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Chimpanzees steal less from their friends and expect them to do the same

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ABSTRACT

Are chimpanzees able to inhibit anti-social behavior towards their friends? And how do they react when a friend acts anti-socially towards them? Past work has demonstrated that chimpanzees are selectively prosocial towards their friends: they groom them more, help them more, and share more food with them. However, the influence of friendship on anti-social behavior remains underexplored. Here, we use food theft as a test case to examine (1) the influence of friendship on anti-social behavior and (2) emotional responses to anti-social behavior. We assigned 26 chimpanzees to pairs of friends (friend condition) and non-friends (non-friend condition) based on 800 h of observations of naturally occurring interactions. The pairs then participated in a stealing task, in which one chimpanzee (the "thief") could pull a tray with pieces of pineapple, on which the other was feeding (the "victim"). Friends and non-friends were matched on sex and dominance rank. We found that chimpanzees stole less from their friends. When theft did occur, chimpanzees tended to initially express more negative emotions in the friend condition than in the non-friend condition, but then attenuated this response with increasing trial number. Thieves, meanwhile, expressed more negative emotions in the non-friend condition, suggesting that they treated interactions with non-friends as more hostile. These results speak to the complex role of friendship in regulating anti-social behavior and emotional responses to it.

Friendship is a close collaborative relationship characterized by a lack of concern with equity or direct reciprocity (Silk, 2003). Unlike purely transactional relationships, friendships involve providing support without an immediate expectation of return. This property helps solve a limitation inherent to tit-for-tat relationships: in a free market of partner choice, individuals become poor investment prospects precisely when they need help most—during times of illness, resource scarcity, or other hardships that limit their ability to reciprocate (Tooby & Cosmides, 1996). However, in the complete absence of any form of long-term tracking or monitoring, relationships among nonkin are susceptible to freeriding and eventual collapse (McElreath et al., 2003). For friendships to work, individuals therefore need to limit the costs they inflict—and those that their would-be friends inflict on them.

The need to balance costs and rewards in the absence of short-term accounting makes friendship something of an evolutionary puzzle (Tooby & Cosmides, 1996). Studying friendship in other species can therefore deliver insights into the natural history of friendship in humans. Chimpanzees are particularly informative in this regard as they are known to form strong and long-lasting relationships, which are associated with improved cooperative exchange and fitness benefits (Feldblum et al., 2021; Samuni et al., 2018, 2021). These relationships tend to be stable and endure over the years (Mitani, 2009). Experimental work has demonstrated that chimpanzees trust their friends significantly more than non-friends (Engelmann & Herrmann, 2016), and are more

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likely to help them than a neutral peer (Engelmann et al., 2019). Observational work has shown that they selectively console their friends after conflict with a third party (Fraser et al., 2008), and that friendship is the strongest predictor of food sharing in this species – over and above harassment, direct signaling, and trade (Samuni et al., 2018). Taken together, the empirical findings paint a picture of a relationship characterized by a prosocial attitude manifesting across domains.

Like human friendships, close social bonds in nonhuman primates have important fitness consequences (De Moor & Brent, 2025; Seyfarth & Cheney, 2012; Silk, 2007). Beyond grooming and food-sharing, chimpanzees cooperate with their friends to climb the status hierarchy (Feldblum et al., 2021), defend their territory (Samuni et al., 2021), and even guard mates (Watts, 1998) – behaviors directly related to survival and reproduction. The challenges of choosing the right friends and keeping them therefore warrant the emergence of adaptations designed to solve them. What might these adaptations look like?

Affective processes play a crucial role in the formation and maintenance of cooperative relationships (Fessler & Haley, 2003). Affective processes are uniquely suited to implement the two defining features of friendship – (i) loyalty in the face of difficulty; and (ii) long-term tracking of costs and benefits, rather than short-term tit-for-tat (Hruschka, 2010; Tooby & Cosmides, 1996; see Silk, 2003 for a related discussion of reciprocity without explicit accounting in friendship). Narrow cost-benefit calculations would lead individuals to defect from friendships as soon as they are more trouble than they are worth; the basic architecture of our motivational systems, which tends to place a premium on short-term rewards, would likewise encourage defection. Affective bonds overcome these barriers by changing the perceived reward structure of such decisions, making the prosocial choice – to stick by one's friend – rewarding in its own right, and defection aversive (Frank, 2011; Gervais & Fessler, 2017). In chimpanzees, grooming with bonded partners is associated with increased urinary oxytocin compared with grooming with non-bond partners (Crockford et al., 2013). The neuroendocrinological oxytocinergic system is thought to link cooperative acts with the dopaminergic reward system, reinforcing prosocial choices as well as partner preferences (Wittig et al., 2014).

