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Does relationship quality affect cooperation in common raven (Corvus corax) pairs during the breeding season?

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Zusammenfassung

Kooperation spielt in vielen Lebenslagen eine wichtige Rolle und bringt Vorteile für kooperierende Individuen, beispielsweise in der Akquirierung von Futter oder in der Aufzucht der Nachkommen. Eine Voraussetzung für erfolgreiche Kooperation ist das Verständnis über die Notwendigkeit eines Partners und dessen Aufgabe während der Kooperation. Ein Test, der sich hervorragend dazu eignet, dieses Verständnis zu testen, ist der Loose String Task, bei dem zwei Partner gleichzeitig an den beiden Enden einer Schnur anziehen müssen, um an eine Belohnung zu gelangen. Ein Faktor, der den Kooperationserfolg beeinflussen kann, sind soziale Beziehungen. Die Qualität einer Beziehung lässt sich auf verschiedene Weisen messen, beispielsweise über die drei Beziehungskomponenten Wertigkeit, Kompatibilität und Sicherheit.

Raben eignen sich hervorragen dazu, beide Forschungsfelder zu untersuchen. Sie sind langzeitmonogam und bekannt für ihre komplexen sozialen Beziehungen. Auch über Kooperation bei Raben gibt es bereits zahlreiche Forschungsarbeiten, die zeigen, dass Raben bevorzugt mit ihren Sozialpartnern kooperieren.

In der vorliegenden Arbeit wurden die Effekte von Paarqualität sowie von Distanz und Gleichwertigkeit der Belohnung auf den Kooperationserfolg untersucht. Dafür wurden bei acht Rabenbrutpaaren in drei Brutphasen (Brut, frühe Nestlings Phase und späte Nestlings Phase) Fokusprotokolle aufgenommen und sechs verschiedene Konditionen eines Loose String Tasks durchgeführt. Die Ergebnisse zeigen, dass der Kooperationserflog von einer Kombination aus Paarqualität und Distanz und Gleichwertigkeit der Belohnung abhängig ist. Dennoch ließ sich eine Tendenz erkennen, dass höhere Paarqualität sowie größere Distanz und gleiche Belohnung den Kooperationserfolg erhöhten. Die Brutphase hatte sowohl auf den Kooperationserfolg als auch auf die Paarqualität einen Einfluss. Der Kooperationserfolg war gegen Ende der Brutzeit höher, auch der Wert der Paarqualität nahm gegen Ende der Brutzeit etwas zu.

Die Ergebnisse entsprechen in weiten Teilen den Erwartungen und den Ergebnissen früherer Forschung an nicht-brütenden Raben. Interessante Fragen für zukünftige Forschung sind, wie sich die Beziehungsqualität auf den Kooperationserfolg während des Jahres auswirkt, und ob es noch andere Einflussfaktoren für den Erfolg gibt, etwa Persönlichkeit.

Abstract

Social relationships play an important role in cooperation. Previous studies in mammals and corvids have shown that individuals prefer to cooperate with familiar individuals. Ravens as a long-term monogamous species are highly social and well known for cooperation. So far, no studies have yet been conducted on the effect of relationship quality on cooperative success during the breeding season. In the present study, eight raven breeding pairs were tested in a loose string task with six different conditions (varying in number and distance between pieces of reward) over three different breeding phases. For relationship quality variables, a factor analysis was conducted with data of focal observations. The effect of relationship quality on the proportion of successful trials and on tolerance regarding distance between pieces of reward and reward equity was tested. In addition, the effect of breeding phase on success and on relationship quality was analysed. Significant three-way interactions were found in models with proportion of success in the presence of both partners depending on relationship quality components, reward distance and reward equity. It was further found that the breeding phase had a significant effect on both relationship quality and cooperative success. These findings are consistent with previous research on non-breeding ravens, according to which social relationships have a positive influence on success of individuals in performance of a cooperative task. Taken together, it has been shown that ravens are cooperative in an experimental problem solving task during the breeding season and that their tolerance regarding reward distance and equity is depending on their social relationship.

Keywords: ravens, relationship quality, cooperation, breeding season, loose string task;

Introduction

Social life means facing problems that a solitary living organism never has. Nonetheless, in the animal kingdom, living in social groups has evolved independently on many occasions for several good reasons. A big advantage of group living is the possibility of cooperation with others. There are varying definitions for the term cooperation: according to Brosnan & De Waal (2002), cooperation can be defined by its intention, i.e., the goal of the involved parties and the effort needed therefor, or its outcome. Sachs et al. (2004) defined cooperation as an interaction between at least two individuals that has benefits for the recipient but not always for the donor. Even though cooperation is a risky strategy, because of direct costs resulting from the required investments and because of possible exploitation, the benefits of cooperative behaviour tend to predominate. Clutton-Brock (2002) defined cooperative behaviour as adapting activities to increase the fitness of others which – in turn – directly or indirectly increase one`s own fitness. However, it is not always clear on which factors cooperative success is based on.

Cooperation is widespread in the animal kingdom and can be explained by different models like direct reciprocity, shared genes, or byproduct benefits (Sachs et al., 2004). The examples of various forms of cooperative behaviour are broadly distributed, like the collaboration in colonies of eusocial insects (Rodrigues et al., 2022). Other forms of cooperation are brood helpers in birds and highly social mammals that help raising the offsprings of near kin (Clutton-Brock, 2002), or cooperative hunting such as in wolves (MacNulty et al., 2014) or chimpanzees (Boesch, 1994). Benefits of cooperation could include protection against predators or against harsh environmental conditions, as well as access to resources like food or shelter (Robinson & Barker, 2017). Other examples of cooperative behaviour can be agonistic support in conflicts with other group members (Fraser & Bugnyar, 2012), shared parental care in raising one`s own offsprings like in many bird species (Ersoy et al., 2021), or solving of problems which cannot be solved by an individual on its own (Marshall-Pescini et al., 2018).

Many factors can influence the success of any kind of cooperation. One facilitator is social tolerance between partners, as determined – for example – by low dominance rank distance, kinship or friendship (Asakawa-Haas et al., 2016). A study in wolves (Dale et al., 2020) showed that social components, i.e. rank distance, affiliation and tolerance, have a significantly higher effect on behaviour during cooperation tasks than non-social factors like inhibitory control, learning speed, persistence or causal understanding of the task.

Familiarity with the cooperation partner could play an important role. Group living animals tend to associate with familiar individuals over a longer time period. Choosing a familiar partner can be beneficial, since the likelihood that both are available to cooperate again is high. Individuals which know each other and already worked together are also well coordinated and have a higher chance to be successful (Asakawa-Haas et al., 2016). Although proximity to group members can be a big challenge, like due to competition for resources, spatial proximity is required for cooperative problem solving. Social tolerance influences how individuals accept closeness to other group members. With a group of chimpanzees, Suchak et al. (2014) showed that individuals prefer to approach a cooperation test set-up if the partner was kin or a similar ranked individual. Due to higher social tolerance, agonistic behaviour and competition in these partnerships is lower, which leads to higher chances of cooperative behaviour in future tasks. These findings provide evidence that social relationships between the partners seem to be a key factor for successful cooperation.

Relationships are defined as interactions between individuals that are repeating several times. An interaction implicates at least two individuals performing one or more types of behaviour. An interaction can be unidirectional or bidirectional. Interactions are characterized through their content (what the animals are doing together, like preening) and the quality (how they do it, like intensity or symmetry). For definitions of relationships, it is also relevant how the interactions are patterned over time (Hinde, 1976). There are various types of relationships, for example dominance hierarchies, affiliative and sexual relationships, or care dependent relationships (Scott, 1956). Relationships are composed of various dimensions, like for example frequency (how often social interactions occur), diversity (what social interactions include), symmetry (balance in showing behaviours between partners), tenor (individuality of participants), tension (coexisting of individuality and togetherness), predictability (how expectable social interactions are) or stability (how social interactions persist over time), and they differ along these continua and in their valence.

Furthermore, social relationships can affect breeding success. A study in zebra finches showed that individuals who formed a stable social relationship outside the breeding season had a higher chance of forming a successful breeding pair. Couples with a stable social relationship divorce each other less often, and thus, the likelihood of maintenance of partnership over several breeding attempts is high (Maldonado-Chaparro et al., 2021). The strength of relationships can vary over time, like in an annual rhythm. Right before the start of the breeding season in particular, relationship quality plays an important role in species with biparental care to strengthen the pair bond for a successful brood (Kubitza et al., 2015). These findings suggest that social relationships are a key factor in successful breeding.

