Annals of Applied Biology, 88(2), 329-334.

Feddersen-Petersen, D.U., 1991. The ontogeny of social play and agonistic behaviour in selected canid species. Bonner Zool. Beitr., 42(2), 97-114.

Foster, E.A., Franks, D.W., Morrell, L.J., Balcomb, K.C., Parsons, K.M., van Ginneken, A., Croft, D.P., 2012. Social network correlates of food availability in an endangered population of killer whales, Orcinus orca. Anim. Behav. 83, 731–736. doi:10.1016/j.anbehav.2011.12.021

Foster, W.A., Treherne, J.E., 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. Nature 293, 466–467. doi:doi:10.1038/293466a0

Franz, M., Mclean, E., Tung, J., Altmann, J., Alberts, S.C., 2015. Self-organizing dominance hierarchies in a wild primate population. Proc. R. Soc. B Biol. Sci. 282, 20151512. doi:10.1098/rspb.2015.1512

Fraser, O.N., & Bugnyar, T., 2010a. Do ravens show consolation? Responses to distressed others. PLoS One 5, e10605. doi:10.1371/journal.pone.0010605

Fraser, O.N., Bugnyar, T., 2010b. The quality of social relationships in ravens. Anim. Behav. 79, 927–933. doi:10.1016/j.anbehav.2010.01.008

Fraser, O.N., Bugnyar, T., 2011. Ravens reconcile after aggressive conflicts with valuable partners. PLoS One 6, e18118. doi:10.1371/journal.pone.0018118

Fraser, O.N., & Bugnyar, T., 2012. Reciprocity of agonistic support in ravens. Anim. Behav. 83, 171–177. doi:10.1016/j.anbehav.2011.10.023

Fraser, O.N., Schino, G., Aureli, F., 2008. Components of relationship quality in chimpanzees. Ethology 114, 834–843. doi:10.1111/j.1439-0310.2008.01527.x

Frère, C.H., Krützen, M., Mann, J., Connor, R.C., Bejder, L., Sherwin, W.B., 2010. Social and genetic interactions drive fitness variation in a free-living dolphin population. Proc. Natl. Acad. Sci. 107, 19949–19954. doi:10.1073/pnas.1007997107

G

Gaston, A.J., 1977. Social behaviour within groups of jungle babblers (Turdoides striatus). Anim. Behav. 25, 828–848. doi:10.1016/0003-3472(77)90036-7

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. doi:10.1007/s00265-012-1457-6

Goodwin, D., 1976. Corws of the world. Cornell University Press.

Goodwin, D., 1955. Some observations on the reproductive behavior of rooks. Br. Birds 48, 97–107.

Greenwood, P., 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 1140–1162.

Griffin, L.R., 1999. Colonization patterns at Rook (Corvus frugilegus) colonies: implications for survey strategies. Bird Study 46, 170–173. doi:10.1080/00063659909461128

Griffin, L.R., Thomas, C.J., 2000. The spatial distribution and size of rook (Corvus frugilegus) breeding colonies is affected by both the distribution of foraging habitat and by intercolony competition. Proc. Biol. Sci. 267, 1463–7. doi:10.1098/rspb.2000.1165

Griffith, S. C., Owens, I. P., & Thuman, K. A. (2002). Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular ecology*,*11*(11), 2195-2212.

Grodzinski, U., Clayton, N.S., 2010. Problems faced by food-caching corvids and the evolution of cognitive solutions. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 365, 977–87. doi:10.1098/rstb.2009.0210

Grueter, C.C., Chapais, B., Zinner, D., 2012. Evolution of Multilevel Social Systems in Nonhuman Primates and Humans. Int. J. Primatol. 33, 1002–1037. doi:10.1007/s10764-012-9618-z

Grüter, C., Menezes, C., Imperatriz-Fonseca, V.L., Ratnieks, F.L.W., 2012. A morphologically specialized soldier caste improves colony defense in a neotropical eusocial bee. Proc. Natl. Acad. Sci. 109, 1182118–6. doi:10.1073/pnas.1113398109

Gueron, S., Levin, S. a., Rubenstein, D.I., 1996. The dynamics of herds: From individuals to aggregations. J. Theor. Biol. 182, 85–98. doi:10.1006/jtbi.1996.0144

H

Halupka, K., & Osińska-Dzienniak, A. 2013. Group foraging by wintering rooks: combined effects of safety and energy requirements. Behaviour, *150*(3-4), 381-395.

Hamilton, W.D., 1964. The genetical evolution of social behaviour. II. J. Theor. Biol. 7, 17–52. doi:10.1016/0022-5193(64)90039-6

Hare, B., Melis, A.P., Woods, V., Hastings, S., Wrangham, R., 2007. Tolerance Allows Bonobos to Outperform Chimpanzees on a Cooperative Task. Curr. Biol. 17, 619–623. doi:10.1016/j.cub.2007.02.040

Hatchwell, B.J., 2009. The evolution of cooperative breeding in birds: kinship, dispersal and life history. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 364, 3217–27. doi:10.1098/rstb.2009.0109

Heinrich, B., 1988. Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven, Corvus corax. Behav. Ecol. Soc., 23(3), 141-156.

Hemelrijk, C. K., 1990a. A matrix partial correlation test used in investigations of reciprocity and other social interaction patterns at group level. Journal of theoretical Biology, 143(3), 405-420.

Hemelrijk, C. K., 1990b. Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. Animal Behaviour, 39(6), 1013-1029.

Hemelrijk, C. K., 1994. Support for being groomed in long-tailed macaques, Macaca fascicularis. Animal Behaviour, 48(2), 479-481.

Henderson, I. G., & Hart, P. J. B., 1991. Age-specific differences in the winter foraging strategies of rooks Corvus frugilegus. Oecologia, 85(4), 492-497.

Henzi, S.P., Lusseau, D., Weingrill, T., Van Schaik, C.P., Barrett, L., 2009. Cyclicity in the structure of female baboon social networks. Behav. Ecol. Sociobiol. 63, 1015–1021. doi:10.1007/s00265-009-0720-y

Heppner, F.H., Grenander, U., 1990. A Stochastic nonlinear model for bird flocks. The ubiquity of chaos, 233-238.

Herbert-Read, J.E., Perna, A., Mann, R.P., Schaerf, T.M., Sumpter, D.J.T., Ward, A.J.W., 2011. Inferring the rules of interaction of shoaling fish. Proc. Natl. Acad. Sci. 108, 18726–31. doi:10.1073/pnas.1109355108

Hillemann, F., Bugnyar, T., Kotrschal, K., Wascher, C. A. F., 2014. Waiting for better, not for more: corvids respond to quality in two delay maintenance tasks. Anim. Behav. 90, 1–10. doi:10.1016/j.anbehav.2014.01.007

Hinde, R.A., 1976. Interactions, Relationships and Social Structure. Man 11, 1–17.

Hinde, R.A., Simpson, M.J.A., 1975. Qualities of mother-infant relationships in monkeys. In Parent-Infant Interactions. CIBA Found. Symp. 33, 39–67.

Hobson, E.A., Avery, M.L., Wright, T.F., 2014. The socioecology of Monk Parakeets: Insights into parrot social complexity. Auk 131, 756–775. doi:10.1642/AUK-14-14.1

Hohmann, G., Gerloff, U., Tautz, D., Fruth, B., 1999. Social bonds and genetic ties: kinship, association and affiliation in a community of bonobos (Pan paniscus). Behaviour 136(9), 1219–1235. doi:10.1163/156853999501739

Holekamp, K.E., Sakai, S.T., Lundrigan, B.L., 2007a. Social intelligence in the spotted hyena (Crocuta crocuta). Philos. Trans. R. Soc. Lond. B. Biol. Sci. 362, 523–38. doi:10.1098/rstb.2006.1993

Holekamp, K.E., 2007b. Questioning the social intelligence hypothesis. Trends Cogn. Sci. 11, 65–9. doi:10.1016/j.tics.2006.11.003

Holekamp, K.E., & Smale, L., 1991. Dominance acquisition during mammalian social development: the “inheritance” of maternal rank. Am. Zool. 31(2), 306–317.

