

How do gibbons solve social dilemmas?

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Abstract

Social primates face conflicts of interest with other partners when their individual and collective interests collide. Despite living in small, primarily dyadic, groups compared to other social primates, gibbons are not exempt from these conflicts in their everyday lives. In the current task, we asked whether pairs of gibbons would solve a conflict of interest over food rewards. We presented pairs of gibbons with a situation in which one pair member, the actor, could release food rewards at a distance, giving the passive partner a chance to take an advantageous position to obtain the rewards. Gibbons participated in three conditions: A No Food control, an Altruistic situation in which the actor could not obtain a direct reward from the cooperative act and a Test condition in which the actor could secure a small fraction of the total rewards. We found that gibbons acted more often in the two conditions involving food rewards, and waited longer when no direct rewards were available for the actor, thus suggesting that they understood the mechanism and that they faced a social trade-off between making the rewards available and waiting for each other to act. However, we found that in a majority of pairs, acting individuals benefitted more than the passive partners in both altruistic and test conditions. Furthermore, in some occasions actors actively refused to approach the location where the food was released. These results suggest that while gibbons strategize to solve the social dilemmas, they often allowed their partners to obtain better rewards. Our results highlight the importance of social tolerance and motivation as drivers promoting cooperation in these pair-living species.

Introduction

Social animals constantly face conflicts of interest with other group members. In primates, decisions about different travel routes, group defense, or access to limited resources may result in divergent preferences for individuals and hence potential conflicts between group members¹⁻⁶. To resolve these conflicts, primates may engage in different sets of strategies including dominance, mutual cooperation or majority rules. For instance, Lar gibbon females (*Hylobates lar*) lead travel routes and access high value rewards before males despite the lack of a clear dominance of one sex over the other⁷. In olive baboons (*Papio anubis*) instead, travel routes seem to be driven by majority rule despite their highly hierarchical social system⁵. However, while these observations allow us to understand different aspects of primate behavior, it is often difficult to dissect the factors contributing to specific behavioral patterns in nature. Accordingly, experimentally controlled studies with primates can shed crucial light on the decision-making strategies underlying the observed behavior.

To that end, over the last years numerous studies have adapted game theory models to explore the strategies that different primates use to overcome social dilemmas in which their interests come into conflict⁸⁻¹¹. That is, the free rider benefits the most from the interaction. For instance, computerized tasks have presented primate species including chimpanzees, capuchin monkeys and rhesus macaques with different economic games borrowed from the game theory literature¹²⁻¹⁴. These studies have found that, in general, primates can converge to a Nash Equilibrium (i.e. the optimal outcome from an

interaction given the strategy of your partner) during coordination and conflict games between pairs. Using a different approach, other researchers have presented great apes, mostly chimpanzees (*Pan troglodytes*), with non-computerized social dilemmas in which apes had to decide between different physical actions to obtain rewards from an apparatus. In general, these studies have found that chimpanzees and bonobos develop strategies to outcompete their partners and obtain the most from the social dilemma, either through monopolization of rewards⁹, by waiting for their partner to act before them^{8,10,15} or by influencing them to change their strategy¹¹.

The use of game theory models to explore how different primate species coordinate actions for mutual goals, as well as how they overcome conflicts of interest, is a growing field in comparative psychology¹⁴. For example, a very recent study presented squirrel monkeys, a primate species that rarely cooperates in nature, with a set of computerized social dilemmas previously presented to more cooperative species such as the capuchin monkeys (*Cebus apella*). Vale and colleagues¹⁶ found that squirrel monkeys (*Saimiri boliviensis*) behaved similar to capuchin monkeys in cooperative scenarios such as the stag hunt game. In another recent study, Sánchez-Amaro and colleagues (under review) presented for the first time pairs of common marmosets (*Callithrix jacchus*) with a social dilemma modeled after the snowdrift game^{10,17}. In this study, marmosets could access an unequal reward distribution in the form of a rotating tray. In the social dilemma condition, the preferred reward could only be obtained by waiting for the partner to act, with the risk that if none of the two accessed the tray they would both lose the rewards. The authors explored whether cooperative breeding marmosets would engage in more cooperative strategies due to their natural tendency to act proactively toward others in different contexts including food sharing. They found similarities between marmosets and great apes' strategies to maximize benefits (e.g. waiting for the partner to act before them). They also found sex differences between females and males' strategies, where the former was more willing to forego a cooperative act and maximize rewards. The results fit the natural history of this species in which males usually donate food to females in food sharing tasks. However, we still know very little about the socio-cognitive strategies that other primate species may develop to deal with similar conflicts of interest.

