Received: 19 April 2019 | Revised: 2 August 2019 | Accepted: 6 August 2019

DOI: 10.1111/eth.12947

RESEARCH PAPER

ethology | WILEY

Tentative evidence for inequity aversion to unequal work-effort but not to unequal reward distribution in Goffin's cockatoos

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Funding information
This work was funded by FWF projects P29084 and P 29075 to Alice Auersperg. During the writing of this manuscript Jorg Massen was funded by a Templeton Grant (# TWCF0267) to M.E. Kret.

Editor: Walter Koenig

Abstract

One hallmark in the evolution of cooperation is the ability to evaluate one's own payoff for a task against that of another person. To trace its evolutionary history, there has recently been a surge in comparative studies across different species. In non-human animals, evidence of inequity aversion has so far been identified in several primate species, dogs, and rats. Research in birds revealed mixed findings so far: among corvids, crows and ravens did react sensitively to unequal payoffs and work-effort, while New Caledonian crows did not. Among psittacids, kea were studied so far: Yet, despite the fact that they live in large, hierarchically organized social groups that show complex interactions, they did not show a significant reaction to inequitable payoffs. Here we tested for the first time a Cacatua, the Goffin's cockatoo, using a standardized token exchange paradigm in which first the partner and then the subject could exchange a token for a food reward. Our results show that subjects did not react to unequal reward distributions. However, in comparison to the Equity Condition, the likelihood to exchange was lower in the condition in which the partner received the same reward as a gift (without having to work for it) whereas the subject had to perform a task involving substantial work-effort, suggesting that the Goffin's cockatoos do react aversively to work-effort inequity. In a follow-up experiment, subjects never received a reward but observed a conspecific receive a high-quality reward depending on condition. We found again no evidence for an aversion for the unequal reward distribution, but only that, independent of condition, subjects quickly lost their motivation to participate due to not receiving a reward. In summary, Goffins showed some sensitivity to increased unequal work-effort, but did not react to unequal reward distribution.

KEYWORDS

avian cognition, decision-making, inequity aversion, inequity response, problem solving, social cognition

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1 | INTRODUCTION

Inequity aversion, defined as the ability to detect and react negatively to unequal payoffs (Adams, 1963; Fehr & Schmidt, 1999), is an important component for cooperative interactions in humans. Children respond negatively to inequitable outcomes already at the age of three to four years (Lobue, Nishida, Chiong, Deloache, & Haidt, 2011).

From an evolutionary perspective, cooperation, especially between unrelated individuals, and inequity aversion seem to be closely linked (Fehr & Rockenbach, 2003) and are believed to have co-evolved alongside one another (Brosnan, 2011; Price & Brosnan, 2012). Having a sense of equitable payoff is beneficial in cooperative interactions, as cheating is easily detected, can be punished, and avoided in future interactions, while stable cooperative partnerships can be formed (Bräuer, Call, & Tomasello, 2006; Fehr & Schmidt, 1999; Price & Brosnan, 2012).

To trace the evolutionary history of inequity aversion, as well as the socio-ecological selection pressures that may have promoted its evolution, recently there has been considerable effort to compare reactions to inequity across species. In non-human animals, inequity aversion can be assessed using a standardized token exchange paradigm, in which two subjects are placed next to each other in adjacent compartments. Subjects are asked to exchange the same token while one individual receives a more preferred reward than the other for the same action (Brosnan & Waal, 2003). Using such a task, comparative evidence across non-human primates suggests that species that habitually cooperate in the wild are more likely to show inequity aversion (Massen, van den Berg, Spruijt, & Sterck, 2012; Price & Brosnan, 2012), in comparison to those that do not (Brosnan, 2011), and that the reaction to unequitable payoffs varies between contexts and individuals (Price & Brosnan, 2012). Within apes, chimpanzees (*Pan troglodytes*) show sensitivity toward unequal reward distribution (Brosnan, Schiff, & De Waal, 2005; Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010; Kim, Choe, Jeong, Kim, & Tomonaga, 2018), but see (Bräuer, Call, & Tomasello, 2009)), while semi-solitary orangutans (*Pongo sp.*), that, in contrast to chimpanzees, do not show cooperation in the wild (Muller & Mitani, 2005; van Schaik, 2004) and did not react to inequity (Bräuer et al., 2009; Kim et al., 2018). Additionally, inequity aversion is found in some Old World monkeys (rhesus & long-tailed macaques (*Macaca mulatta & M. fascicularis*): (Hopper, Lambeth, Schapiro, Bernacky, & Brosnan, 2013; Massen et al., 2012)) and in some New World monkeys (brown capuchins (*Cebus apella*): (Brosnan & De Waal, 2003; Brosnan & De Waal, 2004; Fletcher, 2008; van Wolkenten, Brosnan, & de Waal, 2007) but see (Silberberg, Crescimbene, Addessi, Anderson, & Visalberghi, 2009), cotton-top tamarins (*Saguinus Oedipus*) (Neiworth, Johnson, Whillock, Greenberg, & Brown, 2009), but, for example, not in squirrel monkeys (*Saimiri sciureus*) (Talbot, Freeman, Williams, & Brosnan, 2011) that also do not cooperate habitually. For a review on all primate species tested so far see Brosnan (2011).