Holekamp, K.E., Smith, J.E., Strelioff, C.C., Van Horn, R.C., Watts, H.E., 2012. Society, demography and genetic structure in the spotted hyena. Mol. Ecol. 21, 613–632. doi:10.1111/j.1365-294X.2011.05240.x

Holzhaider, J.C., Sibley, M.D., Taylor, A. H., Singh, P.J., Gray, R.D., Hunt, G.R., 2011. The social structure of New Caledonian crows. Anim. Behav. 81, 83–92. doi:10.1016/j.anbehav.2010.09.015

Horik, J.O. Van, Clayton, N.S., Emery, N.J., 2011. Convergent Evolution of Cognition in Corvids, Apes and Other Animals 80–101.

Huber, L., Rechberger, S., Taborsky, M., 2001. Social learning affects object exploration and manipulation in keas, Nestor notabilis. Anim. Behav. 62, 945–954. doi:10.1006/anbe.2001.1822

Humphrey, N.K., 1976. The social function of intellect.pdf.

Hunt, G.R., Gray, R.D., 2003. Diversification and cumulative evolution in New Caledonian crow tool manufacture. Proc. Biol. Sci. 270, 867–74. doi:10.1098/rspb.2002.2302

I

Isbell, L., Young, T., 2002. Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. Behaviour 139, 177–202. doi:10.1163/156853902760102645

Izawa, E., Watanabe, S., 2008. Formation of linear dominance relationship in captive jungle crows (Corvus macrorhynchos): Implications for individual recognition. Behav. Processes 78, 44–52. doi:10.1016/j.beproc.2007.12.010

J

Jacobs, A., Petit, O., 2011. Social network modeling: a powerful tool for the study of group scale phenomena in primates. Am. J. Primatol. 73, 741–7. doi:10.1002/ajp.20932

Janson, C.H., Van Schaik, C.P., 1988. Recognizing the many faces of primate food competition: methods. Behaviour 105, 165–186.

Jarman, P., 1974. The social organisation of antelope in relation to their ecology. Behaviour 48(1), 215–267.

Jarvis, J.U.M., Series, N., May, N., 2008. Eusociality in a Mammal : Cooperative Breeding in Naked Mole-Rat Colonies Eusociality in a Mammal : Cooperative 212, 571–573.

Jeanson, R., Rivault, C., Deneubourg, J.L., Blanco, S., Fournier, R., Jost, C., Theraulaz, G., 2005. Self-organized aggregation in cockroaches. Anim. Behav. 69, 169–180. doi:10.1016/j.anbehav.2004.02.009

Jennings, A., 1955. Diseases in Wild Birds. Bird Study 2, 69–72. doi:10.1080/00063655509475813

Johnson, K.P., McKinney, F., Sorenson, M.D., 1999. Phylogenetic constraint on male parental care in the dabbling ducks. Proc. R. Soc. B Biol. Sci. 266, 759. doi:10.1098/rspb.1999.0702

Johnstone, R.A., 2006. Negotiation over offspring care--how should parents respond to each other's efforts? Behav. Ecol. 17, 818–827. doi:10.1093/beheco/arl009

Jolles, J.W., King, A.J., Manica, A., Thornton, A., 2013a. Heterogeneous structure in mixed-species corvid flocks in flight. Anim. Behav. 85, 743–750. doi:10.1016/j.anbehav.2013.01.015

Jolles, J.W., Ostojić, L., Clayton, N.S., 2013b. Dominance, pair bonds and boldness determine social-foraging tactics in rooks, Corvus frugilegus. Anim. Behav. 85, 1261–1269. doi:10.1016/j.anbehav.2013.03.013

Jolly, A., 1966. Lemur social behavior and primate intelligence. Science 153(3735),501-506. doi:http://dx.doi.org/10.1126/science.153.3735.501

Jovani, R., Grimm, V., 2008. Breeding synchrony in colonial birds: from local stress to global harmony. Proc. Biol. Sci. 275, 1557–1563. doi:10.1098/rspb.2008.0125

K

Kappeler, P.M., 1993. Variation in Social Structure - The Effects of Sex and Kinship on Social Interactions in 3 Lemur Species. Ethology 93, 125–145.

Kappeler, P.M., Van Schaik, C.P., 2002. Evolution of primate social systems. Int. J. Primatol. 23, 707–740. doi:10.1023/A:1015520830318

Kasprzykowski, Z. 2003. Habitat preferences of foraging Rooks Corvus frugilegus during the breeding period in the agricultural landscape of eastern Poland. *Acta Ornithologica*, *38*(1), 27-31.

Kasprzykowski, Z., 2008. Nest location within the tree and breeding parameters of Rooks Corvus frugilegus. Bird Study 55, 59–65. doi:10.1080/00063650809461505

Kerth, G., Perony, N., Schweitzer, F., 2011. Bats are able to maintain long-term social relationships despite the high fission-fusion dynamics of their groups. Proc. Biol. Sci. 278, 2761–7. doi:10.1098/rspb.2010.2718

King, A.J., Sueur, C., Huchard, E., Cowlishaw, G., 2011a. A rule-of-thumb based on social affiliation explains collective movements in desert baboons. Anim. Behav. 82, 1337–1345. doi:10.1016/j.anbehav.2011.09.017

King, A.J., Clark, F.E., Cowlishaw, G., 2011b. The dining etiquette of desert baboons: the roles of social bonds, kinship, and dominance in co-feeding networks. Am. J. Primatol. 73, 768–74. doi:10.1002/ajp.20918

King, A.J., Sumpter, D.J.T., 2012. Murmurations. Curr. Biol. 22, 112–114. doi:10.1016/j.cub.2011.11.033

King C.E., 2006. Pink flamingos: atypical partnerships and sexual activity in colonially breeding birds. In: Sommer V, Vasey PL (eds) Homosexual behaviour in animals. An evolutionary perspective. Cambridge University Press, New York, pp 77–106

Klass, K., & Cords, M., 2011. Effect of unknown relationships on linearity, steepness and rank ordering of dominance hierarchies: simulation studies based on data from wild monkeys. Behav. Processes 88(3), 168–176.

Komdeur, J., 1994. The Effect of Kinship on Helping in the Cooperative Breeding Seychelles Warbler (Acrocephalus sechellensis). Proc. R. Soc. B Biol. Sci. 256, 47–52. doi:10.1098/rspb.1994.0047

Koski, S.E., de Vries, H., van de Kraats, A., Sterck, E.H.M., 2012. Stability and Change of Social Relationship Quality in Captive Chimpanzees (Pan troglodytes). Int. J. Primatol. 33, 905–921. doi:10.1007/s10764-012-9623-2

Kotrschal, K., Hemetsberger, J., Weiß, B.M., 2006. Making the best of a bad situation: homosociality in male greylag geese. Homosexual Behaviour in Animals. An Evolutionnary Perspective. Cambridge Univ. Press, New York, 45–76.

Krams, I., Krama, T., Igaune, K., 2006. Mobbing behaviour: Reciprocity-based co-operation in breeding Pied Flycatchers Ficedula hypoleuca. Ibis 148, 50–54. doi:10.1111/j.1474-919X.2006.00480.x

Krause, J., Ruxton, G.D., 2002. Living in groups. Oxford University Press.