Perhaps surprisingly, one of the primate families we know less about in terms of their socio-cognitive abilities are the gibbons (family *Hylobatidae*). These small apes are key species in the sense that they are closely related to both old world monkeys and great apes¹⁸. Furthermore, unlike any other ape species, gibbons primarily live in small groups mainly composed of a bonded breeding couple and their kin¹⁹. Thus, the study of their socio-cognitive abilities is crucial to understand whether some cognitive traits are shared by common descent in all apes or have instead arise through convergent evolution in distinct primate species. Up to date, the study of gibbons has mainly focused on elucidating aspects of their biology, ecology and phylogeny^{20,21}, with little work assessing their socio-cognitive abilities in experimentally controlled settings. For instance, in a recent literature review on primate cognitive studies published by the Manyprimates initiative²², it was found that gibbons only appeared in 2 of the 574 studies surveyed between 2014 and 2019.

Gibbons may have been excluded from cognitive studies due to difficulties securing a sufficient sample size to conduct experimental studies or due to their limited motivation to participate in cognitive tasks^{23–25}. While limited sample size is a problem that a majority of comparative psychologists and primatologists face when studying primate behavior, a lack of motivation is often the product of experimental designs and methods not suited to the biology of the species. In the case of gibbons, early work by Beck²⁶ already showed, for example, that adaptations to the way gibbons could interact with an apparatus (e.g. lifting the access to the ropes instead of leaving them on the ground on a flat surface) improved their participation and performance when compared to previous studies^{27,28}.

Furthermore, as Liebal emphasizes²⁵, it has been sometimes assumed that gibbons' are less interesting than other primate species due to their relatively simpler social system based on pair-living, which presupposes low socio-cognitive abilities in relation to other primates. However, mounting evidence over the last 20 years has challenged the assumption that gibbons are truly monogamous^{19,20,29–31}. Some gibbon species have been found to engage in extra-pair copulations³² and a number of studies have reported different group structures in addition to pair-living^{31,33–36}. Furthermore, the fact that gibbons live in reduced groups does not necessarily presuppose a lack of social complexity. According to Freeberg³⁷, pair-bonded individuals would form more complex and intense relationships than those living in large polygamous groups—possibly because they are more interdependent. In other words, social complexity is not only a matter of group size but of relation quality. It is thus possible that gibbons would engage in more prosocial strategies between closely bonded partners when conflicts of interest take place.

Nevertheless, despite the lack of studies on gibbons' socio-cognitive abilities in relation to other primate species²², researchers have made significant advancements on this area. For instance, it has been investigated whether gibbons recognize themselves in the mirror (see²⁵ for review) or whether they are able to follow others gaze to discover an unseen object^{38–42}. In the case of gaze-following studies, researchers have found that gibbons are able to shift their gaze in response to a previous experimenter gaze shift but it remains unclear whether gibbons are taking the perspective of the experimenter into account, including her mental states. However, a recent study found that when gibbons were presented with a competitive scenario in which they could only retrieve uncontested rewards—when the experimenter did not orient his body, head or eyes towards the rewards, gibbons avoided the contested table by paying attention to the orientation of the body and the head of the experimenter but not to his eyes⁴³. This later result suggests that, in line with previous socio-cognitive studies in other primate species^{44–46}, gibbons may perform better in competitive settings compared to neutral ones. However, in previous gaze-following studies the interaction only occurred between the human experimenter and the ape and not between conspecifics. Considering the competitive task presented by Sánchez-Amaro and colleagues⁴³ as an example, the experimenter and the gibbon faced a conflict of interest every time the gibbon approached the contested table since the experimenter and the gibbon competed for the same food reward. Therefore, one open question is how pairs of gibbons would solve conflicts of interest in a

more naturalistic context. That is, when they need to deal with other conspecifics over access to resources such as food rewards.

