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MASTERARBEIT

Titel der Masterarbeit

**„Group integration in captive grey parrots (*Psittacus erithacus*):
Changes of group dynamics after the integration of two newcomers“**

Verfasserin

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angestrebter akademischer Grad

Master of Science (MSc)

Wien, 2015

Studienkennzahl lt. Studienblatt: A 066 831

Studienrichtung lt. Studienblatt: Masterstudium Zoologie

Betreuerin / Betreuer: Univ.-Prof. Mag. Dr. Thomas Bugnyar

Master Thesis

**Group integration in captive grey parrots (*Psittacus erithacus*):
Changes of group dynamics after the integration of two newcomers**

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Key words:

Grey parrot (*Psittacus erithacus*) • Integration

Newcomer • Group dynamics • Social cohesion

• Bond formation

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ABSTRACT

African Grey parrots (*Psittacus erithacus*) live in fission-fusion social systems which are composed of flock formations and monogamous pair bonds formed throughout lifetime. In such communal species individuals frequently face competition over valuable resources and thus conflicts of interest. Changes in group composition need to be coped with requiring adequate conflict management behaviors. This study aims at providing insight into grey parrots' social systems and intragroup behavior, as well as into existing mechanisms of conflict solutions in captivity. Therefore, two newcomers were integrated in an existing group while observing behaviors and interactions. In order to control for naturally occurring interaction changes, behaviors and interactions of a group without integrated individuals was observed and compared to the integration group. The results suggest that individuals are avoiding direct aggression, i.e. they tend to manage potential conflict situations passively by showing territory ownership and social cohesion due to flexible use of bond strengthening and recruiting social support from others. These findings highlight the importance of available affiliation partners as well as territories in captivity. The social group dynamics of grey parrots detected in this study provide insights into their social skills and potential of conflict management strategies. How much the observed pattern can be generalized to wild populations is discussed.

INTRODUCTION

Individuals are required to deal with conspecifics to a variable extent depending on their social organization. Dynamic social systems are represented, for example, by fission-fusion societies where group size changes flexibly (Aureli et al. 2008). Due to the spatial and temporal distribution of resources groups split into smaller subunits (Bradbury & Vehrencamp 2011). Such a society is typical for primates (Aureli et al. 2008), elephants, spotted hyenas, dolphins (Bradbury & Vehrencamp 2011) and also birds like parrots (Del Hoyo et al. 1997) and corvids (Braun et al. 2011). Living in a group has advantages due to the presence of others (Aureli & De Waal 2000). Predators can be detected earlier, information about food and water locations can be shared, resources can be defended better (Silk 2007, Dagg 2011), and sometimes individuals may cooperate to raise offspring (Aureli & De Waal 2000). On the other hand, since group members of the same species have equal needs, competition increases over limited resources like mates, food, resting sites and sleeping sites (Aureli et al. 2002, Aureli & De Waal 2000, Cheney & Seyfarth 1990, Preuschoft & Van Schaik 2000). Further diseases can spread easier among group members (Dagg 2011).

Considering unavoidable conflicts of interest as mentioned above, in communal species signals, which need to be interpreted correctly from individuals, are the key for managing interactions (Bradbury & Vehrencamp 2011). Therefore, social cues and behaviors need to be attended to and information about group members concerning their relationships (like novel separations) should be understood to some extent (Aureli et al. 2008, Bond et al. 2003, Bradbury & Vehrencamp 2011, Cheney & Seyfarth 1990). Furthermore, in contrast to fixed groups, group members of fission-fusion groups need to often remember information over a long period of time since they are scattered consistently (Aureli et al. 2008). Bradbury

& Vehrencamp (2011) suggested that the development of a sophisticated “social brain” was necessary to accomplish these social skills including long-term memory. In general, cognitive abilities are often linked to social living suggesting a higher cognitive development in more social animals (Kummerer et al. 1997). In many social primates, for example, extensive interactions within the group correlate with brain size and complexity (Dagg 2011). Recent studies revealed that the social brain hypothesis does not only apply to mammals (Byrne & Whiten 1988) but also to birds like corvids (Bond et al. 2003). The large brain in relation to body weight is only one of the many convergences between birds and mammals offering comparisons between them in different categories (Burish et al. 2003).

A very important part in daily life of social animals is dealing with potential conflicts. For instance, goals of group members may be incompatible (Aureli & De Waal 2000, Preuschoft & Van Schaik 2000), individual space may be limited (Dagg 2011, Del Hoyo et al. 1997), competition over rank and resources may be omnipresent, and thus may jeopardize social harmony (Aureli & De Waal 2000). Conflict situations between individuals brought up by overlapping interests can lead to aggression (Aureli et al. 2002) involving increased costs that reduce the net benefit of group living (Bradbury & Vehrencamp 2011). Nevertheless, in order to prevent group living benefits (e.g. being safer from predators, being more able to defend resources, profiting from shared information, Silk 2007), alleviation of competition is necessary (Aureli & De Waal 2000). Clarification can result from body condition, experience and age, which is often the case in solitary species (Preuschoft & Van Schaik 2000). Another solution is dominance, since priority over limited resources is clarified once a dominance hierarchy is established (Bradbury & Vehrencamp 2011, e.g. vervet monkeys Cheney & Seyfarth 1990, De Vries et al. 2003). Therefore group members need to know and recognize each other (Bradbury & Vehrencamp 2011).

It is likely that permanent change in social consistency is a cognitive and sometimes stressful challenge (Connor 2007). Changes within group composition like dispersal or immigration can occur at any time (Cockrem 2007), which demands individuals to cope with new situations and react to changes accordingly. Immigration periods often increase stress, indicated by elevated cortisol concentrations (e.g. yellow baboons, Alberts et al. 1992), for both the immigrant and the group members (e.g. olive baboons, De Vries et al. 2003), since newcomers usually face aggressive encounters at first contacts (e.g. vervet monkeys, Cheney & Seyfarth 1990). Potentially disadvantageous situations generate stress reactions (Cockrem 2007), which have like social stress in general negative influence on welfare (De Vries et al. 2003). Furthermore aggression can lead to fighting which is not only stressful but often includes high physical costs (Smith et al. 2010) and is therefore usually the last resort in solving conflicts (Preuschoft & Van Schaik 2000).

Considering consequences and costs resulting from conflicts, aggression and stress any group-living species should have evolved mechanisms to prevent escalation (Preuschoft & Van Schaik 2000) and manage conflicts accordingly (Aureli & De Waal 2000, De Waal 2000). Support of this prediction is seen in many animal societies using behavioral tactics and learned flexible expressed mechanisms in order to deal with conflicts (Aureli & De Waal 2000, De Waal 2000, Matsumura & Okamoto 2000) without fighting (Preuschoft & Van Schaik 2000). These specific actions are called conflict resolution (Aureli et al. 2002), and turn out to be more flexible in species living in environments that are more fluctuating than constant (Cockrem 2007). De Waal and colleagues (1976) framed a categorization of different possible agonistic interaction types (e.g. java-monkeys, *Macaca fascicularis*), depending on the number of individuals involved. Referring to this, interactions could be called “dyads”, “triads” or “polyads” all with the intention of support, protection or alliance respectively. An alliance, mostly formed between genetic relatives (e.g. vervet monkeys), implies an

uninvolved individual intervening in an ongoing agonistic encounter between two group members by taking sides and supporting one of both (Cheney & Seyfarth 1990). Support can either consist of “active social support” by participating actively (Horrocks & Hunte 1983) or of “passive social support” by only being present and indicating social alliance (Von Holst 1986). Alliance relationships are characterized by consistent cooperation and thus can be distinguished from coalitions (Harcourt & De Waal 1992). The advantages of alliances or support in general can be on the one hand higher reproductive success due to better access to resources like food, mates, grooming partners, nests-sites or rest-sites. And on the other hand being able to successfully defend rank positions (e.g. males usually) or resources against neighbors and rivals (De Waal 1978, Cheney & Seyfarth 1990); therefore, winning agonistic encounters more frequently (Schreiber et al. 2005, 2009). Moreover, support can buffer hormonal stress (due to a decrease in corticosterone metabolites which function as hormonal stress response) and as a result stress-mediated responses as well (e.g. greylag geese, Schreiber et al. 2005, 2009; ravens, Stöwe et al. 2008; pigs, Kaiser et al. 2003).

Social support and cooperation has been long known for mammals (Von Holst 1986; e.g. lion, wolf, De Waal 1978; dolphins Connor 2007; spotted hyena, Smith et al. 2010) and is particularly well studied in primates (Bermann 1980, Horrocks & Hunte 1983; e.g. vervet monkeys, macaques, baboons, Cheney & Seyfarth 1990), but comparably little investigated in birds (Schreiber et al. 2005). Nevertheless, triadic interactions and agonistic support also occur in group-living birds (e.g. jackdaw, De Waal 1978; goose, Schreiber et al. 2005; ravens, Fraser & Bugnyar 2012) considering the convergence in social strategies between birds and mammals (Braun & Bugnyar 2011). Burish and colleagues (2003) support this hypothesis by referring to the convergent evolution of the brain structure in birds and mammals, and also highlight existing solutions for social problems in birds.