An inequity response can be provoked by different triggers, such as an unequal reward distribution, by the presence of an unreachable preferred reward or by unequal work-effort. Aside from primates, inequity aversion is well studied in dogs (*Canis familiaris*; reviewed in (McGetrick & Range, 2018)). Interestingly, pet dogs react negatively to inequality when being unrewarded in the presence of a rewarded partner, but not when they receive a lesser reward nor when their work-effort is unequal (Range, Horn, Viranyi, & Huber, 2009). However, pack living dogs, as well as wolves (*Canis lupus*), do react negatively to both reward inequity (receiving a reward or not) and inequity in reward quality (Essler, Marshall-Pescini, & Range, 2017).

Research in birds started in the corvid line and has produced mixed results so far. Carrion crows (*Corvus corone corone*) and ravens (*Corvus corax*), tested in a token exchange paradigm, exchanged the token less when the partner received a better reward or received the food reward as a gift in comparison to baseline, and refused to eat the reward more often when the partner received a better reward (Wascher & Bugnyar, 2013). However, they also refused the reward when tested in a non-social control where the high-quality food rewards were still present, which may indicate that they might have reacted merely to the quality difference (frustration effect (Bräuer et al., 2006; Dubreuil, Gentile, & Visalberghi, 2006)). When tested in a cooperative string-pulling task, ravens did seem to pay attention to the reward distribution and refused to continue cooperating with partners that cheated and took both available rewards (Massen, Ritter, & Bugnyar, 2015). New Caledonian crows (*Corvus moneduloides*) were also tested in a cooperative setup, in which the amount and the quality of the rewards for the subject and its partner did differ depending on the condition. Nevertheless, the crows did not alter their behavior compared to a non-social control condition, suggesting that they did not pay attention to the reward distribution or were not aversive to inequity (Jelbert, Singh, Gray, & Taylor, 2015).

Within parrots, the sensitivity to inequitable outcomes has been studied only recently. In a cooperation study similar to that with ravens (Massen et al., 2015), kea (*Nestor notabilis*) also showed to pay attention to the reward distribution after cooperation and were less likely to cooperate with a partner that took more than its share (Schwing, Jocteur, Wein, Noe, & Massen, 2016). However, when kea were tested in a classic token exchange paradigm, subjects did not react sensitively toward unequal payoffs nor increased work-effort (Heaney, Gray, & Taylor, 2017). Note, however, that the kea did not have to perform substantial work-effort, which has been shown to enhance inequity aversion (Massen et al., 2012; van Wolkenten et al., 2007). In sum, to truly understand the socio-ecological selection pressures that have promoted the evolution of inequity aversion and to test the generalizability of the results found in primates so far, the mixed results among birds call for further investigation.

Goffin's cockatoos (*Cacatua goffiniana*) are endemic to the Tanimbar islands in Indonesia. They can be observed in nomadic fission–fusion groups of up to one hundred individuals on the cultivated parts of the coastline of the islands. Mated pairs can be observed in the rainforest areas, with median group sizes of four individuals (O'Hara et al., 2018). They are cavity breeders and both parents feed their offspring. Goffin's cockatoos compete with Eclectus parrots (*Eclectus roratus*) over these cavities. Notably, they

have been observed mobbing and chasing away the Eclectus as well as predatory birds in small groups in a seemingly cooperative effort (Mioduszewska et al., 2019).

Although Goffin's cockatoos do not use tools in the wild, they can use, manufacture, and innovate tools in captivity (Auersperg, Köck, O'Hara, & Huber, 2018; Auersperg, Szabo, von Bayern, & Kacelnik, 2012; Laumer, Bugnyar, & Auersperg, 2016; Laumer, Bugnyar, Reber, & Auersperg, 2017). They have high social tolerance, show tolerated theft and active food sharing in the wild (Mioduszewska B., personal communication) and even between unrelated conspecifics of the same sex in captivity (IBL, AA, personal observation). Finally, they show high levels of impulse control (Auersperg, Laumer, & Bugnyar, 2013), which is known to be a prerequisite for being able to respond to inequity as to, for example, refuse a food reward (Price & Brosnan, 2012). Taken together, these features make them interesting psittacid test subjects to test inequity aversion.

By using a standardized token exchange paradigm (Brucks, Essler, Marshall-Pescini, & Range, 2016; Heaney et al., 2017; Range et al., 2009), we presented Goffin's cockatoos with a series of conditions (Equity, Inequity, Non-social and Free-gift Condition) designed to investigate sensitivity toward an unequal qualitative reward distribution. Furthermore, we added additional work-effort to the token exchange paradigm by having the Goffin's cockatoos using a tool to retrieve the token from a tube apparatus, as to address the additional effects of work-effort to reward inequity aversion as well as to investigate the effect of unequal work-effort. In order to investigate the cockatoos' reaction to a more extreme qualitative unequal reward distribution, we conducted a second experiment in which subjects received no reward at all while their partner received a high-quality reward depending on the condition (Range et al., 2009). Since inequity aversion is typically found in species which live in complex social groups and engage in cooperative behaviors (Brosnan, 2011; Price & Brosnan, 2012), we predicted that Goffin's cockatoos should show signs of inequity aversion toward unequal treatment. Additionally, we assumed that by adding additional work-effort to the token exchange procedure, the degree of inequality might be substantially increased to provoke an even stronger aversive reaction (note that Goffin's cockatoos, when given the choice between an immediate food reward or using a tool to obtain a food reward of the same quality, avoid additional work-effort (Laumer et al., 2016)).

