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# STRUCTURAL COMPLEXITY AND SOCIAL COHESION IN GREGARIOUS ANIMALS: FROM CONFLICT TO COOPERATION

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## CONTENTS

<b>ABSTRACT .....</b>	<b>4</b>
<b>TIIVISTELMÄ .....</b>	<b>5</b>
<b>LIST OF ORIGINAL PUBLICATIONS AND AUTHOR CONTRIBUTIONS ...</b>	<b>6</b>
<b>1. INTRODUCTION .....</b>	<b>7</b>
1.1 Effects of the local environment on social structure.....	8
1.2 Structural organization and dynamic fluctuations in social systems.....	9
1.3 Conflict resolution and stability of group structure.....	10
1.4 Study species.....	12
1.4.1 Water striders, <i>Aquarius paludum</i> (I).....	12
1.4.2 Jackdaws, <i>Corvus monedula</i> (II, III).....	13
1.4.3 House sparrows, <i>Passer domesticus</i> (IV) .....	14
1.5 Aims of the thesis.....	14
<b>2. MATERIAL AND METHODS .....</b>	<b>16</b>
2.1 Study areas and subjects.....	16
2.2 Observations of social behavior.....	18
2.2.1 Generating distinct interaction networks .....	18
2.2.2 Dominance rank and dominance hierarchies .....	19
2.2.3 Social network measures .....	19
2.3 Experiments.....	20
2.3.1 Manipulation of local population density (I).....	20
2.3.2 Manipulation of group composition (IV) .....	21
2.4 Data analysis.....	22
2.4.1 Statistical analysis .....	22
2.4.2 Social network analysis.....	23
<b>3. RESULTS AND DISCUSSION .....</b>	<b>25</b>
3.1 Effects of the local environment on social structure.....	25
3.2 Structural organization and dynamic fluctuations in social systems.....	25
3.3 Conflict resolution and stability of group structure.....	26
<b>4. CONCLUSIONS AND FUTURE DIRECTIONS .....</b>	<b>30</b>
<b>5. ACKNOWLEDGMENTS .....</b>	<b>33</b>
<b>6. REFERENCES .....</b>	<b>36</b>
<b>ORIGINAL PUBLICATIONS.....</b>	<b>43</b>

## ABSTRACT

A social lifestyle is abundant in nature. The social interactions between animals form the basis for complex, highly dynamic structures and may determine group-level processes such as group cohesion. Social behavior is influenced by local environmental conditions, varies over time and has diverse, context-dependent functions. In my thesis I have investigated the spatial, temporal, contextual and structural aspects of social complexity in three model species.

First, I explored effects of increasing population density on aggression and contact behavior within and between sexes in water striders (*Aquarius paludum*). The current, local density regime affected male mating behavior as males sought more frequent contacts to available mates in denser groups. Frequencies of male-to-male conflicts and the duration of male harassment behavior were unaffected by local density, however. Overall, males in high-density groups may experience intense scramble competition over reproductively active females. Current environmental conditions crucially affect the species' mating system; yet, also the previously experienced environment should be considered.

Second, in a flock of free-flying jackdaws (*Corvus monedula*) I studied seasonal variation in patterns of positive interactions between pair mates and linked the pair bond to group level dynamics. Jackdaw groups are dynamic social units into which mutualistic pair bonds are embedded. Both sexes invested into the bond with different social behaviors and at different times of the year; yet, these are likely the proximate mechanisms employed by males and females to perpetuate a successful bond and secure annual reproductive output. Third, I determined the factors regulating dyadic and polyadic conflict resolution in jackdaws and investigated patterns of social support between the sexes. Conflict aggressors receiving active, aggressive support had high chances of winning encounters and were probably at low risk of receiving counter-aggression. Females cooperated very closely with their mates during conflicts. In doing so, they likely secured male investment into offspring provisioning and care, whereas males might seek conflicts strategically to maintain or improve their social status. Conflicts and interventions hence constitute a vital aspect of jackdaws' social system.

Finally, I used a captive house sparrow (*Passer domesticus*) flock to determine the destabilizing effects of perturbations of group composition on social structure and behavior. The group's dominance hierarchy destabilized after a second perturbation and did not re-establish itself quickly. Yet, irrespective of experimental treatment, birds fed regularly and interacted based on their initially determined dominance rank. Only females joined, rather than supplanted, feeding conspecifics more frequently following the second perturbation treatment, thereby shifting to a non-aggressive social foraging strategy. Thus, sparrows in this study might have tolerated and compensated for structural instability to some degree.

In conclusion, environmental factors, like population density, may alter the social structure of animal groups, creating a potential for both conflict and cooperation. Cooperation is constantly threatened by the selfish interests of individuals, leading to intra-group conflicts, and group members must resolve these conflicts efficiently. Enduring social stability is likely required for maintaining higher-order structures, such as social alliances or linear hierarchies, but relatively simple mechanisms for mitigating conflicts may exist in fluctuating fission-fusion groups.

## TIIVISTELMÄ

Sosiaalinen elämäntapa on luonnossa yleinen. Eläinyksilöiden väliset sosiaaliset vuorovaikutukset ovat perusta monimutkaisille ja hyvin dynaamisille sosiaalisille rakenteille. Sosiaalinen käyttäytyminen riippuu vallitsevista ympäristön olosuhteista. Esimerkiksi sosiaalista yhteenkuuluvuutta edistävä käyttäytyminen vahvistaa sosiaalisia siteitä, kun taas vihamielinen käyttäytyminen liittyy ryhmänsisäisiin ja ryhmien välisiin ristiriitoihin. Nämä sosiaalisen käyttäytymisen kaksi ääripäätä ovat sosiaalisten rakenteiden peruspilareita, ja vaikuttavat yhdessä ryhmän toimintaan ja tiiveyteen. Sosiaaliset järjestelmät vaihtelevat tilassa ja ajallisesti sekä ovat rakenteellisesti hyvin monimutkaisia. Väitöskirjatyössäni olen tutkinut kolmella mallilajilla näitä sosiaalisen kompleksisuuden eri ilmenemismuotoja.

Tutkin vesimittareilla (*Aquarius paludum*) populaatiotiheyden kasvun vaikutuksia sukupuolten sisäiseen ja sukupuolten väliseen aggressioon ja pariutumiskäyttäytymiseen. Populaatiotiheys vaikutti koiraiden pariutumiskäyttäytymiseen niiden etsiessä saatavilla olevia kumppaneita. Paikallinen populaatiotiheys ei kuitenkaan vaikuttanut koiraiden välisten häirintäkäyttäytymisten lukumäärään tai kestoon. Kaiken kaikkiaan koiraat saattavat kuitenkin tiheissä populaatioissa kokea voimakasta kilpailua aktiivisesti lisääntyvistä naaraista. Sekä vallitsevat että aiemmissa elämänvaiheissa koetut ympäristön olosuhteet vaikuttavat merkittävästi pariutumisympäristöön.

Tutkin vapaana elävässä naakkaparvessa (*Corvus monedula*) parinsisäisten positiivisten vuorovaikutusten esiintyvyyttä eri vuodenaikoina sekä parisiteen vaikutusta parven toimintaan. Naakkaparvessa kummallakin sukupuolella parisidettä ylläpitävät sosiaalisen käyttäytymisen muodot vaihtelivat vuodenajoittain. Kyseessä lienevät proksimaattiset mekanismit, joita naaraat ja koiraat käyttävät varmistaakseen lisääntymisensä onnistumisen vuosittain. Tutkin naakoilla myös kahden- ja monenkeskisiin konfliktinratkaisutapoihin vaikuttavia tekijöitä sekä niitä tapoja, joilla naakkapuolisot tukivat toisiaan ristiriitaisissa tilanteissa. Ristiriitatilanteissa hyökkäävät osapuolet, jotka saivat muilta yksilöiltä aktiivista sosiaalista tukea, voittivat useimmin ja yleensä välttyivät uusilta ristiriidoilta. Naaraat tukivat puolisoitaan ristiriitatilanteissa. Tämä todennäköisesti auttoi niitä varmistamaan koiraan osallistumisen jälkeläisten ruokintaan ja hoitoon. Koiraat puolestaan hakeutuivat ristiriitatilanteisiin joko ylläpitääkseen tai parantaakseen omaa sosiaalista asemaansa. Ristiriitatilanteet ja niiden ratkaiseminen ovat tärkeä osa naakkojen sosiaalista järjestelmää.

Lopuksi tutkin tarhaoloissa pidetyillä varpusilla (*Passer domesticus*) parvirakenteen hajoamisen ja yhdistymisen vaikutusta sen sosiaaliseen rakenteeseen ja yksilöiden käyttäytymiseen. Parven valtajärjestys hajosi häirinnän jälkeen, eikä enää palautunut ennalleen. Tästä huolimatta parven jäsenet ruokailivat säännöllisesti, ja yksilöiden väliset suhteet noudattivat kokeen alussa vakiintunutta valtajärjestystä. Parven häirintäkerran jälkeen naaraat olivat ruokaillessaan vähemmän aggressiivisia. Tutkimukseni siis osoitti, että varpuset pysyvät palauttamaan valtajärjestelmän sen hajottua ja uudelleen yhdistyessä.