Considering parrots' cognitive abilities and convergence with primates in both physiology and life history (Del Hoyo et al. 1997, Pepperberg 2002), grey parrots (*Psittacus erithacus* LINNAEUS, 1758) represent a suitable species for further investigations on social coping mechanisms. The natural habitat of African Grey parrots covers lowland moist forest across Africa depending on available food and nesting sites (Del Hoyo et al. 1997). Concerning social group composition they can be classified as a fission-fusion system like *Psittacidae* in general (Del Hoyo et al. 1997, Bradbury & Vehrencamp 2011) with a transactional social structure (Burish et al. 2003). The monogamous pair is the primary social unit since they bond for life even beyond breeding season, and support each other to increase reproductive success (Duff 2011, Del Hoyo et al. 1997, Lantermann 1990, Luft 1994). But they also socialize with others (Martin 2001) and roost communally especially after the nesting period, when parents including subadults integrate into larger flocks again (Del Hoyo et al. 1997). Flock formations occur in different sizes (e.g. family-, group- or swarm-flocks of five up to 10.000 individuals) in order to share information about foraging areas (Lantermann 1990, Luft 1994, Del Hoyo et al. 1997). Resting and feeding trees are used as social centers to interchange friendly and agonistic interactions (Garnetzke-Stollmann & Franck 1991). During fusion situations they exchange complex vocal signals in order to recognize each other and assess novel situations (Bradbury & Vehrencamp 2011). Interspecific communication, which involves perception of and appropriate response to complex signals, may have supported the development of their intelligence (Pepperberg 1981, 2002). According to this Emery and colleagues (2007) outlined the association between brain size and mating system in birds, more precisely the fact that species with long-term pair bonds show the largest brains in relation to size. This argument is supported by the studies of Irene M. Pepperberg, who investigated grey parrots' cognitive and communicative abilities (e.g. categorical concepts, Pepperberg 1983, 1987, 1990; counting-like strategies, Pepperberg 2006; vocal plasticity, Pepperberg 1981), concluding that they are comparable to those of non-human primates and

young human children (Pepperberg 2002, 2006). Also the parrots' social structure is similar to that of primates, considering their corresponding system of hierarchy, which is also based on experience, seniority and union, but not as complex due to the monogamy of parrots (Del Hoyo et al. 1997). Unlike the aforementioned hypothesis, scientists observing these parrots in the field suggest that within a wild flock, individuals do not form social hierarchies resembling those of mammals (e.g. fixed hierarchies between respective individuals) but rather restricted their hierarchy to family groups (Lantermann 1990, Luft 1994, Martin 2001). However high competition about nesting sites exists (Lantermann 1990) in the wild and according to Luft (1994) birds also compete for fruitful trees of the African oil palm (*Elaeis guineensis*) where more assertive birds have priority over inferior ones. In order to protect resources aggressive behavior is exhibited especially when bonded pairs defend breeding territories (Martin 2001). Therefore, disputes appear to be highly ritualized in order to prevent serious injuries (Lantermann 1990). Most disputes in the wild are resolved without physical contact, and birds use visual and vocal displays to keep intruders off (Martin 2001).

Birds live in complex social environments where, due to limited distance in feeding and roosting situations (Del Hoyo et al. 1997), potential conflicts and changes in flock compositions occur at any time (Cockrem 2007). Thus evolution should have provided individuals with different behavioral "tools" for conflict solutions (Aureli & De Waal 2000). Recent studies focus on how species deal with conflicts and what mechanisms they use to regulate them (Aureli & De Waal 2000). But studying parrots in the wild is difficult, since they are difficult to mark, follow and observe. Thus, knowledge about regulatory mechanisms on a population level and social systems remains limited (Del Hoyo et al. 1997). So far, little is known about group dynamics in general and mechanisms of conflict management (Aureli et al. 2002) or the influence of conflicts in intragroup behavior (Radford 2011) in particular. Observations on grey parrots in captivity were often limited to single birds or individual pairs

and did not help increase our knowledge about their group life (Luft 1994). So how do parrots manage conflicts or deal with competitive situations? Do they show similar conflict resolutions and mechanisms as, for example, primates?

The present study aims at gaining insight into grey parrots' social group dynamics as well as into intragroup behavior. Further I try to investigate how individuals manage changes as well as potential conflicts and what conflict solutions exist. Therefore, two unknown individuals were subsequently integrated into an existing captive group, and both individual room use and interactions were observed before and after the integrations. Since in captivity the integrity of the group should be of priority as well, mechanisms for conflict management could be expected (Aureli & De Waal 2000).

Considering the unlimited access to food in captivity competition could be expected to revolve around restricted space and partner choice. Therefore, I hypothesize that group members change their room use and approach the new individual. As novel individuals may change the social hierarchy, aggressive interactions between newcomers and established group members would be expected to occur in the beginning of the introduction phase. Newcomers on the one hand should try to gain support of others, whereas group members on the other hand should try to defend their space and partners against the intruder. Due to the limited space, avoidance is possible only to a certain degree, which may increase the necessity of active management in competitive situations. Within this framework alliances between neighbors or between newcomers among themselves or/and unaffiliated individuals could occur. If individual history and experience influences group integration, it could be expected that the first integrated bird, which was housed in a group, might pose a higher threat and would predict a stronger reaction to her introduction.

MATERIAL AND METHODS

SUBJECTS

The study was conducted on seventeen grey parrots that were kept in two different aviaries at the ARGE-Papageienschutz in Vösendorf, Austria, a non-profit association that supports the protection of parrots and species-appropriate husbandry under the supervision of Mag. Nadja Ziegler. Each aviary had a size of about 20 m² plus an open-air enclosure the access of which was closed during observation. The aviaries were equipped with structures, items, toys and necessary components like water basins and thus as appropriate for the species as possible. The ground was covered with sand. Their diet consisted of a fruit and vegetable mix combined with carbohydrates in the morning and a seed-mix in the afternoon. Additionally oil seed was provided each day and water was accessible ad lib.

We focused on two groups: the so-called integration group originally consisted of eight subjects and received two more individuals in the course of the study, whereas the composition of the control group (n=7 birds) remained constant over the course of the study. Detailed information of the two groups is shown in Tab.1. The birds had different origins and backgrounds. Most were private hand offs and were kept alone or with a partner. The first integrated bird Mucki was kept in group-housing prior to introduction, whereas the second integrated bird Pimienta came from an individual housing. Most birds of the integration group including the integrated individuals showed a plucked plumage due to self-plucking behavior, and were therefore limited in or incapable of flying (e.g. Rocky, Romy, Gogo, Kunibert, Chica, Mucki, Pimienta). A lack of stimulation and social isolation during private captivity in the past is the most likely explanation for self-plucking behavior and other stereotypes (Lantermann 1990, Luft 1994, Del Hoyo et al. 1997).

Table 1. Overview of study subjects.

Group	Name	Short name	Sex	Subspecies	Year of Birth
Integration	CocoH.	Co.H	Male	<i>P.e.erithacus</i>	?
Integration	Rocky	Roc	Male	<i>P.e.erithacus</i>	2005
Integration	Gigi	Gi	Male	<i>P.e.erithacus</i>	?
Integration	Romy	Rom	Female	<i>P.e.timneh</i>	?
Integration	Gogo	Go	Female	<i>P.e.erithacus</i>	?
Integration	Kunibert	Ku	Male	<i>P.e.erithacus</i>	?
Integration	CocoR.	Co.R	Male	<i>P.e.timneh</i>	?
Integration	Chica	Ch	Female	<i>P.e.erithacus</i>	1967
Integrated Birds:					
Integration	Mucki	Mu	Female	<i>P.e.erithacus</i>	2003
Integration	Pimienta	Pi	Female	<i>P.e.erithacus</i>	2002
Control	Pauli	Pa	Female	<i>P.e.erithacus</i>	?
Control	Coco	Co	Male	<i>P.e.erithacus</i>	?
Control	Kasi	Ka	Female	<i>P.e.erithacus</i>	?
Control	Chica	Ch	Female	<i>P.e.erithacus</i>	1998
Control	Joki	Jo	Male	<i>P.e.erithacus</i>	1999
Control	Maxi	Ma	Female	<i>P.e.erithacus</i>	1987/88
Control	Billi	Bi	Female	<i>P.e.erithacus</i>	1991

EXPERIMENTAL SET-UP

All experiments and observations were conducted within the aviary for the integration group and in- and outside the aviary for the control group. After a pilot monitoring phase each aviary was virtually subdivided into seven different areas, labeled from A to G each. The boarder of every area was defined according to physical structures and landmarks the subjects appeared to perch on (Fig.1 and 3), although they could run free inside the whole aviary. Due to feeding bowls and roosting sites in nearly all areas, those areas can be considered as territories (control group: A, B, C, E, F; integration group: A, C, D, E, F, G).

The set-up for the integration group consisted of four phases of successive observation with a break of four weeks after the phase “integration pimienta”. Consisting of eight birds at the beginning, the first bird was integrated into the group during phase “integration mucki”. In addition the second bird was integrated in phase ”integration pimienta”. Both integrated birds are henceforth referred to as “newcomers”. Due to health reasons the first newcomer had to be taken out after phase “integration pimienta” (Fig. 1).