2 | METHODS

2.1 | Subjects, housing, and experimental histories

Eleven Goffin's cockatoos participated in this study (Table 1). They were housed at the Goffin's Lab, Lower Austria, associated with the Messerli Research Institute, Austria. All birds were hand-raised and were individually marked with colored leg bands. Subjects were housed together in indoor and outdoor area (indoor: 45 m^2, 3–6 m height; outdoor: 150 m^2, 3–6 m height). The birds had ad libitum access to fresh water and food (variety of seeds, fruits, vegetables, and mineral supplements). Nuts were only available as rewards during test sessions, in which the cockatoos participated on a voluntary basis. All subjects had CITES certificates and were registered at the district's administrative animal welfare bureau (Bezirkshauptmannschaft St. Pölten Schmiedgasse 4–6, A-3100, St. Pölten, Austria). These housing conditions were in accordance with the Austrian Federal Act on the Protection of Animals (Animal Protection Act—§24 Abs. 1 Z 1 and 2; §25 Abs. 3—TSchG, BGBl. I Nr. 118/2004 Art. 2). As our experiments were appetitive, non-invasive, and based exclusively on behavioral tests, they were not classified as animal experiments under the Austrian Animal Experiments Act (§2. Federal Law Gazette No. 501/1989). Research at the Goffin's Lab so far has mainly been focused on physical cognition, and all of the animals had experience with using stick tools (Laumer et al., 2016). Subjects, however, had no experience with being tested in dyads.

TABLE 1 Detailed subject information: division into two testing groups (A&B; Group A started with treatment 1 and group B with treatment 2, see ii) below), names, roles in the test, sex, and age of the eleven cockatoos

Group	Name	Role	Sex	Hatch date
A	Muppet	Partner	Male	2010
	Figaro	Subject	Male	2007
	Pipin	Subject	Male	2008
	Heidi	Subject	Female	2010
	Muki	Subject	Male	2011
	Olympia	Subject	Female	2010
B	Zozo	Partner	Male	2010
	Fini	Subject	Female	2007
	Dolittle	Subject	Male	2011
	Mayday	Subject	Female	2011
	Kiwi	Subject	Male	2010

2.2 | Apparatus

Subjects were sitting in two adjacent test compartments, separated by a wire mesh (see Figure 1). The cockatoos could exchange a token for food with the experimenter through a transfer slit at the front. At the beginning of each trial, subjects were separated to the front part of their compartment close to the transfer slit by a removable transparent plexiglass divider (see Figures 1 and 2.). Depending on the condition, either a token or a token inside a transparent tube apparatus and a stick (see Figure 2) were placed in the back part of each compartment, which were separated from the subject and its partner by transparent dividers. At the start of the trial, these dividers were removed.

In Experiment 1 whole pieces of sunflower (less preferred) and same sized pieces of cashew (more preferred) and in Experiment 2 only pieces of cashew were placed on plates in front of the test apparatus such that the food rewards were visible to both birds the entire testing time, as to control for frustration effects solely due to

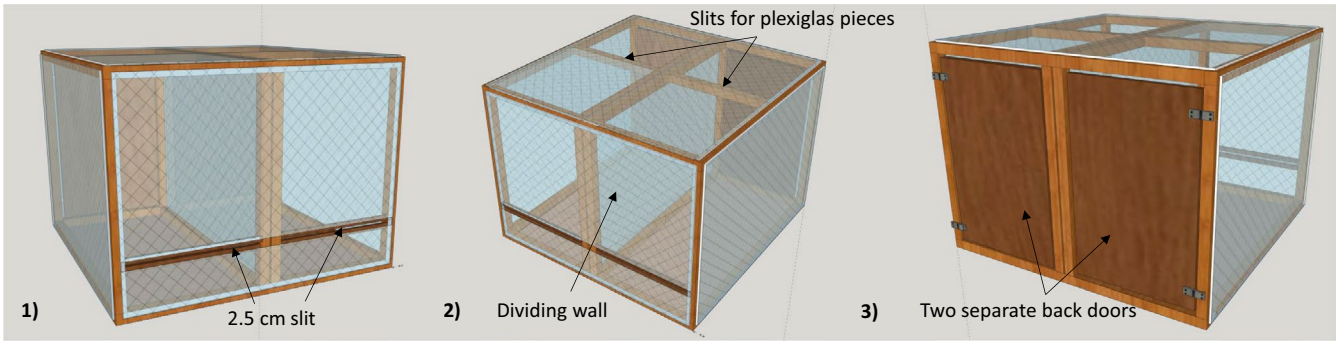

FIGURE 1 Illustration of the testing apparatus, shown from 1) front: transfer slit at head level. 2) View from above: The two compartments were divided by a wire mesh. Two plexiglas dividers could be inserted from above to separate subjects to the front part of their compartment close to the transfer slit. Depending on the treatment a token or a token in a tube apparatus was placed in the back part of each compartment. 3) Back view: ubjects could be placed into their compartment by opening the back doors