There are multiple ways to measure relationship quality, like for example the rate of affiliative behaviour or the absence of agonistic behaviour (Silk et al., 2013). Cords & Aureli (2000) defined three main components of relationship quality: value, compatibility, and security. Relevant behaviours for relationship quality are for example preening, contact sitting or agonistic support. In the model of Cords & Aureli, the relationship quality components are the result of a principal component analysis based on behavioural observations. Value refers to direct benefits that an individual gains from the interaction with a partner, such as food sharing or agonistic support. Compatibility, the second component resulting from their analysis, measures tolerance between individuals and the general tenor of social interactions. Security describes the predictability and consistency of relationships over time.

Experiences earlier in life could influence future interactions between individuals (Hinde, 1976). Thus, a connection between content and quality of interactions on the one hand and the components of relationship quality on the other hand seems to be likely. Value and security may not be shared between the social partners symmetrically, while compatibility is directly related to shared experiences and therefore the same for both social partners (Cords & Aureli, 2000). The three components of relationship quality have mainly been investigated in chimpanzees (Fraser et al., 2008), but there is further research in some other species as well, for example in corvids.

Common ravens (*Corvus corax*), a member of the well-studied corvid family, are perfectly suited for research in both the fields of relationship quality and cooperation. The species is distributed worldwide and kept in captivity like in zoos. Ravens are long-term monogamous and build strong relationships with partners or friends (Braun & Bugnyar, 2012), who can be remembered even after a long time-period (Boeckle & Bugnyar, 2012). In order to understand relationship quality in ravens in more detail, Fraser & Bugnyar (2010) investigated the three relationship quality components in young ravens, showing that kinship and sex combination have an influence on relationship quality, thus underpinning previous knowledge on strong relationships between ravens.

Ravens regularly cooperate in the wild, for example in sharing information about food resources (Marzluff et al. 1996), in fighting against competitors (Heinrich & Marzluff, 1991) or during breeding (Ersoy et al., 2021). Previous studies in ravens suggest that the relationship between the performers plays an important role for cooperation. Asakawa-Haas et al. (2016) showed that ravens prefer to cooperate with a friend. Furthermore, Massen et al. (2015) showed that ravens of a non-breeder group successfully cooperated in a cooperative task, with success being dependent on inter-individual tolerance. Dyads with a higher inter-individual tolerance had a higher cooperative success, suggesting that relationship quality between individuals plays an important role in cooperation.

Many studies on cooperative problem solving are focusing on the understanding of the need of a partner and its role in solving the problem. A commonly used way to test the understanding of a partner's role is a cooperative pulling task like the loose string paradigm. Originally, Crawford (1937) established a string-pulling test where two or more individuals have to pull simultaneously on a string, to move a board with food into reaching distance, with chimpanzees who are well known for cooperative behaviour. The current design, a loose string setup in which two individuals need to pull on each end of the string at the same time, was introduced by Hirata (2003) and advertised by Melis et al. (2006). Since that time, it has been used with various species including wolves (Marshall-Pescini et al., 2018; Dale et al., 2020), elephants (Plotnik et al., 2011), and parrots (Péron et al., 2011).

Raven breeding pairs have a long-term social relationship and cooperate in raising their chicks. However, there are no studies about stability of relationship quality during the actual breeding season. Furthermore, it is not known yet if the quality of relationship influences cooperation between pair partners during the breeding season and whether cooperation success varies between different breeding phases.

In order to fill this knowledge gap, the present work aims to investigate whether relationship quality affects cooperation in common raven pairs during the breeding season. The study took place in cooperation with another study that investigated inequity and tolerance in cooperative behaviour. To start with, three hypotheses on the relation between relationship quality and cooperation success in different breeding phases were established. The first hypothesis was that relationship quality has an effect on cooperation success. The prediction was that higher relationship quality will lead to higher cooperation success. The second hypothesis was that relationship quality influences tolerance regarding distance and inequity. The prediction was that the acceptance of closeness between pieces of reward and the tolerance against unequal reward is higher, when the relationship quality is high. Finally, the third hypothesis was that the breeding phase has no effect on relationship quality but on cooperation success. It was predicted that the relationship quality is stable over time; however, cooperation success should increase given that the parents need more food during the nestling phase.

Methods

Study subjects and Housing

The study subjects were eight breeding pairs of common ravens (*Corvus corax*): three pairs living at Konrad Lorenz Research Center (KLF) in Grünau im Almtal, Upper-Austria, four pairs living at Haidlhof Research Station (HH) in Bad Vöslau, Lower-Austria, and one pair living at the Zoo Vienna (Tiergarten Schönbrunn; TGS). All ravens were marked with coloured leg-rings for individual recognition. All individuals were born in captivity and were housed pairwise in outdoor aviaries. The aviaries had an average size of 80 m^2 (TGS: ~ 160 m^2) and a hight of 5 to 7 m, and contained trees, branches, stones, a nestbuilding site, and a water tank for bathing. Subjects were fed twice per day, morning and afternoon, with an appropriate and varying diet, containing meat in the afternoon. During the nestling phase, there was a third feeding around noon. In Schönbrunn, the ravens were fed two to three times a day, in the morning, around noon and in the afternoon. Water was provided *ad libitum*.

Ethical note

The study was conducted in the home aviaries of each dyad, and participation in the experiments was voluntary. The whole data collection was non-invasive and complied with the Austrian law. The study was authorized by the ethical board of the behavioural research group of the Faculty of Life Sciences of the University of Vienna (case number: 2023-028).

Data collection

Data collection included focal observations and recordings of a cooperation task and occurred during the breeding season 2024 from end of February until beginning of May. It was divided into three blocks of three weeks each: the first block covered the nesting phase, which started three days after the first egg was laid. The subsequent nestling phase was divided into the early nestling phase (second block of three weeks) and the late nestling phase (third block). The early nestling phase started the day after the first chick hatched, while the late nestling phase started immediately after the end of block two. Each block contained twelve days of data collection. Given that there were multiple dyads at KLF and HH, there were four slots of data collection per day, two in the morning and two in the afternoon (see *Table 1*). The slot of data collection was randomised every day for each dyad. Focal protocols and the cooperation task always happened on the same half day within one dyad. To include the raven pairs from all three sites, data collection was accomplished by three different people.

Table 1: Exemplary day schedule of data collection at HH.

<table>
<tr><td rowspan="4">morning</td><td>feeding focals dyad 1</td></tr>
<tr><td>feeding focals dyad 2</td></tr>
<tr><td>normal focals & cooperation task dyad 1</td></tr>
<tr><td>normal focals & cooperation task dyad 2</td></tr>
<tr><td rowspan="4">afternoon</td><td>normal focals & cooperation task dyad 3</td></tr>
<tr><td>normal focals & cooperation task dyad 4</td></tr>
<tr><td>feeding focals dyad 3</td></tr>
<tr><td>feeding focals dyad 4</td></tr>
</table>

<u>Focal observations</u>

Focal observations (normal and feeding focals) were carried out on each day of data collection in order to assess relationship quality. For the focals, each individual was filmed with a hand-held camera for five minutes in order to record interactions between the pair partners. Affiliative behaviour, agonistic behaviour, and food related behaviour (see *Table 1* in appendix) were recorded in each focal. Both the normal focals and the feeding focals were carried out in a randomised order with regard to male or female. Normal focals were conducted right before the cooperation task.

Feeding focals were taken during the morning or the afternoon feeding occasion (notably, feeding focals at TGS were only conducted during the second feeding around noon). The feeding focal of the first raven of the dyad started one minute after the keeper left the aviary.

<u>Cooperation task</u>

The cooperation test was conducted by using the loose string task. The apparatus for this task (see *Figure 1*) included the feeding platform (100 x 15 cm) with wheels, which was placed on a bigger board (125 x 30 cm) outside of the aviary. A loose string (150 cm) was threaded through two metal loops (placed in a distance of 90 cm in-between them on the feeding platform), and each end of the string (with a length of 10-15 cm each) was placed into the aviary. On the feeding platform, five nails were mounted pointing towards the aviary. The outer two nails were equidistant positioned as the two metal loops. The other nails were in regular intervals between the outer nails (distance between them 22.5 cm).

The partners had to pull on the string simultaneously - each partner on one end of the string - to move the feeding platform towards the aviary; if only one of the ravens was pulling, the string became unthreaded, and the platform would not move. Rewards were placed on the nails on the feeding platform; the number of rewards and the nails on which they were placed depended on predefined conditions (described in detail in the section "Testing").