Krützen, M., Mann, J., Heithaus, M.R., Connor, R.C., Bejder, L., Sherwin, W.B., 2005. Cultural transmission of tool use in bottlenose dolphins. Proc. Natl. Acad. Sci. 102, 8939–43. doi:10.1073/pnas.0500232102

Kudo, H., Dunbar, R.I.M., 2001. Neocortex size and social network size in primates. Anim. Behav. 62, 711–722. doi:10.1006/anbe.2001.1808

Kulahci, I. G., Rubenstein, D. I., Bugnyar, T., Hoppitt, W., Mikus, N., & Schwab, C. 2016. Social networks predict selective observation and information spread in ravens. Royal Society Open Science, 3(7), 160256.

Kulik, L., Muniz, L., Mundry, R., Widdig, A., 2012. Patterns of interventions and the effect of coalitions and sociality on male fitness. Mol. Ecol. 21, 699–714. doi:10.1111/j.1365-294X.2011.05250.x

Kummer, H., 1968. Social organization of hamadryas baboons (Vol. 765). Chicago: Univ. Press.

Kutsukake, N., 2000. Matrilineal rank Inheritance varies with absolute rank in Japanese macaques. Primates 41, 321–335. doi:10.1007/BF02557601

Kurvers, R. H., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S. E., Ydenberg, R. C., & Prins, H. H. 2009. Personality differences explain leadership in barnacle geese. Animal Behaviour, 78(2), 447-453.

L

Lamprecht, J., 1985. Structure and causation of the dominance hierarchy in a flock of bar-headed geese (Anser indicus). Behaviour 96, 28–48. doi:10.1163/156853986X00207

Landeau, L., Terborgh, J., 1986. Oddity and the “confusion effect” in predation. Anim. Behav. 34(5), 1372–1380. doi:10.1016/S0003-3472(86)80208-1

Langergraber, K.E., Mitani, J.C., Vigilant, L., 2007. The limited impact of kinship on cooperation in wild chimpanzees. Proc. Natl. Acad. Sci. U. S. A. 104, 7786–90. doi:10.1073/pnas.0611449104

Le Bohec, C., Gauthier-Clerc, M., Le Maho, Y., 2005. The adaptive significance of crèches in the king penguin. Anim. Behav. 70, 527–538. doi:10.1016/j.anbehav.2004.11.012

Lefebvre, L., Reader, S.M., Sol, D., 2004. Brains, innovations and evolution in birds and primates. Brain. Behav. Evol. 63, 233–46. doi:10.1159/000076784

Lehmann, J., Boesch, C., 2004. To fission or to fusion: effects of community size on wild chimpanzee (Pan troglodytes verus) social organisation. Behav. Ecol. Sociobiol. 56, 207–216. doi:10.1007/s00265-004-0781-x

Lehmann, J., Korstjens, A. H., Dunbar, R.I.M., 2007a. Group size, grooming and social cohesion in primates. Anim. Behav. 74, 1617–1629. doi:10.1016/j.anbehav.2006.10.025

Lehmann, J., Korstjens, A.H., Dunbar, R.I.M., 2007b. Fission-fusion social systems as a strategy for coping with ecological constraints: A primate case. Evol. Ecol. 21, 613–634. doi:10.1007/s10682-006-9141-9

Leiva, D., de Vries, H., 2014. Testing Steepness of Dominance Hierarchies. R Package version 0.2-2.

Lewis, S., Roberts, G., Harris, M.P., Prigmore, C., Wanless, S., 2007. Fitness increases with partner and neighbour allopreening. Biol. Lett. 3, 386–9. doi:10.1098/rsbl.2007.0258

Lincoln, G.A., Racey, P.A., Sharp, P. J., &, Klandorf, H., 1980. Endocrine changes associated with spring and autumn sexuality of the rook, Corvus frugilegus. J. Zool. 190(2), 137–153.

Linklater, W.L., 2000. Adaptive explanation in socio-ecology: lessons from the Equidae. Biol. Rev. Camb. Philos. Soc. 75, 1–20. doi:10.1111/j.1469-185X.1999.tb00039.x

Lockie, J. D. 1955. The breeding and feeding of Jackdaws and Rooks with notes on Carrion Crows and other Corvidae. Ibis, 97(2), 341-369.

Lockie, J. D. 1956. Winter fighting in feeding flocks of rooks, jackdaws and carrion crows. *Bird Study*, *3*(3), 180-190.

Logan, C.J., Emery, N.J., Clayton, N.S., 2012. Alternative behavioral measures of postconflict affiliation. Behav. Ecol. 24, 98–112. doi:10.1093/beheco/ars140

Logan, C.J., Ostojić, L., Clayton, N.S., 2013. Rook, But Not Jackdaw, Post-Conflict Third-Party Affiliation Reduces Aggression for Aggressors. Ethology 119, 427–435. doi:10.1111/eth.12078

Loretto, M.-C., Fraser, O.N., Bugnyar, T., 2012. Ontogeny of Social Relations and Coalition Formation in Common Ravens (Corvus corax). Int. J. Comp. Psychol. 25, 180–194.

Lott, D.F., 1991. Intraspecific variation in the social systems of wild vertebrates (Vol. 2). CambridgeUniv. Press.

Lou, T., Tang, J.I.E., Hopcroft, J., Fang, Z., Ding, X., 2013. Learning to Predict Reciprocity and Triadic Closure in social networks. ACM Trans. Knowl. Discov. Data (TKDD), 7(2), 5.

Lusseau, D., 2003. The emergent properties of a dolphin social network. Proc. Biol. Sci. 270(Suppl 2), S186–8. doi:10.1098/rsbl.2003.0057

Lusseau, D., Newman, M.E.J., 2004. Identifying the role that animals play in their social networks. Proc. Biol. Sci. 271 Suppl , S477–81. doi:10.1098/rsbl.2004.0225

Lusseau, D., Schneider, K., Boisseau, O.J., Haase, P., Slooten, E., Dawson, S.M., 2003. The bottlenose dolphin community of doubtful sound features a large proportion of long-lasting associations: Can geographic isolation explain this unique trait? Behav. Ecol. Sociobiol. 54, 396–405. doi:10.1007/s00265-003-0651-y

Lusseau, D., Wilson, B., Hammond, P.S., Grellier, K., Durban, J.W., Parsons, K.M., Barton, T.R., Thompson, P.M., 2006. Quantifying the influence of sociality on population structure in bottlenose dolphins. J. Anim. Ecol. 75, 14–24. doi:10.1111/j.1365-2656.2005.01013.x

M

Mackinson, S., 1999. Variation in structure and distribution of pre-spawning Pacific herring shoals in two regions of British Columbia. J. Fish Biol. 55, 972–989. doi:10.1006/jfbi.1999.1104

Madge, S., Burn, H., 1993. Crows and jays: a guide to the crows, jays and magpies of the world.

Majolo, B., Ventura, R., Schino, G., 2010. Asymmetry and Dimensions of Relationship Quality in the Japanese Macaque (Macaca fuscata yakui). Int. J. Primatol. 31, 736–750. doi:10.1007/s10764-010-9424-4

Maklakov, A.A., 2002. Snake-directed mobbing in a cooperative breeder: anti-predator behaviour or self-advertisement for the formation of dispersal coalitions? Behav. Ecol. Sociobiol. 52(5), 372–378. doi:DOI 10.1007/s00265-002-0528-5

Mariette, M.M., Griffith, S.C., 2015. The adaptive significance of provisioning and foraging coordination between breeding partners. Am. Nat. 185, 270–80. doi:10.1086/679441

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. doi:10.1111/j.1600-048X.2012.05555.x

Marshall, A.J., Coombs, C.J.F., 1956. The interaction of enviromental, internal and behavioral factors in the rooks, Corvus frugilegus.