To answer this question, we presented pairs of gibbons with a simplified version of a social dilemma resembling a snowdrift game¹⁷. This is the first time a game theory model has been implemented to shed light on the nature of gibbons' socio-cognitive abilities. In this situation, one pair member should volunteer to provide a common good that becomes accessible for both of them. The dilemma occurs when the passive individual takes advantage of her position. In other words, the costs to volunteer may hinder the actor's chances to benefit herself in relation to the passive partner. In our task, one gibbon could pull from a handle attached to a rope. By pulling the handle, the rope would lift a release mechanism and rewards would fall at a distance to the actor, giving the passive individual the chance to position herself in front of the released rewards and hence benefit from the actors' action (although the actor could potentially benefit from those rewards as well).

Pairs of gibbons were presented with three conditions varying in the number of available rewards: a Test condition in which the actor could obtain one reward attached to the handle while releasing five rewards at a distance from herself; an Altruistic condition in which the actor did not obtain any reward from pulling the handle but could still release the five rewards at a distance and a No Food control condition with no rewards involved.

We expected gibbons to act more often in the Test and the Altruistic conditions compared to the No Food condition. This would show that gibbons understood the contingencies of the game. Furthermore, given that gibbons were living with closely bonded partners one possibility is that they would cooperate to solve the dilemma by sharing the volunteer costs. If that were the case, we would expect pairs of gibbons to obtain similar amounts of food in both conditions. Furthermore, we would not expect pairs members to show significant differences in their rate of participation and in their latencies to release the rewards between Altruistic and Test conditions.

If, in contrast, gibbons would react competitively as other great ape species did in previous social dilemmas, we would expect them to try to maximize their food rewards by hesitating to act and by taking advantage of their passive role—placing themselves in front of the release mechanism. In that sense, we would expect passive partners to benefit from their position and obtain more rewards than the actors. Furthermore, we would also expect gibbons to be more likely to act in Test trials given that they could obtain direct benefits from their actions.

Results

Rate of participation and latencies

Gibbons decisions to participate (i.e. to manipulate the handle and release the food container) were affected by the condition presented (GLMM: $\chi^2 = 19.8$, $df = 2$, $p < 0.001$, $N = 532$, Fig. 1). Pair-wise comparisons indicated that gibbons participated significantly more often in the Test condition compared

to the Altruistic (GLMM: $\chi^2 = 19.8$, $df = 2$, $p < 0.001$, $N = 532$, CI [4.05, 16.33]) and the No Food control condition (GLMM: $\chi^2 = 19.8$, $df = 2$, $p < 0.001$, $N = 532$, CI [4.58, 16.76]). Gibbons pulled in all Test trials but one while in Altruistic and No Food control trials gibbons pulled less frequently (62.5% and 53.1% respectively). Interestingly though, gibbons pulled significantly more often in the Altruistic condition compared to the No Food control condition (GLMM: $\chi^2 = 19.8$, $df = 2$, $p = 0.049$, $N = 532$, CI [-1.02, 0.005]), suggesting that the potential release of food rewards at a distance also motivated gibbons' decisions and that they could distinguish between the three conditions presented.

Next, we found that gibbons' latencies to pull were also affected by the condition presented (see the Electronic Supplementary Materials (ESM) Fig. S1). That is, in those trials in which individuals pulled (71.8% of trials), they clearly acted faster in the Test condition (when one piece of food was directly accessible from the pipe) compared to the Altruistic condition (coxme, HR = 4.97, $p < 0.001$, $N = 532$, CI [3.65, 6.11]) and to the No Food condition (coxme, HR = 6.38, $p < 0.001$, $N = 532$, CI [4.6, 7.91]). Despite gibbons being more likely to participate in Altruistic compared to No Food control trials, their latencies to act did not statistically differ between those two conditions in those trials in which they accessed the rope (coxme, HR = 0.78, $p = 0.075$, $N = 532$, CI [0.59, 1.03]).

Strategies by actors and passive partners

We also analyzed whether actors received less rewards than passive partners. That is, whether there was a conflict of interest in place. To answer this question, we analyzed whether a previous volunteering action would predict the amount of released food that individuals obtained across conditions.