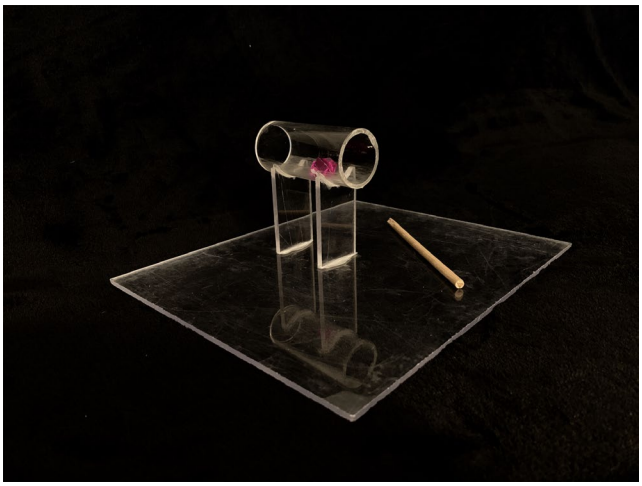

FIGURE 2 Tube apparatus used in the work-effort conditions. Pink plastic stones (2cm in diameter) were used as tokens. The token could be retrieved by the use of a stick tool (length 12 cm)

the expectation of a visible high-quality food reward in both Equity and Inequity Conditions (Silberberg et al., 2009).

2.3 | Experimental procedure

Prior to testing, the birds were first trained to exchange a pink colored plastic token for a food reward. The cockatoos were already trained in the token exchange procedure in a previous study (Auersperg et al., 2013). Therefore, the training with the unknown token served as reminder.

Before the trial started, the partner bird was always placed in the right and the subject in the left compartment (viewed from the front). Upon encouraging the cockatoos to move to the front part of their compartment, the plexiglass dividers were carefully inserted. Depending on the treatment, either the tokens were placed on the floor of each compartment (treatment 1) or the tube apparatuses were placed baited with a token and a stick tool next to it (treatment 2). Then, the doors were closed. During testing, the experimenters (either MLT or BW in Experiment 1, CC in Experiment 2) wore mirrored sunglasses and did not speak nor move. In order to ensure that birds were motivated to participate, each cockatoo received at the beginning of the session three "warm-up" baseline trials, in which both birds received a low-value food reward in exchange for the token.

First the partner's divider was lifted in order to give the partner bird access to the token. The experimenter immediately sat down on a chair in front of the test apparatus and held out her open right hand with the palm facing upward about 2 cm close to the slit in order to invite the bird to exchange the token. The open hand was held steady at the slit. As soon as the cockatoo arrived with the token in its beak within a 10 cm radius close to the slit, the experimenter changed her hand position. The index finger and thumb were extended, while the hand still remained steady at the same position, so that the cockatoo could place the token between her fingers. If the bird refused to exchange the token and moved out of the 10 cm radius, the experimenter still kept the finger in the same position. If the bird put the token between her fingers, the experimenter took and removed the token and placed a food reward into her open palm visible to both birds for a duration of three seconds. Then, she gave the reward to the partner.

The subject received the same procedure and was always tested after the partner bird received its reward. A trial was ended when the subject exchanged the token, after 90 s from lifting of the divider, if the cockatoo threw the token through the side, the backside of the compartment or dropped the token into the partner's compartment. In treatment 2, a trial was also terminated when the stick was thrown out of the compartment before the token was retrieved from the tube apparatus.

2.4 | Experiment 1

Eleven adult Goffin's cockatoos were tested. Prior to testing, the birds were randomly divided in two testing groups (see Table 1). Although it was originally planned to test half of the subjects with partner Zozo (high-ranking) and the other half with Muppet (low-ranking), due to a motivation loss of Zozo to exchange the token and interindividual aggression, subjects that were initially partnered up

TABLE 2 Detailed information on each testing condition: rewards for partner and subject, descriptions and purpose of each condition

Condition	Partner reward	Subject reward	Description	Purpose of condition
Equity	Sunflower	Sunflower	Both partner and subject receive the same reward.	Baseline condition
Inequity	Cashew	Sunflower	Partner receives high-quality reward, subject receives low-quality reward.	Control for sensitivity to unequal reward distribution
Non-social	Partner not present	Sunflower	A high-quality reward is moved toward the empty partner's compartment, subject receives a low-quality reward.	Control for reward movement in the Inequity Condition
Free-gift	Sunflower	Sunflower	Partner receives a low-quality reward as a gift, subject has to exchange the token to receive a low-quality reward.	Control for sensitivity to work-effort

Note: The quality of the rewards differed between Experiments 1 & 2 and are numbered accordingly.

with Zozo had to be tested with Muppet from the second block of treatment 1 onwards (in the 4th testing block, see below).