Yhteenvetona voidaan todeta ympäristötekijöiden kuten populaatiotiheyden voivan vaikuttaa eläinryhmien sosiaaliseen rakenteeseen, mikä luo paitsi ristiriitatilanteita myös yhteistyötä. Yksilöiden itsekkäät vaikuttimet vaarantavat jatkuvasti yhteistyön mahdollisuuksia, mikä johtaa ryhmänsisäisiin ristiriitoihin, joita ryhmän jäsenten tulisi voida tehokkaasti ratkoa. Sosiaaliset rakenteet kuten yksilöiden yhteenliittymät tai lineaariset valtajärjestykset edellyttävät pitkäkestoista sosiaalisten suhteiden vakautta. Alati koostumukseltaan muuttuvissa, toistuvasti hajoavissa ja uudelleen muodostuvissa eläinryhmissä voivat kuitenkin toimia melko yksinkertaiset ristiriitoja lieventävät toimintamallit.

## LIST OF ORIGINAL PUBLICATIONS AND AUTHOR CONTRIBUTIONS

This thesis consists of the following publications and manuscripts, which are referred to in the text by their Roman numerals:

- I** Kubitzka RJ, Kaunisto KM, Suhonen J & Vuorisalo T. Density-dependent effects on social interactions and sexual conflict: an experimental test in water striders. – Submitted manuscript.
- II** Kubitzka RJ, Bugnyar T & Schwab C. 2015. Pair bond characteristics and maintenance in free-flying jackdaws *Corvus monedula*: effects of social context and season. – *Journal of Avian Biology* 46: 206-215. doi: 10.1111/jav.00508
- III** Kubitzka RJ & Schwab C. Patterns of dyadic conflict and third-party interventions in free-flying jackdaws, *Corvus monedula*. – Submitted manuscript.
- IV** Kubitzka RJ, Suhonen J & Vuorisalo T. 2015. Effects of experimental perturbation of group structure on hierarchy formation and behaviour in House Sparrows. – *Ornis Fennica* 92: 157-171.

Articles **II** and **IV** reprinted with permission from John Wiley & Sons and BirdLife Finland, respectively.

### Author contributions to the original publications

	<b>I</b>	<b>II</b>	<b>III</b>	<b>IV</b>
Original idea and study design	JS, TV	CS	CS, RK	RK, JS, TV
Sampling and preparation	KK, RK	RK, CS	RK, CS	RK, JS, TV
Experimentation	KK, RK			RK, JS
Empirical data collection	RK	RK	RK, CS	RK
Analyses	RK, JS	RK, CS	RK, CS	RK, JS
Manuscript preparation	RK, TV, JS, KK	RK, CS, TB	RK, CS	RK, TV, JS

RK=Robin Kubitzka, JS=Jukka Suhonen, CS=Christine Schwab, TV=Timo Vuorisalo, KK=Kari Kaunisto, TB=Thomas Bugnyar

## 1. INTRODUCTION

Group-living is taxonomically widespread in nature. Social animals must reconcile the associated costs of social life – intra-group competition over natural resources and mates (Alexander 1974; van Schaik et al. 1983), the potential for inbreeding and infanticide (Alexander 1974; Michener 1983), and a high risk of disease outbreak or transmission of parasites (Godfrey et al. 2009; Hamede et al. 2009) – with its corresponding benefits: improved avoidance and protection from predators (Hamilton 1971; Milinski and Heller 1978; Lima 1995; Krause and Ruxton 2002), the joint acquisition of resources (Emlen 1982; Johnson et al. 2005; Lucia et al. 2008), use and propagation of information (Galef and Giraldeau 2001), enhanced thermoregulation (Canals et al. 1989; Ebensperger 2001) or cooperative breeding (Balshine et al. 2001; Clutton-Brock et al. 2001).

Local environmental conditions set the physiological and ecological boundaries in which complex social systems can develop: environmental factors of influence are, for example, habitat quality and composition (Edward and Gilburn 2007), food abundance and distribution (Brashares and Arcese 2002; Shochat 2004; Smith et al. 2008; Henzi et al. 2009), predation pressure (Hoare et al. 2004; Edenbrow et al. 2011; Kelley et al. 2011), population density (Jirotkul 1999; Kokko and Rankin 2006; Cureton et al. 2010) and the operational sex ratio (OSR; Vepsäläinen and Savolainen 1995; Clark and Grant 2010). Animals adapt to these local selective regimes accordingly, which influences the pathways and patterns in which they interact with each other (Brashares and Arcese 2002; Pinter-Wollman et al. 2014). Both of these factors – local environmental conditions and variable social behavior – shape the relationships between individuals in a group and, ultimately, the group's overarching structure (Hinde 1976; Pinter-Wollman et al. 2014). Social groups interact with and alter their current environments in turn.

As individuals attempt to tip the cost-benefit ratio of group-living in their favor, conflicts over access to resources and reproduction can be common in social groups (Aureli et al. 2002). Aggressive conflicts are potentially harmful but may also impose ecological disadvantages on individuals, for example, reducing the time spent foraging after a conflict due to the need to remain vigilant (Aureli 1992). Conflicts may even lead to a tragedy of the commons scenario (Eldakar et al. 2009). In addition, intra-group conflicts have potentially severe social effects by disturbing valuable relationships and impairing future cooperation between individuals (de Waal 1986; Aureli et al. 2002). Repeated conflicts as well as severe environmental stressors threaten the social cohesion of populations, and thus, the basis for cooperation and survival (Flack et al. 2006). Hence, animals are required to resolve conflicts efficiently.

In the far end of the dynamic social spectrum are the so-called fission-fusion societies in which animals travel repeatedly between groups depending on the distribution and abundance of resources or the presence of predators (Kummer 1971; Janson 1988; Krause and Ruxton 2002; Smith et al. 2008). As a result, group size and composition frequently change and intra-group aggression can be common in some species (Aureli and Schaffner 2007; Couzin and Laidre 2009; but see Asensio et al. 2008). Under constant environmental and social conditions, however, animals may develop mechanisms of conflict management. One such behavioral mechanism that is thought to stabilize social groups is the establishment of a dominance hierarchy. By making the outcome of social encounters more predictable, animals in dominance-structured societies need to expend less time and energy in entering repeated conflicts and they face a lower risk of receiving physical injury (Clutton-Brock et al. 1986; Aureli and de Waal 2000). Thus, in constant social groups hierarchies and other mechanisms of conflict mitigation (e.g. reconciliation; Aureli et al. 2002) help to foster group stability and cohesion.

In this way, group-living animals form organized yet highly dynamic social structures. Below, I describe three aspects of social complexity in greater detail.

### **1.1 Effects of the local environment on social structure**

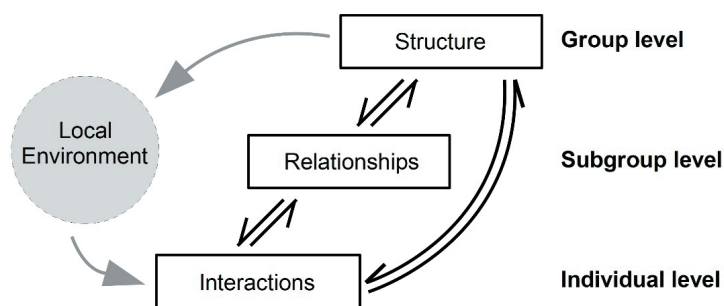
Environmental effects on patterns of social behavior, mating behavior in particular, have been investigated with a strong focus on sexual conflict (e.g. Krupa and Sih 1993; Rowe et al. 1994; Edenbrow et al. 2011). Environmental conditions greatly affect the intensity of sexual conflict, and hence, mating patterns vary both spatially and temporally depending on local conditions (Rowe et al. 1994). For example, a strongly male-biased operational sex ratio (the proportion of ready-to-mate males to receptive females in a mating pool; Vepsäläinen and Savolainen 1995; Alonso-Pimentel and Papaj 1996) leads to increased frequencies of male harassment behavior (Rowe 1992) and prolongs the duration of mating and post-copulatory mate guarding (Arnqvist 1992a; Rowe 1992). Population density, conversely, influences intra-sexual competition as well as associated male mating tactics (Emlen and Oring 1977; Jirotkul 1999; Mills and Reynolds 2003; Kokko and Rankin 2006): at high local densities conflicts among males over potential mates become more common (Kokko and Rankin 2006; Cordoba-Aguilar 2009) and large, aggressive males usually gain a selective competitive advantage (Tomkins and Brown 2004; Bertin and Cezilly 2005). Males also harass females more frequently (Arnqvist and Rowe 2005; Cureton et al. 2010) while simultaneously reducing courtship efforts (Jirotkul 1999; Grant et al. 2000; Clark and Grant 2010). Females, in turn, are



predicted to become choosier at high male densities (Crowley et al. 1991; Kokko and Rankin 2006). Some empirical evidence, however, shows that females in high-density populations are in fact less reluctant to mate (Arnqvist 1992a). This is termed convenience polyandry: females are believed to be less choosy when the associated fitness costs of prolonged mating struggles (e.g. predation; Fairbairn 1993; Rowe 1994) exceed the costs of mating multiple times (Rowe 1992; Ronkainen et al. 2010).