Surprisingly, we found a significant two-way interaction between condition and the presence/absence of previous volunteer act suggesting that passive individuals obtained less food than actors and that this difference was especially salient in Altruistic compared to Test trials (GLMM: $\chi^2 = 7.57$, $df = 2$, $p = 0.006$, $N = 572$, CI [-1.64, -0.19], see ESM Fig. S2). Therefore, actors were still able to obtain the majority of the food released in both conditions, despite the fact that passive individuals could benefit from their position in Test trials compared to Altruistic trials—most likely due to the time that the actors required to obtain the food from the pipe. In line with this finding, Fig. 2 shows the percentage of trials in which individuals release food against the number of rewards that each individual obtained in Altruistic and Test trials. Interestingly, in only one pair (Betty and Khim Maung Win) the more active individual obtained less benefits than the passive partner in both conditions.

Next, we evaluated whether passive gibbons (those not releasing the food) acted strategically by placing themselves in front of the ramp at the moment the actor released the food and whether they would act more strategically in Test compared to Altruistic trials given that the actor gibbon would spend some time retrieving the food baited inside the pipe.

There were 287 instances in which the food was released by the actor in the Altruistic and Test conditions. In 235 (81.9%) of those trials the passive individual was not in front of the ramp by the time the food was released. The passive individual only placed herself in front of the ramp by the time the food was released in 52 trials (18.1%) and there were no differences between conditions (GLMM: $\chi^2 =$

0.31, $df = 1$, $p = 0.58$, $N = 287$). We also explored whether gibbons would take an advantageous position by the time the actor arrived to the location where the food had been released. That is, whether the passive individual was there at that time. After releasing the food, the actor arrived to the food location in 237 of those 287 trials (82.6%). Passive individuals were not in front of the ramp in 161 trials (67.9%). They were in front of the ramp by the moment the actor arrived in 76 occasions (32.1%). We found no differences between conditions (GLMM: $\chi^2 = 0.69$, $df = 1$, $p = 0.41$, $N = 237$).

We found that actors did not approach the released food in 50 trials in which they released it. A majority of those trials were Test trials (37 of 50, binomial test $p < 0.001$). This makes sense since actors spent some time obtaining the food reward placed inside the pipe. Nevertheless, in a great majority of these trials (44 of 50 trials; 88%) the actors ended up obtaining their food reward from the handle before the passive individual finished to obtain her last reward. Furthermore, we only found one case in which the actor showed an intention to approach the partner by getting closer to him.

Social measurements: displacement and cofeeding events

We examined whether displacement and cofeeding events differed between Altruistic and Test conditions. We only found 13 displacements out of 287 trials (4.5%). In a majority of displacement events the passive was already in front of the food when the actor arrived (11 of 13) but only in 3 trials the partner was already there from the moment the food was released. Furthermore, in 10 of 13 trials the active individual displaced the passive one and 10 of these 13 displacements occurred in test trials.

Finally, we found cofeeding in 44 trials out of 287. A majority of cofeeding events occurred during Test trials (27 of 44; 61%). However, we found that cofeeding did not significantly vary between Altruistic and Test conditions (GLMM: $\chi^2 = 1.58$, $df = 1$, $p = 0.21$, $N = 287$).

Discussion

The results of the study suggest that pairs of gibbons can solve a conflict of interest where one pair member has the opportunity to volunteer to activate a release mechanism containing potential food rewards for both partners. In line with previous studies with great apes, gibbons avoided mutual defection in a Test condition where they could obtain a direct reward from their actions^{10,47}. In contrast, in an Altruistic condition where gibbons could not obtain direct benefits, their likelihood to volunteer and release potential food rewards dropped significantly in comparison to the Test condition. In our opinion, two primary reasons could explain this pattern of results.

First, it is possible that gibbons were only motivated to participate when they could directly benefit from their own actions. However, if that were the case, how can we explain that in the Altruistic condition gibbons still participated significantly more than in a No Food control condition? In that sense, gibbons showed that they did not just act for the sake of pulling the rope. Most likely, their actions were motivated by the prospect of obtaining rewards, especially when those were directly available.