2.4.1 | The four test conditions

Subjects received four test conditions: Equity, Inequity, Non-social, and Free-gift Condition (see Table 2 for an overview). In the Equity Condition (baseline condition), both subject and partner received the same reward (low quality, sunflower seed). In the Inequity Condition, the partner received a high-quality reward (cashew) while the subject received a low-quality reward (sunflower seed). In the Non-social Condition, the partner was not present. The partner's reward (high quality, cashew) was displayed for three seconds in the open palm and moved toward the slit of the empty compartment, imitating the same hand movements and procedure as in the social conditions. Subsequently, the subject had to exchange its token to receive a low-quality reward. In the Free-gift Condition, the partner bird did not have to retrieve a token but was offered a low-quality reward as a gift. The subject had to retrieve and exchange the token to receive the same quality reward. Note that irrespective of the condition the subject always got the same, low-quality reward (Table 2).

2.4.2 | Treatment 1 & 2

Experiment 1 consisted of two treatments. In treatment 1 ("without work-effort"), the token had to be retrieved from the bottom of the back compartment. In treatment 2 ("with work-effort"), the token rested in a tube apparatus and had to be retrieved by the means of a stick tool (see Figure 2). Each treatment was tested in two testing blocks. The order of the four test conditions within one block was randomized for each bird and stayed the same for both blocks within one treatment. Group A started with two blocks of treatment 1 and group B with two blocks of treatment 2, and this was subsequently reversed. Subjects received one session of 12 trials of each condition within each block, so that they received a total of 24 trials of each condition per treatment.

2.5 | Experiment 2

Nine birds participated in Experiment 2 (note that two birds from Experiment 1 could not be tested due to motivation loss). Muppet and Zozo stayed in the partner role as in Experiment 1. Although it was originally planned to test half of the subjects (Heidi, Figaro, Pipin) with partner Zozo (high-ranking) and the other half (Fini, Dolittle, Mayday, Kiwi) with Muppet (low-ranking), due to interindividual aggression, Figaro and Pipin had to be tested with Muppet from session 1 and 5 out of a total of six sessions on, respectively.

2.5.1 | Experimental procedure and test conditions in Experiment 2

The experimental procedure stayed the same as in Experiment 1 with work-effort. Depending on the test condition, the partner received either a high-quality reward or no reward, while the subject never received a reward (see Table 3). Subjects were tested in the Equity, Inequity, and Non-social Conditions. The order of the three conditions within one block was randomized for each subject and stayed the same for the second block.

Birds were tested in the Equity, Inequity, and Non-social Conditions for two sessions of 12 trials each. Therefore, similar to Experiment 1, each condition in Experiment 2 consisted of a total of 24 trials. In the Equity Condition, both the partner and the subject received no reward in exchange for the token. In the Inequity Condition, the partner received a high-quality reward (cashew), while the subject did not receive a reward for exchanging the token. In the Non-social Condition, the partner was not present. The partner's reward (high quality, cashew) was displayed for three seconds in the open palm and moved toward the slit of the empty compartment, imitating the same hand movements and procedure as in the social conditions. Afterward, the subject received no reward in exchange for the token.

Note that, as in Experiment 1, the high-quality rewards were always visibly present during the whole experiment.

2.6 | Analysis

Trials were recorded using two HD video cameras filming from different angles (JVC HD Everio Camcorder GZ-HM30 and Samsung Galaxy 4S mini). The videos were coded afterward using the video coding software BORIS (Friard & Gamba, 2016). We checked interobserver reliability (5% of the videos were double coded) and found excellent agreement (ICC ≥ 0.908; $p < .001$). Per trial, we measured whether the

TABLE 3 Overview of the testing blocks and partner & subject rewards in Experiment 2

Experiment 2 (with work-effort)		Partner reward	Subject reward
Block 1	Equity	None	None
	Inequity	Cashew	None
	Non-Social	Cashew	None
Block 2	Equity	None	None
	Inequity	Cashew	None
	Non-Social	Cashew	None

focal bird exchanged the token for the reward (y/n), and how long it took the birds to do so (in seconds). Since in the conditions with work-effort, the birds first needed to retrieve a token from a puzzle box, which may pose difficulties for the birds independent of the condition they were in, we also calculated how long it took the birds from the point that they picked up the token they retrieved until the point at which the exchange took place. We analyzed what influenced the likelihood of an animal refusing to participate using a binomial generalized linear mixed model with a logit link function with whether the birds exchanged (y/n) per trial as target variable in IBM SPSS v23. We entered condition and treatment as well as the interaction between condition and treatment as fixed factors. Since we had repeated measures per individual, we structured our data nested within individual. Moreover, we entered individual ID, partner ID, and trial number as random effects into our model. We ran the full model and reduced models and chose the best fitting model based on comparisons of the corrected Akaike Information Criteria of those models.