Martin, T.E., 1988. Processes organizing open-nesting bird assemblages: competition or nest predation? Evol. Ecol. doi:10.1007/BF02071587

Marzluff, J.M., Heinrich, B., 1991. Foraging by common ravens in the presence and absence of territory holders: an experimental analysis of social foraging. Anim. Behav. 42, 755–770. doi:10.1016/S0003-3472(05)80121-6

Massen, J.J.M., Pašukonis, A., Schmidt, J., Bugnyar, T., 2014a. Ravens notice dominance reversals among conspecifics within and outside their social group. Nat. Commun. 5, 1–7. doi:10.1038/ncomms4679

Massen, J. J., Szipl, G., Spreafico, M., & Bugnyar, T. 2014b. Ravens intervene in others' bonding attempts. Current Biology, 24(22), 2733-2736.

Mason, C. F., & MacDonald, S. M. 2004. Distribution of foraging rooks, Corvus frugilegus, and rookeries in a landscape in eastern England dominated by winter cereals. Folia Zoologica, 53(2), 179.

Matsumura, S., 1999. The evolution of “egalitarian” and “despotic” social systems among macaques. Primates 40(1), 23–31.

McFarland Symington, M., 1990. Fission-fusion social organization in Ateles and Pan. Int. J. Primatol. 11, 47–61. doi:10.1007/BF02193695

McGraw K.J., Hill G.E. 1999. Induced homosexual behaviour in male house finches (Carpodacus mexicanus): the “Prisoner effect”. Ethol Ecol Evol 11:197–201

McFarland, R., Majolo, B., 2011. Exploring the components, asymmetry and distribution of relationship quality in wild barbary macaques (macaca sylvanus). PLoS One 6(12),. doi:10.1371/journal.pone.0028826

Melis, A.P., Hare, B., Tomasello, M., 2006. Engineering cooperation in chimpanzees: tolerance constraints on cooperation. Anim. Behav. 72, 275–286. doi:10.1016/j.anbehav.2005.09.018

Menard, N., 2004. Do ecological factors explain variation in social organization?, in: Macaque Societies: A Model for the Study of Social Organization (Vol. 41). pp. 237.

Mendoza, S.P., Mason, W.A., 1986. Contrasting responses to intruders and to involuntary separation by monogamous and polygynous New World monkeys. Physiol. Behav. 38, 795–801. doi:10.1016/0031-9384(86)90045-4

Milinski, M., 1984. A predator's costs of overcoming the confusion-effect of swarming prey. Anim. Behav. 32(4), 1157–1162. doi:doi:10.1016/S0003-3472(84)80232-8

Minias, P., 2014. Evolution of within-colony distribution patterns of birds in response to habitat structure. Behav. Ecol. Sociobiol. 68, 851–859. doi:10.1007/s00265-014-1697-8

Mirabet, V., Auger, P., Lett, C., 2007. Spatial structures in simulations of animal grouping. Ecol. Modell. 201, 468–476. doi:10.1016/j.ecolmodel.2006.10.018

Mitani, J., Merriwether, D., Zhang, C., 2000. Male affiliation, cooperation and kinship in wild chimpanzees. Anim. Behav. 59, 885–893. doi:10.1006/anbe.1999.1389

Møller, A.P., 1987. Advantages and disadvantages of coloniality in the swallow, Hirundo rustica. Anim. Behav. 35, 819–832. doi:10.1016/S0003-3472(87)80118-5

Moore, J., 1992. Dispersal, nepotism, and primate social behavior. Int. J. Primatol. doi:10.1007/BF02547823

Mooring, M.S., Hart, B. L., 1995. Costs of allogrooming in impala: distraction from vigilance. Anim. Behav. 49, 1414–1416. doi:10.1006/anbe.1995.0175

N

Nagy, M., Akos, Z., Biro, D., Vicsek, T., 2010. Hierarchical group dynamics in pigeon flocks. Nature 464, 890–3. doi:10.1038/nature08891

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., 2011. Assessing dominance hierarchies : validation and advantages of progressive evaluation with Elo-rating. Anim. Behav., 82(4), 911–921. doi:10.1016/j.anbehav.2011.07.016

Nohria, N., 1992. Is a network perspective a useful way of studying organizations, in Nohria, N. & Eccles, R.G., Networks and Organizations: Structures, Form and Action. HBS Press, Boston, pp. 1–22.

O

Ogilvie, C.M., 1951. The building of a rookery. Br. Birds 44, 1–5.

Oh, K.P., Badyaev, A. V, 2010. Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. Am. Nat. 176, E80–9. doi:10.1086/655216

Okubo, A., 1986. Dynamical aspects of animal grouping: Swarms, schools, flocks, and herds. Adv. Biophys. 22, 1–94. doi:10.1016/0065-227X(86)90003-1

Ossi, K., Kamilar, J.M., 2006. Environmental and phylogenetic correlates of Eulemur behavior and ecology (Primates: Lemuridae). Behav. Ecol. Sociobiol. 61, 53–64. doi:10.1007/s00265-006-0236-7

Owen, D.F., 1959. The breeding season and clutch-size of the rooks Corvus frugilegus. Ibis 101(2), 235–239.

P

Parrish, J.K., Viscido, S. V., Grünbaum, D., 2002. Self-organized fish schools: an examination of emergent properties. Biol. Bull. 202(3), 296–305.

Paz-y-Mino, G.C., Bond, A.B., Kamil, A.C., & Balda, R.P., 2004. Pinyon jays use transitive inference to predict social dominance. Nature 430(7001), 778–781. doi:10.1038/nature02720.1.

Pérez-barbería, F.J., Nores, C., 1994. Seasonal variation in group size of Cantabrian chamois in relation to escape terrain and food.Acta Ther., 39(3), 295–305.

Pérez-Barbería, F.J., Shultz, S., Dunbar, R.I.M., 2007. Evidence for Coevolution of Sociality and Relative Brain Size in Three Orders of Mammals. Evolution, 61(12), 2811–2821. doi:10.1111/j.1558-5646.2007.00229.x

Prum, R.O., 1994. Phylogenetic analysis of the evolution of alternative social behavior in the manakins (Aves: Pipridae). Evolution, 1657–1675.

Pulliam, H.R., 1973. On the advantages of flocking. J. Theor. Biol. 419–422.

Q

Queller, D.C., 1989. The evolution of eusociality: Reproductive head starts of workers). Proc. Nat. Ac. Sci. 86, 3224–3226. doi:10.1073/pnas.86.9.3224

R

Radford, A.N., Fawcett, T.W., 2014. Conflict between Groups Promotes Later Defense of a Critical Resource in a Cooperatively Breeding Bird. Curr. Biol. 24, 2935–2939. doi:10.1016/j.cub.2014.10.036

Ramos-Fernández, G., Boyer, D., Aureli, F., Vick, L.G., 2009. Association networks in spider monkeys (Ateles geoffroyi). Behav. Ecol. Sociobiol. 63, 999–1013. doi:10.1007/s00265-009-0719-4

Ratcliffe, J.M., Ter Hofstede, H.M., 2005. Roosts as information centres: social learning of food preferences in bats. Biol. Lett. 1, 72–4. doi:10.1098/rsbl.2004.0252

Rebecchini, L., Schaffner, C.M., Aureli, F., 2011. Risk is a Component of Social Relationships in Spider Monkeys. Ethology 117, 691–699. doi:10.1111/j.1439-0310.2011.01923.x

Reeve, H.K., Westneat, D.F., Noon, W.A., Sherman, P.W., Aquadro, C.F., 1990. DNA “fingerprinting” reveals high levels of inbreeding in colonies of the eusocial naked mole-rat. Proc. Natl. Acad. Sci. 87, 2496–2500. doi:10.1073/pnas.87.7.2496

Richards, P.R., 1976. Pair Formation and Pair Bond in Captive Rooks. Bird Study 23(3), 207–211.

Richardson, S.C., Patterson, I.J., & Dunnet, G.M., 1979. Fluctuations in colony size in the Rook, Corvus frugilegus. J. Anim. Ecol. 103–110.