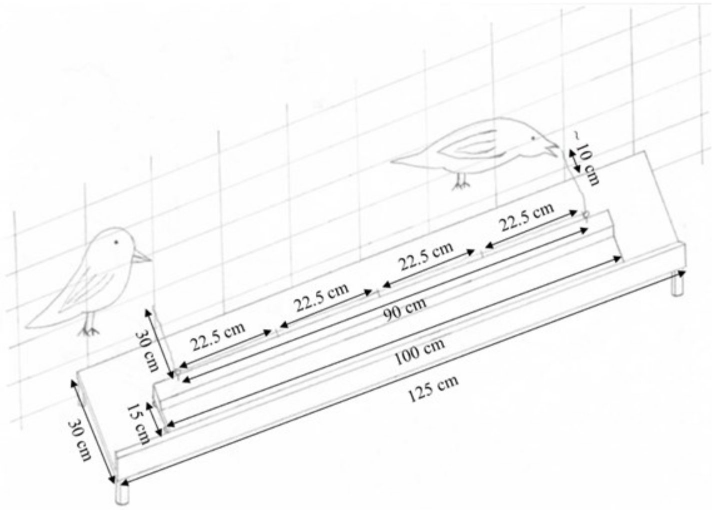

Figure 1: Loose string setup for the cooperation task (© Rita Götz).

Training

At the beginning of the training, the ravens were habituated to the experimenter by feeding them dry cat food until they approached the person outside the aviary without hesitation; they were also habituated to the big board outside, directly placed next to the fence of each aviary, by providing them treats from the platform until they did not hesitate to approach the board. Simultaneously, the ravens were habituated to the feeding platform, which - at the beginning - was placed inside the aviary approximately one meter next to the feeding site. A string was attached to the board, secured with a knot. As soon as the ravens were completely habituated, the feeding platform was removed from the aviary, and the training began.

Training took place as often as possible during the training phase (December 2023 until beginning of breeding phase 2024) and had been designed to sequentially meet three criteria. The first criterion was that each raven learned by itself to pull the string. To that end, the string was secured with a knot on the board to prevent it from becoming loose; this was carried out in order to habituate to the movement and the sound of the platform. As soon as both partners became familiar with pulling the string, the training continued with the second criterion in which the ravens had to pull together, each on one end of the string. During criterion two, the string was still secured with a knot to prevent it from becoming loose. In this training phase, the experimenter blocked the feeding platform from movement if only one raven pulled. Upon successful achievement of the second criterion, training with the last criterion started. To that end, the string was not secured with a knot anymore; it was loose (threaded through the metal loops) as during the testing phase. The aim of this criterion was to learn that only cooperation will be rewarded, i.e. that simultaneous pulling on both ends of the string was needed in order to move the feeding platform for getting the reward.

Dyads that reached criterion three before the end of the training phase continued the training with two sessions of fifteen trials each per week until the start of the testing phase to keep them on the same level. (Notably, before achieving criterion three, there was no fixed number of trials during the training.) With dyads who did not reach criterion three before the end of the training phase, training was continued during the testing phase until they achieved the criterion. Training was adapted a little bit to individual differences in the dyads, like presenting the pieces of rewards at the beginning of the training from inside the aviary, presenting the pieces in front of the board instead of directly from the board, or distracting the partner from the board to avoid acting against the dominance hierarchy. At the beginning of the training phase, the rewards were pieces of dry dog food (Frolic); later they were replaced with commercially obtainable greaves. At TGS, the rewards during the training were pieces of beef meat (size ~ 1 cm^3). During the training, the rewards were always placed on both outer nails.

Testing

The setup for the cooperation task was the same as during the training phase, and the test sessions were recorded with a camera on a tripod (see *Figure 2*). Six conditions were tested in the cooperation task (see *Figure 3*). The conditions were grouped into equity and inequity conditions. The conditions varied by the distance between the rewards (the nails, on which the rewards were placed). The first condition (equity-distant) was with rewards placed on each of the outer nails (termed "lo" and "ro" – "left outer" and "right outer"). The second condition (equity-middle) was with rewards placed on the nails next to the outer nails (middle nails; "lm" and "rm"), while in the third condition (equity-close), there were two pieces of reward on the innermost nail ("i"). In the fourth condition (inequity-distant), there was only one piece of reward on one of the outer nails (lo/ro). In the fifth condition (inequity-middle), there was one piece of reward on one of the middle nails (lm/rm), and in the sixth condition (inequity-close), there was one piece of reward on the innermost nail (i). For the unequal reward conditions, the side of reward placement was randomised with no more than three consecutive trials on the same side.

Figure 2: Test situation for the cooperation task (© Rita Götz).

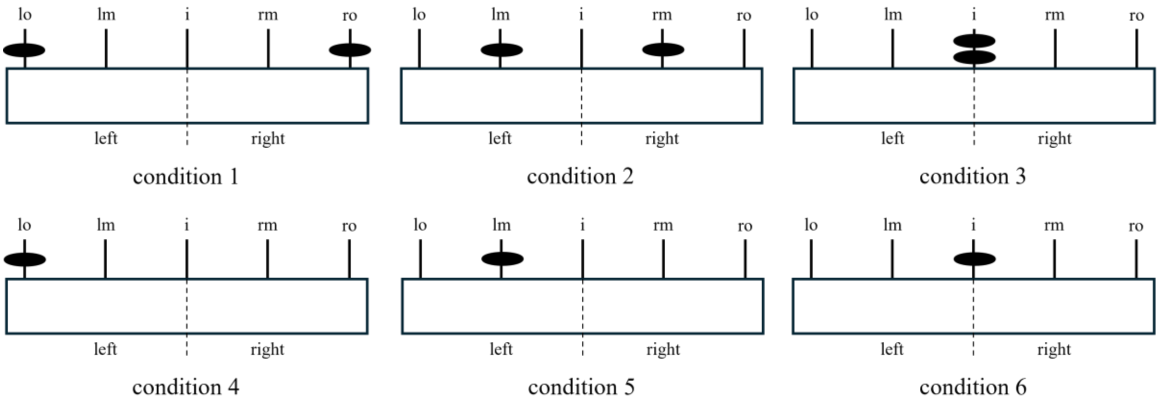

Figure 3: Illustration of the six conditions for the cooperation task.

On each day of data collection (twelve per block), one of the six conditions was conducted in a single test session of fifteen trials. Each condition was conducted twice per breeding phase, once in the morning and once in the afternoon (on separate days). The series of six conditions was conducted in a randomized order. Within a breeding phase, each of the six conditions was conducted for the first time before the second set of the six conditions was conducted. Additionally, the testing in morning or afternoon session was randomized.

In each test session of fifteen trials, the interval between completion of the trial and start of the next trial was twenty seconds. A trial ended when the string had successfully (cooperatively) or unsuccessfully been pulled (only one partner pulled, resulting in no movement of the feeding platform and in no reward), or after a maximum of two minutes after start of the trial. At the beginning of the trial, the ravens were called by their names. If they were both in front of the setup, the strings were provided immediately. If one or both ravens were absent, the strings were provided after five seconds. The trial started with providing the strings. If needed, the ravens were called again after one minute. The rewards in the testing phase were greaves (TGS: beef meat). Since participation in the task was low during the nesting phase, from the early nestling phase onwards, the session started with providing up to two treats per raven directly at the board to motivate them to participate in the task.

Data analysis

The whole data collection was videotaped. The focals (normal and feeding) were coded with Solomon coder (Péter, 2019). Normal and feeding focals of ten days per breeding phase per dyad were used. For each individual, affiliative (approach, allopreening, touch, follow, play), agonistic (avoid, displacement, aggressive behaviour) and food related (co-feeding, allofeeding, begging, theft) behaviour was coded, as well as self-assertive displays (SADs) and the proximity towards the partner (see *Table 1* in appendix). To include each interaction, the behaviour was coded as active when the focal individual performed it and as passive when the focal individual received it. To check for interobserver reliability (IOR), a randomized sample of 48 videos (normal and feeding focals) were coded by an independent person. The IOR for more than half of the relationship quality variables was excellent (ICC above 0.8), another sixth of the variables had a moderate IOR (ICC above 0.4; detailed results see *Table 2* in appendix). Most of the differences in coding could be referable to varying notion of distances.

The videos of the cooperation task were coded manually. Counts included presence of individuals, number of successful and unsuccessful trials, recipients of the pieces of rewards and number of thefts (see *Table 1* in appendix). For the IOR, the coding results of 26 sessions from another person were used. The IOR for successful trials (ICC = 0.998, $n_{subjects}$ 26, = n_{raters} = 2, $p < 0.001$;) and for trials in which both were present (ICC = 0.996, $n_{subjects}$ 26, = n_{raters} = 2, $p < 0.001$;) was excellent.

Issues and deviations from study protocol

Only six out of eight pairs solved the cooperation task during the testing phase (two at KLF, four at HH). Thereof, three pairs only solved the task in the late nestling phase (one at KLF, two at HH). One pair at HH only completed one series of six conditions at the very end of data collection. Moreover, some videos from HH were missing. For one dyad, two feeding focals for the nesting phase and two feeding focals for the early nestling phase were missing, and for a second dyad, two normal focals for the early nestling phase were missing. In addition, several cooperation task sessions were missing or represented the wrong conditions. Most of the missing sessions from the late nestling phase were repeated right after the end of the phase. An additional issue with the videos from HH was that some trials were missing in several sessions and that the length of the trials as well as the intertrial intervals were too long. However, given that measure of success was a proportion (see session "Statistics"), the fact of missing trials was not a major issue. Some sessions contained more than 15 trials; in this case, extra trails were not considered in the analyses. Several focal videos from HH were of low quality, in that sometimes much time elapsed until following the individuum when it was moving, or in that the wrong individual was focused on or in that the focus individual was partially or fully out of sight for an extended time. This affected the coding of social interactions.