We log-transformed the recorded latencies as to enhance normality of these data. Since the latencies we used were very much dependent on the treatment, we analyzed them separately per treatment, again using GLMM's with the data nested within individual. Here, we entered condition as fixed factor and trial number as covariate, and individual ID, partner ID, and testing block as random effects into our models. α was set at .05, and we used a Holm–Bonferroni correction (Holm, 1979) when multiple post hoc comparisons were conducted.

3 | RESULTS

3.1 | Experiment 1

On average, the birds were very willing to participate and successfully exchanged a token in 95.7% ±*SEM* 1.2% of all cases (see Movie S1). The best fitting model on the likelihood of a bird to exchange/ refuse to exchange only contained the two main effects of treatment and condition (cAIC = 12.39, in comparison to the full model that also included the interaction between these two conditions: cAIC = 18.75); we a) found a significant effect of both treatment ($F_{1,1717}$ = 20.45, p < .001; Figure 3), with the likelihood of exchanging being significantly higher in the treatment without work-effort (β = 1.61; Figure 3) and b) a significant effect of condition ($F_{3,1717}$ = 3.55, p = .014). Between condition, comparisons revealed that specifically the Free-gift condition resulted

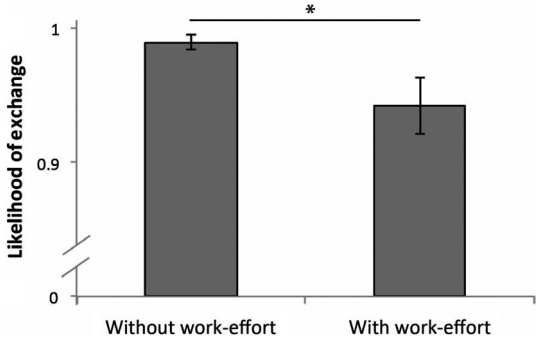

FIGURE 3 Mean ± *SEM* likelihood of an exchange in the treatment with and without work-effort. *indicates a p-value below .05

in lower likelihoods of exchange, and significantly so when compared with the Equity Condition (β = −1.06, t = 2.51, p = .012) and with the Inequity Condition (β = −1.06, t = 2.52, p = .012) (Figure 4). Even though the interaction between treatment and condition was not maintained in the best fitting model, visual inspection of the data (see Figure 5) suggests that this effect is mainly driven by the data from the treatment with additional work-effort; namely when in the Free-gift Condition the inequity in work-effort between the partner (who received the reward without any effort) and the subject (who had to perform a tool-use task to retrieve the token) was at its peak. Furthermore, we found a difference between the Non-social control and the Inequity Condition, albeit only marginally significant (β = −0.86, t = 1.97, p = .05; Figure 3).

With regard to the latencies of those exchanges that took place, in the no work-effort treatment we found no effect of condition on either the full duration before exchange or the duration between picking up the token and exchanging it, though did find that both variables could be predicted by trial number, with durations increasing over trials (total duration: $F_{1,839}$ = 7.33, β = 0.011, p = .007; picking up token exchange: $F_{1,839}$ = 8.24, β = 0.011, p = .004). Within the work-effort treatment, we found similar results: no effect of condition and an increase of both latencies over trials, albeit as non-significant trends only (p = .08, and p = .09 respectively).

3.2 | Experiment 2

The results of a GLMM revealed no significant effect for condition on the number of trials, in which subjects refused to exchange the token ($F_{2,34}$ = 1.59, p = .22). From session 2 on six out of the seven subjects refused at high rates in all test conditions. Overall, we found a significant effect of session on the number of refused trials ($F_{5,34}$ = 13.66, p < .001). The mean number of refused trials per session increased by the number of sessions (Figure 6; see Movie S3).

4 | DISCUSSION

Here we tested Goffin's cockatoos reactions to both, inequity in reward quality and inequity in the work-effort required between themselves and a partner. We found no evidence for any aversion

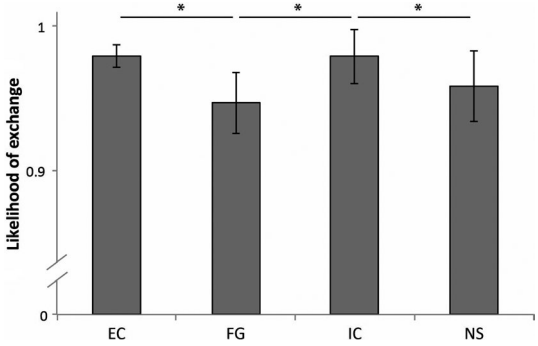

FIGURE 4 Mean ± *SEM* likelihood of an exchange in the Equity Condition (EC), the Free-gift Condition (FG), the Inequity Condition (IC) and the Non-social Control Condition (NS)