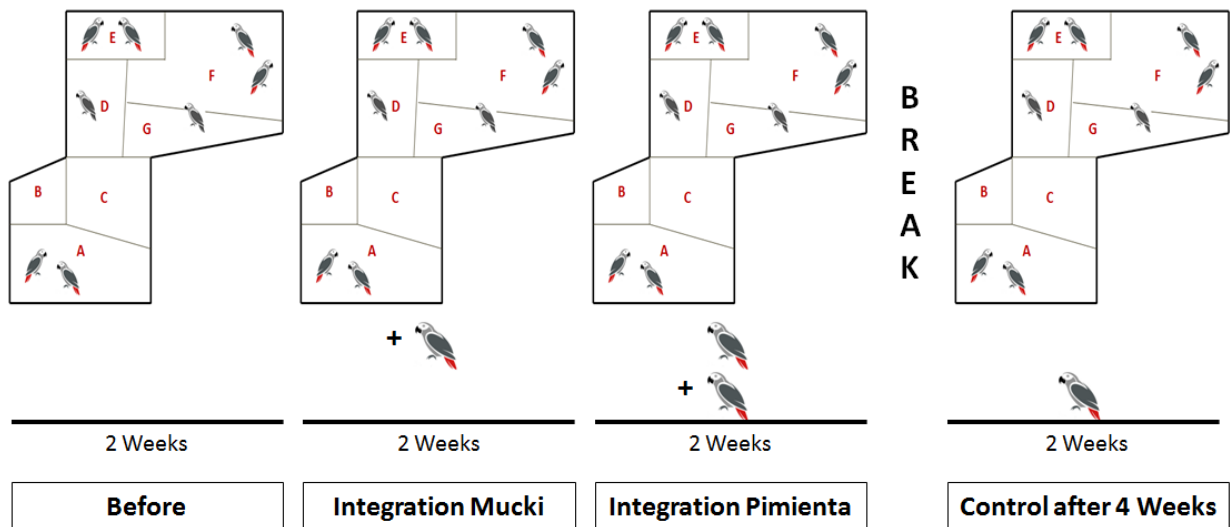


Figure 1. Experimental set-up for the integration group: Conditions of the group during four phases (before, integration mucki, integration pimienta, control after 4 weeks) consisting of eight birds at the beginning. Each phase of observation lasted for two weeks.

The observation spot was chosen to offer an overview of the whole aviary and to reduce the disturbance of area owners to a minimum. During observation I was sitting in a folding chair that was integrated into the existing area's framework. The two newcomers were integrated into two different spots of the aviary. In order to reduce agonistic behavior by group members, new structures were built for the newcomers before integration. Therefore, spots between existing territories (integration pimienta) or in big territories with only one owner (integration mucki) were chosen (Fig. 2), as the new structures, including own feeding bowls, distracted the group members. By immediately placing the newcomer into the new structures group members could not occupy the structures in the meantime, and were likely to accept the newcomer there.

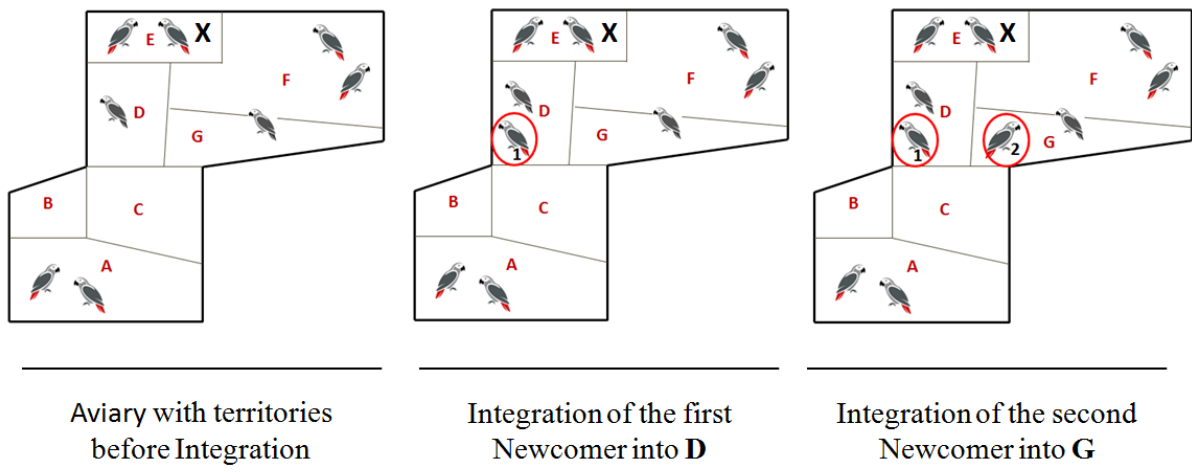


Figure 2. Integration spots of the two newcomers. The first newcomer Mucki was integrated into area D, identified with number one. The second newcomer Pimienta was integrated into area G, identified with number two. Spot of observation, identified with X, was constantly in area E.

The procedure for the control group consisted of two phases of observation with a break of four weeks between, and was to see if group dynamics remained constant over longer times. In order to keep conditions continuous no structural or individual changes were performed (Fig.3).

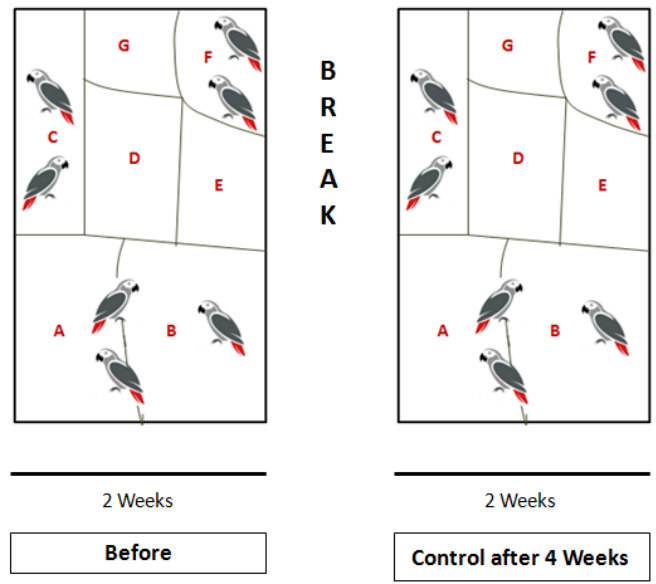


Figure 3. Experimental set-up: Conditions of control group consisting of seven birds during two phases (before, control after 4 weeks). Each phase lasted for two weeks of observation with a break of four weeks between.

DATA COLLECTION

Observation

Observation took place for four hours per day, eight days per phase, in total 128 hours for the integration group and 64 hours for the control group. Observation time alternated between morning and afternoon. To detect social interactions between individuals in both groups, behavioral sampling and “all occurrence recording” was chosen (Martin & Bateson 2007, similar to Woppel 2003, Zeppetzaer 2004). Specifically, all agonistic and affiliative interactions between individuals were recorded. Allopreening, copulating and contact sitting were collected as frequencies. Unidirectional interactions that did not count for both individuals were written down as directed or received interaction for the particular individuals (Tab. 2). Relationship-pairs are defined as dyads that show series of interactions with each other, thus constant interactions during observation (see Hinde 1976). Therefore, relationship-pairs can be monogamous couples (male-female), as wells as friends or even rivals with same-sex relationships, respectively (male-male, female-female). Relationships can be seen as “friendships” when individuals share time together and interchange affiliative interactions (Van Schaik & Aureli 2000).

Table 2. Noted interactions between individuals (Behavioral parameters due to Luft 1994 and Woppel 2003)

Agonistic interactions	Affiliative interactions
Threatening	Courting
Chasing	Billing
Attacking	Courtship feeding
Beak battling	Allopreening
Stealing	Copulating
Fleeing	Contact sitting
	Bowing down
	Using same feeding bowl

To reconstruct individual room use during observation, the method of “instantaneous sampling” was chosen to note individual positions (Martin & Bateson 2007). Therefore, every ten minutes the position of every individual according to the seven different areas, each divided in “on the ground” and “structure above”, was noted (similar to Fischer 2001, Horauer 2002).

Experiments

To test if birds show different reactions to interruptions depending on the position in the aviary, known female persons positioned themselves first in the middle of the aviary and then successively in each territory for about three minutes without making any communicative contact with the birds. Behavioral reactions of each individual were noted during the time. Known persons were chosen to exclude shy behavior of neophobic birds. Using other birds instead of humans for this test was not possible due to stress exposure. The test was performed twice per aviary, each before and after the four-week pause, with different

people. For the integration group testing was only conducted if birds remained at the ground of the aviary, except for those who stayed mainly at structures above.

DATA EVALUATION AND STATISTICAL ANALYSIS

For the detection of significant differences between frequencies of interactions Pearson's Chi-squared test was used. To determine whether means differed significantly, data were tested for normal distribution using Shapiro-Wilk normality test. If data were normally distributed further treatment was performed with Paired t-test due to interdependency; if not, further analysis followed using Wilcoxon signed rank tests. The significance level was set to $p < 0.05$. Note that data analysis excludes Bonferroni correction whereby results could turn out otherwise.

To measure how widespread individuals use the aviary indexes were calculated. Therefore, the frequencies of each area used by every individual were evaluated. A similar method for diet breadth index calculation by Saikia (2012) was applied to evaluate room use indexes. This way the proportion of the maximal value of an area use to total possible area use was measured. For example, if an individual used one area the most with a frequency of 56 out of 205 total observations, then the index will be 56 divided by 205 equaling an index of 0.27. Individuals can reach a minimal index of 0.14 if they use all areas equally and a maximal index of 1 if only one area is used during total observation time. Note that there is no information which area is used. The lower the index the more widespread is the room use.

For data calculation and graph creation Microsoft Office Excel 2007 and Rcmdr Version 2.1-6 (R Core Team 2014) were used.