Statistics

All statistical analyses were conducted with R, Version 4.1.1 (R Core Team, 2021). The packages "psych" (version 2.4.6; Revelle, 2020), "tidyverse" (Wickham et al., 2019), "lme4" (Bates et al., 2014), "tidyr" (version 1.3.0; Wickham & Girlich, 2022), and "emmeans" (version 1.10.3; Russell, 2024) were used. Using the "anova" function, a full-null model comparison (likelihood ratio test) was conducted for each model, whereas the null model only contained the response variable and the random effects. The significance level was set to ≤ 0.05. The IOR was conducted with the package "irr". For some of the plots, the packages "ggplot2" (Wickham, 2016) and "cowplot" (version 1.1.3; Wilke, 2015) were used. The function "boot_glmm" (Mundry, 2023) was used to obtain the confidence intervals (CI) for plotting.

Factor analysis for relationship quality components

Following the methodology outlined in Fraser & Bugnyar (2010), a principal component analysis (PCA) was run at first in order to identify the underlying factors (principal components) of relationship quality. Therefor, a Kaiser-Meyer-Olkin test of sampling adequacy (MSA = 0.56) and a Bartlett's test of sphericity ($\chi^2 = 101.74$, df = 36, $p < 0.001$) was applied.

However, none of the variables loaded strongly on the first PCA component. For further analyses, a factor analysis with varimax rotation was applied which turned out to fit better to the data of this study. Only components with a minimum eigenvalue of 1.0 were extracted from the factor analysis. Nine behavioural variables were entered into the factor analysis (see *Table 2*). For the factor analysis, all behavioural variables were split up into the three different breeding phases, and active and passive behaviour shown was summed up on a dyadic level. All other coded behaviours (see *Table 1* in appendix) were excluded from the analysis, due to the fact that they occurred in less than half of the dyad/breeding phase combinations only.

Table 2: Variables used for the factor analysis.

Allofeeding	Total number of food sharing from beak to beak
Co feeding	Sum of time the partners ate together in a reaching distance
Proximity	Sum of time the partners spent next to each other within 1 m
Contact sitting	Sum of time the partners were sitting next to each other on a perch (up to 15 cm)
Allopreening	Sum of time the partners spent preening each other
Touch	Sum of time the partners touched each other with their beaks
Approach	Total number of approaching the partner within 1 m
Follow	Total number of following the partner immediately
SAD	Total number of self-assertive displays

Generalized linear mixed model with relationship quality

A generalized linear mixed model (GLMM) with a binomial error distribution was fitted to analyse the effects of relationship quality as well as of reward distance and reward equity on the proportion of success in the cooperation task. The number of successful trials and non-successful trials (unsuccessful male or female, or unfinished) were included as the response variable in the model, using the "cbind" function. For each relationship quality variable from the factor analysis, an individual model was fitted. Distance (distant, middle, close) and equity (equal, unequal) were included as additional fixed effects. There was a three-way interaction between the three fixed effects (relationship quality variable, distance, equity). The dyad was included as a random effect. A second model was run for each relationship quality variable with the proportion of successful trials and unsuccessful trials for trials in which both partners were next to the board during the trial. For each model, an overdispersion test was conducted. The dispersion parameter was in most cases below 0.5 which means an overly conservative model.

Generalized linear mixed model with breeding phase

In order to analyse the effect of the breeding phase on cooperative success, a second GLMM was fitted with again the proportion of success as the response variable, the breeding phases as a fixed effect and the dyad as a random effect. Two models were run, one with the total number of trials and the second with trials in which both partners were next to the board. For both models, an overdispersion test was conducted which showed an underdispersion.

Linear model with breeding phase

For measuring the effect of the breeding phases on relationship quality, a linear model (LM) was fitted with the relationship quality variables as the response variable, the breeding phases as a fixed effect and the dyad as a random effect. An individual model was fitted for each of the relationship quality variables.

Results

Three relationship quality components were extracted from the factor analysis (see *Table 3*). The proportion of approaches was used as an individual behavioural variable as it was the only behavioural variable that fitted to the fourth factor of the factor analysis. A higher value of the factor means a higher relationship quality. The variables co-feeding and SAD loaded weakly on the factors and may have had a limited influence.

Table 3: Factor analysis matrix

Behaviour variables	Factor 1	Factor 2	Factor 3
Contact sitting	**0.99339843**	-0.02338429	0.08739500
Allopreening	**0.82016971**	-0.10085125	-0.21348144
Touch	**0.70794041**	0.19589898	0.10657133
Approach	0.08629848	**0.95194146**	0.28525932
Proximity	0.57189647	**0.69275024**	-0.04814526
Co feeding	-0.09574742	**0.45951802**	-0.17799156
Allofeeding	-0.08918794	-0.43629716	**0.67749090**
Follow	-0.15118149	-0.01329268	**0.89061232**
SAD	0.10782419	0.08888551	**0.41267237**

Values represent correlation between each relationship quality variable and each factor. Bold values marked the factor to which each of the behaviours belongs.

Effects of relationship quality on cooperative success and tolerance regarding reward distance and equity

For all models, the number of observations was 131 and the number of dyads was six. Over all trials, neither one of the four relationship quality variables nor reward distance or equity or their interaction had a significant effect on cooperation success (full-null model comparison with Factor 1: $\chi^2 = 8.64$, df = 11, p = 0.655; full-null model comparison with Factor 2: $\chi^2 = 14.032$, df = 11, p = 0.231; full-null model comparison with Factor 3: $\chi^2 = 14.175$, df = 11, p = 0.223; full-null model comparison with proportion of approach: $\chi^2 = 11.238$, df = 11, p = 0.424).

In those trials where both partners were at the board during the trial, there was a significant three-way interaction between factor 1, distance, and equity effecting the proportion of success (full-null model comparison: $\chi^2 = 19.995$, df = 11, p = 0.045; see *Figure 4*). The conditions equity-distant and inequity-distant (estimate = -1.252, SE = 0.507, p = 0.014), and inequity-close and inequity-distant (estimate = -1.114, SE = 0.482, p = 0.021) were significantly different from each other. The proportion of success was higher in conditions equity-distant and inequity-close than in inequity-distant (see *Figure 4*).

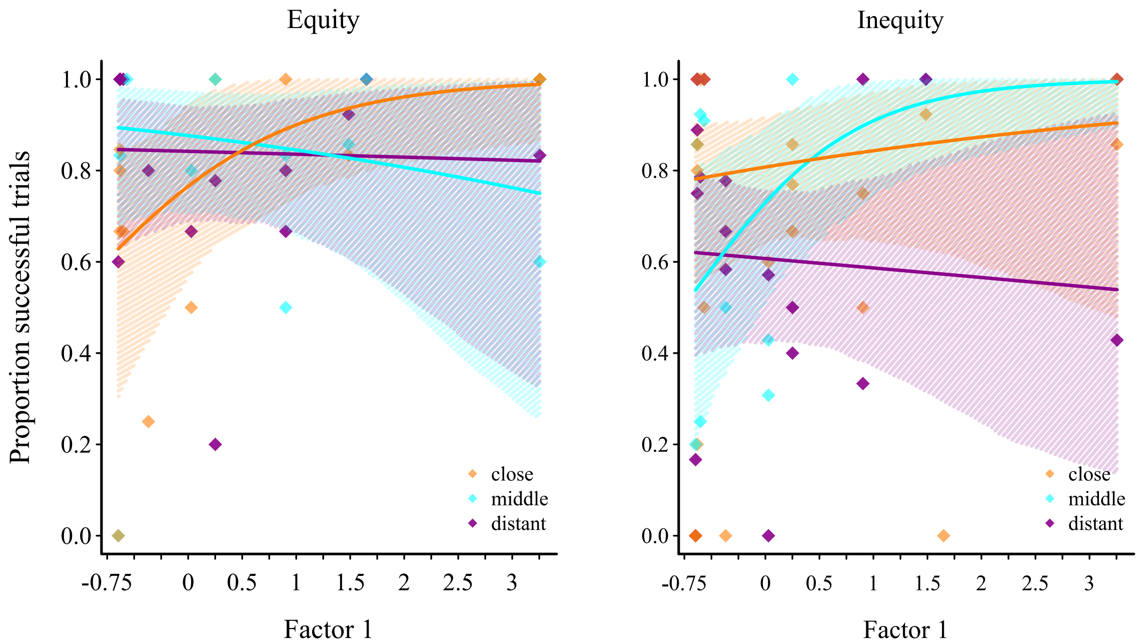

Figure 4: Proportion of successful trials in equity (left) and inequity (right) condition with close (orange), middle (blue), or distant (purple) conditions depending on relationship quality factor 1. Points represent the individual data point, lines the model lines and ribbons the CIs.