## 1.2 Structural organization and dynamic fluctuations in social systems

Group-living animals typically occupy very distinct social positions within their groups and interact with each other in non-random patterns, from which biologically meaningful relationships and organized yet highly dynamic social structures arise (Krause and Ruxton 2002; Krause et al. 2007; Whitehead 2008). Social structure is hence distinct from feeding aggregations, in which animals are spread out according to scattered food resources, and other assemblages based on shared use of space (Krause and Ruxton 2002; Croft et al. 2008). Instead, socially structured systems can be represented as interaction (or association) networks in which individuals exchange social services, resources or information. Hinde (1976) proposed to analyze social structure according to interconnected hierarchical levels of organization (**Figure 1**): interactions between animals on the individual level form the basis of social structure and distinct social relationships arise from repeated interactions over time. These relationships may cause the emergence of structured sub-groups (the subgroup level), which are themselves embedded in the larger social structure of the group (the group level; Hinde 1976; **Figure 1**). Each organizational level gives rise to unique emergent properties (Hinde 1976), such as division of labor and the evolution of cooperation (e.g. Kummerli et al. 2010). Social structure on the group level, in turn, determines how individuals interact and exchange information, resulting in intricate feedback-loops between dyadic interactions and population dynamics (Krause and Ruxton 2010). The structural properties that underlie animal social systems are complex and dynamic over space and time and still puzzle behavioral ecologists today (Krause et al. 2007; Pinter-Wollman et al. 2014; Rands 2014). In particular, questions of how animals integrate into existing social structures or how higher-level structure arises from dyadic and polyadic interactions between individuals remain exciting areas of research (Krause and Ruxton 2002; Krause et al. 2007).



**Figure 1.** Social organization and structural levels in animal groups. Each successive level yields emergent properties. Independent, nonsocial variables (shown here: the local environment) affect social organization on certain levels. (Modified from Hinde 1976 *Man* 11:1-17).

### 1.3 Conflict resolution and stability of group structure

Repeated intra-group conflicts, rapid changes in group composition and other perturbations pose serious challenges for the social structure of animal groups (e.g. Ansmann et al. 2012). The efficient resolution of conflicts becomes necessary for the internal stability of a group (Aureli et al. 2002; Flack et al. 2006). As such, dominance hierarchies enable individuals to better predict their social environment as well as their own status in the group: physically aggressive conflicts are supplemented or replaced by displays of social status (Perry et al. 2004); thus, by gauging their chances of winning, combatants are able to avoid drawn-out, repeated battles (Aureli and de Waal 2000; East and Hofer 2010). Linear (or transitive) hierarchies are structured in a way that individuals can be ranked from top to bottom: the highest-ranking individual is dominant over all others, the one second in rank dominates all except the top-ranking one, and so forth (Martin and Bateson 2007; East and Hofer 2010). Hierarchy formation is brought upon through recurring dyadic encounters and various factors have been identified in determining rank, including differences in intrinsic attributes such as size and age asymmetries (Valderrábano-Ibarra et al. 2007) on the one hand and social factors on the other hand. Social factors incorporate trained winning and losing (Dugatkin 1997; Hsu et al. 2006) and bystander-effects (Dugatkin 2001; Chase et al. 2002), in which an animal observing an agonistic conflict alters its behavior accordingly when facing either one of the contestants in a future encounter. Social factors appear to play a large role in maintaining stable hierarchies, particularly in larger groups (Chase 1982; Chase et al. 2002). As long as group composition (Senar et al. 1990; Graham and Herberholz 2009) and environmental conditions (Sloman et al. 2002) remain constant, hierarchies remain relatively stable and rank order rarely needs to be re-negotiated. Dominants benefit from their high-ranking position by receiving prime access to limited resources (Ekman and Askenmo 1984; Henderson

and Hart 1995), such as food, mates and breeding sites. Subordinates are left with less predictable access (Ficken et al. 1990; Polo and Bautista 2002) but they may still be better off in a low-ranking position within their social group than leading a solitary life (Ekman and Askenmo 1984).

Conflict resolution occasionally involves bystanders to physically intervene into ongoing conflicts, supporting one of the opponents against the other and thus affecting the conflict outcome. This type of conflict management is known as third-party intervention and has been commonly ascribed to primates (e.g. de Waal and Harcourt 1992; Watts 1997; Petit and Thierry 2000; Roeder et al. 2002; Flack et al. 2005; von Rohr et al. 2012) as well as some non-primate mammals (Connor et al. 1992; de Villiers et al. 2003; Ward et al. 2009; Schneider and Krueger 2012) and only relatively recently also to non-mammalian species such as birds (Scheiber et al. 2005; Scheiber et al. 2009; Fraser and Bugnyar 2012; Massen et al. 2014b). Support during agonistic conflicts constitutes a vital element of many social alliances in which intervener and recipient of support share a close social bond (e.g. Watts 1997; Braun and Bugnyar 2012; Krueger et al. 2015). While the support recipient will benefit directly from the assistance during the conflict, the intervener not only pays time and energy costs in supporting an ally but also faces the risk of physical injury (Smith et al. 2010). By cooperating the provider of social support may, however, gain indirect and potentially delayed benefits (Clutton-Brock 2009; Fraser and Bugnyar 2012): for example, reciprocation of support in the future (Trivers 1971; Hemelrijk and Ek 1991; Krams et al. 2008; Krama et al. 2012), solidification or rise in dominance rank with the associated benefit of greater resource access (Ekman and Askenmo 1984; Drews 1993; Lendvai et al. 2006; Smith et al. 2010), or higher connectivity and prominence within the group, which provides access to social information (Lusseau and Conradt 2009) and may even increase reproductive success (McDonald 2007). Impartial third-party interventions, known as policing (Flack et al. 2006), are the rarest form of conflict management (von Rohr et al. 2012). Here, a small subset of individuals with high social power (Flack et al. 2005; Flack et al. 2006) effectively represses the escalation of intra-group conflicts. Policing may thus increase cohesion within a social group and enable cooperative interactions among its members (Frank 2003; Gardner and Grafen 2009; von Rohr et al. 2012).

It is still a matter of debate what set of attributes and behavioral mechanisms are involved in establishing and maintaining hierarchies in natural populations (Dugatkin 1997; Valderrábano-Ibarra et al. 2007; Chase and Seitz 2011): no single factor is likely to explain the process of hierarchy formation and the factors involved in stabilizing hierarchies appear to vary across groups of different sizes (Chase and Seitz 2011) and at different points in time. Also knowledge regarding the processes that destabilize hierarchies and social systems alike is further needed.

## 1.4 Study species

In my thesis I have used three social taxa to study the dynamic and structural complexity of social systems, including both invertebrate (water striders, *Aquarius paludum*) and vertebrate species (gregarious passerines). First, I explored how the local density regime affects aggression and contact behavior within and between sexes in water striders (**I**). Second, I studied dynamic patterns of positive interactions shared among pair-bonded birds and the linkage between pair bonds and group structure in jackdaws, *Corvus monedula* (**II**), and determined the factors involved in the resolution of agonistic conflicts in this species (**III**). Finally, I investigated the destabilizing effects of a rapidly fluctuating group composition on social structure and dyadic interactions in a captive house sparrow (*Passer domesticus*) flock (**IV**).

### 1.4.1 Water striders, *Aquarius paludum* (I)

Polyandrous water striders (Gerridae, Heteroptera) are well established models of sexual conflict and aggression (e.g. Rowe et al. 1994; Arnqvist and Rowe 1995; Eldakar et al. 2009; Han and Jablonski 2010; Eldakar and Gallup 2011; Wey et al. 2015). Polyandrous mating systems are characterized by strong sperm competition; hence, males are selected to pursue repeated matings with one or several available females to improve their own reproductive success (Rubenstein 1989). By mounting a female's back during and after copulation males further attempt to guard their mate against competitors; however, the morphologically larger female is typically able to dislodge the male and eventually terminate the mating struggle (Rowe 1992; Weigensberg and Fairbairn 1994). Female fertility, conversely, does not increase further after passing an initial threshold (Ronkainen et al. 2010) and, in fact, female water striders face severe costs to individual fitness when being harassed by males (Wilcox 1984; Chapman et al. 2003): violent pre- and post-mating struggles make females more detectable to natural predators (for example, frogs and predatory backswimmers) while at the same time lowering mobility across the water surface and, thus, the potential for escape (Fairbairn 1993; Rowe 1994; Amano and Hayashi 1998; Arnqvist and Rowe 2002). As a result, females often end up mating out of convenience to escape harassment (Rowe 1992; Weigensberg and Fairbairn 1994; Ronkainen et al. 2010), particularly at high male densities (Arnqvist 1992a). Intense sexual selection has led both sexes to develop morphological adaptations in order to gain the upper hand in conflicts over mating frequency: male genital claspers that aid them in grasping and overpowering reluctant mates (Arnqvist 1989; Andersen 1991; Arnqvist 1992b; Fairbairn et al. 2003) and female abdominal spines that enable resisting such attempts (Arnqvist and Rowe 1995) pose as adaptations and counter-adaptations in a co-evolutionary arms-race.