Emotional responses to social interactions not only help form and dissolve social relationships, but are also shaped by them in complex ways. This includes anger, an emotion that – perhaps counterintuitively – plays an important role in regulating our close relationships (Sell et al., 2017). Among the negative emotions, anger is particularly relevant to social cooperation because it signals violations of expectations between partners. Theorizing on anger suggests two opposing manners in which friendship might affect the victim's emotional response to the infliction of undue costs. Emotional expressions serve communicative functions in the context of close relationships (Keltner & Haidt, 1999). In particular, anger is a response to a violation of social expectations, grounded in the appraisal that the target should have treated us better (Engelmann & Tomasello, 2017; Sell et al., 2009; Wallace, 1994). How much weight we expect others to place on our welfare depends on the nature of the relationship we share with them. Since we expect more of our friends (Delton & Robertson, 2016; Krems et al., 2023), we might react with more anger when they violate these expectations – compared to more distant others, of whom we expect less. However, affective bonds such as friendship also act on our emotions in ways that may lessen our anger. The attitudinal representations we hold towards others change how we appraise situations involving them (Gervais & Fessler, 2017). For example, when a friend steals food from us, we may focus less on our loss, and more on the fact that our valued cooperative partner gets to enjoy the sweet taste of pineapple. Furthermore, our attitudinal representations of the fitness value afforded by specific relationships are thought to act on our emotions more directly, dampening and potentiating specific emotional reactions based on features of the relationship (Gervais & Fessler, 2017). Thus, the *liking* we feel towards a friend – grounded in our implicit representation that they are beneficial to our fitness – may weaken our tendency to feel anger at them, an emotion which risks damaging the relationship.

In a species capable of the long-term tracking of costs and benefits, an individual motivated to maintain their friendships must seek to provide their friends with more benefits, and inflict fewer costs, than potential competitors. The research on grooming, food sharing, consolation and trust reviewed above suggests that chimpanzees are indeed selectively motivated to confer benefits onto their friends. In contrast, the role of chimpanzee friendships in inhibiting anti-social behavior – i.e., the imposition of costs – remains underexplored. Here, we address this gap in the literature by using stealing behavior to study the relationship between friendship and anti-social behavior.

Stealing behavior represents an ideal test case for investigating the influence of friendship on anti-social behavior and associated emotional responses. Chimpanzees are thought not to respect ownership, understood as a cooperative arrangement where individuals refrain from taking each other's property (Brosnan et al., 2008). For example, Kanngiesser et al. (2020) had dyads of chimpanzees participate simultaneously in a foraging task, where each was able to retrieve an easily recognizable, unique set of food rewards. In one condition, the access of one of the participants to the rewards was blocked for 45 s, allowing the other to monopolize them. In 95% of trials, the participant able to monopolize the rewards chose to do so, reflecting a complete lack of respect for ownership in this task. However, chimpanzees do generally refrain from grabbing a resource in a conspecific's immediate *possession.* It remains unclear whether this is the product of a normative-like sense of respect or lower-level cost-benefit calculations (Brosnan, 2011). Supporting the latter interpretation, while forced food theft is uncommon in observational work (Silk, Brosnan, et al., 2013), experiments that give chimpanzees the possibility to steal food at a low energetic cost and with no opportunity for immediate retaliation find that they are rather inclined to do so. For example, Jensen et al. (2007) found that theft occurred in 74% of trials. Chimpanzees could steal a tray with food rewards from a conspecific by pulling a rope. The "victims" responded with displays and tantrums, and avenged themselves by pulling a (different) rope to collapse the tray, making the food inaccessible to either party. Importantly, participants collapsed the tray at higher rates after stealing than in a control condition, in which a human experimenter pushed the tray from the subject to the partner – isolating the effect of the thief's agency on the decision to retaliate. This pattern suggests that chimpanzees are highly motivated to steal food, while also seeing theft as an undue imposition of costs.

In the present study, we combined observational with experimental methods to investigate two interrelated research questions: (1) Do chimpanzees steal less from their friends? (2) Does friendship affect chimpanzees' emotional reactions to theft situations? In the observational phase of the study, we collected 800 h of data from naturally occurring interactions. We then used this data to determine the strength of the relationships between individuals in the group based on the relative frequency with which they groomed, co-fed, touched, or were within arm's length of each other. Using this measure, we assigned each subject one friend and one non-friend, who were matched in sex and dominance. These dyads then participated in a stealing task, where one individual (the "thief") could pull a rope to steal a food tray from the other (the "victim"). In a within-subjects design, each victim participated in one session of three trials with a friend and one session of three trials with a non-friend. We counterbalanced whether the victim participated first in the friend condition or the non-friend condition. We coded stealing decisions and a range of behaviors known to express affective states in both the victim and the thief. The theorizing presented above posed contrasting predictions: friendship could either dampen or intensify anger at anti-social behavior. We therefore remained agnostic with regards to the direction of the effect of friendship on the expression of negative emotions. We tested the following predictions:

- P1: Chimpanzees will steal less from their friends.