Richner, H., & Heeb, P., 1996. Communal life: honest signaling and the recruitment center hypothesis. Behav. Ecol. 115–119.

Ridley, A.R., Nelson-Flower, M.J., Thompson, A.M., 2013. Is sentinel behaviour safe? An experimental investigation. Anim. Behav. 85, 137–142. doi:10.1016/j.anbehav.2012.10.017

Riehl, C., Jara, L., 2009. Natural History and Reproductive Biology of the Communally Breeding Greater Ani (Crotophaga major) at Gatún Lake, Panama. Wilson J. Ornithol. 121, 679–687. doi:10.1676/09-017.1

Righi, S., Takács, K., 2014. Triadic Balance and Closure as Drivers of the Evolution of Cooperation, Advances in Computational Social Science and Social Simulation: Proc. Europ. Soc. Simul. Assoc. (ESSA), Conference 2014. pp. 121–124.

Robichaud, D., Lefebvre, L., Robidoux, L., 1996. Dominance affects resource partitioning in pigeons, but pair bonds do not. Can. J. Zool., 74(5), 833–840.

Roell, A., Bossema, I., 1982. A comparison of nest defence by Jackdaws, rooks, magpies and crows. Behav. Ecol. Sociobiol. 11, 1–6. doi:10.1007/BF00297658

Rolland, C., Danchin, E., & Fraipont, M.D., 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. Am. Nat. 151, 514–529.

Romano, V., Duboscq, J., Sarabian, C., Thomas, E., Sueur, C., MacIntosh, A.J., 2016. Modeling infection transmission in primate networks to predict centrality-based risk. Am. J. Primatol.

Røskaft, E., 1983. Male promiscuity and female adultery by the rook Corvus frugilegus. Ornis Scand. 175–179.

Røskaft, E., Espmark, Y., 1984. Sibling recognition in the rook. Behav. Processes 9, 223–230.

Roulin, A., 1999. Nonrandom pairing by male barn owls (Tyto alba) with respect to a female plumage trait. Behav. Ecol. 10, 688–695. doi:10.1093/beheco/10.6.688

Rubenstein, D.I., 1978. On predation, competition, and the advantages of group living. Soc. Behav. doi:10.1007/978-1-4684-2901-5_9

Rutz, C., Burns, Z.T., James, R., Ismar, S.M.H., Burt, J., Otis, B., Bowen, J., St Clair, J.J.H., 2012. Automated mapping of social networks in wild birds. Curr. Biol. 22, R669–71. doi:10.1016/j.cub.2012.06.037

Ryder, T.B., McDonald, D.B., Blake, J.G., Parker, P.G., Loiselle, B. A, 2008. Social networks in the lek-mating wire-tailed manakin (Pipra filicauda). Proc. Biol. Sci. 275, 1367–74. doi:10.1098/rspb.2008.0205

S

Sánchez-Macouzet, O., Rodríguez, C., Drummond, H., 2014. Better stay together: pair bond duration increases individual fitness independent of age-related variation. Proc. Biol. Sci. 281, 20132843. doi:10.1098/rspb.2013.2843

Schaffner, C.M., Aureli, F., Caine, N.G., 2005. Following the rules: Why small groups of tamarins do not reconcile conflicts. Folia Primatol. 76, 67–76. doi:10.1159/000083614

Schaik, V.C.P., Van Noordwijk, M.A., Warsono, B., Sutriono, E., 1983. Party size and early detection of predators in Sumatran forest primates. Primates 211–221.

Scheiber, I. B., Weiß, B. M., Hirschenhauser, K., Wascher, C. A., Nedelcu, I. T., & Kotrschal, K. 2008. Does 'relationship intelligence'make big brains in birds?. The open biology journal, 1, 6.

Scheid, C., Noë, R., 2010. The performance of rooks in a cooperative task depends on their temperament. Anim. Cogn. 13, 545–53. doi:10.1007/s10071-009-0305-1

Scheid, C., Schmidt, J., Noë, R., 2008. Distinct patterns of food offering and co-feeding in rooks. Anim. Behav. 76, 1701–1707. doi:10.1016/j.anbehav.2008.07.023

Schino, G., 2000. Beyond the primates: expanding the reconciliation horizon, in Aureli, F., Waal, F.B.,Natural Conflict Resolution, Univ. of California Press. p. 225e242.

Schino, G., di Sorrentino, E.P., Tiddi, B., 2007. Grooming and coalitions in Japanese macaques (Macaca fuscata): partner choice and the time frame reciprocation. J. Comp. Psychol. 121, 181–8. doi:10.1037/0735-7036.121.2.181

Schradin, C., 2013. Intraspecific variation in social organization by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors. Philos. Trans. R. Soc. B Biol. Sci. 368, 20120346. doi:10.1098/rstb.2012.0346

Schradin, C., Koenig, B., Pillay, N., 2010. Reproductive competition favours solitary living while ecological constraints impose group-living in African striped mice. J. Anim. Ecol. 79, 515–521. doi:10.1111/j.1365-2656.2009.01651.x

Schradin, C., Lindholm, A.K., Johannesen, J., Schoepf, I., Yuen, C.H., Koenig, B., Pillay, N., 2012. Social flexibility and social evolution in mammals: A case study of the African striped mouse (Rhabdomys pumilio). Mol. Ecol. 21, 541–553. doi:10.1111/j.1365-294X.2011.05256.x

Schülke, O., Bhagavatula, J., Vigilant, L., Ostner, J., 2010. Social bonds enhance reproductive success in male macaques. Curr. Biol. 20, 2207–2210. doi:10.1016/j.cub.2010.10.058

Seed, A., Emery, N., Clayton, N., 2009. Intelligence in Corvids and Apes: A Case of Convergent Evolution?. Ethology 115, 401–420. doi:10.1111/j.1439-0310.2009.01644.x

Seed, A.M., Clayton, N.S., Emery, N.J., 2008. Cooperative problem solving in rooks (Corvus frugilegus). Proc. Biol. Sci. 275, 1421–9. doi:10.1098/rspb.2008.0111

Seed, A.M., Clayton, N.S., Emery, N.J., 2007. Postconflict third-party affiliation in rooks, Corvus frugilegus. Curr. Biol. 17, 152–8. doi:10.1016/j.cub.2006.11.025

Seed, A.M., Tebbich, S., Emery, N.J., Clayton, N.S., 2006. Investigating physical cognition in rooks, Corvus frugilegus. Curr. Biol. 16, 697–701. doi:10.1016/j.cub.2006.02.066

Seibert, L.M., Crowell-Davis, S.L., 2001. Gender effects on aggression, dominance rank, and affiliative behaviors in a flock of captive adult cockatiels (Nymphicus hollandicus). Appl. Anim. Behav. Sci. 71, 155–170. doi:10.1016/S0168-1591(00)00172-6

Seyfarth, R.M., 1980. The distribution of grooming and related behaviours among adult female vervet monkeys. Anim. Behav. 28, 798–813. doi:10.1016/S0003-3472(80)80140-0

Seyfarth, R.M., Cheney, D.L., 1984. Grooming, alliances and reciprocal altruism in vervet monkeys. Nature 308, 541–543. doi:10.1038/308541a0

Shizuka, D., McDonald, D.B., 2015. The network motif architecture of dominance hierarchies. J. R. Soc. Interface 12, 20150080–20150080. doi:10.1098/rsif.2015.0080

Shizuka, D., McDonald, D.B., 2012. A social network perspective on measurements of dominance hierarchies. Anim. Behav. 83, 925–934. doi:10.1016/j.anbehav.2012.01.011

Shultz, S., Dunbar, R.I.M., 2006. Both social and ecological factors predict ungulate brain size. Proc. R. Soc. Biol. Sci. 273, 207–15. doi:10.1098/rspb.2005.3283

Shultz, S., Dunbar, R.I.M., 2009. Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment - SHULTZ - 2010 - Biological Journal of the Linnean Society - Wiley Online Library 111–123.