### 1.4.2 Jackdaws, *Corvus monedula* (II, III)

Social corvids are an ideal study system for animal sociality: these cognitively advanced birds (Emery and Clayton 2004; Bugnyar et al. 2007) establish, maintain and remember valuable relationships with conspecifics for prolonged periods of time (Fraser and Bugnyar 2010; Boeckle and Bugnyar 2012). Moreover, they closely follow the relationships between other members of their social group (Massen et al. 2014a) and may even infer transitive dominance relationships among them (Bond et al. 2003; Lazareva et al. 2004; Paz-y-Mino et al. 2004; Mikolasch et al. 2013). The jackdaw is an exceptionally social corvid that lives and breeds (semi-)colonially (Haffer 1993; Henderson et al. 2000). Winter roosts and foraging aggregations may number up to several thousand individuals (Goodwin 1976; Haffer 1993; Clayton and Emery 2007). Social stability in colonies is achieved through organization into strongly linear hierarchies (Tamm 1977; Röell 1978; Wechsler 1988). Males and females maintain their own social hierarchies but generally male jackdaws are dominant over females (Tamm 1977; Röell 1978; Wechsler 1988) and mated individuals dominate singletons (Röell 1978; Haffer 1993). Once mated, females acquire a rank corresponding to their mate's (Lorenz 1931; Wechsler 1988). Socially dominant birds are better able to secure and defend valuable but limited resources such as nesting cavities and food (Röell 1978). Dominance also affects breeding success in jackdaws, albeit equivocally (cf. Henderson and Hart 1995; Verhulst and Salomons 2004). Shifts and turnovers in the rank order, however, can be common both during the winter and the breeding season (Tamm 1977; Röell 1978).

Despite the sheer size of social colonies, long-term monogamous pair bonds predominate jackdaw society and are widely regarded as its elementary unit (Goodwin 1976; Röell 1978; Wechsler 1989; Emery et al. 2007). This combination of monogamous bonds embedded in the framework of an exceptionally social species may lead to high structural complexity. Birds pair up at 1-2 years of age when they reach sexual maturity and the resulting bond commonly lasts until one partner dies (Goodwin 1976; Henderson et al. 2000). Pair mates cooperate extensively across various social contexts: they share food and social services (Röell 1978; Wechsler 1989; chapter II), jointly acquire and defend a suitable nesting site (Haffer 1993), provide for the offspring during and after the breeding season (Henderson and Hart 1993) and support the pair mate during conflicts (Röell 1978; Haffer 1993; chapter III). Pair bond management requires time and energy investments, and birds effectively trade off fitness benefits gained from mating polygamously (Volland 2000) against enhanced offspring survival (Henderson and Hart 1993).

### **1.4.3 House sparrows, *Passer domesticus* (IV)**

The gregarious house sparrow is a highly suitable model organism for studies of social behavior, learning and dominance (e.g. Møller 1987; Lendvai et al. 2006; Liker and Bókony 2009; Buchanan et al. 2010; Bókony et al. 2010; Katsnelson et al. 2011). House sparrows live year-round in dynamic social groups (Andersson 2006) and fission-fusion events can be common. Moreover, the birds share a close commensalistic relationship with humans (Andersson 2006; de Laet and Summers-Smith 2007): the size of sparrow populations is often positively correlated with human population density and, indeed, sparrows are among the most numerous and dominant bird species in cities (Vuorisalo and Tiainen 1993; Jokimäki et al. 1996; Jokimäki and Suhonen 1998). Group mates are attracted quickly to the food discoveries of conspecifics (Turner 1964) and sparrows appear to be highly skilled at obtaining social information. The dominance structure in house sparrow flocks is formed both by intrinsic factors (current level of testosterone and the size of the male ‘badge of status’; Bókony et al. 2006; Nakagawa et al. 2007) as well as extrinsic factors (birds’ history of preceding dominance interactions; Buchanan et al. 2010). Females are known to dominate males at the nest during the breeding season (Haffer 1997) and in autumn flocks (Hegner and Wingfield 1987). In winter flocks, however, male-female aggression can be frequent and victory appears to depend largely on male bib size (Møller 1987; Liker and Barta 2001; Hein et al. 2003). Dominant sparrows are able to forage in high-quality patches and frequently exploit others’ food discoveries (termed scrounging; Barnard and Sibly 1981; Liker and Barta 2002; Lendvai et al. 2006), whereas subordinates are forced to feed more opportunistically and under a greater threat of starvation (cf. Polo and Bautista 2002).

## **1.5 Aims of the thesis**

Dyadic interactions constitute the building blocks of higher-order structures, vary across environments and socially diverse contexts and change over time. Animal sociality hence poses an exciting area of research and, in particular, the confounding effects imposed by the environment, the interrelatedness of structural organization, the mechanistic basis and fitness implications of social behavior and the proximate mechanisms that facilitate cohesion in animal populations warrant further study. In my thesis I have set out to investigate these aspects of structural complexity.

I have used novel analytical tools, such as social network analysis (SNA) and generalized linear models (GLM), alongside conventional statistical analyses. I have further used a mixture of experimental manipulation of social structure in wild-

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caught populations (**I, IV**) and long-term observations of social behavior in nature (**II, III**). Experimental manipulation is important for detecting the processes underlying social organization, whereas observation of animals in their natural environment is necessary to draw proper conclusions regarding their ecology. Here, I aim to answer the following questions:

- I. How do local environmental conditions, such as population density, affect mating interaction patterns and the intensity of sexual conflict? (**I**)
- II. How are basic social units, such as monogamous pair bonds, nested into the overarching structure of the group? How do interaction patterns differ throughout the breeding cycle, between diverse social contexts and between the sexes? (**II**)
- III. What factors determine the outcome of agonistic conflicts and how do mechanisms of conflict management, such as third-party interventions, function? Do sexes differ in providing social support? (**III**)
- IV. Does perturbation of social structure, such as a rapidly fluctuating group composition, destabilize social hierarchies and lead to intra-group conflicts? Do group members adjust their behavior to unstable conditions? (**IV**)

## 2. MATERIAL AND METHODS

### 2.1 Study areas and subjects

In mid-May 2011 water striders were sampled over a nine-day period from stagnant, semi-natural ponds in Maskun Riviera and Hauninen, located near the city of Turku, SW Finland (I). Both sites started as gravel pits between 30–80 years ago, then gradually filled up after digging terminated. In total 90 individuals from five populations were collected, i.e., 18 adult individuals ( $N=9$  males,  $N=9$  females) per population. The ponds were separated by stretches of gritty lakefront or low grassland and located at least 240 m (up to 5.4 km) apart from each other. Populations were assumed to be independent replicates. All 18 individuals from a population were collected during the same 1–2 h sampling session. Sex was identified on spot in the field. Subjects were jointly brought to the laboratory facilities of the University of Turku in polystyrol transport boxes with added dampened moss for moisture.

Chapters II and III were conducted at the Konrad Lorenz Research Station for Ethology (KLF) and the Herzog von Cumberland game park Grünau, Upper Austria, where I observed social interactions in a free-flying flock of jackdaws between November 2008 and September 2009. The research station and game park are located in an alpine valley through which the river Alm flows (Figure 2). Over the course of the study period the dispersal and death of resident birds as well as the immigration of wild jackdaws passing through the valley were commonly observed. Jackdaws were predominantly preyed upon by the Eurasian sparrow hawk, *Accipiter nisus*. Consequently, the size and composition of the study flock varied over the study period. The core of the flock consisted of birds that were hand-reared in 2005 and 2006 and released into free-flight in 2007 (Wagner et al. 2011). Since then, wild migrants as well as biological offspring have joined the flock. Mated pairs of mixed origin (wild and hand-reared birds) were common and can be considered as a reliable indicator that the semi-natural flock was socially intact with a functioning mating system. In chapter II I thus observed the social behavior of 27 jackdaws ( $N=15$  males,  $N=12$  females), including seven offspring fledged during the breeding season of 2009. For chapter III, which examines agonistic conflicts, I used only data between November 2008 – April 2009, excluding the post-fledging parental care period during which conflicts were rare, and group size was 18 ( $N=10$  males,  $N=8$  females). The majority of birds were color-banded for individual identification; wild jackdaws that could not be trapped and marked could nevertheless be identified by unusual phenotypic characteristics, such as a



rare coloration of the iris. Sex was determined by taking blood samples and the age of birds was either known or, in the case of wild migrants, was estimated based on plumage maturation and coloration of the oral cavity. Jackdaws older than 1 year of age were considered to be adults.