There was another significant three-way interaction in the model with Factor 2 and the proportion of successful trials when both partners were present (full-null model comparison: χ^2 = 25.106, df = 11, p = 0.009; see *Figure 5*). Factor 2 had a significant positive effect on success in the conditions equity-close, inequity-close, equity-middle, inequity-middle, and inequity-distant (see *Table 4*). There was a significant difference between inequity-close and inequity-distant (estimate = -0.995, SE = 0.392, p = 0.011), and equity-distant and inequity-distant (estimate = -1.212, SE = 0.442, p = 0.006). The success in the inequity-distant condition was lower than in equity-distant and inequity-close (see *Figure 5)*.

Table 4: Significant effects of Factor 2 on several cooperation task conditions.

condition	estimate	SE	p
equity-close	0.856	0.412	0.038
inequity-close	1.135	0.349	0.001
equity-middle	1.574	0.515	0.002
inequity-middle	1.017	0.383	0.008
inequity-distant	0.952	0.325	0.003

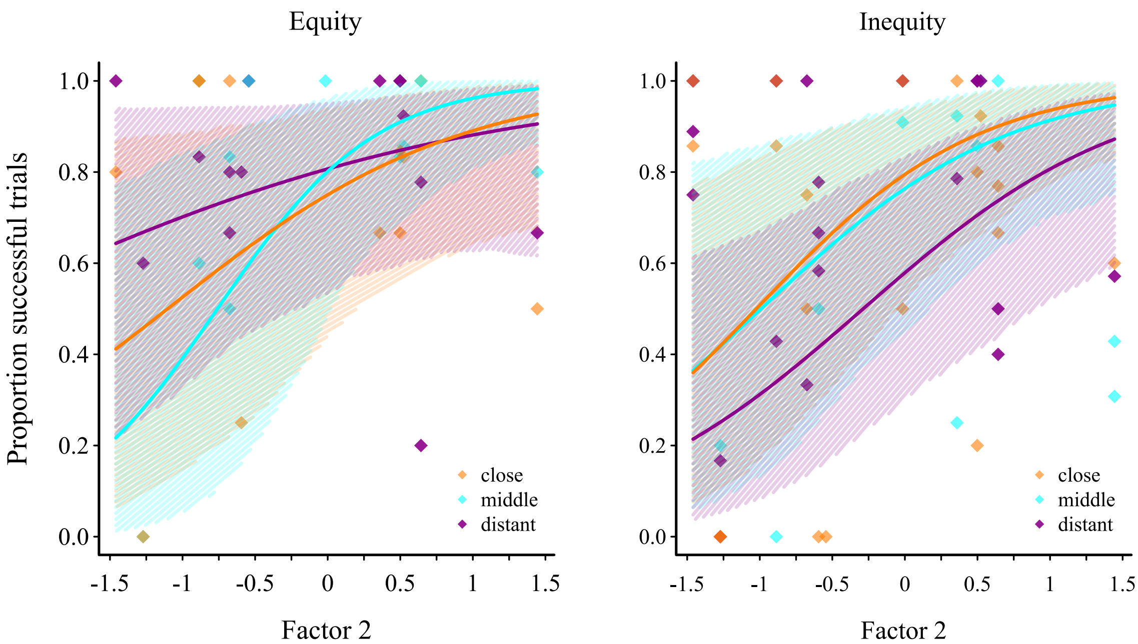

Figure 5: Proportion of successful trials in equity (left) and inequity (right) condition with close (orange), middle (blue), or distant (purple) conditions depending on relationship quality factor 2. Points represent the individual data point, lines the model lines and ribbons the CIs.

In the model with Factor 3 and proportion of successful trials when both partners were present, there was again a significant three-way interaction (full-null model comparison: χ^2 = 27.023, df =11, p = 0.005; see *Figure 6*). The proportion of success in the conditions inequity-close (estimate = 1.268, SE = 0.64, p = 0.048), and inequity-middle (estimate =

2.207, SE = 0.82, p = 0.007) was significantly positive affected by Factor 3. Between the conditions inequity-close and inequity-distant (estimate = -1.548, SE = 0.51, p = 0.002), inequity-middle and inequity-distant (estimate = -1.079, SE = 0.541, p = 0.046), and equity-distant and inequity-distant (estimate = -1.379, SE = 0.501, p = 0.006) there was a significant difference. The success in the inequity-distant condition was lower than in the other conditions (see *Figure 6)*.

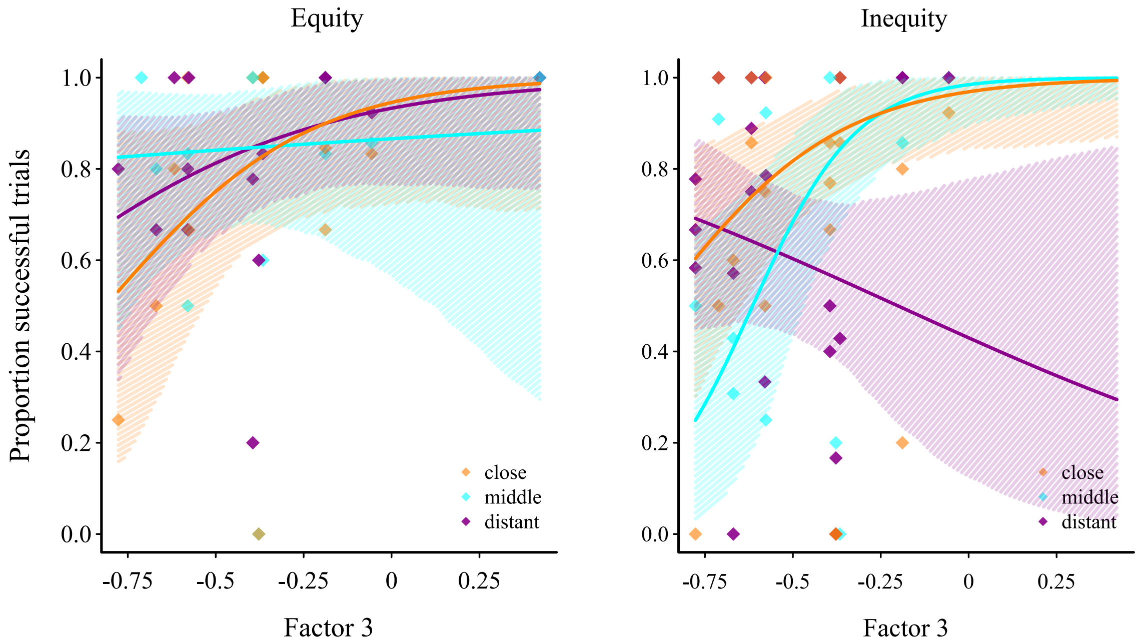

Figure 6: Proportion of successful trials in equity (left) and inequity (right) condition with close (orange), middle (blue), or distant (purple) conditions depending on relationship quality factor 3. Points represent the individual data point, lines the model lines and ribbons the CIs.

In the model with proportion of approach and the proportion of successful trials when both partners were present, there was no such significant interaction (full-null model comparison: $\chi^2 = 11.647$, df = 11, p = 0.391; see *Figure 1* in appendix).

Effects of breeding phase on relationship quality and cooperative success

For models with cooperative success as response, the number of observations was 131 and the number of dyads was six. Breeding phase had a significant effect on cooperative success in the model with all trials (full-null model comparison: $\chi^2 = 19.313$, df = 2, p < 0.001; see *Figure 7*). There was a significant difference between early nestling and nesting (estimate = -1.624, SE = 0.575, p = 0.005), and late nestling and nesting (estimate = -2.243, SE = 0.522, p < 0.001). The proportion of success was lower in the nesting phase than and the nestling phases (see *Figure 7)*.