RESULTS

ROOM USE

Integration group

During all four phases of observation group members (excluding newcomers) significantly preferred staying on the ground over staying on structures above (“before”: $\chi^2 = 49.3204$, $df = 7$, $p < 0.001$; “integration mucki”: $\chi^2 = 64.6618$, $df = 7$, $p < 0.001$ “integration pimienta”: $\chi^2 = 39.1655$, $df = 7$, $p < 0.001$; “control after four weeks”: $\chi^2 = 63.8594$, $df = 7$, $p < 0.001$). During phase “integration mucki” and “control” group members used the structures above significantly more often as compared to phase “before” (“integration mucki”: $t = 2.8838$, $df = 7$, $p = 0.024$; “control after four weeks”: $t = 2.5287$, $df = 7$, $p = 0.039$). Both newcomers used structures above almost exclusively (Mucki stayed on the ground four out of 400 times and Pimienta seven out of 400 times).

Due to calculating indexes, I found out how widespread the room use of each individual was. In phase “before” most individuals showed a preference for two or three areas. CocoH ($i = 0.47$) and Rocky ($i = 0.74$) preferred area A, B & C while CocoR ($i = 0.56$) and Chica ($i = 0.65$) preferred area F & G. Gigi showed the most widespread room use and thus had the lowest index ($i = 0.27$). He used all areas of the aviary. Three birds showed a clear preference for only one area during all phases: Romy only used area D, whereas Gogo and Kunibert only used area E.

In phase “integration mucki” five individuals revealed different indexes compared to “before”, both lower or higher ones (CocoH, $\chi^2 = 19.3215$, $df = 6$, $p = 0.004$; Rocky, $\chi^2 = 26.7393$, $df = 3$, $p < 0.001$; Gigi, $\chi^2 = 25.221$, $df = 6$, $p < 0.001$; Chica, $\chi^2 = 35.9694$, $df = 4$, $p < 0.001$). CocoH and Rocky focused on area A & B. Chica, CocoR and Gigi focused on area

F. Mucki preferred area D where she was integrated in, but also used area E (ratio D to E 157:43).

After the integration of Pimienta nearly all individuals demonstrated higher indexes than in phase “integration mucki” (CocoH, Rocky, Gigi, CocoR, Mucki) and a significant different index to phase “before”, respectively (CocoH, $\chi^2 = 26.2125$, $df = 6$, $p < 0.001$; Rocky, $\chi^2 = 12.8088$, $df = 3$, $p = 0.005$; Gigi, $\chi^2 = 68.5027$, $df = 6$, $p < 0.001$; $\chi^2 = 48.2865$, $df = 4$, $p < 0.001$; Chica, $\chi^2 = 30.271$, $df = 4$, $p < 0.001$; Mucki, $\chi^2 = 45.9644$, $df = 1$, $p < 0.001$). Except for Chica, Pimienta and those individuals who already showed the maximum index 1, all other group members also reached their highest indices of all four phases after the introduction of Pimienta. In doing so CocoH and Rocky strongly focused on area A. CocoR, Chica and Gigi all showed a strong focus an area F. Pimienta stuck to the area G where she was integrated.

In the last phase “control after 4 weeks” (after a break of four weeks), all individuals, except for Pimienta and those who never changed their room use, had a lower index than in the previous phase “integration pimienta”. Some individuals still revealed significant differences between this phase and phase “before” (CocoH, $\chi^2 = 29.6296$, $df = 6$, $p < 0.001$; Gigi, $\chi^2 = 57.2146$, $df = 6$, $p < 0.001$; CocoR, $\chi^2 = 45.0194$, $df = 4$, $p < 0.001$; Chica, $\chi^2 = 23.733$, $df = 4$, $p < 0.001$; Pimienta, $\chi^2 = 400$, $df = 2$, $p < 0.001$). Most of the individuals diminished the focus they showed in phase “integration pimienta” as described above, and used two or more areas again. Pimienta switched her position and did not use area G as in the previous phase but only area D, where Mucki used to stay before she had to be taken out of the group (Tab.3).

Table 3. Individual indexes of the room use in each phase for the integration group. Asterisks mark significant differences to phase “before”, respectively, and in the case of Mucki and Pimienta to the former phase in each case (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Values in bold represent maximal indexes of each individual.

Phases	Individuals									
	Co.H	Roc	Gi	Rom	Go	Ku	Co.R	Ch	Mu	Pi
<i>index</i>										
before	0.47	0.74	0.27	1.00	1.00	1.00	0.56	0.65	n.a.	n.a.
integration mucki	0.46**	0.51***	0.46***	1.00	1.00	1.00	0.66	0.89***	0.79	n.a.
integration pimienta	0.65***	0.85**	0.65***	1.00	1.00	1.00	0.84***	0.87***	1.00***	0.96
control after 4 weeks	0.55***	0.67	0.55***	1.00	1.00	1.00	0.80***	0.83***	n.a.	1.00***

Control group

During the two phases of observation in the control group, group members preferred structures above significantly more than the ground (“before”: $\chi^2 = 25.8511$, $df = 6$, $p < 0.001$; “control after 4 weeks”: $\chi^2 = 19.7908$, $df = 6$, $p = 0.003$). The total percent of the room use concerning structures above or on ground did not change over observation time ($V = 7$, $p = 0.525$).

According to the index calculation, individuals showed different indexes and uses of areas. In phase “before” most individuals preferred mainly one or two areas. Pauli ($i = 0.60$), Coco ($i = 0.39$) and Kasi ($i = 0.44$) favored area A & B while Chica ($i = 0.74$) and Joki ($i = 0.76$) favored area C, and Maxi ($i = 0.89$) and Billi ($i = 0.93$) area F. The individuals’ focus did not change after the break concerning what areas were used except for Pauli, who concentrated more on area B after the break. Still five individuals revealed a significant

difference between both phases with respect to the index (Pauli, $\chi^2 = 24.5213$, $df = 5$, $p < 0.001$; Kasi, $\chi^2 = 19.3236$, $df = 5$, $p = 0.002$; Chica, $\chi^2 = 34.0523$, $df = 4$, $p < 0.001$; Maxi, $\chi^2 = 10.8378$, $df = 4$, $p = 0.028$; Billi, $\chi^2 = 9.9649$, $df = 4$, $p = 0.041$). Some showed an increase and some a decrease in the index value. None exhibited the maximally achievable index of 1 in the control group. The individually highest indices are distributed unequally between both phases, namely three in phase “before” and three in phase “control after 4 weeks” (Tab.4).

Table 4. Individual indexes of the room use in both phases for the control group. Asterisks mark significant differences to phase “before” (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Values in bold represent maximal indexes of each individual.

Phases	Individuals						
	Pa	Co	Ka	Ch	Jo	Ma	Bi
<i>index</i>							
before	0.60	0.39	0.44	0.74	0.76	0.89	0.93
control after 4 weeks	0.82***	0.38	0.61**	0.77***	0.76	0.82*	0.84*

INTERACTIONS

Integration group

In order to detect relationships between individuals agonistic and affiliative interactions of all ten birds were noted. Accordingly the following setting arose in phase “before” and was valid for all other phases excluding for the dyad-type rivals (see Gigi & CocoR page 22 and following). Categorization of single newcomers is entered as well since that never changed during observation. The rival dyad Gigi & Rocky is in brackets due to the fact that this relationship was unidirectional with Gigi always trying to affiliate with Rocky but not the other way round (Tab.5).

Table 5. Overview of relationship-pairs with respective type and singles within the integration group.

Dyad-type	Relationship-pairs		
Monogamous couple	Gigi & Chica	Kuniber & Gogo	
Affiliative partners / friends	CocoR & Chica	Gigi & CocoH	Rocky & CocoH
Rivals	Gigi & CocoR	(Gigi & Rocky)	
Single			
Romy, Mucki, Pimienta			

In the course of the integrations total interactions within the group, excluding the newcomers changed both in affiliative and agonistic way. During the integration and control phases total agonistic interactions within the group decreased successively (significantly different to phase “before”: “integration mucki”, $\chi^2 = 4.09$, $df = 1$, $p = 0.043$; “integration pimienta”, $\chi^2 = 5.9578$, $df = 1$, $p = 0.015$; “control after 4 weeks”, $\chi^2 = 38.4497$, $df = 1$, $p < 0.001$). After the integration of Pimienta total affiliative interactions within the group increased successively (significant difference to phase “before”: “integration pimienta”, $\chi^2 = 8.9253$, $df = 1$, $p = 0.003$; “control after 4 weeks”, $\chi^2 = 52.2246$, $df = 1$, $p < 0.001$) (Fig.4).

In the observation phase “before” total affiliative interactions within the group were significantly higher compared to agonistic interactions ($\chi^2 = 73.1217$, $df = 1$, $p < 0.001$). This difference was less distinctive in phase “integration mucki” ($\chi^2 = 19.0431$, $df = 1$, $p = 0.013$) since total affiliative interactions significantly decreased ($\chi^2 = 39.2861$, $df = 1$, $p < 0.001$) and reached the minimal value during the course of observation (Fig.4).