**Figure 2.** Study site for long-term observational studies **II** and **III** was the Konrad Lorenz Research Station for Ethology (KLF) in Grünau, Upper Austria (left), located in the alpine Alm valley (right). (Photos: R. Kubitza).

The jackdaws roamed the valley freely in search for naturally occurring food sources such as small invertebrates (flies, beetles and spiders) and seeds. They had *ad libitum* access to water from the Alm river. In the early mornings, before data were collected, I provided the flock with additional supplementary food. This was done to habituate the shy birds to the close presence of a human observer and to discourage autumn dispersal. However, the birds acquired the main portion of their diet by foraging eagerly in the meadows for the rest of the day.

In late October 2012 house sparrows were captured out of natural habitats from three urban locations in Turku, SW Finland (**IV**). The sparrows were caught from multiple locations and later combined into a single flock in order to simulate fission-fusion dynamics in wild autumn and winter flocks. Birds were expected to establish novel social relationships and to re-negotiate dominance rank order since pre-existing social ties were likely disrupted during sampling. The three sampling sites were Sirkkala in central Turku, the north-eastern district of Käsämäki and Muhkuri in the northwest. The sites were located at least 4.5 km apart from each other. Sirkkala and Muhkuri are residential areas with relatively high vegetation cover, whereas Käsämäki is a largely industrial area interspersed with green spaces and forests. Birds from Käsämäki were caught out of the open storage area of an agricultural market. We captured 17 house sparrows in total ( $N=11$  males,  $N=6$  females; one female died near the end of the study and was excluded from analysis) on four consecutive days using mist nets and baited live traps. Birds were sexed, weighed and color-banded on spot for individual identification. All birds with the exception of one

male possessed the fully matured plumage of adults. The sparrows were transferred to the Botanical Garden of the University of Turku, located a short way from the city center on Ruissalo island, where they were housed as one social group in an indoor aviary. The birds were released together back into the wild in mid-December 2012 and additional wintering food for passerine birds was provided at the release site (Sirkkala) over the course of one week.

## **2.2 Observations of social behavior**

I collected empirical data on dyadic social interactions by conducting 1-min focal samples in observational studies (**II**, **III**) and continuous sampling in experimental studies (**I**, **IV**), respectively. Digital video cameras were used for continuous sampling and all occurring interactions could be captured. Interactions were always analyzed as frequencies of occurrence, except for the duration of male harassment behavior (**I**). I then compared the mean frequencies of initiated social interactions among functionally distinct contexts of social behavior (**I**, **II**, **III**, **IV**) and between observational periods (**II**) or experimental treatments (**I**, **IV**).

### **2.2.1 Generating distinct interaction networks**

In a first step, I tentatively classified discrete behavioral parameters into specific social contexts based on their social function. These contexts were relevant to the study questions being investigated and were biologically meaningful for the ecology of the species. For example, in chapter **II** I categorized social interactions that either involved keeping close spatial proximity, the sharing of food, or affiliative (sociopositive) behavior – all of which are important contexts for socially monogamous pairs. This allowed me to compare social contexts both temporally and directly with each other. In a second step, I computed matrix correlations (Mantel tests with 10000 permutations each; Mantel 1967) between pairs of behavioral parameters within each of the previously defined contexts. This was done to test whether behavioral parameters that were assigned to a context due to perceived common function correlated also statistically with each other. I implemented sequential Bonferroni corrections to control for multiple testing (Holm 1979) and included only significantly correlating parameters in a context. The program MatMan 1.1 by Noldus Technologies (de Vries et al. 1993) was used for matrix correlations. Parameters in a context were then pooled together (summed up) and corrected for individual sampling effort, i.e., variation between individuals in the number of focal observations (**II**, **III**) or in the time observed interacting in the arena (**I**, **IV**), to minimize observational skew. All interaction data were standardized to a 1-min time interval. I ended up with a sociomatrix (i.e., an interaction matrix or network) computed for each social context, observational period or experimental condition. Lastly, for chapters **I** and **II** I have

filtered sociomatrices to include either solely interactions initiated by males towards other males or towards females (I), or solely interactions shared among pair mates (II).

### **2.2.2 Dominance rank and dominance hierarchies**

In chapters III and IV I have calculated the dominance rank of individuals and tested the linearity of hierarchies across observational periods (III) or experimental conditions (IV). Dominance rank was calculated from strongly asymmetric agonistic behaviors, for example, fights and displacements. Similar to generating interaction networks (see above), I computed matrix correlations between agonistic parameters (Mantel tests with 10000 permutations each), applied sequential Bonferroni corrections due to multiple testing and pooled significantly correlated parameters. From this pooled data set de Vries et al.'s (2006) modified version of David's score (David 1987; hereafter MDS) was calculated for each individual in the group. MDS quantifies an individual's wins and losses against every other group member, weighted by the estimated dominance of the opponent (de Vries et al. 2006). I standardized the MDS to values between 1 (the top-ranking individual) and 0 (the bottom-ranking individual). Lastly, I calculated MDS separately for observational periods (III) on the one hand, due to changes in group composition over the study period, and for experimental conditions (IV) on the other hand, to detect effects of the experimental treatment on the behavior of dominants and subordinates. I followed Whitehead (2008) in assigning and interpreting dominance ranks only when hierarchies were linear. The linearity of hierarchies was tested with a randomization routine (de Vries 1995). The program SOCPROG 2.5 (Whitehead 2009) was used for calculating dominance ranks and testing the linearity of hierarchies.

### **2.2.3 Social network measures**

I have used social network measures in all my chapters in an attempt to characterize and analyze the social behavior exchanged between individuals. Social network analysis (SNA) is a highly suitable methodological framework for the study of animal sociality (Croft et al. 2008; Wey et al. 2008; Whitehead 2008). Many empirical studies have successfully implemented SNA in recent years and, in doing so, have uncovered complex underlying structures across a broad species spectrum (e.g. McDonald 2007; Sundaresan et al. 2007; Wolf et al. 2007; Hamede et al. 2009; Mann et al. 2012; Aplin et al. 2013). Social networks consist of nodes, i.e., individual actors, connected by ties that commonly represent some form of interaction or association (Wasserman and Faust 1994). Connections of essentially any kind can be analyzed: previous studies used SNA to explore such diverse biological contexts like cooperative male displays at a lek (McDonald 2007), transmission networks of ectoparasitic ticks in social

lizards (Godfrey et al. 2009; Leu et al. 2010) and the impact of commercial fisheries on dolphin community structure (Ansmann et al. 2012). (Even in popular culture, Beveridge and Shan (2016) took a recent social network approach to the popular Game of Thrones television show.) The SNA framework thus integrates dyadic connections (interactions or associations) on the individual level into higher-order structures, and by doing so, addresses the interrelatedness of social structure (Hinde 1976; Wasserman and Faust 1994). The non-independent nature of relational data is duly accounted for (see e.g. Hemelrijk 1990a).

I have calculated the centrality measures of outdegree, i.e., the mean frequency of initiated social interactions (**I-IV**), and mean degree, i.e., the average number of interaction partners (**II**), for each present individual and in the relevant social contexts. Centrality measures describe individuals' social positions within a group (Whitehead 2008). Outdegree is a directed measure, being addressed from an initiator towards a receiving individual, and was calculated from so-called weighted data, i.e., the observed frequencies of social interactions. In network terms, outdegree represents the number and strength of ties an actor directs towards other group members (Newman 2003). Outdegree was corrected for variation in group size by dividing through the number of available interaction partners ( $N-1$ , excluding self-directed ties). In contrast, mean degree is an undirected measure and was calculated from binary data, i.e., the presence or absence of a tie. In other words, mean degree represents the average number of ties that connect to an actor in a given network (Croft et al. 2008). Mean degree was used in its normalized version as the percentage of available interaction partners (Borgatti et al. 2002). All social network measures were computed with the Ucinet 6 for Windows software package (Borgatti et al. 2002).

## **2.3 Experiments**

Recent literature has highlighted the importance of manipulating the social structure of animal groups in order to detect underlying patterns of organization (Krause and Ruxton 2010; Croft et al. 2011; Pinter-Wollman et al. 2014; Rands 2014). In this thesis, I have experimentally manipulated local population density on the one hand (**I**) and group composition on the other hand (**IV**) and recorded the effects on dyadic interaction patterns and the robustness of social structure.