While this reason is plausible, it does not necessarily explain their refusal to participate in almost 40% of Altruistic trials. The second possible reason is that the conflict of interest was higher in the Altruistic condition compared to the Test condition. In Altruistic trials, cooperative gibbons obtained no direct benefits from their participation. In these trials, gibbons ran the risk of losing any potential reward, especially if their passive partner positioned herself in front of the release mechanism. Supporting this view, gibbons waited for each other to act, often delaying their participation over the 90 seconds time limit that they had to participate in a trial. In fact, gibbons did not differ in their latencies to pull from the handle between Altruistic and No Food control trials.

Our results thus suggest that gibbons understood some aspects of the social dilemma, preferring to participate in Test over Altruistic trials. As in previous studies with great apes^{8,10}, this propensity could be explained through the combination of two opposing factors: the possibility to obtain direct benefits and the fear to lose all potential rewards.

So far, we have discussed gibbons' decisions whether to participate or not. The next question is whether gibbons strategized when they took a passive role. In other words, did they try to maximize their own rewards when their partners volunteered? The main source of conflict between participants lied on the possibility that passive individuals could position themselves in front of the release mechanism during Altruistic and Test trials. In Test trials, this could be particularly beneficial for passive partners given that actors could lose some valuable seconds trying to obtain the food reward attached to the PVC pipe.

However, we found that actors actually obtained most of the rewards in both conditions, with a special advantage over passive partners during Altruistic trials. In fact, in only one pair of gibbons the passive individual obtained more rewards than the actor in Altruistic and Test trials. Furthermore, passive individuals rarely took advantage of the situation (they position themselves in front of the release mechanism in 18.1% of trials) and they did not distinguish between conditions. That is, during Test trials passive partners did not benefit from the time that the actors spent trying to obtain the reward located inside the PVC pipe. In that sense, gibbons did not solve the social dilemma cooperatively. For that to be the case, pair members would have benefited more or less equally on both conditions and they would have not hesitated to manipulate the PVC pipe in Altruistic trials. It is also very unlikely that gibbons' decisions were driven by proactive prosocial motivations such as releasing food rewards to favor their pair members given that actors benefited the most from their own actions.

One possible explanation to understand why actors obtained more rewards than passive partners is that passive individuals tried to pull from the handle during Test trials. This possibility could partially explain why passive gibbons rarely position themselves in front of the release mechanism during Test trials, but it cannot explain why in Altruistic trials they did not take advantage of their passive role. An alternative explanation is that only the most dominant individuals participated and obtained the majority of rewards. However, there are numerous reasons to suggest that a dominance component cannot fully explain our pattern of results as opposed to previous findings in chimpanzees⁹. First, only three of 12 individuals released rewards in less than 20% of Altruistic and Test trials suggesting that in half of the pairs both

individuals exchanged roles relatively often. Furthermore, our results are also in line with literature suggesting that there is no clear dominance of one sex over the other⁴⁸. Importantly, conflict avoidance does not seem to support this alternative either. The number of co-feeding events tripled the number of displacements events, suggesting that individuals were usually tolerant to each other. A third alternative explanation is that once a gibbon decided to manipulate the handle, the other one totally disengaged from the task. This could explain why passive partners did not take an advantageous position in front of the release mechanism and why, as a consequence, actors did not face a social dilemma in many trials. After all, actors benefit more than passive partners despite the volunteer costs. Nevertheless, this is unlikely because passive individuals still obtained a significant fraction of the food rewards (38% of rewards across conditions).

All these previous arguments cannot fully explain why passive partners rarely took advantage of their position, especially given how successful this strategy was: passive partners obtained almost 75% of rewards when they position themselves in front of the release mechanism by the time the actor manipulated the pipe. We thus propose that the reason why passive gibbons did not always take advantage of their partner actions could be explained through combined processes of motivation from the side of the actor and a general high level of social tolerance towards inequities. That is, individuals that were more motivated to obtain food and more attentive were also more likely to take the actors' role in our task. Through participation, they could become more aware of the situation as a whole and react faster to obtain the rewards despite their volunteer costs –the distance they covered from the location of the PVC pipe to the location where the rewards were released. This gave them an advantage over their passive partners, who at the same time tolerated actors to obtain the majority of rewards (as if actors would have called “dibs” on the rewards). Importantly, tolerance towards reward inequities also came from the actors' perspective. In support of this interpretation we also found that in a number of trials the actors seemed to adopt a prosocial attitude towards their passive partners by letting them access all the released rewards.