- P2: Friendship will affect emotional responses of chimpanzees to theft.
- P3: Friendship will affect the emotional expressions of thieves in theft situations.

1. Methods

1.1. Subjects

Twenty-six chimpanzees (fourteen females and twelve males) ranging in ages from 16 to 39 (M = 27.73 years, SD = 6.56) participated in the study. Twenty-three subjects participated in the victim role. Of these, twenty-one also participated in the thief role. Three chimpanzees participated only in the thief role. The chimpanzees live at Ngamba Island Chimpanzee Sanctuary, Uganda, where they have access to a large outdoor enclosure during the day and receive regular daily feedings, daily enrichment, and water ad libitum. Subjects voluntarily participated in the study and were never deprived of food or water. For more information on the subjects, refer to Table S1 in the electronic supplementary material.

Experimental protocols adhered to the Institutional Animal Care and Use Committee at the University of California, Berkeley and were carried out in accordance with the guidelines of the Pan African Sanctuary Alliance and the regulations of the Ngamba Island Chimpanzee Sanctuary, Wildlife Conservation Trust in Uganda. The procedures were approved by the Sanctuary ethics committee (including the board members and veterinarian), the Uganda Wildlife Authority, and the Ugandan National Council for Science and Technology. Chimpanzees' daily participation in these studies was completely voluntary, and the research was non-invasive and not harmful to the animals. Animal husbandry complied with international standards (the Weatherall report, The use of nonhuman primates in research).

1.2. Materials

The testing area consisted of two opposing rooms (see SI Fig. 1). The rooms are separated by a 2 m wide corridor, which is not accessible to the chimpanzees. The chimpanzees had visual and auditory access to each other when in these rooms.

The testing apparatus consisted of a 60 × 11.5 cm tray with a row of three bolts. A long rope was attached to two sides of the back of the tray. We used medium-sized (approximately 3 × 7 cm) pieces of pineapple.

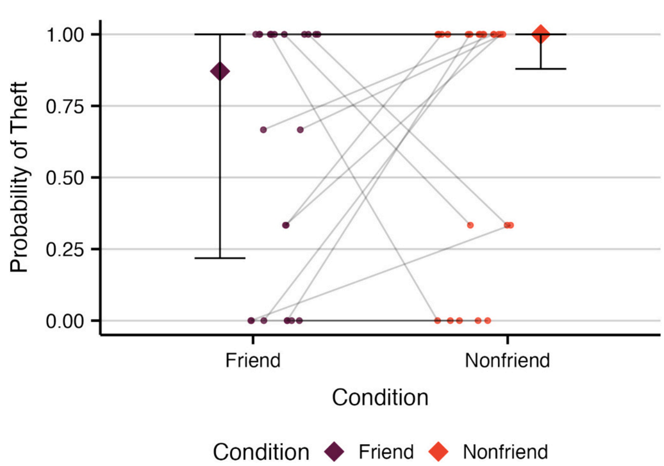

Fig. 1. Thieves were significantly more likely to steal in the non-friend than in the friend condition. *Note.* Each dot represents the mean probability of theft for a given subject. The lines connect between sessions of the same victim in both conditions. The diamond represents the model predictions, with error bars representing bootstrapped 95% confidence intervals.

1.3. Observational phase

1.3.1. Collection of observational data

A research assistant collected 800 h of observational data. Observations took place four times a day, during the chimpanzees' feeding times, for approximately 30 min.

1.3.2. Analysis of observational data

We followed exactly the same procedure as Engelmann and Herrmann (2016) to calculate the composite index of sociality (CSI) for each pair. We first calculated the frequency with which each individual was grooming, in contact, at arm's reach, or co-feeding with all other individuals (by, for example, dividing the number of grooming events between individual A and B by the number of times A and B were simultaneously present). The frequencies of the four activities were positively correlated within dyads (mean Pearson's $R = 0.56$, range 0.18–0.97), indicating moderate convergence across the measures. While not fully redundant, they cannot be considered independent sources of information about relationship quality. Using the obtained frequencies, we then calculated the CSI for each dyad using the following formula based on Silk, Cheney, and Seyfarth (2013):

$$CSI_{x,y} = \frac{\sum_{i=1}^{4} \frac{f_{ixy}}{\underline{f_i}}}{4}$$

In this equation, f_{ixy} is the frequency of behavior i for dyad xy, and $\underline{f_i}$ is the mean frequency of behavior i across all dyads. Since the CSI involves the division of the frequency of a given behavior within a dyad (f_{ixy}) by the average of that behavior across all dyads $\left(\underline{f_i}\right)$, its outcome describes the extent to which a particular dyad deviates from the average of all dyads. The average across all dyads is thus 1. Dyads with a high score are more closely bonded than the average dyad, and, conversely, dyads with a low score are less closely bonded than the average dyad.