### **2.3.1 Manipulation of local population density (I)**

In chapter I I exposed water striders to environments varying in population density in order to determine how these local conditions affect mating patterns and the intensity of sexual conflict. Within each sample population I randomly assigned

individuals either to the low ( $N=4$ ), the intermediate ( $N=6$ ) or the high density treatment ( $N=8$ ). The sex ratio was kept constant at  $N_{\text{males}}=N_{\text{females}}$ . At the beginning of each density treatment the corresponding number of water striders was transferred simultaneously to a large plastic bucket (46 cm Ø) filled with water to a height of 50 cm. The bucket was covered with plates of glass, leaving a gap for ventilation. No food or vegetation cover was provided. After individuals had settled down for 5 min we recorded their interactions for a period of 30 min with a digital video camera poised directly above the bucket. After experimentation the water striders were collected back into their individual storage containers. We repeated this process in each of the three density treatments for all five sample populations. The order in which density treatments were conducted during the day was randomized.

### 2.3.2 Manipulation of group composition (IV)

In chapter IV I experimentally tested whether perturbations of group composition would destabilize the social structure of a captive house sparrow flock. To this end, I used an experimental removal design, capturing sparrows out of their group and subsequently re-introducing them back into the group. The study was performed in an indoor aviary setting, located at the Botanical Garden of the University of Turku. Initially, the sparrows were housed together as one social flock. The room (L: 5.20 m, B: 2.44 m, H: 2.42 m) was outfitted with feeding platforms (L: 121 cm, B: 59 cm, H: 85 cm), several perching branches, a sheltering spot and a small sand box for dust bathing. The room contained a side compartment (L: 2.10 m, B: 1.00 m, H: 2.42 m) that was later used to keep the experimentally removed birds separate from the remainder of the group for a limited period of time. The side compartment was partitioned off from the main room by opaque heavy cotton curtains that prevented physical and visual contact to the remainder of the group but allowed limited vocal communication. The side compartment similarly contained perching branches, a feeding platform, sheltering spot and a separate ventilation opening. Birds had *ad libitum* access to water at all times and were housed at a light: dark period of 8:16 h, which represented natural conditions at their time of capture. The temperature was kept constant at 14°C during the day and 10°C at night. I recorded social interactions and feeding behavior at the feeding platform by pointing a digital video camera through a Plexiglas window. The window could be covered with opaque cloth to avoid disturbing the birds through the presence of a human observer.

Prior to data collection I allowed the sparrows to habituate to their novel environment for a minimum of three days. I then collected behavioral data over a six-week period and during four consecutive experimental conditions: perturbation period 1 (P1), stability period 1 (S1), perturbation period 2 (P2) and stability period 2 (S2). In the beginning of the experiments (the P1 condition), I assumed that the

semi-naïve birds from different urban locations would need to establish novel social ties and re-organize the social structure of their flock. The P1 condition lasted for one week, after which a dominance hierarchy had presumably been established (Hegner and Wingfield 1987). During the following two weeks (the S1 condition), group structure was expected to remain stable. At the beginning of week four we captured three randomly determined sparrows (two males, one female) out of the group and released them into the side compartment. Birds in the main room and in the side compartment were kept physically separate from each other, unable to interact, for ten days in total. During this time no data were collected. In the evening of day ten the side compartment was re-opened and the removed birds re-joined the group. Data collection commenced the following day and during the following week (the P2 condition) sparrows were expected to re-negotiate rank order once more. I collected data for one final week (the S2 condition) during which group structure was assumed to have stabilized again. Unfortunately, the experimentally removed female sparrow died during this last week of the study and was hence excluded from statistical analyses.

## 2.4 Data analysis

### 2.4.1 Statistical analysis

In general, I have used  $\log_{10}$ -transformations on response variables that failed to fulfill the assumption of normality. In the instances a factor reached statistical significance I conducted Posthoc tests with sequential Bonferroni corrections to control for multiple comparisons. All statistical tests were two-tailed with an alpha level of 0.05. Data were analyzed using SPSS Statistics 20.0–23.0 by IBM.

In chapter I I used MANOVA to analyze the effects of local population density on frequencies of intra- and inter-sexual interactions (agonistic and neutral contact interactions) as well as on the duration of male harassment behavior. Density treatment and population were used as main factors in the models. Males and females were analyzed separately. Follow-up univariate ANOVA on the response variables were computed in case the MANOVA reached statistical significance ( $p \leq 0.05$ ).

In chapter II I used non-parametric tests to compare the number of interaction partners (mean degree) between observational periods (Kruskal–Wallis tests and Mann–Whitney U tests) and between social contexts (Friedman tests and Wilcoxon signed rank tests), respectively. Moreover, I used Kruskal–Wallis tests and Mann–Whitney U tests to determine differential patterns of male and female investment into the pair bond at different times of the year. For this, frequencies of initiated spatial proximity, feeding and sociopositive interactions (outdegree) between pair

mates were analyzed. Mann–Whitney U tests between observational periods were conducted as planned comparisons with repeated contrasts.

In chapter III I analyzed what factors determine the outcome of unsupported conflicts on the one hand and third-party interventions on the other hand in a generalized linear model (GLM). Subjects in unsupported conflict models were both aggressors and victims of aggression; in third-party intervention models the subjects were the providers of social support. Conflicts won vs. lost and interventions won vs. lost, respectively, were used as binomial target variables with a logit link function. The best-fitting model was achieved through step-wise backwards selection from the full model, containing all model factors, by deleting the least-significant factor based on p-values, starting from interaction factors. Null models, including only the intercept, were used as a control. Comparisons of the best-fitting model against the null model were based on the  $AIC_c$ , the Akaike information criterion corrected for small samples, whereby differences in  $AIC_c > 2$  indicated a better relative fit for the model with the lower score. Male and female patterns of providing social support were analyzed with Wilcoxon signed rank tests. Lastly, I compared males and females regarding the total number of individuals to whom they gave social support using Mann-Whitney U tests.

In chapter IV I analyzed the effects of experimental perturbation on feeding duration and frequencies of dyadic social interactions (agonistic, joining and supplanting interactions) with mixed within-between subjects ANOVA. This design combines factorial analysis with repeated-measures analysis. The initial models contained experimental treatment (the within-subjects factor) and either sex or dominance rank (the between-subjects factors). Due to the low sample size of  $N=16$  it was not possible to analyze sex and dominance rank in conjunction; instead, I selected the model containing the factor that fitted the data better, based on the  $AIC_c$ , and rejected the other. In case the experimental treatment was statistically significant I carried out planned comparisons with repeated contrasts.

#### **2.4.2 Social network analysis**

In addition to conventional statistical analyses I have carried out social network analyses in some of my studies. In particular, I have used relative reciprocity (II) and homophily models (I, II). Relative reciprocity tests whether actors that receive frequent social interactions from certain group members reciprocate interactions of the same kind towards the same individuals and at a similar frequency (Hemelrijk 1990b). In chapter II I thus compared jackdaws' tendencies for reciprocating positive social behavior in various contexts and at different times of the year. For this, sociomatrices were compared with their corresponding transposed form using row-

wise matrix correlations (Tau- $K_r$ -Tests with 10000 permutations each; Hemelrijk 1990b; de Vries 1993). Relative reciprocity was computed with the program MatMan 1.1 by Noldus Technologies.

I have implemented both variable homophily models (**I**) and constant homophily models (**II**). Homophily models investigate whether individuals that share a common trait – such as sex or age group – interact preferentially among each other (homophily) rather than with those that are dissimilar to them (heterophily; Hanneman and Riddle 2005). The models suppose the null hypothesis that individuals interact entirely at random. Variable homophily models test whether within- or between-group ties occur significantly more often than expected by chance. The model accounts for variation between groups in preference for homophily (Hanneman and Riddle 2005). Constant homophily models, by comparison, assume that all groups have a similar preference for within-group ties (homophily). Both the variable and constant homophily models were analyzed with the program Ucinet 6 for Windows. In chapter **I** I used sex as the grouping variable for variable homophily models in order to determine whether female water striders would direct neutral contact interactions preferentially towards other females. Males were used as a control. I calculated discrete models for each population and within each of the density treatments (10000 permutations each). In chapter **II** I used constant homophily models to test whether jackdaws preferentially exchanged interactions in various social contexts with their pair mate. Membership in discrete pair bonds was used as the grouping variable, resulting in a number of groups equivalent to the number of mated pairs plus the number of singletons. I computed homophily models within each social context and observational period (10000 permutations each).