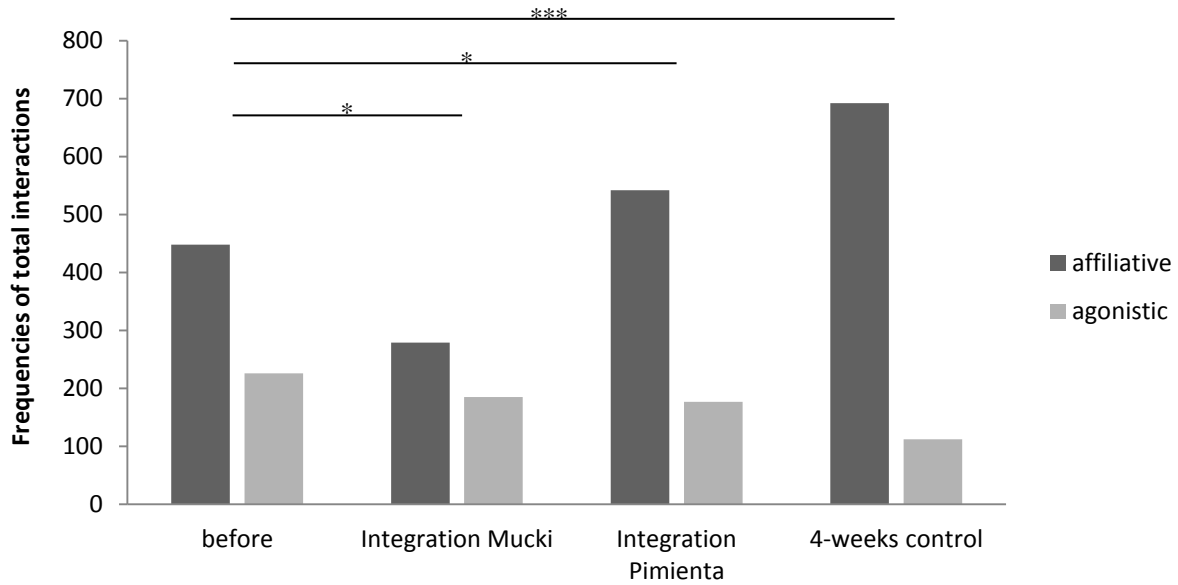


Figure 4. Total affiliative and agonistic interactions within the integration group during all four phases excluding interactions of newcomers. Asterisks mark significant differences between the phases both affiliative and agonistic interactions (* $p < 0.05$; *** $p < 0.001$).

Taking a closer look at interactions between relationship-pairs over observation time, a similar picture emerged as outlined above concerning the total agonistic and affiliative interactions within the group. In phase “integration mucki” a trend of decreasing affiliative and agonistic interactions was visible. Only after the integration of Pimienta agonistic interactions were significantly decreasing compared to phase “before” ($\chi^2 = 24.4353$, $df = 5$, $p < 0.001$) and even lower during the phase “control after 4 weeks” ($\chi^2 = 130.1877$, $df = 4$, $p < 0.001$). Conversely affiliative interactions were increasing significantly in phase “integration pimienta” ($\chi^2 = 89.012$, $df = 6$, $p\text{-value} < 0.001$) and even more in phase “control after 4 weeks” ($\chi^2 = 49.1893$, $df = 6$, $p\text{-value} < 0.001$) (Fig.5). Besides, all interaction-pairs had their maximal frequency of affiliative interactions after the integration of Pimienta, either in phase “integration pimienta” (Roc & Co.H, Ku & Go, Co.R & Gi) or in phase “control after 4 weeks” (Gi & Co.H, Gi & Roc, Gi & Chi, Co.R & Chi).

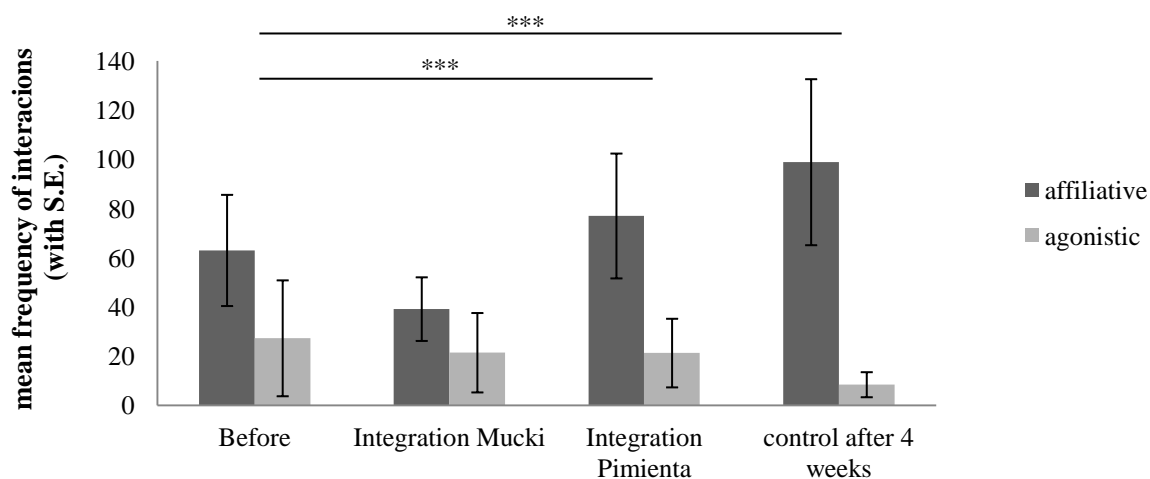


Figure 5. Mean frequencies of affiliative and agonistic interactions between relationship-pairs during all four phases. Asterisks mark significant differences between the phases both affiliative and agonistic interactions (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

To determine what affiliative interactions were increased between relationship-pairs, I calculated means of main affiliative interactions within all relationship-pairs (e.g. contact sit, billing and others). Relationship-pairs significantly increased all three categories of affiliative interactions in both phases “integration pimienta” (contact sit, $\chi^2 = 29.7898$, $df = 5$, $p < 0.001$; billing, $\chi^2 = 41.9561$, $df = 5$, $p < 0.001$; others, $\chi^2 = 37.3801$, $df = 5$, $p = 0.001$) and “control after 4 weeks” (contact sit, $\chi^2 = 11.9502$, $df = 5$, $p = 0.035$; billing, $\chi^2 = 22.4089$, $df = 5$, $p < 0.001$; others, $\chi^2 = 38.0144$, $df = 5$, $p < 0.001$) compared to phase “before” (Fig.6).

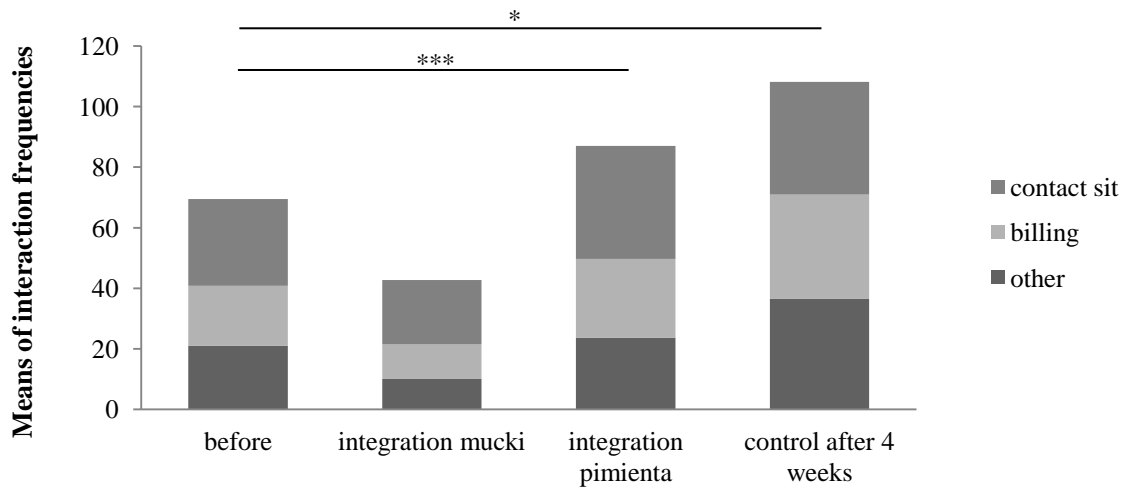


Figure 6. Mean frequencies of detailed affiliative interactions between relationship-pairs during all four phases. Asterisks mark significant differences between the phases (* $p < 0.05$; *** $p < 0.001$).

In the process of integrations and afterwards types of relationships did not change for monogamous couples, friends and singles but the intensity did change. Most affiliative relationships were weak during the phase “integration mucki” and got intensified after the integration of Pimienta recognized by a greater frequency of affiliative interactions. That was also the case in the relationship between Gigi & Chica as well as between Gigi & CocoH. Strength of the relationship (regarding affiliative behaviors) between Gigi & Chica was increased in phase “integration pimienta” and between Gigi & CocoH in phase “control after four weeks.

In contrast the relationship type between the rival dyad Gigi & CocoR changed. As noted above, relationship-pairs in general increased affiliative interactions and decreased agonistic interactions, particularly after the integration of Pimienta. This trend was also observable in the rivalry relationship. During integrations agonistic interactions between them decreased gradually. Gigi reduced his threatening, chasing and attacking behavior towards CocoR while CocoR showed gradually less flight behavior. The decreased trend is shown in

Fig.7 with a significant difference between the initial phases (“before”, $\chi^2 = 9.5899$, $df = 2$, $p = 0.008$; “integration mucki”, $\chi^2 = 7.3889$, $df = 1$, $p = 0.007$) and the last phase “control after 4 weeks”.