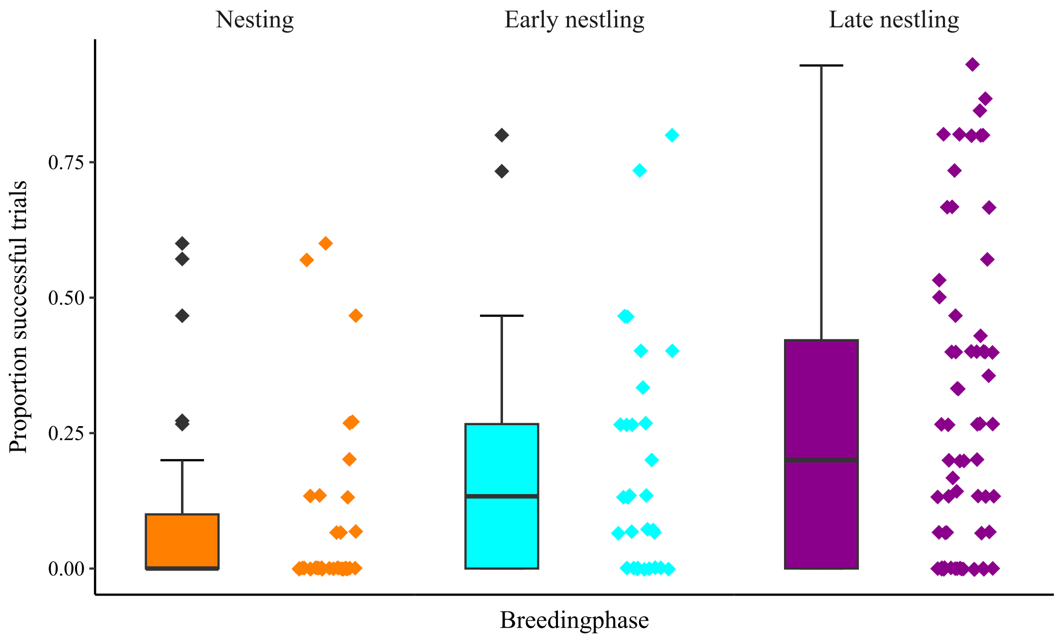

Figure 7: Proportion of successful trials in the breeding phases nesting (orange), early nestling (blue) and late nestling (purple) over all trials. Boxes represent the interquartile range, thick black horizontal bars the median, whiskers the range of data points within 1.5 times the interquartile range from the upper and lower hinge, and black points the outliers. Coloured points represent the individual data points in the nesting (orange), early nestling (blue) and late nestling (purple) phase.

In the model with trials in which both partners were present, there was a significant effect as well (full-null model comparison: $\chi^2 = 11.863$, df = 2, p = 0.003; see *Figure 2* in appendix). Between early nestling and late nestling (estimate = 1.02, SE = 0.422, p = 0.016), and late nestling and nesting (estimate = -1.617, SE = 0.486, p = 0.001), there was a significant difference. In the late nestling phase, proportion of success was higher than in nesting and early nestling phase (see *Figure 2* in appendix).

For all models with relationship quality variables as response, the number of observations was 24 and the number of dyads was eight. Breeding phase had a significant effect on Factor 1 (full-null model comparison: $\chi^2 = 48.286$, df =2, p = < 0.001; see *Figure 8a*). There was a significant difference between early nestling and late nestling (estimate = -0.795, SE = 0.11, p < 0.001), and late nestling and nesting (estimate = 0.574, SE = 0.105, p < 0.001), as Factor 1 was higher in late nestling phase than in the other phases.

Factor 2 was significantly affected by breeding phase (full-null model comparison: χ^2 = 89.402, df = 2, p < 0.001; see *Figure 8b*). Between early nestling and nesting (estimate = 0.763, SE = 0.094, p < 0.001), and late nestling and nesting (estimate = 0.959, SE = 0.09, p < 0.001) was a significant difference. Relationship quality Factor 2 increased over time.

In addition, breeding phase had a significant effect on Factor 3 (full-null model comparison: $\chi^2 = 82.632$, df = 2, $p < 0.001$; see *Figure 8c*). All breeding phases were significantly different from each other (see *Table 5*). Factor 3 had the highest value in the nesting phase, and during the late nestling phase it was higher than in the early nestling phase.

Table 5: Effects of breeding phase on relationship quality factor 3.

breeding phase	estimate	SE	p
early nestling - late nestling	-0.236	0.044	< 0.001
early nestling - nesting	-0.475	0.044	< 0.001
late nestling - nesting	-0.239	0.042	< 0.001

There was a significant effect of breeding phase on the proportion of approach (full-null model comparison: $\chi^2 = 67.181$, df = 2, $p < 0.001$; see *Figure 8d*). Between early nestling and late nestling (estimate = -0.158, SE = 0.018, $p < 0.001$), and late nestling and nesting (estimate = 0.126, SE = 0.018, $p < 0.001$), there was a significant difference, as proportion of approach was higher in late nestling phase than in the other phases.

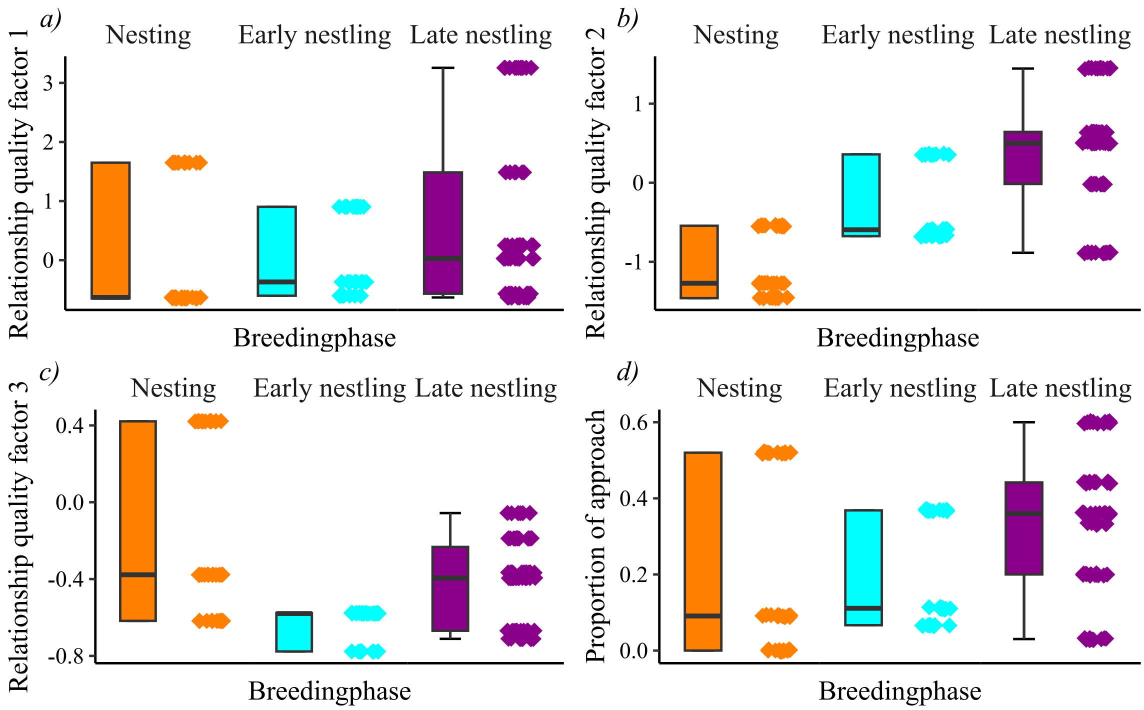

Figure 8: Effects of nesting (orange), early nestling (blue) and late nestling (purple) phase on the relationship quality variables: panel a) Factor 1, panel b) Factor 2, panel c) Factor 3 and panel d) Proportion of approach between partners. Boxes represent the interquartile range, thick black horizontal bars the median, and whiskers the range of data points within 1.5 times the interquartile range from the upper and lower hinge. Points represent the individual data points in the nesting (orange), early nestling (blue) and late nestling (purple) phase. Values in panels a) – c) are from the factor analysis, panel d) is a proportion of balance in behaviour shown.

Discussion

The central question to answer in the present study was, whether relationship quality effects success in cooperation tasks. Other aspects of interest were, whether relationship quality also has an effect on tolerance regarding reward distance and equity, and whether breeding phase influences cooperative success and relationship quality.

The results of this work showed that the effect of relationship quality on cooperative success depends on the condition (depending on reward distance and equity). In particular, relationship quality factor 2 (approach, proximity and co-feeding) had an impact on success in the cooperation task, meaning that higher relationship quality led to higher cooperative success (significant increase in five out of six conditions, increase in condition equity-distant not significant). Relationship quality factor 3 (allofeeding, follow and SAD) influenced the success in inequity conditions with less of a distance between pieces of reward (middle and close condition). Here, the cooperative success was higher when the relationship quality was higher. Relationship quality factor 1 (contact sitting, allopreening and touch) had no significant impact on a specific condition but like in the models with factor 2 and 3, there were significant differences between specific conditions affected by relationship quality. This supported the suggestion that relationships are a key factor in cooperative behaviour.