### 3. RESULTS AND DISCUSSION

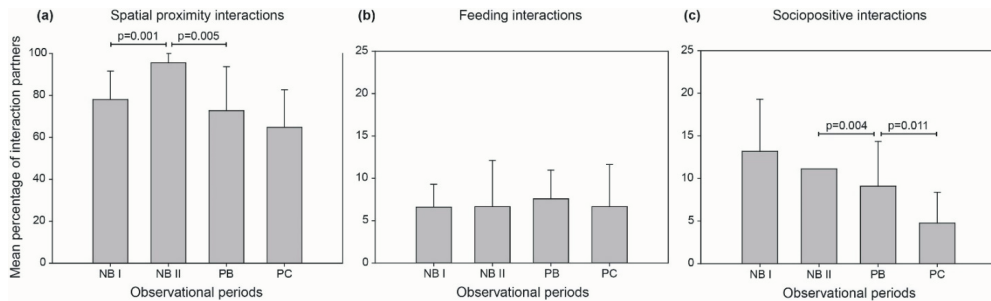
#### 3.1 Effects of the local environment on social structure

In chapter I I show that male water striders seek the proximity of female conspecifics – but not of other males – more frequently at high local densities, as was predicted by sexual conflict theory (Kokko and Rankin 2006; Cureton et al. 2010). Thus, the current, local environment affected mate searching behavior. However, contrary to predictions, males did not harass females for prolonged durations as density increased. I had also assumed that male water striders would fight more frequently among each other as groups become denser (cf. Emlen and Oring 1977; Kokko and Rankin 2006) but such an effect was not found. This result may indicate that contest competition among *A. paludum* males in densely populated habitats could be a less significant factor compared to scramble competition, in which males are forced to locate and reach potential mates faster than others. Female water striders were expected to preferentially seek contacts with other females (homophily) at higher local densities in an attempt to better escape harassing males; yet, only females from a single population behaved in this way and a consistent female strategy was not apparent. Indeed, populations varied both in observed interaction frequencies and homophily patterns, irrespective of the density treatment. The previously experienced environment, in addition to current environmental conditions, may determine behavioral patterns in *A. paludum* water striders (cf. Vepsäläinen and Savolainen 1995).

#### 3.2 Structural organization and dynamic fluctuations in social systems

In chapter II I show that jackdaws establish and maintain valuable monogamous bonds; yet, these bonds are embedded into the social structure of the group in an intricate way. Importantly, pair partners interacted more or less pro-socially also with other group members, depending on both the type of interaction considered and the current period of the breeding cycle. Birds exchanged spatial proximity interactions, which carry a comparatively low energetic demand, with the great majority of group members, particularly in late winter (**Figure 3a**). Previous research has shown that jackdaws gather information about foraging opportunities from spatially distant, non-affiliated conspecifics (Schwab et al. 2008). Hence, staying in close proximity to other group members in winter may enable jackdaws to learn about scarce food resources in their surroundings. In this manner the spatial proximity network may represent an interaction platform for group members to exchange social information, while simultaneously facilitating cohesion in winter flocks. By contrast, sociopositive (affiliative) interactions were exchanged among fewer birds during winter but became exclusive to the pair mate at the onset of the breeding season and during the parental care period, when fledged

offspring had joined the group (**Figure 3c**). Feeding interactions, by comparison, were consistently the most exclusive interactions of all (**Figure 3b**) and were almost entirely focused on the pair mate. Furthermore, with just a single exception, jackdaws reciprocated interactions within all social contexts and periods of the year.



**Figure 3.** The proportion of conspecifics [%] jackdaws interacted with across various social contexts and periods of the year. Shown are normalized mean degrees (mean  $\pm$  SD) in a) the spatial proximity, b) the feeding and c) the sociopositive context. Note the different scales on the y-axes. Observational periods were: NB I: non-breeding period I (N=14); NB II: non-breeding period II (N=10); PB: pre-breeding period (N=12); PC: parental care period (N=21). Mann–Whitney U tests (two-tailed). (Reproduced from Kubitz et al. 2015. *Journal of Avian Biology* 46:206-215. doi: 10.1111/jav.00508; see original article II).

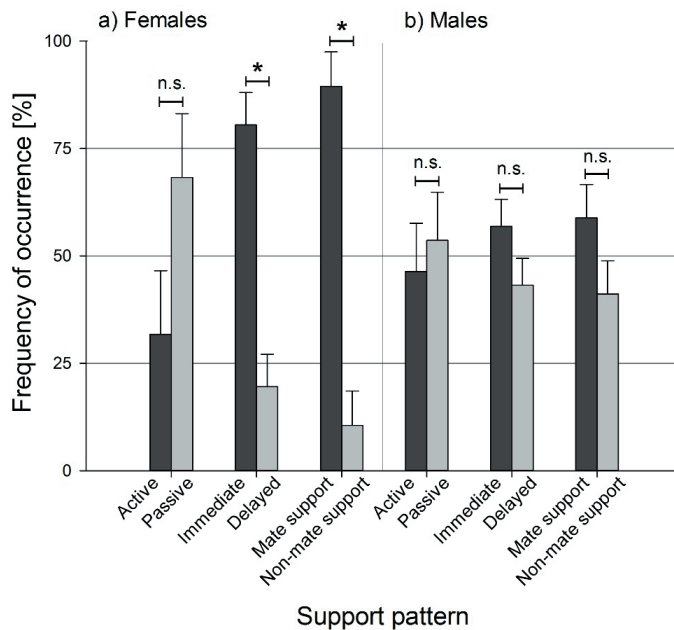
Pair mates preferentially shared social interactions with each other in all the contexts investigated. Male and female mates similarly invested most into mutual proximity during late winter, which resembled the pattern of mean degrees on the group level. By maintaining mutual proximity mated jackdaws may refresh their social bond before the start of the upcoming breeding season. When determining pair partner effort in the other two contexts, however, the sexes markedly differed: whereas males fed their mates throughout the entire year, presumably signaling their provider qualities (Scheid et al. 2008), females hardly fed their mates at all. Instead, female jackdaws invested strongly into sharing sociopositive behavior with their partner directly before the onset of breeding. Thus, feeding and sociopositive interactions are likely the proximate mechanisms employed by male and female jackdaws, respectively, to perpetuate a valuable bond.

### 3.3 Conflict resolution and stability of group structure

In chapter III I focus on another characteristic of monogamous jackdaw pair bonds: mutual cooperation during agonistic conflicts. Without the intervention from bystanders success during dyadic conflicts depended on both intrinsic factors (sex) and extrinsic factors (pair status, dominance rank and agonistic outdegree). Sex, pair status and dominance rank in jackdaws are likely linked (cf. Tamm 1977; Wechsler 1988). Yet, in our study flock receiving social support improved birds' chances of winning a conflict.

Providing active rather than passive support and the role of the support recipient (being the aggressor during the prior conflict rather than the victim) further determined success in third-party interventions. Since conflict victims may not be able to defend against two aggressors at once, both the conflict aggressor and support provider likely faced low risks of receiving counter-aggression, while sharing the resulting benefits (Smith et al. 2010).

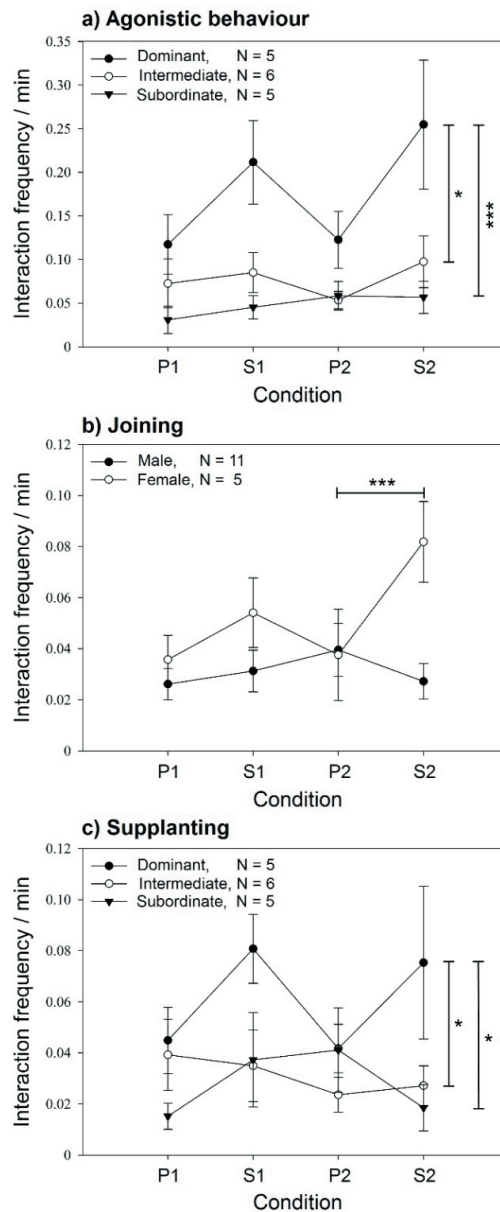
Also in the conflict arena the sexes markedly differed in their patterns of providing social support: whereas females intervened immediately into ongoing conflicts and preferentially supported their pair mate during encounters (**Figure 4a**), males, on the whole, showed no clear preference for providing certain types of support (**Figure 4b**). Hence, female jackdaws may be more prominently involved in conflict resolution than previously thought. Supporting their mate during ongoing conflicts, akin to providing sociopositive behavior prior to breeding (**II**), may further constitute a female's investment into maintaining a stable pair bond. Females likely cooperate and take certain risks during conflicts in return for their mate's cooperation during offspring provisioning. Male investment into care is a highly valuable asset: in jackdaws biparental care is indispensable for the survival of the offspring (Henderson and Hart 1993) and pair mates must work together early on to secure annual reproductive output. Additionally, females might benefit indirectly from securing their mate's social position in the group (Röell 1978).