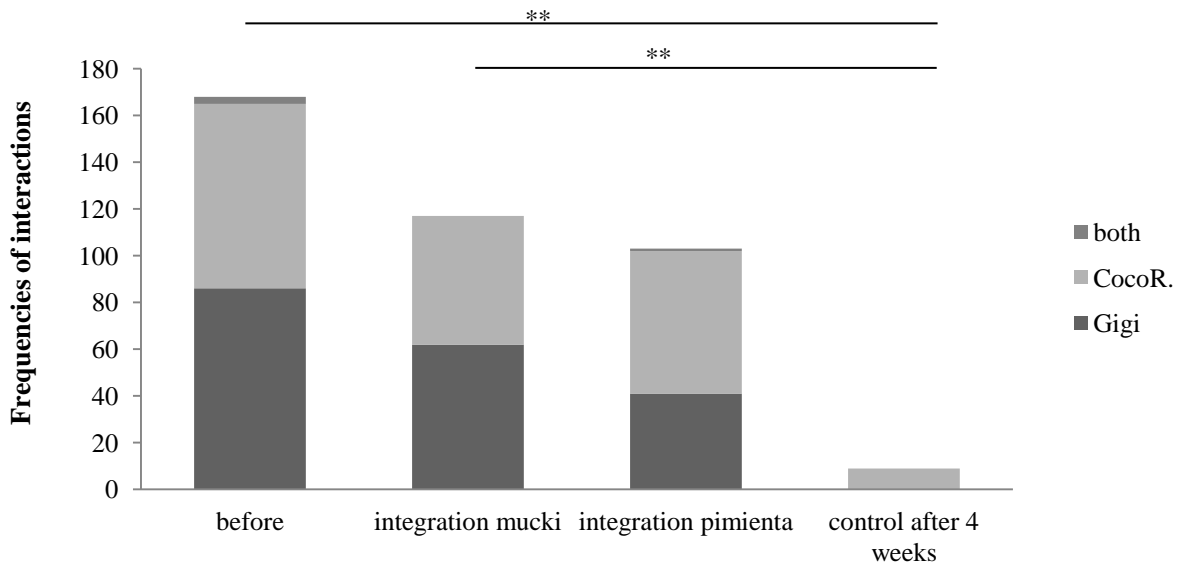


Figure 7. Frequencies of mutually addressed agonistic interactions between Gigi and CocoR during all four phases. Asterisks mark significant differences between the phases (** $p < 0.01$).

Moreover, affiliative interactions between the former rivals arose. This change of relationship occurred after the integration of Pimienta and was most distinctive in phase “integration pimienta”. The first two phases were significantly different to both last phases (“integration pimienta”, $\chi^2 = 24.1429$, $df = 1$, $p < 0.001$; “control after 4 weeks”, $\chi^2 = 14.2222$, $df = 1$, $p\text{-value} < 0.001$). Most exchanged affiliations were contact sitting and billing. Furthermore, Gigi performed friendly behaviors towards CocoR like allofeeding, allopreening and courtship display, while CocoR submitted to Gigi and fed and preened him as well (Fig. 8).

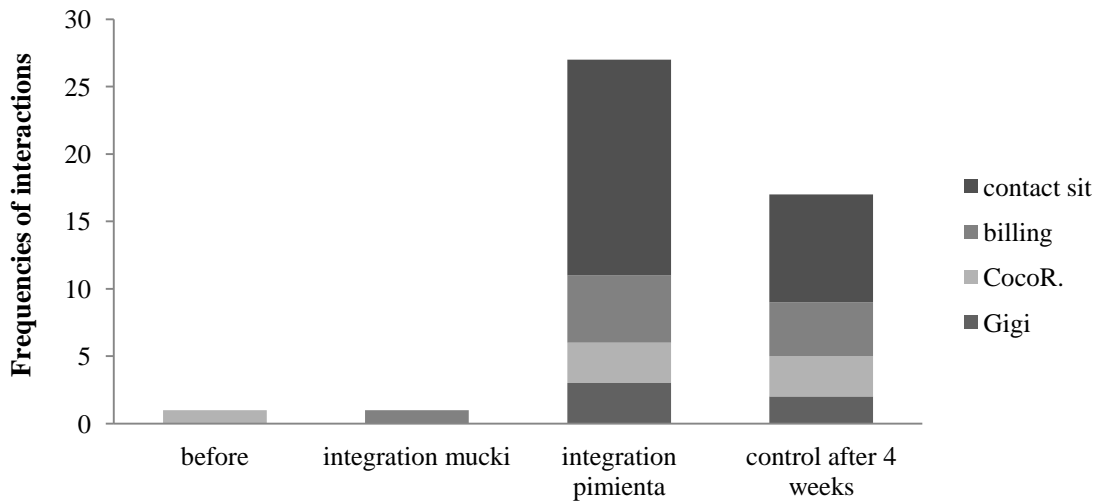


Figure 8. Frequencies of mutually addressed affiliative interactions between Gigi and CocoR during all four phases.

As mentioned earlier, relationships of both newcomers did not change over time. Both newcomers stayed single and did not affiliate with any group member or vice versa. The only interactions Mucki had were agonistic disputes with Romy. Agonistic interactions occurred on both sides in phase “integration mucki” and were higher in phase “integration pimienta” where Mucki fled more frequently and where fights were initialized more often by Romy.

Pimienta had no affiliative interactions with others either and exhibited hardly any agonistic interactions during phase “integration pimienta”. In the last phase, Pimienta had only agonistic interactions with Romy, which were significantly higher compared to agonistic interactions between Romy and Mucki ($\chi^2 = 46.4876$, $df = 1$, $p < 0.001$). Initialization of disputes occurred on both sides at equal ratios.

Control group

To determine whether changes between interactions within a group occur in general even without integration, affiliative and agonistic interactions were detected in the control group as well. According to interactions between all seven individuals the following setting of relationships arose (Tab.6). Relationship-pairs consisted of two monogamous couples, three friend-dyads and one rival-dyad. Unlike in the integration group, the control group contained no single birds. Relationship types did not change over observation time and were valid for both phases “before” and “control after 4 weeks”.

Table 6. Overview of relationship-pairs, with respective type and singles within the control group.

Dyad-type	Relationship-pairs		
Monogamous couple	Coco & Kasi	Chica & Joki	
Affiliative partners / friends	Coco & Pauli	Kasi & Pauli	Maxi & Billi
Rivals	Joki & Coco		
Single			
-			

Observation of the control group showed that total affiliative interactions within the group were higher than agonistic ones ($\chi^2 = 5.6177$, $df = 1$, $p = 0.018$). This was also true for the last phase after the break ($\chi^2 = 4.3261$, $df = 1$, $p = 0.038$). In the last phase after the break a trend of increasing affiliative interactions was visible. Contrary to the integration group, agonistic interactions were increasing as well, at significant levels ($\chi^2 = 4.8126$, $df = 1$, $p = 0.028$) (Fig.9).

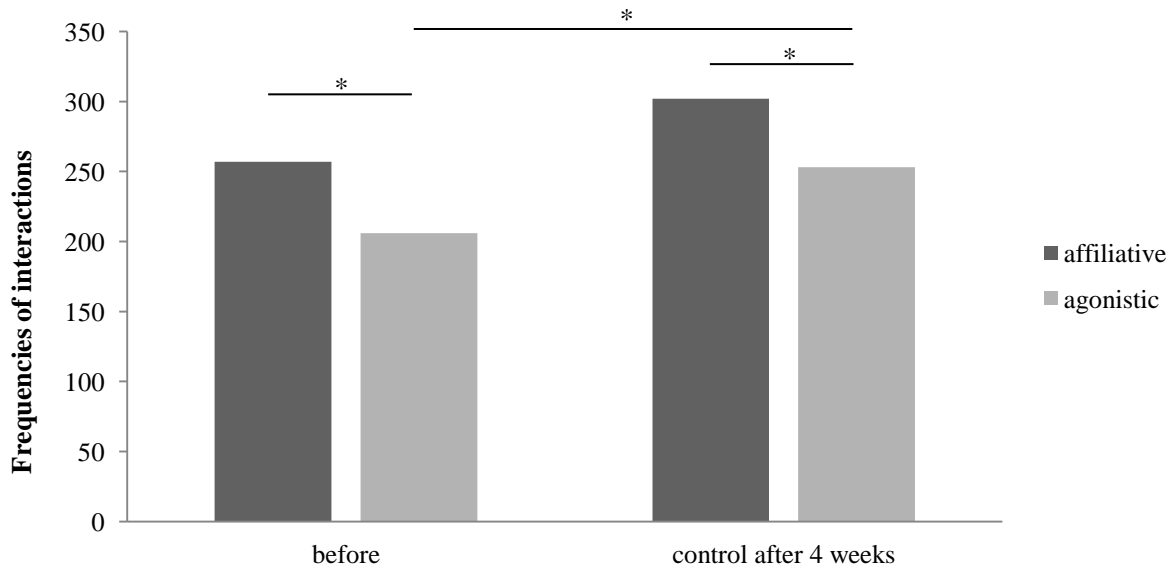


Figure 9. Total affiliative and agonistic interactions within the control group in both phases.

Asterisks mark significant differences within and between phases (* $p < 0.05$).

Taking a closer look at the relationships concerning the different dyads, all friends increased their affiliative interactions and two even significantly (Kasi & Pauli, $\chi^2 = 9$, $df = 1$, $p = 0.003$; Maxi & Billi, $\chi^2 = 7.1111$, $df = 1$, $p = 0.008$). Concerning the monogamous couples, only Joki & Chica increased their affiliative interactions while Coco & Kasi decreased them. In contrast to the integration group, the relationship type of the rival dyad did not change. Instead they even increased their agonistic interactions ($\chi^2 = 18.023$, $df = 1$, $p < 0.001$). In both phases Coco was always the initiator of the disputes, and Joki fled from him.

EXPERIMENTS

Integration group

Interruptions dependent on different spots inside the aviary revealed different reactions from the individuals. All individuals showed passive reactions and no active reactions if the interruption occurred in the middle of the aviary in the first session (nr. of succ. = 0, nr. of trials = 10, $p = 0.002$), and only one bird (Gigi) showed an active reaction in the second session (nr. of succ. = 1, nr. of trials = 9, $p = 0.039$). In contrast five birds (CocoH, Rocky, Gigi, CocoR, Chica) showed active interactions if the interruption was within their territory in both sessions (nr. of succ. = 5, nr. of trials = 10, $p = 1$).