The results match with findings of Massen et al. (2015) that social tolerance (as a part of relationship quality) affected cooperative success in ravens. Friendship led to earlier future cooperation after being cheated, and the probability of successful cooperation was higher in group settings (where the ravens could choose their preferred partner, usually a friend) than in dyadic settings (Massen et al., 2015). In general, a part of relationship quality is knowledge about the social partner and the stability of the relationship over the time (Maldonado-Chaparro et al., 2021), which facilitates predictions about future cooperative behaviour and the chances of positive outcomes of cooperation for the individual itself. This could be an explanation for higher proportion of success in the cooperation task in dyads with high relationship quality, as previously shown in a study with ravens (Asakawa-Haas et al., 2016).

In contrast to the models with the factor analysis factors, the model with proportion of approach (balance between partners in approaches) was not significant. A possible explanation is that a well-balanced proportion in approaching the partner is not a good indicator for social tolerance. Other aspects of relationship quality like staying in proximity or contact sitting could be more important for social tolerance (i.e. tolerating closeness to partner over a longer period, as it is needed for cooperation). Furthermore, as reward sharing is often part of cooperation tests (to keep partner motivated for further cooperation), high values of co-feeding and allofeeding seem to be better requirements for successful cooperation than high balance in approaching the partner.

In all three significant models with the relationship quality factors, a difference in successful trials between equal and unequal reward in the distant conditions was seen in that the proportion of success was lower in the inequity condition. A possible explanation for differences in the distant conditions but not in middle or close conditions could be that in middle and close distance, rewards were more easily accessible from both sides of the board. A single piece of reward on the distant position on the other side of the board could be less motivating to cooperate, because the perceived chance of getting the reward is lower. Furthermore, a previous study in ravens showed that the probability of future successful cooperation was higher after an equal reward division (Massen et al., 2015).

However, higher relationship quality led to higher cooperative success in inequity conditions, which could be explained by higher tolerance regarding food sharing and unequal outcomes for same effort. In addition, in trials with both partners present at the board, a significant difference in success between the distant and the close condition was seen with the unequal reward in each of the three models including the relationship quality factors. The proportion of success was higher with lower distance between the pieces of reward. Additionally, in the model with relationship quality factor 3, there was a significant difference between the middle and the distant inequity condition: proportion of success was lower in the distant condition.

These findings match with the results mentioned above, that proportion of successful trials in the inequity-distant condition is low. In middle and close conditions, compared to distant conditions, probability of theft is higher even in the equity conditions. Thus, likelihood of cooperation in equal and unequal reward conditions is similar. Both partners have similar chances for gaining the reward. In inequity conditions with great distance between pieces of reward, probability of theft is higher, and thus, one partner has lower chances for gaining the reward. This could explain why in inequity conditions, success in distant condition is lower than in middle or close conditions.

All these effects could only be found when trials were excluded from the analysis in which only one of the two partners or none of them was available. This can be explained by the fact that it was only possible to complete the task when both partners were present; there was a large number of trials, though, in which one or both partners were absent. Excluding these trials enabled it to measure the proportion of success when both partners had the possibility to cooperate. This offered more accurate information when individuals chose to cooperate.

Furthermore, breeding phase had a significant impact on cooperative success. In the model including all trials, it was found that cooperative success was higher in both nestling phases than in the nesting phase. In the model including only trials in which both partners were present, the proportion of successful trials was higher in the late nestling phase than in the nesting phase and the early nestling phase.

A simple explanation for the results with all trials is that as the females spent most of their time in the nest during the nesting phase and therefore were not available to cooperate. Moreover, right after the chicks hatched, they were not available to participate in the cooperation task due to the chicks requiring body heat from the parents. As soon as the chicks were old enough to stay in the nest on their own, the females started to participate in the cooperation task more often, thus leading to a higher rate of success over all trials. In contrast, against the prediction, there was no evidence that they needed an additional amount of food for their chicks. Thus, gaining additional food seems to be an unlikely explanation for success. Results of the study seem to confirm previous findings that ravens are highly cooperative, especially during the breeding season (Ersoy et al., 2021). However, the study was only conducted during the breeding season, thus there is no comparison to cooperative success throughout the rest of the year.

Additionally, one explanation for higher success rates in the late nestling phase could be that the ravens had more experience with the task at the end of the breeding season than at the beginning. Another reason could be that some pairs only reached criterion three of the training right before the late nestling phase. They had intense training with high rewarding rate before participating in the test during the late nestling phase, and therefore, it could be possible that motivation in participation in the cooperation task was higher.

Breeding phase significantly effected relationship quality, too. Factor 1 was higher in the late nestling phase than in the nesting phase and the early nestling phase. Furthermore, Factor 2 was lower in the nesting phase than in both nestling phases. Factor 3 was highest in the nesting phase and lower in the early nestling phase than in the late nestling phase. The proportion of approach (how well-balanced the partners approached each other; the higher the proportion of approach, the more imbalanced was the number of approaches of each partner) was higher in the late nestling phase than in the nesting phase and the early nestling phase.

These findings did not support the hypothesis that relationship quality is stable over time. One possible explanation could be that the females were sitting on the nest most of the time in the nesting phase; thus, there were fewer interactions to count during the focal protocols. The results suggest that the relationship quality was higher towards the end of the breeding season. A possible explanation for this observation could be that there was less time for social interactions with the pair partner during the nesting and the early nestling phase due to the fact that females spent a considerable amount of the day in the nest. For the short durations the females were out of the nest, they usually spent their time for eating, defending their territory by calling, or preening themselves rather than affiliating with their partner. When the chicks were old enough to be alone in the nest for a longer time period, the females had more time to engage in other activities, and the frequency of social interactions during the focal observations increased.

Relationship quality factor 3 including allofeeding and SADs was highest in the nesting phase, which seems comprehensible. SADs strengthen the pair bond and show dominance against intruders (Luef et al., 2020), whereas allofeeding is a form of male care taking occurring mostly during the nesting phase when the female spent most of the time in the nest. In contrast, relationship quality factors 1 and 2, including proximity, contact sitting, co-feeding, and allopreening, were higher at the end of the breeding season. Due to that the female was in the nest most of the time, behaviours that required spatial proximity occurred less often at the beginning of the breeding season. In addition, as a support for the female, the males overtook the incubation in some cases when the females left the nest, as is also common in other bird species (Møller & Cuervo, 2000). Therefore, the time both partners spent outside of the nest was even shorter, and probability of proximity to the partner which is needed for social behaviour like contact sitting or allopreening was low.

In the end, there were three major limitations in this study causing difficulties. A longer training period could have increased the number of dyads participating in the cooperation task. If the ravens had more experience with the procedure than in the present study, that could also influence how much time the females, in particular, invest in the cooperation task during the breeding season. Additionally, consistently accurate data collection in the cooperation task, in particular, like exact time intervals without delays within or during the trials, could lead to more meaningful results. Furthermore, more accurate focal observations could increase the number of recorded social interactions, which leads to more accurate relationship quality data. A minor aspect to improve would be the procedure during the testing, like keeping the intertrial intervals as short as possible to hold the ravens` attention on the task.

Conclusion

In conclusion, the present study showed that cooperation success is influenced by different aspects. The hypothesis that relationship quality has an effect on cooperative success was supported by these results. However, the influence of relationship quality on cooperative success depended on the condition. Furthermore, the effect of reward distance and equity on success depended on relationship quality. However, the proportion of successful trials was in large parts higher in conditions with lower distance between the pieces of reward and reward inequity, which is against the expectations. Overall, as predicted, high relationship quality had a positive effect on cooperation success. These findings are consistent with previous research. The results only partially supported the third hypothesis though. Breeding phase had not only an effect on cooperation success but also on relationship quality.

Further research is needed to investigate whether the effect of relationship quality on cooperative success is consistent over multiple breeding seasons, as ravens are a long-term monogamous species, and how relationship quality influences cooperation outside the breeding season. Another interesting question for further research is if there are any other aspects influencing cooperation, like individual personality or previous experience in the cooperation task with the current partner or other conspecifics. Another gap in knowledge relates to the stability of relationship quality during the breeding season, as changes in the social behaviour between pair partners may influence their behaviour in different situations, i.e. during a cooperation test.

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Appendix

Table 1: Ethogram, including displays, position, affiliative, agonistic and food related behaviour for relationship quality index and cooperation related behaviour for analysis of cooperation test.