1.3.3. Determination of friends and neutral peer

For each subject, we selected as a friend the chimpanzee that exhibited the highest CSI with them. For four chimpanzees, the partner with the highest CSI was not an individual who regularly participates in testing (participation in research is voluntary and some chimpanzees are known by the caregivers to decline participation). In these cases, we assigned the individual with the second highest CSI as the friend. This procedure resulted in mutual pairings for 10 of the 23 subjects who participated in the victim role (i.e., they were assigned as their friend's friend).

To assign a neutral peer to each individual, we selected the individual closest to the median CSI for that individual who is of the same sex and equivalent rank as the individual's friend. We determined rank equivalence based on the consensus of four senior caregivers, who have been working with this group of chimpanzees for an extended period of time (4–20 years). The caregivers were blind to the experimental hypotheses. The mean CSI in the friend condition was 10.5 (SD = 7.42); the mean CSI in the non-friend condition was 0.528 (SD = 0.454). For all pairings and the corresponding CSI values and ranks, refer to Table S2 in the electronic supplementary material.

1.4. Procedure and design

1.4.1. Design

In a within-subjects design, each subject participated in one session with a friend and one session with a neutral peer. To the extent possible under the testing conditions, we attempted to counterbalance the order of the sessions such that half of the subjects participated first in the friend condition, and such that half of the subjects participated first as a thief (of subjects who participated in both roles). Subjects did not participate in more than one session a day as a victim and, where possible, we did not test subjects the day after they participated as a victim. Subjects could participate in more than one session as a thief per day (but not as a victim and a thief on the same day). Apart from the identity of the thief, the procedure was identical in the friend and in the non-friend condition. Each session consisted of one (re-)familiarization trial of the thief to the experimental apparatus and three test trials.

1.4.2. Procedure

1.4.2.1. Familiarization trials. At the beginning of each testing session, we conducted a familiarization of the thief to the testing apparatus (or re-familiarized them to it when it was not their first session). The experimenter baited the middle bolt of the tray with one large piece of pineapple, placed the tray on the ground and against the bars of the victim's room, and laced the rope through the bars of the thief's room. Before the trial, the thief waited in the thief's waiting room, with the door to the waiting room locked. The thief had visual access to the baiting process. Each familiarization trial began when the experimenter asked a caregiver to open the door to the thief's room, and ended once the thief pulled the rope to make the tray accessible to themself and consumed the pineapple (which all thieves did, for every single familiarization trial). The victim was in the victim's waiting room for the duration of the familiarization trial.

1.4.2.2. Test trials. Before each trial, the thief waited in the thief's waiting room and the victim waited in the victim's waiting room. The experimenter baited the tray with three pieces of pineapple (one on each bolt). Each trial began when the experimenter asked the caregiver to open the door to the victim's room. Once the victim entered the victim room and consumed one piece of pineapple, the experimenter asked another caregiver to open the door to the thief's room, allowing the thief to enter the thief's room to pull the rope and "steal" the tray with the two remaining pineapple pieces from the victim. (Note that since the victims needed to retrieve the pineapple pieces through the bars, they could only retrieve them one at a time, giving the thieves ample time to steal.) The trial concluded 90 s after the thief was allowed to enter the thief's room.

1.5. Behavioral coding

Trials were videotaped with four cameras, all placed in the corridor: two facing the victim and two facing the thief. The victim and the thief behaviors were coded separately, with all coders blind to experimental conditions. We coded the decision to steal, as well as several behaviors known to indicate negative affect: rough self-scratching, a displacement activity, which is thought to express an internal state of uncertainty or anxiety in this species (Baker & Aureli, 1997); banging (a type of temper tantrum) which is believed to express anger (Rosati & Hare, 2013); and vocalizations, which express a range of emotions. Following Crockford (2019), we distinguished between three different vocalizations that express negative affect: whimpers, screams, and barks. We coded these behaviors for the duration of the trial for the victims (90 s from the time point the thief enters the room). For the thieves, we coded these behaviors for 45 s after they were allowed to enter the thief's room, thus capturing the emotions most relevant to the stealing event (when theft occurred, it was always within a few seconds of the thief entering the room; 83.7% of target behaviors occurred within the first 20 s).

The first author coded all behaviors in all videos. For tray pulls (i.e. stealing decisions), self-scratching, and banging, a graduate student with extensive behavioral coding experience scored 25% of the videos. Reliability was perfect for tray pulls, excellent for banging (ICC = 0.95), and good for self-scratching (ICC = 0.79). The vocalizations were all additionally coded by the seventh author. Disagreements between the first and the seventh author were resolved by the third author, a field primatologist with over a decade of experience coding chimpanzee behavior (68 out of 204 vocalization bouts).