Control group

In the control group no individual showed active reactions due to disturbances neither in the middle of the aviary nor in each territory, respectively. This was true for both test sessions (nr. of succ. = 0, nr. of trials = 7, $p = 0.0156$).

DISCUSSION

The study demonstrated that grey parrots flexibly adapt to intragroup interactions and behaviors according to changes in group composition. After the integration of newcomers group dynamics changed but not as expected with an increase in aggression towards the intruders. On the contrary, agonistic interactions successively decreased, whereas the intragroup affiliation increased after the second integration. These results indicate that group members avoid aggressive encounters and try to prevent fights. Thus they rather choose to manage potential conflict situations passively.

At a more detailed level, total affiliative interactions increased not only within the whole integration group but also within relationship-pairs after the introduction of Pimienta. The results lead me to conclude that all relationship-pairs including individuals with multiple relationships tried to strengthen their bonds, and this way intensified social cohesion generally. Dagg (2011) reported that allopreening in crows contributes to maintain their pair bonds, which is most likely also true for parrots. Furthermore, individuals showed an increase in frequency of contact sitting, billing and other affiliative behaviors thereby displaying a strong cohesion to newcomers. These results support several findings in the literature, where it is suggested that disputes or even potential conflicts with others influence intragroup affiliation (Radford 2008), and that affiliation should be highest the greater the threat (West et al. 2006). For example, green wood hoopoes increase intragroup allopreening rates after (Radford 2008) and also before potential conflicts (Radford 2011). Captive rook pairs increase bill-twinning after conflicts (Seed et al. 2007), captive ravens increase allopreening and contact sitting after conflicts (Fraser & Bugnyar 2010, 2011) and captive Japanese macaques increase allogrooming rates due to conflicts within the group (Schino et al. 1998). The results of the current study support the hypothesis that social relationships can keep up group integrity (Cords 1997).

However, as has been shown in previous studies, increased affiliative behavior in relationship-pairs may be one mechanism to cope with increased stress levels (De Vries 2002; House et al. 1988). Many authors suggest that the presence of a social partner or friendly social contact and affiliative behaviors reduce or buffer stress (e.g. monkeys, Coe et al. 1982; Dagg 2011; Gonzalez et al. 1982; humans, House et al. 1988; Levine 1993; green wood hoopoe, Radford 2008; macaques, Schino et al. 1998; ravens, Fraser & Bugnyar 2010), and thus influence well-being and health positively (Cohen 1988, De Vries 2002, De Vries et al. 2003). This was also found in a captive group of grey parrots, where not only individuals with stable social relationships exhibited decreased stress levels (lower glucocorticoid excretion, Zeppetzauer 2004) but also individuals with passive social support (Horauer 2002). Therefore, in this study, behavioral changes concerning the increase of intragroup affiliations may act as a stress (see also Cockrem 2007) indicating the integration of newcomers as potential stressors.

Altogether, individual reactions favor the conclusion that newcomers represent potential threats for both, group harmony and bonds of relationship-pairs. Therefore, newcomers could be seen as intruders imposing increased competition for group members. De Vries and colleagues (2003) already detected that due to the striking responses to an intruder the relevance of mate-guarding becomes obvious. They concluded that the importance of social partners is illustrated by the exposure to stressful stimuli. Moreover, in previous studies with parrots bond strengthening and social support between partners also occurred if the partnership was at risk or defense against rivals was necessary (e.g. spectacled parrotlet, Garnetzke-Stollmann & Franck 1991; grey parrots, Lantermann 1990).

In addition, single newcomers not only represented a high threat for relationship-pairs considering the limits of available partners. But due to limited space in captivity intruders may also challenge previously established territory claims. In contrast to nature, strong

territorialism was possible due to locally concentrated single feeding stations in captivity (Del Hoyo et al. 1997). Thus group members established individual “territories” within the aviary surrounding areas with feeding bowls. They used and defended them as territories, most likely to avoid feeding competition. Due to Preuschoft & Van Schaik (2000) a territory can be seen as an area that is defended by its inhabitant, from which he drives other conspecifics away. Throughout all phases of this study individuals displaced all other birds entering their territories, except affiliated partners. Therefore, hierarchies were difficult to evaluate (similar to Fischer 2001) since most individuals had higher ranks over others only within their own territory but not outside of it. Territory occupation was illustrated especially after the integrations when group members focused strongly on their individual territories. Due to this high frequency of territorial use it seemed that “owners” tried to demonstrate presence and readiness to defend their territories, if necessary. For most birds the results of the experiment, following a disturbance within the aviary, confirmed territory occupation. Nearly all group members reacted in an aggressive way, but only if the disturbance was within their territory and not in the middle of the aviary or in neighboring territories.

In summary, intragroup affiliation increase and territory guarding was used to better protect relationship bonds and territories including resources. This supports findings in the literature where successful defense of resources and prevailing over competitors was achievable by closely bonded individuals (e.g. monkeys, Cheney & Seyfarth 1990; ravens, Braun & Bugnyar 2012; grey parrots, Martin 2001). In addition, social bond protection affected territory defense since due to combined efforts the latter was more effective.

Concerning the reactions to both newcomers, group members reacted different to them, and not as expected stronger to Mucki (regarding her social experience), but rather less to this first integrated individual. Less frequent affiliative interactions between relationship-pairs after the integration of Mucki could be explained by different, not necessarily mutually

exclusive reasons: Mucki may have been perceived as a potential affiliative partner, thus relationship-pairs lowered their bonds and considered bonding with her. But group members' lack of attempt and withdrawal including territory occupation makes this rather unlikely. Another reason could be that group members' bond strengthening was not necessary since Mucki was not such a high threat regarding her lack of affiliative advance. She seemed to correctly respond to signals and displays of group mates which might be ascribed to the social skills she developed during her previous experience with conspecifics (see Garnetzke-Stollmann & Franck 1991). In order to inform opponents about her status she displayed submissive and withdrawal behaviors what seemed to have appeased the superior Romy (Preuschoft & van Schaik 2000). Considering her integration spot its position may have been to her advantage since it concluded only one territory and thus endangered no other group members except for Romy. Furthermore less strong reactions towards Mucki from group members could be due to the integration of only one bird so far, which was easier manageable for group members.

It could be argued that the group reacted stronger to Pimienta due to the different spot she was integrated at, and as the second newcomer the group reached a group size coping threshold. However, these explanations seem unlikely, as reactions to her were the same or even stronger when she changed her position and was the only newcomer left in the group. This can be illustrated impressively by focusing on the disputes between the territory owner Romy and both newcomers, as Romy exhibited significantly more disputes with Pimienta than with Mucki.

Since both newcomers were nearly of the same age (one year difference) and both were females, sex and age can be safely excluded as reasons for the different reactions. However, without sexual dimorphism the opposite sex can often be recognized only by its specific behavior, namely with males being more aggressive (Lantermann 1990). Therefore,

group members may have not interpreted the sex correctly. Instead, a more plausible explanation for the stronger reaction towards Pimienta was probably her single housing background and due to this background, her lack of social experience with conspecifics (Garnetzke-Stollmann & Franck 1991). In contrast as expected, her social inexperience did not seem to make her cautious in interactions but appear more threatening to group members. On the one hand, she could have had misinterpreted received signals or social cues and thus behaved inappropriately. And on the other hand, she also could have had problems sending out correspondent signals to group members.

Newcomers did not only differ in their background but also in their individual behavioral characteristics. Animals show different “personalities” that can be categorized as “proactive-type” (corresponding to bold/fast) such as more aggressive individuals that are likely to take risks, or as “reactive-type” (corresponding to shy/slow) who are less aggressive and more fearful individuals (Cockrem 2007, Carere & Eens 2005, Carere et al. 2003/2005, Verbreeck et al. 1996). Since this study lacks any evaluation of individual personalities, assumptions referring to this remain speculative. However, during observation Mucki appeared fearful and panicked as soon as humans or other birds came near her, which could make her a possible candidate for a rather “reactive-type”. Pimienta, in contrast, never showed fearful behavior during observation, and initiated aggressive displays with Romy in the same manner as Romy did, thus behaving rather as a “proactive-type”. In this respect emphasis must be placed on the fact that humans in general focus strongly on verbal communication and therefore body language of parrots is often being misinterpreted (Martin 2001). Altogether, the stronger reaction to Pimienta was likely due to a combination of her background and her more proactive approach.

As much as group members lacked aggression towards newcomers, newcomers seemed to avoid agonistic encounters. Considering their arranged integration spots including

feeding bowls, both newcomers had no need to expand their “territories” or compete for food elsewhere. Considering the importance and positive impact of social contacts and affiliative partners, the lack of affiliative behaviors from both newcomers was unexpected. They neither affiliated with group members nor with each other. According to the strong bonds of group members coinciding with territory guarding, affiliative behavior by newcomers was difficult. This is probably also the reason why both remained at the area they were introduced in. Only Pimienta switched to the spot of Mucki after she was taken out. It might be argued that Pimienta tried to affiliate with Romy, since she was the only single in the group and therefore a potential affiliative partner. But considering their frequently exhibited disputes this seems unlikely and Romy treated Pimienta as an intruder competing over her feeding station. However, Garnetzke-Stollmann & Franck (1991) concluded that in spectacled parrotlets, any partnership was better than being alone since singles tried to affiliate with others independent of sex or kin if no mate was found. Furthermore, many authors found existing same-sex relationships in other birds (rooks, Emery et al. 2007; grey parrots, Fischer 2001), whereas female-female dyads were not as strong and stable as male-male dyads (ravens, Braun & Bugnyar 2012, Fraser & Bugnyer 2010). Fischer (2001) found in grey parrots additional relationships with the same sex only for males. Therefore, the sex of the only single bird and both newcomers was likely a factor prohibiting the establishment of affiliations or bonds.