Position	
Proximity (d)	Individual sits in proximity to partner (up to 1 m)
Contact sitting (d)	Individual sits on a perch in reaching distance to partner, close enough to enter body contact within one step (up to 15 cm)
Affiliative behaviour	
Approach (f)	Individual approaches partner within 1 m; either active (initiator) or passive (receiver);
Allopreening (d)	Individual runs its beak through feathers of partner; either active or passive;
Touch (d)	Individual touches feathers/beak/foot of partner; either active or passive;
Follow (f)	Individual moves in the same direction as partner after being in proximity/contact with it and enters again in proximity/contact; follower moves shortly after partner; either active or passive
Play (d)	Partners interact with each other through a wide variety of motor patterns, postures, vocalizations, which do not explicitly express aggressive intentions and appears functionless
Displays	
SAD (f)	Self-assertive display; individual makes multimodal display (sound, body movement, feather position)
Agonistic behaviour	
Avoid (f)	Individual leaves before approaching partner is less than 1 m away; either active or passive
Displacement (f)	Individual enters partner (less than 1 m), who leaves immediately, and takes its place; with or without physical contact; either active or passive
Aggressive behaviour (f)	Negative action against partner (threat, peck, pull, push, fight,…) excluding other described agonistic behaviours; either active or passive
Food related behaviour	
Co feeding (d)	Partners eat the same piece of food or distinct food pieces within a reaching distance (up to 1 m)
Allofeeding (f)	Individual actively transfers food from its beak to partners beak; either active or passive

Begging (f)	Individual vocalises and/or flapping wings towards partner and/or touches partners beak to request for food; either active or passive; either successful (food transfer) or unsuccessful (no food transfer)
Theft (f)	Individual steals food item from partner and either stays or leaves with it; either active or passive; either successful (steals food) or unsuccessful (owner keeps/leaves with item)
Cooperation related behaviour	
Present (f)	Individual is visible within 1 m in front of the board during the trial; either male or female
Successful (f)	Both partners pull at the same time, board rolls towards them
Unsuccessful (f)	Only one partner pulls, string gets loose; either male or female
Unfinished (f)	Neither of the partners pull within 2 min
Rewarded (f)	Individual gets one or both pieces of reward; either male or female
Theft cooperation (f)	One partner steals reward from the other side; gets one or both rewards; either male or female

f = frequency, d = duration;

Table 2: Results for the IOR of each observed behaviour. Italicized behaviours were used for the behavioural analyses.

Behaviour variable	**ICC**	**$n_{subjects}$**	**n_{raters}**	**p-value**
Allofeeding active	*1*	*48*	*2*	*0*
Allofeeding passive	*0*	*48*	*2*	*0.5*
Begging successful active	NaN	48	2	NaN
Begging successful passive	NaN	48	2	NaN
Begging unsuccessful active	NaN	48	2	NaN
Begging unsuccessful passive	NaN	48	2	NaN
Theft successful active	NaN	48	2	NaN
Theft successful passive	< 0.001	48	2	0.5
Theft unsuccessful active	NaN	48	2	NaN
Theft unsuccessful passive	< 0.001	48	2	0.5
Co feeding	*0.516*	*48*	*2*	*< 0.001*
Proximity	*0.417*	*48*	*2*	*0.001*
Contact sitting	*0.386*	*48*	*2*	*0.003*
Play	NaN	48	2	NaN
Allopreening active	*1*	*48*	*2*	*< 0.001*
Allopreening passive	*NaN*	*48*	*2*	*NaN*
Touch active	*0.996*	*48*	*2*	*< 0.001*
Touch passive	*< 0.001*	*48*	*2*	*0.5*
Approach active	*0.607*	*48*	*2*	*< 0.001*
Approach passive	*0.94*	*48*	*2*	*< 0.001*
Follow active	*NaN*	*48*	*2*	*NaN*
Follow passive	*NaN*	*48*	*2*	*NaN*
SAD	*0.998*	*48*	*2*	*< 0.001*
Avoid active	NaN	48	2	NaN
Avoid passive	NaN	48	2	NaN
Displacement active	< 0.001	48	2	0.5
Displacement passive	0.729	48	2	< 0.001
Aggressive behaviour active	< 0.001	48	2	0.5
Aggressive behaviour passive	< 0.001	48	2	0.5

NaN = not a number (behaviour never occurred)

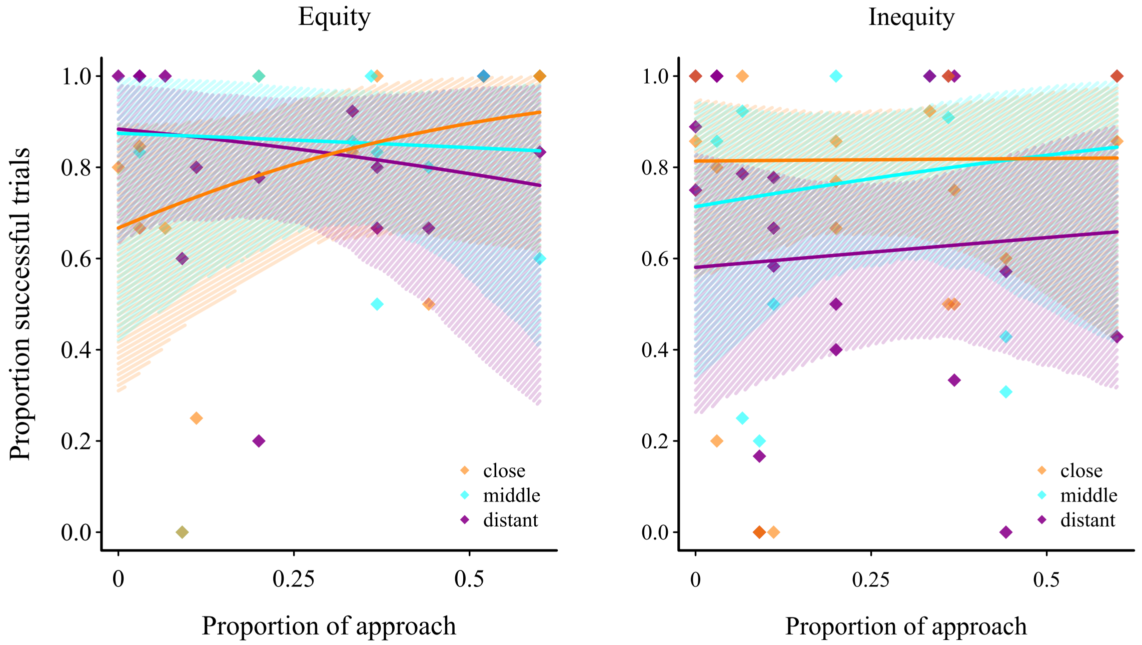

Figure 1: Proportion of successful trials in equity (left) and inequity (right) condition with close (orange), middle (blue), or distant (purple) conditions depending on proportion of approach. Points represent the individual data point, lines the model lines and ribbons the CIs.

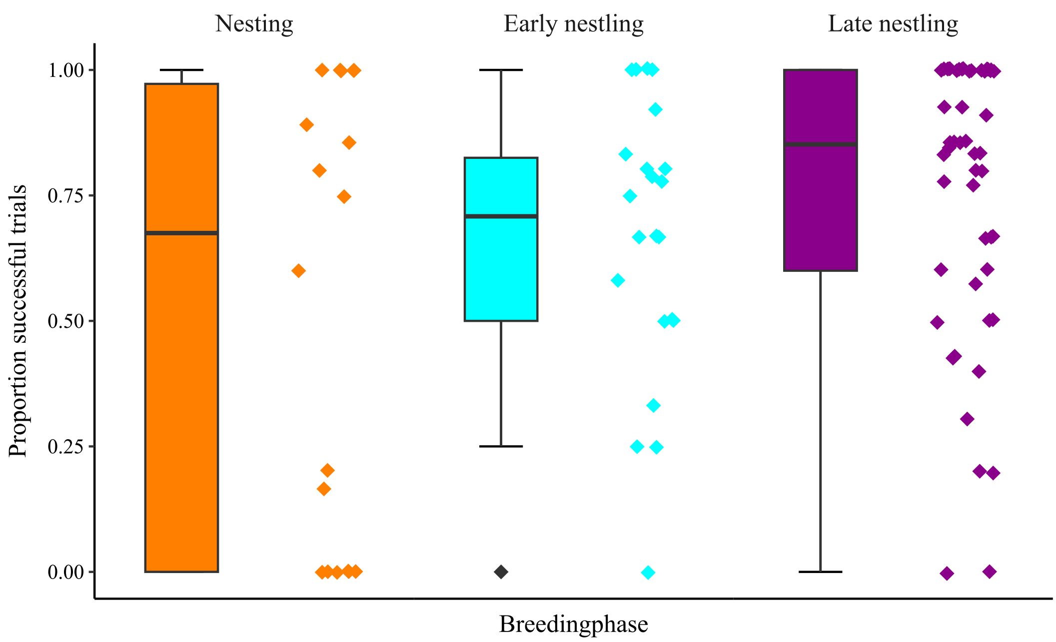

Figure 2: Proportion of successful trials in the breeding phases nesting (orange), early nestling (blue) and late nestling (purple) in trials when both partners were present. Boxes represent the interquartile range, thick black horizontal bars the median, whiskers the range of data points within 1.5 times the interquartile range from the upper and lower hinge, and black points the outliers. Coloured points represent the individual data points in the nesting (orange), early nestling (blue) and late nestling (purple) phase.