**Figure 4.** Patterns of social support in a) female and b) male jackdaws. Alternating dark and light grey bars show the relative frequency (mean  $\pm$  SE) of providing active versus passive support, immediate versus delayed support and support of the mate versus a non-mate. Wilcoxon signed rank tests (two-tailed).  $N_{\text{Females}}=6$ ;  $N_{\text{Males}}=6$ . \*:  $p \leq 0.05$ ; n.s.: not significant.

Male jackdaws supported on average four other group members during conflicts. As one possible explanation for this behavior, they might intervene strategically into the conflicts of others in order to advance or solidify their social rank and position within the group, earning them greater access to valuable resources (Drews 1993; Henderson and Hart 1995).

Finally, in chapter IV I show that severe perturbations of group composition can destabilize a group's hierarchical structure: in this captive flock, house sparrows established a stable hierarchy quickly after the group was initially fused together (already during perturbation period 1) but the experimental removal and reintroduction of conspecifics effectively destabilized their hierarchy (perturbation period 2) and birds were unable to reach stability again afterwards (during the following stability period 2). Nevertheless, dominant sparrows consistently showed more frequent agonistic and supplanting behavior than subordinates, irrespective of the experimental treatment (**Figure 5a, c**). Also the duration of birds' feeding bouts was unaffected by experimental perturbations. These findings might indicate that the sparrows in this study tolerated disruptions of the group's social organization to some degree. Yet, female but not male house sparrows joined conspecifics at the feeding platform more frequently during stability period 2 (**Figure 5b**) and thereby behaved less aggressively when feeding socially. When animal groups are very large and open, linear dominance hierarchies are thought to be rare in the wild (Drews 1993). Having likely experienced fission-fusion events in nature prior to their capture, female sparrows may have responded to perceived structural instability by shifting to a non-aggressive social foraging strategy (joining, rather than supplanting conspecifics) in the absence of a possibility for dispersal. Dominance-related behavior, by comparison, appeared to be less phenotypically plastic. I note, however, that results were limited to a single flock and should ideally be repeated in a setting with replicate groups and/or treatments.



**Figure 5.** Behavioral responses to experimental perturbations of group composition in a captive house sparrow flock. Shown are frequencies (mean  $\pm$  SE) of a) agonistic, b) joining and c) supplanting interactions either for classes of dominance rank (a, c) or for sexes (b). Conditions were: P1: perturbation period 1; S1: stability period 1; P2: perturbation period 2; S2: stability period 2. Repeated contrasts between conditions; Posthoc tests (two-tailed) with sequential Bonferroni corrections between dominance rank classes.  $N=16$ . \*:  $p \leq 0.05$ ; \*\*\*:  $p \leq 0.001$ . (Reproduced from Kubitzka et al. 2015. *Ornis Fennica* 92:157–171. See original article IV).

## 4. CONCLUSIONS AND FUTURE DIRECTIONS

Here I have studied the social interactions and individual relationships between animals that form the basis for complex, highly dynamic social structures. The social behavior of animals is influenced by local environmental conditions (Hinde 1976; Pinter-Wollman et al. 2014), such as population density, and it also varies over time with the current phase of the breeding cycle. Moreover, social interactions occur across diverse social contexts: affiliative behavior, for example, serves to strengthen the social bonds and alliances between animals (Fraser and Bugnyar 2010; Tiddi et al. 2010), whereas agonistic behavior is involved in competition, aggressive intra- and inter-group conflict and its resolution (Aureli and de Waal 2000; Flack et al. 2006). Both modalities constitute the building blocks of higher-order structures, such as social hierarchies, and they may be prominently involved in group-level processes such as group cohesion. These higher-order structures, in turn, regulate dyadic social behavior and determine the local environment, which leads to intricate feedback loops (Krause and Ruxton 2010). Thus, social systems are spatially, temporally, contextually and structurally complex. In my thesis I have investigated these aspects of social complexity in three model species.

Current, local population density affected the frequency of mate searching behavior (neutral contact interactions) in male water striders (**I**). Elevated population density has previously been shown to increase also the intensity of direct male-to-male competition (e.g. Jirotkul 1999; Mills and Reynolds 2003; Kokko and Rankin 2006); yet, in the present study, the frequency of agonistic conflicts among males was apparently unaffected by local density. Scramble competition may hence be a prominent factor among *A. paludum* males in dense aggregations. Further research is still needed in this species in order to evaluate the differential mating success of males competing under contest vs. scramble competition as well as under different environmental conditions. Variation in interaction frequencies and homophily patterns between populations was high in all density treatments, and thus, there is a clear need to control for individuals' previous experiences of environmental conditions in future studies. Finally, investigating effects of environmental conditions in conjunction – for example, population density in combination with the operational sex ratio (de Jong et al. 2009; Clark and Grant 2010; Cureton et al. 2010) – will further unravel the interrelatedness between local environmental conditions and social behavior.

Groups of jackdaws are dynamic social assemblages into which mutualistic pair bonds are embedded (**II**). Birds actively maintained positive social ties (close proximity, sociopositive behavior) to other members of the flock, particularly in early

to late winter. This reflected the interaction patterns exchanged between pair mates. I show here that the social behavior within pair bonds is asymmetric in jackdaws: both sexes invested into their bond with different social behaviors and at different times of the year. Paired males fed their mates consistently throughout the year (II). They also intervened into other group members' conflicts (III), presumably to improve their social rank and thus their own status of being a valuable mate (cf. Henderson and Hart 1993; Henderson and Hart 1995). Females, conversely, exchanged sociopositive behavior with their mates prior to breeding (II) but also provided pro-active social support during agonistic conflicts (III). In this way, they likely secured their mate's later investment into paternal care. Male and female pair partners hence cooperate closely to maintain a valuable bond that enables them to successfully raise offspring together. By integrating functionally diverse social contexts, such as allo-feeding, affiliative and agonistic behavior, it is possible to gain a broader picture of the species' social system and its nested pair bonds.

Finally, the hierarchical structure in a group of house sparrows destabilized after an invasive experimental perturbation and a linear hierarchy was not re-established again quickly (IV). Disruptions of social organization did not appear to affect sparrows' feeding and dominance behavior, however. Only female sparrows joined, rather than supplanted, feeding conspecifics more frequently following the second experimental perturbation treatment. Individual sparrows may thus be able to tolerate some degree of structural instability caused by a fluctuating group composition and may possibly reduce conflicts by shifting to a less aggressive social foraging strategy. I acknowledge that these results are limited to a single flock of house sparrows; therefore, the setup should ideally be repeated with multiple groups before firm conclusions about the ecology, social structure and fission-fusion dynamics of the species may be drawn. Moreover, in natural fission-fusion populations structural instability and conflicts of interest may compel members to leave their social group (Kummer 1971; Wrangham 1979), which can be stressful for individuals (Stocker et al. 2016). Our experimental setting, however, prohibited dispersal. Further studies on fission-fusion dynamics in natural populations are much needed and will likely yield novel insights. Also the mechanisms that facilitate social cohesion in animal groups pose exciting areas for future research.

In conclusion, a basic environmental factor such as local population density may profoundly affect social groups by altering the animals' contact structure: in larger and denser groups the contacts between individuals become more frequent (I) and from this situation a potential for both conflict and cooperation arises. As aggressive intra-group conflicts increase in frequency the capacity for cooperation decreases (de Waal 1986; Aureli et al. 2002). Cooperation, in turn, is constantly threatened by the selfish interests of individuals (Darwin 1859). Hence, conflicts must be

resolved efficiently in social groups. Enduring social stability is likely required for complex relationships and higher-order social structures to develop and function (Aureli et al. 2002), as may be the case for long-term mutualistic bonds or alliances (**II**, **III**) and linear dominance hierarchies (**III**). It is hence rather unlikely that such higher-order structures would remain stable in the long run or grow very complex in highly dynamic fission-fusion societies (**IV**; Lusseau et al. 2006; but see Kerth et al. 2011; Braun et al. 2012). Whereas complex mechanisms of conflict resolution, such as third-party interventions (**III**) and policing (Wenseleers et al. 2004; Flack et al. 2006), may exist in long-term stable social groups, relatively simple mechanisms for mitigating conflicts may be possible in fluctuating (fission-fusion) groups, for example, behavioral shifts to non-aggressive social foraging (**IV**). The forms of social structure that evolve in fission-fusion societies, how these societies deal with structural instability, and the effects of fission-fusion dynamics on the condition and behavior of individuals are focus areas of ongoing research (e.g. Aureli and Schaffner 2007; Randić et al. 2012; Stocker et al. 2016). It is also important to integrate social behavior with its selective functions and the evolutionary history of a species in order to gain a complete picture of animal sociality. In light of ongoing environmental changes, such as the increasing human impact on natural habitats, a greater understanding of the factors and processes underlying social behavior is much needed.



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