1.6. Variable coding

To assess the affective responses of our subjects, we summed the duration in seconds of all bouts for each of the target behaviors in each trial (e.g., the total time screaming in each trial). The mean durations per trial of the coded behaviors are presented in Table 1. Our main dependent variable for the analyses of affective responses was a combined affective measure, which we calculated by z-transforming each of the target behaviors (scratching, banging, screaming, barking, and whimpering) separately for victims and thieves, and then taking their average. Similar scores have been used to measure stress and negative emotionality in chimpanzees (e.g., Fraser et al., 2008) and have been shown to enhance sensitivity to affective states compared to individual behavioral measures in mice (Guilloux et al., 2011). *Z*-transforming the variables ensures that behaviors differing in variance or base rate contribute equally to the composite score, preventing any one behavior from disproportionately influencing the result (Martin & Bateson, 2007; Song et al., 2013). This approach mirrors common practice in human emotion research, where scale items are routinely standardized before being averaged into composite scores (e.g. Seo et al., 2023).

Trial number was z-transformed for all analyses. Relative rank was determined using the consensus ranking of four senior caregivers (over 50 years of combined experience working with this group), who assigned each chimpanzee in the group to "low", "medium", or "high" status. We treated each male as higher in rank than each female.

2. Data analysis and results

All mixed effects models included random intercepts for victim and thief, as well as random slopes for condition within victim. Data analysis was conducted in R (R Core Team, 2024) with tidyverse (Wickham et al., 2019) used for data wrangling and visualization. Mixed effects models were fitted using lme4 (Bates et al., 2015), with lmerTest (Kuznetsova et al., 2017) used for significance testing. Gamma models were fitted using glmmTMB (Brooks et al., 2017). Significance of individual terms was assessed using likelihood ratio tests using the function drop1.

2.1. Model 1: do chimpanzees steal less from their friends?

To test for the effect of friend/non-friend condition on stealing likelihood, we included condition, trial number, and their interaction, as well as sex of thief and relative rank, in a binomial GLMM (logit link function) predicting the probability of theft occurring in a given trial (of $N = 138$ trials).

Thieves pulled the tray on 65% of trials: 61% in the friend condition and 70% in the non-friend condition. The distribution of stealing events is presented in Fig. 1.

Table 1
Mean total duration of all coded behaviors per trial in *seconds* (with standard deviations).

Role	Behavior	Mean Duration	SD
Victim	screaming	2.15	6.91
	banging	1.57	5.18
	whimpering	2.53	9.34
	scratching	1.12	3.24
	barking	0.13	0.64
Thief	screaming	0.88	4.94
	banging	0.36	1.57
	whimpering	0.23	1.18
	scratching	0.02	0.21
	barking	0.00	0.00

Note. The coding window was larger for victims than for thieves, so the values are not directly comparable.

Thieves were significantly more likely to steal in the non-friend than in the friend condition ($\chi2(1) = 7.57$, $p = 0.006$). The interaction between condition and trial number was non-significant so we dropped it from the model ($\chi2(1) = 0.13$, $p = 0.72$). The effect of relative rank was likewise significant, such that the higher the relative rank of the victim, the lower the likelihood of theft ($\chi2(1) = 6.87$, $p = 0.009$). The effects of trial number and sex of thief were non-significant. The model predictions are presented in Fig. 1.

2.2. Model 2: are victims more or less upset when a friend steals from them?

To test whether the victim's emotional response to theft was greater when friends versus non-friends stole from them, we included condition, trial number, and their interaction, as well as the victim's sex and relative rank, in a linear mixed-effects model predicting the victim's negative response in a given trial. We only included victims who were stolen from in both conditions in this model ($N = 15$; to avoid confounding by subject), and only included trials where theft occurred, leading to a sample of 80 trials. We ran the model with our combined affective measure as the dependent variable, as well as separately with each of the behaviors comprising it as the dependent variable.

In the friend condition, victims expressed significantly less negative emotional responses to theft with increasing trial number ($t(61.58) = -2.90$, $p = 0.005$). In the non-friend condition, there was no significant effect of trial number on affect ($t(61.54) = 0.76$, $p = 0.45$). We thus found an unexpected interaction of condition and trial number on our combined affective measure ($t(61.60) = 2.58$, $p = 0.012$). The effects of sex and of relative rank were non-significant. The interaction is visualized in Fig. 2. The sub-models predicting scratching, screaming, whimpering, barking, and banging did not reveal a significant interaction of condition and trial number, nor main effects of either. Coefficient estimates for all sub-models with the interaction are presented in SI Table 3.

Visual inspection of the qq-plots revealed a non-normal distribution of residuals. Since our dependent variables were right-skewed, we performed a log-transformation (after adding the absolute minimal value $+0.1$ to ensure positivity). This resulted in approximately normally distributed residuals for all dependent variables except for barking. Therefore, for the sub-model predicting the amount of barking in a given trial, we fitted a GLMM with a gamma error structure. For this sub-model, we checked for overdispersion, which was not an issue (dispersion parameter: 0.4). None of the sub-models evidenced collinearity (maximal variance inflation factor: 1.02).