Shultz, S., Dunbar, R., 2010a. Bondedness and sociality. Behaviour 147, 775–803. doi:10.1163/000579510X501151

Shultz, S., Dunbar, R.I.M., 2010b. Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment. Biol. J. Linn. Soc. 100, 111–123. doi:10.1111/j.1095-8312.2010.01427.x

Sigurjónsdóttir, H., Van Dierendonck, M.C., Snorrason, S. & Thórhallsdóttir, A. G., 2003. Social relationships in a group of horses without a mature stallion. Behaviour 140(6), 783–804. doi:10.1163/156853903322370670

Silk, M.J., Croft, D.P., Tregenza, T., Bearhop, S., 2014. The importance of fission – fusion social group dynamics in birds. Ibis, 156(4), 701–715.

Silk, J.B., 2002. Using the ’F'-word in primatology. Behaviour, 139(2-3), 421–446. doi:10.1163/156853902760102735

Silk, J.B., 2002. Kin selection in primate groups. Int. J. Primatol. 23, 849–875. doi:10.1023/A:1015581016205

Silk, J., Cheney, D., Seyfarth, R., 2013. A practical guide to the study of social relationships. Evol. Anthropol. 22, 213–225. doi:10.1002/evan.21367

Silk, J.B., 2007a. Social components of fitness in primate groups. Science 317, 1347–1351. doi:10.1126/science.1140734

Silk, J.B., 2007b. The adaptive value of sociality in mammalian groups. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 362, 539–59. doi:10.1098/rstb.2006.1994

Silk, J.B., Alberts, S.C., Altmann, J., 2006a. Social relationships among adult female baboons (Papio cynocephalus) II. Variation in the quality and stability of social bonds. Behav. Ecol. Sociobiol. 61, 197–204. doi:10.1007/s00265-006-0250-9

Silk, J.B., Alberts, S.C., Altmann, J., 2004. Patterns of coalition formation by adult female baboons in Amboseli, Kenya. Anim. Behav. 67, 573–582. doi:10.1016/j.anbehav.2003.07.001

Silk, J.B., Alberts, S.C., Altmann, J., 2003. Social bonds of female baboons enhance infant survival. Science 302, 1231–1234. doi:10.1126/science.1088580

Silk, J.B., Altmann, J., Alberts, S.C., 2006b. Social relationships among adult female baboons (Papio cynocephalus) I. Variation in the strength of social bonds. Behav. Ecol. Sociobiol. 61, 183–195. doi:10.1007/s00265-006-0249-2

Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., Cheney, D.L., 2010. Strong and consistent social bonds enhance the longevity of female baboons. Curr. Biol. 20, 1359–1361. doi:10.1016/j.cub.2010.05.067

Smith, J.E., Kolowski, J.M., Graham, K.E., Dawes, S.E., Holekamp, K.E., 2008. Social and ecological determinants of fission-fusion dynamics in the spotted hyaena. Anim. Behav. 76, 619–636. doi:10.1016/j.anbehav.2008.05.001

Smith, J.E., Van Horn, R.C., Powning, K.S., Cole, A.R., Graham, K.E., Memenis, S.K., Holekamp, K.E., 2010. Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. Behav. Ecol. 21, 284–303. doi:10.1093/beheco/arp181

Soltis, J., Mitsunaga, F., Shimizu, K., Yanagihara, Y., & Nozaki, M., 1997. Sexual selection in Japanese macaques I: female mate choice or male sexual coercion?. Animal Behaviour, 54(3), 725-736.

Spoon, T.R., Millam, J.R., Owings, D.H., 2007. Behavioural compatibility, extrapair copulation and mate switching in a socially monogamous parrot. Anim. Behav. 73(5), 815–824. doi:10.1016/j.anbehav.2006.10.010

Spoon, T.R., Millam, J.R., Owings, D.H., 2006. The importance of mate behavioural compatibility in parenting and reproductive success by cockatiels, Nymphicus hollandicus. Anim. Behav. 71(2), 315–326. doi:10.1016/j.anbehav.2005.03.034

Spoon, T.R., Millam, J.R., Owings, D.H., 2004. Variation in the stability of cockatiel (Nymphicus hollandicus) pair relationships : the roles of males, females, and mate compatibility. Behaviour 141(10), 1211–1234.

Sridhar, H., Shanker, K., 2013. Using intra-flock association patterns to understand why birds participate in mixed-species foraging flocks in terrestrial habitats. Behav. Ecol. Sociobiol. 68, 185–196. doi:10.1007/s00265-013-1633-3

Stahl, J., Tolsma, P.H., Loonen, M.J.J.E., Drent, R.H., 2001. Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks. Anim. Behav. 61, 257–264. doi:10.1006/anbe.2000.1564

Stander, P.E., 1992. Cooperative hunting in lions: the role of the individual. Behav. Ecol. Sociobiol. 29, 445–454. doi:10.1007/BF00170175

Sterck, E.H.M., Watts, D.P., vanSchaik, C.P., 1997. The evolution of female social relationships in nonhuman primates. Behav. Ecol. Sociobiol. 41, 291–309. doi:10.1007/s002650050390

Stevens, J.M., de Groot, E., & Staes, N., 2015. Relationship quality in captive bonobo groups. Behaviour 152, 259–283. doi:10.1163/1568539X-00003259

Struhsaker, T.T., 1969. Correlates of ecology and social organization among African cercopithecines. Folia Primatol. 11, 80–118. doi:10.1159/000155259

Sue Carter, C., Courtney Devries, A., Getz, L.L., 1995. Physiological substrates of mammalian monogamy: The prairie vole model. Neurosci. Biobehav. Rev. 19, 303–314. doi:10.1016/0149-7634(94)00070-H

Sumpter, D.J., 2006. The principles of collective animal behaviour. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 361, 5–22. doi:10.1098/rstb.2005.1733

Swingland, I.R., 1973. The Social Organisation of Roosting in Rooks and Jackdaws. Ph.D. Thesis, University of Edinburgh

Swingland, I.R., 1977. The social and spatial organization of winter communal roosting in Rooks (Corvus frugilegus). J. Zool. London 182, 509–528.

Szabo, B., Bugnyar, T., & Auersperg, A. M. I. 2016. Within-group relationships and lack of social enhancement during object manipulation in captive Goffin’s cockatoos (Cacatua goffiniana). Learning & Behavior, 1-13.

T

Tamm, S., 1977. Social dominance in captive jackdaws (Corvus monedula). Behav. Processes 2(3), 293–299. doi:10.1016/0376-6357(77)90032-8

Tarvin, K. A, Woolfenden, G.E., 1997. Patterns of Dominance and Aggressive Behaviour in Blue Jays at a Feeder. Condor, 434–444.

Taylor, P., Källander, H., 2010. Food hoarding and use of stored food by Rooks Corvus frugilegus 37–41.

Tebbich, S., Seed, A.M., Emery, N.J., Clayton, N.S., 2007. Non-tool-using rooks, Corvus frugilegus, solve the trap-tube problem. Anim. Cogn. 10, 225–31. doi:10.1007/s10071-006-0061-4

Tebbich, S., Taborsky, M., Winkler, H., Lorenz-institut, K., Verhaltensforschung, V., 1996. Social manipulation causes cooperation in keas. Anim. Behav. 52, 1–10. doi:10.1006/anbe.1996.0147

Thierry, B., 2013. Identifying constraints in the evolution of primate societies. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 368, 20120342. doi:10.1098/rstb.2012.0342

Thierry, B., 2008. Les sociétés animales. Encycl. Universalis 22.