In matters of alliances Romy did not pair up with neighbors either, probably for the same reason as for the newcomers, due to her sex, as well as the strengthened bonds of the other relationship-pairs that made affiliation impossible. The only individual who initiated a new affiliative relationship was Gigi together with his former rival CocoR. This occurred after the integration of Pimienta, while she was as a direct neighbor to his territory. He stopped threatening and chasing CocoR away, but rather tolerated him inside his territory and showed affiliative behavior towards him. Considering Gigi’s most widespread room use and toleration

in all areas together with his numerous relationship partners of each sex, he was the most suitable candidate for the alpha-position in the group. Alpha positions are often kept by monogamous pairs and males with high activity, enlarged space occupation, threatening behavior, and multiple affiliation partners (captive grey parrots, Fischer 2001, Lantermann 1990), especially when in male-male coalitions (ravens, Fraser & Bugnyar 2010). In primate societies alpha males react actively to competitive situations, successively defend resources and maintain their higher position due to social skills, e.g. mobilizing support and forming alliances (Bernstein 1976, De Waal 1978/2000, Harcourt & De Waal 1992). Also in birds, ravens status is mainly dependent on age and bonding, rather than on residency (Braun & Bugnyar 2012). They concentrate on one bond formation according to maximum benefit gain (Braun & Bugnyar 2012) and do so mostly in times when intragroup conflict is likely to occur (Radford 2011). According to Gigi's reaction Pimienta was apparently a high threat to his territory and/or his alpha-position. Combined with the aforementioned lack of social experience these characteristics seemed to pose a threat to Gigi, which could not be resolved by communicative cues alone. In addition, Gigi already had a rivalry relationship and thus most likely elevated baseline stress levels.

One strategy to cope with such a situation, as displayed by Gigi, was to "invest" affiliative behavior in a social relationship with CocoR (the former rival). Such interchanges of affiliation, in return for agonistic support in resource and territory defense have also been reported in other species (baboons, Silk et al. 2004; green woodhopes, Radford 2011). Thus, in case of a dispute CocoR should have shown threatening behavior or aggression towards the opponent of his coalition partner Gigi, in this case Pimienta. Since none of the three had aggressive encounters during observation the triadic interactions were not a classic coalition or alliance (sensu: De Waal 1978, Preuschoft & van Schaik 2000), but a bond formation between Gigi and CocoR including passive social support. Supporting a dominant group

member includes building a valuable relationship and can be a tactical way to increase one's status (Fraser & Bugnyar 2012). Though CocoR faced some effort caring for the new affiliative relationship with Gigi, his advantage of the bond involved no more stressful disputes but affiliative displays from Gigi. Furthermore he was tolerated in the territory of Gigi were also his relationship-partner Chica stayed, which enabled him to care about this relationship more intense. The sudden tolerance and affiliation between the two former opponents was likely to lead to a stress reducing effect and thus repaired the damaged relationship which may have benefited both (De Waal 2000, De Waal & Aureli 1997). The bond ultimately resulted in a status increase for both (De Waal 1978, Emery et al. 2007). Due to the new bond formation Gigi neglected his affiliative partnership with CocoH and hardly joined him in his area.

After the bond formation of Gigi and CocoR, Pimienta changed her room use and only remained at the former spot of Mucki next to Romy. Considering her huge competition with Romy over food access, her choice for moving in Romy's territory and staying there could have due to the deterrent bond formation. However, advanced cognitive capacities are required to detect existing and changing relationships of others (Connor 2007), and individuals need to gather information about each other's strength and motivation in order to estimate opponent superiority (Preuschoft & van Schaik 2000). Lacking these social skills such estimation might have been difficult for Pimienta. However, it could be argued that she quickly developed these skills during her integration. After her moving she was no direct neighbor to Gigi anymore, and affiliative interactions between the bonding partners Gigi and CocoR decreased. That indicates that the strength of the bond was not necessary anymore, at least not to such an extent. Moreover, after the lowered bond with CocoR, Gigi started to show his initially widespread room use and re-strengthened the bond with his affiliative partner CocoH.

When examining the results of the control group a different picture arose. Although total affiliations within the group increased only few relationship-pairs strengthened their bonds, and to a lesser degree than in the integration group. In contrast to the integration group, they did not decrease but even increase agonistic displays, especially the rival dyad Coco and Joki. Furthermore, preferences for territory use remained rather stable.

In sum, these comparisons led to the conclusion that the strong reaction of the integration group was due to the introduction of new individuals in the aviary. With regard to their ability to fly and thus escape the control group differed strongly from the integration group. This may also explain why individuals did not react actively to disturbances within their territory during the experiment.

Overall, the handicap situation in the integration group appears to be a crucial factor and strongly influences individuals in their conflict management strategies. Facing aggressive encounters could have serious consequences particularly without the ability to quickly escape by flying. This probably required them to employ different tactics of conflict resolution and group regulatory mechanisms. At first, group members limited unwelcome encounters by territory occupation. Facing potential conflicts with newcomers forced them to deal with the threatening situation. Hence, most conflicts were resolved by avoidance and managing the situation passively. They did not show dominance in a physical way but rather resorted to partnership cohesion and ownership. Evidence for their behavioral flexibility was exhibited by their social skills in recruiting partners for bond formation against potential competitors if necessary. This type of conflict solution rather led to a tolerance of the newcomers, than an active integration. The passive pre-conflict management and social plasticity of grey parrots provide further evidence of their social cognitive capacities and support convergence with primate strategies. Thus this study reveals important insight and understanding of group dynamics with respect to new situations affecting intragroup processes. Furthermore it

emphasizes the relevance of available partners and territories in captivity. Nevertheless, it is important to be aware that individuals were handicapped, came from various backgrounds and faced special circumstances in captivity. These factors may result in different conflict solutions as employed in the wild. Further research should address these mechanisms in captive birds without handicaps including the integrations of males, to be able to postulate hypothesis, which ultimately can be tested on birds in the wild.

ACKNOWLEDGEMENTS

First of all I would like to thank my supervisor Prof. Dr. Thomas Bugnyar very much for his help, his ideas and his useful advising during this study, as well as his willingness to supervise me in this study in the first place. Special thanks go to Mark O'Hara for his kindly support, help, time and interest in my study. I would like to thank every member of the Department of Cognitive Biology who all taught me so much about cognitive and behavioral biology in many talks and discussions during the past year which highly motivated and inspired me.

I would like to especially thank Mag. Nadja Ziegler for giving me the initial idea to study this topic and the opportunity to carry out my thesis at ARGE Papageienschutz whereby I found my fascination and love for these birds. I would also like to thank the whole team of ARGE Papageienschutz showing so much dedication and effort in the protection of these animals, caring so much about the welfare of each individual, and always trying to get the best for the birds.

Also, I would like to thank all my friends who supported me during my thesis. Finally, I thank my parents for making my education possible, especially my mom for always supporting and believing in me.

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APPENDIX

Deutsche Zusammenfassung

Die soziale Struktur von Graupapageien (*Psittacus erithacus*) ist durch ein Fission-Fusion-System charakterisiert, das durch die Schwarmformation und dem lebenslang bestehenden monogamen Paar gekennzeichnet ist. Das Gruppenleben im Schwarm birgt oft Rivalität um Ressourcen und damit Konfliktsituationen. Änderungen in der Gruppenzusammensetzung müssen gehandhabt sowie entsprechende Konfliktlösungen gefunden werden. Diese Studie soll sowohl Einblick in das Gruppenleben und –verhalten von Graupapageien geben, als auch in vorhandene Mechanismen zur Konfliktlösung. Im Zuge dessen wurden zwei unbekannte Individuen in eine vorhandene Gruppe integriert und Verhaltensweisen beobachtet. Zum Vergleich wurde eine Kontrollgruppe ohne integrierte Individuen beobachtet und mit der Integrationsgruppe verglichen. Anhand der Ergebnisse zeigt sich, dass die Individuen sehr daran interessiert sind, direkte Konflikte zu vermeiden und potentielle Auseinandersetzungen passiv zu handhaben, indem sie deutlich ihren sozialen Zusammenhalt und Territoriumsbesitz anzeigen. Außerdem nutzen sie ihre Partnerschaften, die sie gegebenenfalls verstärken und rekrutieren, und beziehen wenn nötig, soziale Unterstützung von Anderen. Diese Konfliktvermeidung lässt sich auf ihren Gesundheitszustand zurückführen (da eine Gruppe flugunfähige Vögel beinhaltete), welcher sie scheinbar nötig, im Gegensatz zu flugfähigen Vögeln oder Wildtieren, alternative Lösungen zu finden. Die Ergebnisse verdeutlichen die Notwendigkeit von Partnervögeln und Einzelterritorien in Gefangenschaft. Die Gruppendynamik von Graupapageien liefert wichtige Erkenntnisse über ihre sozialen Fähigkeiten sowie über ihr Potential zur flexiblen Lösung von Konflikten.

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Forest and Environmental Sciences, Albert-Ludwigs-Universität Freiburg

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