Many of the emotional responses to the theft occurred in its more immediate aftermath, and emotional expressions towards the end of the trial appeared to be related to boredom. Therefore, as an additional, exploratory analysis, we also ran Model 2 only including emotional responses during the time window starting 3 s before the theft and ending 30 s after it occurred (which captured the first peak in all target behaviors). For these analyses, residuals remained non-normal even after log-transformation for all dependent variables apart from the combined measure. Therefore, we fitted a GLMM with a Gaussian error structure for the combined measure, and GLMMs with gamma error structures for all other dependent variables. For the gamma models, we transformed the dependent variables by adding 0.1 to ensure positivity. We checked for overdispersion and collinearity, neither of which were an issue for any of the sub-models (maximal dispersion parameter across sub-models: 1.124; maximal variance inflation factor: 1.028).

Here, we found a similar but more pronounced pattern compared to the full-trial model: the interaction between condition and trial number significantly predicted the combined affective measure ($t(62.56) = 3.70$, $p < 0.001$), as well as screaming ($\chi^2(1) = 5.88$, $p = 0.015$), whimpering ($\chi^2(1) = 8.08$, $p < 0.01$), and banging ($\chi2(1) = 6.18$, $p = 0.013$). Coefficient estimates for all sub-models with the interaction are presented in SI Table 4.

2.3. Model 3: do thieves express more or less negative affect when stealing from friends?

To test for the effect of friend/non-friend condition on the emotional expression of the thieves, we included condition, trial number, and their interaction, as well as the thief's sex, and relative rank, in a linear mixed-effects model predicting the thief's negative affect in a given trial. We only included trials where theft occurred in this model ($N = 90$). We ran the model with our combined affective measure as the dependent variable, as well as separately with each of the behaviors comprising it as the dependent variable. Thieves expressed more negative affect in the non-friend than in the friend condition. This was the case in the sub-model predicting the combined affective measure ($\chi2(1) = 8.49$, $p = 0.003$) as well as the sub-model predicting screaming ($\chi2(1) = 4.71$, $p = 0.030$). The interaction between condition and trial number was non-significant so we removed it from the model ($\chi2(1) = 0.05$, $p = 0.824$). The fixed

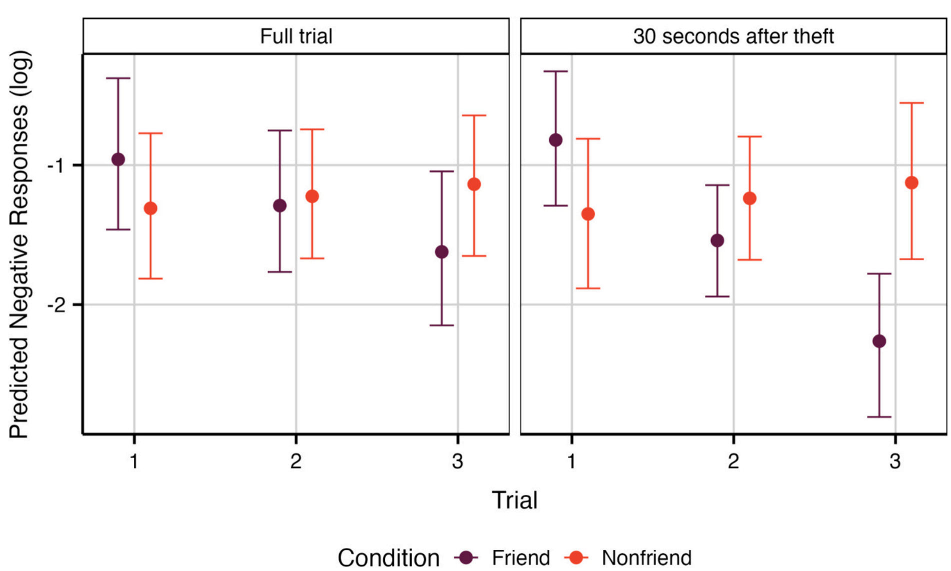

Fig. 2. Victims expressed less negative affect with increasing trial number in the friend condition than in the non-friend condition.
Note. Dots correspond to model predictions, with error bars representing bootstrapped 95% confidence intervals. Predictions are marginalized over sex and relative rank. The left panel shows the predictions for the model looking at the full trial, and the right panel shows the predictions for the first 30 s.

effects estimates for all sub-models are presented in SI Table 5. Model predictions are represented in Fig. 3.

Visual inspection of the qq-plots revealed a non-normal distribution of residuals, which was not resolved by transforming the dependent variables. Therefore, we fitted a GLMM with a gamma error structure. All dependent variables were transformed by adding 0.1 and the absolute minimum value (for the combined measure) to ensure positivity. We checked for overdispersion and collinearity, neither of which were an issue for any of the sub-models (maximal dispersion parameter across sub-models: 0.22; maximal variance inflation factor: 1.29).