Thierry, B., 2007. Unity in diversity: Lessons from macaque societies. Evol. Anthropol. 16, 224–238. doi:10.1002/evan.20147

Thierry, B., Iwaniuk, A.N., Pellis, S.M., 2000. The influence of phylogeny on the social behaviour of macaques (Primates: Cercopithecidae, genus Macaca). Ethology 106, 713–728. doi:10.1046/j.1439-0310.2000.00583.x

Thierry, B., Singh, M., & Kaumanns, W., 2004. Macaque societies: a model for the study of social organization (Vol. 41). Cambridge University press.

Tiddi, B., Aureli, F., Polizzi Di Sorrentino, E., Janson, C.H., Schino, G., 2011. Grooming for tolerance? Two mechanisms of exchange in wild tufted capuchin monkeys. Behav. Ecol. 22, 663–669. doi:10.1093/beheco/arr028

Trivers, R., 1971. The Evolution of Reciprocal Altruism. Q. Rev. Biol. 46, 35–57. doi:10.1086/406755

V

Vail, A.L., Manica, A., Bshary, R., 2013. Referential gestures in fish collaborative hunting. Nat. Commun. 4, 1765. doi:10.1038/ncomms2781

Van De Pol, M., Heg, D., Bruinzeel, L.W., Kuijper, B., Verhulst, S., 2006. Experimental evidence for a causal effect of pair-bond duration on reproductive performance in oystercatchers (Haematopus ostralegus). Behav. Ecol. 17, 982–991. doi:10.1093/beheco/arl036

Van Schaik, C.P., 1989. The ecology of social relationships amongst female primates. In V. Stan. ed. Oxford: Blackwell.

Van Schaik, C. P., & Aureli, F. 2000. The natural history of valuable relationships in primates. *Natural conflict resolution*, 307-33.

Verhulst, S., Geerdink, M., Salomons, H.M., Boonekamp, J.J., 2014. Social life histories: jackdaw dominance increases with age, terminally declines and shortens lifespan. Proc. Biol. Sci. 281. doi:10.1098/rspb.2014.1045

Viblanc, V.A., Pasquaretta, C., Sueur, C., Boonstra, R., & Dobson, F.S., 2016. Aggression in Columbian ground squirrels: relationships with age, kinship, energy allocation, and fitness. Behav. Ecol.

Viblanc, V.A., Valette, V., Kauffmann, M., Malosse, N., Groscolas, R., 2012. Coping with social stress: Heart rate responses to agonistic interactions in king penguins. Behav. Ecol. 23, 1178–1185. doi:10.1093/beheco/ars095

von Bayern, A.M., de Kort, S.R., Clayton, N.S., Emery, N.J., 2007. The role of food- and object-sharing in the development of social bonds in juvenile jackdaws (Corvus monedula). Behaviour 144, 711–733. doi:10.1163/156853907781347826

Vonhof, M.J., Whitehead, H., Fenton, M.B., 2004. Analysis of Spix’s disc-winged bat association patterns and roosting home ranges reveal a novel social structure among bats. Anim. Behav. 68, 507–521. doi:10.1016/j.anbehav.2003.08.025

W

Waite, R. K. 1984. Winter habitat selection and foraging behaviour in sympatric corvids. Ornis Scand. 15, 55-62.

Walker, G., Kogut, B., Shan, W., 1997. Social Capital, Structural Holes and the Formation of an Industry Network. Organ. Sci. 8, 109–125. doi:10.1287/orsc.8.2.109

Ward, P., Zahavi, A., 1973. The imporatance of certain assemblages of birds as “information-centres” for food-finding. Ibis (Lond. 1859). 115, 517–534. doi:10.1111/j.1474-919X.1973.tb01990.x

Wascher, C.A.F., Dufour, V., Bugnyar, T., 2012a. Carrion crows cannot overcome impulsive choice in a quantitative exchange task. Front. Psychol. 3, 1–6. doi:10.3389/fpsyg.2012.00118

Wascher, C.A.F., Fraser, O.N., Kotrschal, K., 2010. Heart rate during conflicts predicts post-conflict stress-related behavior in greylag geese. PLoS One 5. doi:10.1371/journal.pone.0015751

Wascher, C.A.F., Scheiber, I.B.R., Kotrschal, K., 2008. Heart rate modulation in bystanding geese watching social and non-social events. Proc. Biol. Sci. 275, 1653–9. doi:10.1098/rspb.2008.0146

Wascher, C.A.F., Scheiber, I.B.R., Weiß, B.M., Kotrschal, K., 2009. Heart rate responses to agonistic encounters in greylag geese, Anser anser. Anim. Behav. 77, 955–961. doi:10.1016/j.anbehav.2009.01.013

Wascher, C. A., Szipl, G., Boeckle, M., & Wilkinson, A. 2012b. You sound familiar: carrion crows can differentiate between the calls of known and unknown heterospecifics. *Animal cognition*, *15*(5), 1015-1019.

Wasserman, S., & Faust, K., 1994. Social network analysis: Methods and applications (Vol. 8). Cambridge University press.

Watanabe, K., 1979. Alliance formation in a free-ranging troop of Japanese macaques. Primates 20(4), 459–474.

Wechsler, B., 1988. Dominance relationships in jackdaws (Corvus monedula). Behaviour 106(3), 252–264.

Weiß, B.M., Kehmeier, S., Schloegl, C., 2010. Transitive inference in free-living greylag geese, Anser anser. Anim. Behav. 79, 1277–1283. doi:10.1016/j.anbehav.2010.02.029

Weiß, B. M., & Scheiber, I. B. 2013. Long-term memory of hierarchical relationships in free-living greylag geese. *Animal cognition*, *16*(1), 91-97.

West, S.A., Griffin, A.S., Gardner, A., 2007a. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. J. Evol. Biol. 20, 415–32. doi:10.1111/j.1420-9101.2006.01258.x

West, S.A., Griffin, A.S., Gardner, A., 2007b. Evolutionary Explanations for Cooperation. Curr. Biol. 17, 661–672. doi:10.1016/j.cub.2007.06.004

West-Eberhard, M.J., 1979. Sexual selection, social competition, and evolution. Proc. Am. Philos. Soc. 123, 222–234. doi:10.1086/413215

Wey, T., Blumstein, D.T., Shen, W., Jordán, F., 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. Anim. Behav. 75, 333–344. doi:10.1016/j.anbehav.2007.06.020

Wheatcroft, D.J., & Price, T.D., 2008. Reciprocal cooperation in avian mobbing: playing nice pays. Trends Ecol. Evol. 23, 414–416. doi:10.1016/j.tree.2008.05.003

White, F.J., Wood, K.D., 2007. Female Feeding Priority in Bonobos, Pan paniscus, and the Question of Female Dominance. Am. J. Primatol. 1222, 1210–1222. doi:10.1002/ajp

Whitehead, H., Dufault, S., 1999. Techniques for Analysing vertebrate social structure identified individuals: Review and Recommendations. Adv. Study Behav. 28, 33.

Whitehead, H. 2008. *Analyzing animal societies: quantitative methods for vertebrate social analysis*. Chicago: University of Chicago Press.

Wilkinson, G.S., 1984. Reciprocal food sharing in the vampire bat. Nature 308(5955), 181–184.