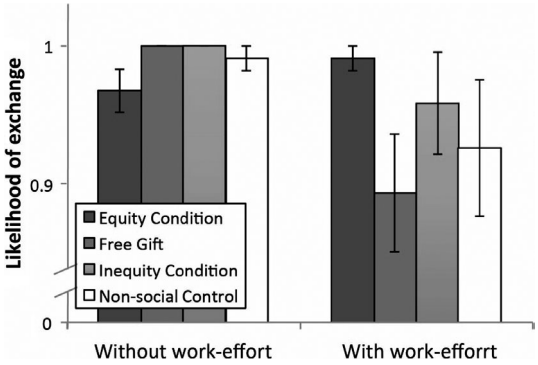

FIGURE 5 Mean ± *SEM* likelihood of an exchange in the Equity Condition, the Free-gift Condition, the Inequity Condition and the Non-social Control Condition, for the treatments with and without additional work-effort separately

with regard to inequity in reward quality. However, we did find some tentative evidence for an averse reaction to inequity in the work-effort required in the Goffin's cockatoos. In particular, when that inequity was increased by adding substantial work-effort for the subjects to first retrieve a token using a tool-use task and then to exchange that token for a reward, whereas the partner was given the reward without any effort whatsoever. Specifically, the likelihood to refuse to participate was higher in the Free-gift Condition, in which the partner received the same reward as a gift, than in the Equity Condition, indicating a responsiveness toward unequal work-effort. A follow-up experiment, that was conducted in order to investigate the cockatoos' reaction to a more extreme qualitative unequal reward distribution, revealed no further insights, since the majority of birds refused at high rates from session 2 onwards. The cockatoos' refusals to exchange in the follow-up experiment were not influenced by the test conditions but by the number of sessions conducted, indicating that subjects continuously lost their motivation to participate early on in the experiment due to not receiving a reward irrespective of whether the partner received a high-quality reward or not, or was present at all. Unfortunately, thus, this ceiling effect may have obscured any other indications for inequity aversion in the Goffin's cockatoos.

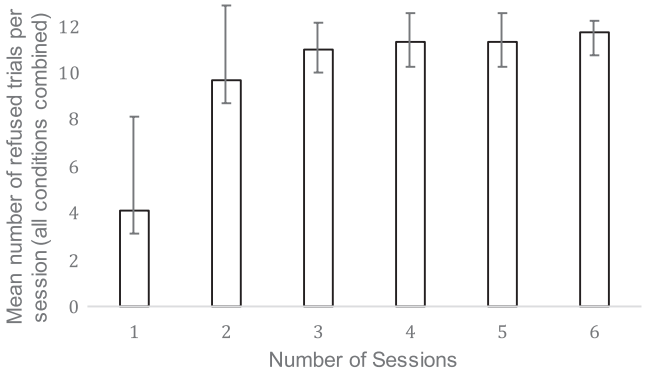

FIGURE 6 Mean number of refused trials per session (all three conditions combined; $n_{trials\ per\ session} = 12$; $n = 7$). Error bars indicate standard deviation

In line with the hypothesis that inequity aversion and cooperation among unrelated individuals co-evolved in primates (Brosnan, 2011), highly social Goffin's cockatoos that, according to anecdotal evidence seem to show cooperation when it comes to nest and predator defense in the wild (Mioduszewska et al., 2019), showed a negative reaction to unequal work-effort, particularly so when the work-effort to obtain the token was substantially increased. This is the first suggestive evidence for any responsiveness to inequity in a parrot so far, since kea did not show any sign of an aversion toward inequity in food value nor work-effort (Heaney et al., 2017). While kea are highly social, this parrot is considered to not engage in cooperative behavior in the wild, although there exist anecdotal reports of kea hunting shearwater chicks (Heaney et al., 2017). Nevertheless, the lack of inequity aversion in kea is surprising as they at least seem to be similarly equipped with the predispositions required for inequity aversion as described by Brosnan, 2011: They are highly social and at least show the capacity for cooperation in various captive settings (Heaney et al., 2017; Schwing et al., 2016), Schwing et al., this issue), and discontinue cooperation with a given partner when the reward distribution with that partner was unequal in the previous trial (Schwing et al., 2016).

Similar to the Goffin's cockatoos, ravens and crows decreased their exchange performance, when the partner received the same reward as a gift (note, however, that for the ravens and crows obtaining the token did not involve additional work-effort (Wascher & Bugnyar, 2013)). In line with the hypothesis (Brosnan, 2011; Price & Brosnan, 2012), carrion crows and ravens are also living in complex social groups and they regularly show cooperative behavior, such as cooperation to rear the offspring and alliance formation in the wild (Baglione, Canestrari, Marcos, & Ekman, 2003; Heinrich & Bugnyar, 2007). In contrast to the Goffin's cockatoos, yet similar to some primates (capuchins: (Brosnan & Waal, 2003); chimpanzees: (Brosnan et al., 2005, 2010); rhesus macaques: (Hopper et al., 2013); long-tailed macaques: (Massen et al., 2012)), the crows and ravens also reacted averse when the partner received a qualitative better food reward for the same work. However, these corvids' reaction to reward quality has to be interpreted with caution, since the corvids also reacted to the reward quality in the *Non-social Control*, which

could be explained by food expectancy effects (the mere presence of a high-quality reward and having received a high-quality food in the immediate past might elicit food expectancy; note that we controlled for this effect by testing subjects only with low-quality rewards in Experiment 1, and with no rewards in Experiment 2. Note also that Experiment 2 was conducted one year later to eliminate a possible food expectation).