3. Discussion

We studied how friendship shapes chimpanzee stealing behavior. To this end, we first observed a community of chimpanzees to ascertain their friendships. We then used this data to assign chimpanzees to sex- and rank-matched friend and non-friend (neutral) dyads. These dyads participated in a simple stealing task, where one subject (the “thief”) could steal a food tray from the other (the “victim”). We analyzed both the decision to steal and behaviors known to communicate negative affect in both the victim and the thief (scratching, banging, screaming, whimpering, and barking). Chimpanzees stole less from their friends than their non-friends. The role of friendship in emotional reactions to theft, meanwhile, appears nuanced: victims were initially angrier with friends but attenuated their responses as trials progressed – whereas their reactions to non-friends remained consistent across the trials. The thieves, meanwhile, expressed more negative affect when stealing from non-friends. These results highlight the complex role of affective processes in mediating friendship-related anti-social behavior and responses to it.

Previous studies have found that chimpanzees are more likely to help (Engelmann et al., 2019), trust (Engelmann & Herrmann, 2016), and console (Fraser et al., 2008) their friends, and to share food with them (Samuni et al., 2018). This set of findings highlights chimpanzees' motivation to engage in prosocial behavior among friends. The present finding that chimpanzees are less likely to steal from their friends demonstrates that friendship not only buttresses prosocial behavior, but also inhibits anti-social behavior. Of note, chimpanzees pulled on the rope to feed on the pineapple in every single familiarization trial without a “victim” present. Refraining from stealing thus requires a high degree of self-control – especially in a species as food motivated as chimpanzees (Parrish et al., 2015).

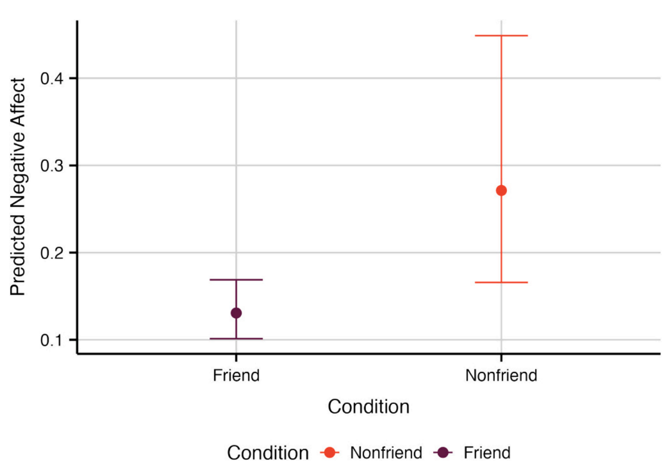

Fig. 3. Thieves expressed more negative affect in the non-friend than in the friend condition.
Note. Model 3 predictions from the sub-model predicting the combined affective measure. Dots correspond to model predictions, with error bars representing bootstrapped 95% confidence intervals. Predictions are marginalized over sex and relative rank.

For a close relationship among non-kin to be beneficial, it should provide more benefits than the costs it imposes. The fact that chimpanzees are able to inhibit an otherwise lucrative course of action when it imposes a cost on their friend suggests that chimpanzees are sensitive to this calculus. Whether this knowledge is explicit or operates through more implicit affective mechanisms, which make the imposition of costs on a friend aversive, remains an open question. In this context, it is noteworthy that the only study to explicitly investigate the link between prosociality and self-control in chimpanzees concluded that chimpanzee cooperation is fast and independent from self-control: prosocial decisions in a resource allocation task were made faster than anti-social decisions, and there was no correlation between individuals' performance in any of the prosociality tasks and their performance in temporal discounting and behavioral inhibition tasks (Rosati et al., 2018). Our results suggest that the role of self-control in chimpanzee cooperation is greater than previously thought.

The theft in the present study also differs from other behaviors studied experimentally in the context of friendship in the cost-benefit calculation involved. Social repercussions notwithstanding, participants in our study stood to gain pieces of pineapple – a highly prized food reward – for the mere low energetic cost of pulling a rope. The cost of choosing *not* to steal from a friend is therefore significantly higher than the modest energetic cost of helping them by pulling a rope to deliver food that is anyway inaccessible to oneself (Engelmann et al., 2019).

Recent theorizing suggests that chimpanzees (and other primates) form specific social expectations towards collaborative partners (Engelmann et al., 2017; Engelmann & Tomasello, 2017; Ritov et al., 2025; Titchener et al., 2023). While it was previously thought that chimpanzees are averse to unequal treatment, a recent meta-analysis has called this finding into question (Ritov et al., 2024). Rather than comparing their own treatment to the treatment of someone else, the data is more consistent with the workings of relationship-specific mechanisms: the subjects reject ostensibly inequitable food offers because the human experimenter is not treating them as well as they could, and not because they are treating someone else better (Engelmann et al., 2017; Titchener et al., 2023). If chimpanzees form social expectations from collaborative partners, it follows that they should expect more from closely bonded others, such as their friends. Our results are largely consistent with this account. Chimpanzees may steal less from their friends because they know that theft would be a violation of their friend's expectation, and hence they avoid damaging the relationship. On the victim's side, the tendency to initially express a greater affective response to theft in the friend condition is consistent with anger as a response to a violation of social expectations.