Williams, R., Lusseau, D., 2006. A killer whale social network is vulnerable to targeted removals. Biol. Lett. 2, 497–500. doi:10.1098/rsbl.2006.0510

Wilson, D.J., 1992. Correlates of agonistic display by great tits parus major. Behaviour 121(3), 168–214. doi:10.1017/CBO9781107415324.004

Wittemyer, G., Douglas-Hamilton, I., Getz, W.M., 2005. The socioecology of elephants: Analysis of the processes creating multitiered social structures. Anim. Behav. 69, 1357–1371. doi:10.1016/j.anbehav.2004.08.018

Wittemyer, G., Getz, W.M., 2007. Hierarchical dominance structure and social organization in African elephants, Loxodonta africana. Anim. Behav. 73, 671–681. doi:10.1016/j.anbehav.2006.10.008

Wittemyer, G., Okello, J.B. a, Rasmussen, H.B., Arctander, P., Nyakaana, S., Douglas-Hamilton, I., Siegismund, H.R., 2009. Where sociality and relatedness diverge: the genetic basis for hierarchical social organization in African elephants. Proc. Biol. Sci. 276, 3513–3521. doi:10.1098/rspb.2009.0941

Wittig, R.M., Boesch, C., 2003. Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. Int. J. Primatol. 24, 847–867. doi:10.1023/A:1024632923180

Wittig, R.M., Crockford, C., Lehmann, J., Whitten, P.L., Seyfarth, R.M., & Cheney, D.L., 2008. Focused grooming networks and stress alleviation in wild female baboons. Horm. Behav. 54(1), 170–177. doi:10.1038/nmeth.2250.Digestion

Woolfenden, G.E., Fitzpatrick, J.W., 1977. Dominance in the Florida Scrub-Jay. Condor 79, 1–12. doi:10.1126/science.100.2609.594

Wrangham, R.W., 1980. An Ecological Model of Female-Bonded Primate Groups. Behaviour 75, 262–300

Wrigh, J., Maklakov, A. A., Khazin, V., 2001. State-dependent sentinels: an experimental study in the Arabian babbler. Proc. Biol. Sci. 268, 821–826. doi:10.1098/rspb.2000.1574

Wrona, F.J., Dixon, R.J., 1990. Group size and predation risk: a field analysis of encounter and dilution effects. Am. Nat. 186–201

Y

Young, A.J., Carlson, A.A, Monfort, S.L., Russell, A.F., Bennett, N.C., Clutton-Brock, T., 2006. Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. Proc. Natl. Acad. Sci. 103, 12005–12010. doi:10.1073/pnas.0510038103

Young, L.C., Zaun, B.J., VanderWerf, E.A., 2010. Successful same-sex pairing in laysan albatross. Biol Lett 4:323–325

Z

Zann R.A., 1996. The zebra finch: a synthesis of field and laboratory studies. Oxford University Press, Oxford

Zandberg, L., Jolles, J.W., Boogert, N.J., Thornton, A., 2014. Jackdaw nestlings can discriminate between conspecific calls but do not beg specifically to their parents. Behav. Ecol. 25, 565–573. doi:10.1093/beheco/aru026

Zuberbühler, K., Noë, R., Seyfarth, R.M., 1997. Diana Monkey long-distance calls: messages for conspecifics and predators. Anim. Behav. 53, 589–604. doi:10.1006/anbe.1996.0334

Zuk M., 2006. Family values in black and white. Nature 439:917

SUMMARY

One of the major issues inherent to our understanding of the evolution of animal sociality is that it remains strongly taxa-biased. For instance, studies on mammals and in particular primates are clearly overrepresented in comparison to birds' social organisation studies. If the current paradigm shift in bird socio-biology is slowly acknowledging that in some species, the social organisation may be far more complex than simple aggregations, numerous assumptions on bird sociality remain untested.

Yet numerous avian species are good candidates to study the emergence of complex forms of sociality. This concern in particular species showing advanced cognitive skills, like corvids or parrots, and living in groups all year long, where individuals necessarily have to cope with both the costs and the benefits of group living. Among corvid species, rooks are then particularly relevant because they form long-term monogamous pair bond and live in colonies all year long. But whether rooks have the ability to bond out of the pair, and whether they live in a stable and integrated social structure characterised by different layers of relationships, remained to be determined. In my thesis, I investigated the diversity and the dynamic of social relationships in a group of captive adult rooks over three years. Overall, my results highlight a picture of rooks' social life that is partially consistent with the prevalent belief, but also raises a few questions about the actual complexity of their social system.

I show that adult rooks have the ability to form non-reproductive social bond, resulting in the formation of a modular social structure. This structure emerges from the inter-connection of intra- and extra-pair relationships (i.e. both mixed-sex and same-sex). More precisely, the dynamic of the relationships points out that pairs have a strong attractor effect on social interactions, providing interesting novel insights on how such a strong bond can influence the shape of the overall group's social structure. In addition, the social structure of the group appeared flexible enough to allow temporal variations of relationships, group composition and sex-ratio, preserving the group stability over time. I also found that rooks are not absolute monogamous, but have the ability to form several pair bond throughout their life. All separations were concomitant to the formation of a new pair (i.e. mate switching), indicating that extra-pair relationships can influence the strength and the stability of the monogamous pair bond. Finally, my results indicate that dominance relationships do not have any long lasting effects on the stabilisation of the social structure in rooks. Indeed, dominance relationships were highly unstable over time, which precluded a reliable assessment of the hierarchy. As it is, my work questions former evidences about hierarchical ranking and linearity in rooks. Indeed, if hierarchies can potentially develop in rooks, how predominant are they on rooks' social organisation remained unclear.

Overall, my work provides a focused view on the proximate mechanisms that sustain the establishment and the stability of rooks' social structure. My results demonstrate that rooks social structure extends far beyond the simple aggregation of reproductive pairs, and may be acknowledged as a multi-level, or modular social organisation. By fostering our knowledge of rooks' social organisation, my thesis contributes to the establishment of a comparative framework in corvids, necessary to a better understanding of the overall evolution of animal sociality. More broadly, it also widen our knowledge on the proximate mechanisms underlying the emergence of social structures, and ultimately on the function of sociality.

UNIVERSITÉ DE STRASBOURG

Palmyre BOUCHERIE

École Doctorale
des Sciences de la Vie
et de la Santé
STRASBOURG

LAYERS OF SOCIAL ORGANISATION IN ROOKS, A MONOGAMOUS BIRD SPECIES

Chez les oiseaux, les espèces aux aptitudes cognitives avancées, et celles faisant face aux coûts et aux bénéfices de la vie en groupe, sont particulièrement intéressantes pour étudier l'émergence de formes complexes de socialité. Dans ma thèse, j'ai étudié les mécanismes comportementaux sous-jacents à la diversité et la dynamique des relations sociales dans un groupe de corbeaux freux captifs, une espèce de corvidé monogame et coloniale. J'ai montré que les freux peuvent former des relations en dehors du contexte reproducteur et changer de partenaire au cours de leur vie. De plus, j'ai montré : une certaine résilience de la structure sociale face aux variations temporelles des relations, de la composition du groupe et du sex-ratio; et l'absence d'effets stabilisateurs des relations de dominance sur la structure. Mon travail démontre que la structure sociale chez le corbeau freux est plus qu'un simple agrégat de paires, et forme la base d'une organisation sociale aux multiples niveaux.

Mots-clés: Corbeaux freux (*Corvus frugilegus*), corvidés, structure sociale, paire, relations extra-paires, relations de dominance.

Numerous avian species are good candidates to study the emergence of complex forms of sociality, in particular the species showing advanced cognitive skills, and the one living in groups all year long, coping with the costs and benefits of group living. In my thesis, I investigated the proximate mechanisms underlying the diversity and dynamic of social relationships in captive adult rooks, a colonial and monogamous corvid species. I found that rooks have the ability to form non-reproductive social bonds and several pair bonds throughout their life. In addition, I found: that the group social structure was flexible enough to allow temporal variations of relationships, group composition and sex-ratio; and that dominance relationships do not have any long lasting effects on the stabilisation of the structure. Overall, my work demonstrates that rooks social structure extends far beyond a simple aggregation of reproductive pairs, and may be acknowledged as a multi-level social organisation.

Keywords: rooks (*Corvus frugilegus*), corvids, social structure, pair bond, extra-pair relationships, dominance relationships.