We can only speculate why the Goffin's cockatoos did not react to inequity with regard to the reward quality, whereas they did with regard to effort inequity. A similar pattern has been observed in dogs (Range et al., 2009), that also did not react when their partner received a better reward than they did. The dogs did, however, react when they received nothing while their partners did receive a reward, much like in our Experiment 2. The Goffin's cockatoos refused to exchange when they did not receive a reward at all, but independently of condition, suggesting that they merely lost the motivation to participate when receiving no reward at all. This ceiling effect may have obscured any indication of inequity aversion with regard to a more extreme reward distribution. This finding also suggests that it is not a lack of impulse control to inhibit exchanging the token (Goffin's cockatoos can wait extended periods of over one minute in order to receive a better reward; Auersperg et al., 2013) that can explain the lack of inequity aversion with regard to reward quality in Experiment 1. Furthermore, in chimpanzees, it has been shown that aversive reactions to inequity are significantly lower among long-term stable relationships (Brosnan et al., 2005). The fact that the Goffin's cockatoos in this experiment have also been living with each other ever since shortly after weaning to solid food and that their relationships and dominance hierarchy are relatively linear and stable (Szabo, Bugnyar, & Auersperg, 2017) may thus explain why they did not react to inequity in reward quality, but that would not explain why they did react to effort inequity. It is further unlikely that the birds are not able to easily distinguish between different food qualities: In a previous study, in which the Goffins had to decide between an immediate food reward and a tool that led to the same reward, the cockatoos avoided the additional work-effort as well and chose the immediately available food, but chose the tool if the food within the apparatus was of higher quality than the immediate food (Laumer et al., 2016). Nevertheless, they may only pay attention to the quality of the food offered to themselves but not to the quality of the food offered to the partner. The fact that they did pay attention to the work-effort of the partner and reacted aversively when there was inequity in the work-effort required may indicate that the aversion for reward quality inequity and aversion for effort inequity are two different mechanisms that can evolve independently.

From a comparative perspective with regard to birds, it is furthermore interesting to see that New Caledonian crows showed no response to inequitable payoffs nor to effort inequity (Jelbert et al., 2015), although it has to be noted that they were tested in a different, possibly more complicated setup. Nevertheless, New Caledonian crows also do not aggregate in large flocks with complex hierarchies (they live in small family groups; (Holzhaider et al., 2011; Rutz et al., 2012)). Although they have been observed to cooperatively mob raptors in the wild (Jelbert et al., 2015). However, anecdotes like this are difficult to interpret as it is hard to differentiate between true cooperation or acting apart together (Noë, 2006). This of course also applies to observations of Goffin's cockatoos mobbing Eclectus parrots seemingly cooperatively at Tanimbar (Mioduszewska et al., 2019). Consequently, as in the primate line (Brosnan, 2011; Price & Brosnan, 2012), the absence of inequity aversion in New Caledonian crows and its presence in other, more cooperative, large-brained birds, suggests that extremely high levels of sociality and cooperation are essential for inequity aversion to evolve.

In summary, similar to ravens, crows and some primates (corvids:(Wascher & Bugnyar, 2013); cotton-top tamarins: (Cronin & Snowdon, 2008; McAuliffe, Shelton, & Stone, 2014)); rhesus macaques: (Hopper et al., 2013); long-tailed macaques: (Massen et al., 2012); chimpanzees: (Brosnan et al., 2010); capuchin monkeys: (van Wolkenten et al., 2007)), Goffin's cockatoos reacted to unequal work-effort, and particularly so when the work-effort was substantially increased. Our results support the notion that inequity aversion toward unequal work-effort may have evolved in large-brained birds in response to living in social groups and engaging in cooperative behaviors with unrelated individuals that require substantial energy. Hence, birds that do not habitually cooperate in the wild or that cooperate but show comparatively rather low levels of social complexity, might therefore not be sensitive to unequal payoffs (Heaney et al., 2017; Jelbert et al., 2015). Our findings indicate that awareness to other individuals' efforts and payoffs may evolve independently of phylogeny, and also independently from each other, in systems with a given degree of social complexity and cooperative behaviors in the wild. So far, the mechanisms underlying cooperation in birds are largely uncharted. Further research in different bird species, that show variations in their socio-ecology and degree of cooperation, might reveal further insights into the evolution of inequity aversion. And finally, further studies are needed to fully understand how effort and reward quality are interrelated in subjects' perception of inequity.

ACKNOWLEDGEMENTS

We thank Thomas Bugnyar for stimulating discussion in the process of designing the experiment and Karsten Kenzel for the construction of the test apparatus.

CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

IBL and JJMM designed the experiment, IBL supervised MLT, BW and CC in conducting the experiments, JJMM analyzed the data. IBL, JJMM and AMIA wrote the paper. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data is available as supplementary material.

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How to cite this article: Laumer IB, Massen JJM, Wakonig B, Lorck-Tympner M, Carminito C, Auersperg AMI. Tentative evidence for inequity aversion to unequal work-effort but not to unequal reward distribution in Goffin's cockatoos. *Ethology*. 2019;00:1–10. https://doi.org/10.1111/eth.12947