Victims attenuated their affective responses towards thieving friends across trials. What may account for this pattern? Theoretically, there are at least two ways friendship may affect emotional responses to theft. The social expectations account discussed above suggests that individuals should be more upset when a friend steals from them. However, friendship may also dampen anger – a socially disengaging emotion that risks destabilizing the relationship (Gervais & Fessler, 2017). It is possible that both motivations played out in our study: the victims may have initially been angrier with their friend, but then inhibited their responses to avoid threatening the relationship (Wallace, 2019). It is also possible that after the first time their friend stole from them, the victims came to expect less of their friends. Since we did not predict this interaction, we are cautious of over-interpreting it; future work should seek to replicate this effect and more explicitly disentangle the two proposed mechanisms. Future work could also examine whether the broader range of bargaining strategies afforded by friendship, such as withdrawal from future interactions, leads to a tempered expression of negative affect (Krems et al., 2021).

Thieves expressed less negative affect when stealing from friends than from non-friends, an effect driven by less screaming in the friend condition. There are at least two possible explanations for this finding.

The thieves may have treated the interaction as less hostile in the friend condition, leading them to scream less. Alternatively, even when they succumbed to the temptation to steal from their friend, they may have inhibited their affective response, seeking to minimize the hostility between themselves and their friends.

Our vocalization coding scheme took a finer-grained approach than previous experimental studies that looked at affective responses as a dependent measure (e.g., Rosati & Hare, 2013). We distinguished between whimpers, screams, and barks – which are all negatively valenced but differ in their emotional content (Crockford, 2019). Whimpers express distress, and are particularly common among infants (Clark, 1993). Barks and screams both occur frequently in the context of agonistic interactions. In one field study on victims of aggression, screams, but not barks, occurred more commonly in the presence of adult or late-adolescent male bystanders; and barks, but not screams, predicted retaliatory aggression (Fedurek et al., 2015). This pattern suggests that screams may serve to recruit coalitionary support, whereas barks may serve to intimidate the opponent. Based on the situations in which these vocalizations occur as well as a comparison to human expressions, theorists have hypothesized that screams express fear and barks express anger (Kret et al., 2020). Interestingly, our model looking at the affective response of the victim revealed a significant effect of condition on the combined measure, but not on any of the individual behaviors comprising it. This suggests that the affective mechanisms distinguishing interactions among closely bonded pairs are orthogonal to the situational features that distinguish between the different response types. Alternatively, it is possible that there are nuances within the vocalization categories that our coding did not capture. Chimpanzee screams have distinct acoustic signatures depending on whether the vocalizer is the aggressor or the victim (Slocombe & Zuberbühler, 2005), and chimpanzees can extract information such as the severity of the aggression (Slocombe et al., 2009) and the dominance relations between the aggressor and the victim (Slocombe et al., 2010) from playbacks of screams. Future work can build on our findings by using an even finer-grained coding system or more advanced technological tools (e.g., machine-learning-based analyses) to measure the animals' affect in friendship-related conflicts.

Friendships are increasingly gaining recognition as an important facet of both human and nonhuman animal sociality. In fact, recent research and theorizing suggest that friendships play an important role in shaping group-level cooperation (Dunbar, 2024; Samuni et al., 2021). Thus, a better understanding of the cognitive and affective mechanisms underlying friendship in our closest living relatives will help explain the emergence of the large-scale cooperation we see in humans (Apicella et al., 2012; Dyble et al., 2016). Much remains to be uncovered regarding the role of social expectations in maintaining nonhuman cooperation. Our study takes a step in this direction by highlighting the role of self-control and affective processes in maintaining chimpanzee friendship.

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CRediT authorship contribution statement

Oded Ritov: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Christoph J. Völter:** Writing – review & editing, Visualization, Methodology, Formal analysis. **Liran Samuni:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Avi Benozio:** Writing – review & editing, Conceptualization. **Dacher Keltner:** Writing – review & editing, Methodology, Conceptualization. **Jan M. Engelmann:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Laura S. Lewis:** Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization. **Esther Herrmann:** Writing – review & editing, Supervision, Conceptualization.

Declaration of Competing Interest

Jan Engelmann, Avi Benozio reports financial support was provided by United States-Israel Binational Science Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.evolhumbehav.2026.106948.

Data availability

All data has been made public and can be accessed at: https://doi.org/10.5281/zenodo.15750049

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