Future studies should improve different aspects of our setup to continue exploring gibbons' decision-making strategies when individuals' interests collide. The main weakness of our design is that we were not able to separate pairs of gibbons before the experimental sessions. In that sense we could not train them with the different task contingencies as it is usually the case in this type of settings [10,50, 51 but see 52–54]. It is thus possible that some individuals were more skillful than others, and that might have affected our results. Nevertheless, all individuals approached the apparatus and obtained rewards and only one never pulled from the PVC pipe during the course of the study. In addition, despite the fact that gibbons distinguished between conditions with food (Test and Altruistic) and the No Food control, their latencies to act did not differ between Altruistic and No Food control trials. We hypothesize that with longer trials we would have found a significant difference between gibbons' latencies in Altruistic and No Food conditions. In that sense, future changes in the trial time or the food rewards can better assess whether gibbons strategize to solve conflicts of interest. Given the quasi-experimental nature of our task, we did not always capture the social dilemma scenario we envisioned. Future tasks should implement

designs in which cooperative acts are clearly costly for those individuals willing to volunteer. In addition, given our restricted sample size we could not test species differences or the presence of individual biases (e.g. bias leading individuals towards becoming actors).

The present study advances our understanding of how primate species overcome conflicts of interest in experimental settings. Specifically, we find that gibbons are able to solve social dilemmas akin to those previously presented to other great apes [10], suggesting a continuity in the way apes solve situations of conflict resembling a snowdrift dilemma. In addition, in our study gibbons exhibit high degrees of social tolerance (in particular in the form of reactive, rather than proactive prosociality⁵⁴). Passive partners tolerate that actors obtain higher benefits in a majority of trials while actors often actively forego opportunities to maximize rewards (e.g. the actor does not try to obtain any of the released rewards). Relatedly, gibbons engaged in cofeeding events relatively often. One possibility is that such a high degree of social tolerance towards conspecifics results from gibbons' unique pair-living social system compared to other great apes, although future studies should inspect this relationship in more detail. Overall, the inclusion of gibbons in studies exploring the nature of primates' socio-cognitive abilities is crucial to elucidate the nature of our prosocial motivations and their relationship to specific socio-ecological pressures and ultimately how they have evolved since the last common ancestor with all living apes.

Materials And Methods

Subjects

Seven eastern hoolock gibbons (*Hoolock leuconedys*), two pileated gibbons (*Hylobates pileatus*), two northern white cheeked gibbons (*Nomascus leucogenys*), and one Siamang (*Symphalangus syndactylus*) participated in the current study (total N = 12, 6M:6F, age in years = 13.98 ± 6.99). See Table S1 in the ESM for info about the subjects.

All subjects were housed at the Gibbon Conservation Center (GCC) in Santa Clarita (CA, USA). They lived in pairs of the same species, with the exception of one eastern hoolock gibbon, who was housed with one siamang. Subjects were tested together in their enclosure and participation was voluntary. Subjects were fed multiple small meals per day outside of testing food. Testing took place between meals to ensure motivation. Water was accessible *ad libitum*.

Ethical Statement

The current research was purely behavioral and non-invasive. The current research has been approved by the IACUC committee of the Gibbon Conservation Center (GCC) and complied with the rules of the IACUC office at University of California, San Diego. The current research was carried out in compliance with the ARRIVE guidelines.

Setup and materials

One experimenter (hence E1) interacted with the apes during a test session while a second experimenter recorded the session and scored the subjects behavior (hence E2). Each experimenter tested half of the pairs. We used high quality rewards (blueberries) that would be easily visible to the subjects.

The apparatus (see Fig. 3) was composed of a plastic folding table with a square wooden plank clamped to the top. At one end of the plank a transparent plastic bin was taped so that it could be lifted up or hang down. The bin, at rest, would hang down and remain unmoved on the top of a wooden ramp. A hole big enough to fit blueberries was drilled on the back side of the bin so that when at rest on the ramp, the experimenter could place five blueberries into the bin. A thin purple rope was tied to the far end of the plastic bin and was routed back to the opposite end of the wooden plank. This was set up so that pulling on the purple rope would reliably lift the plastic bin, so blueberries could fall down the wooden ramp and be easily accessible for subjects to obtain. The extreme end of the rope was attached to the mesh of the enclosure. To allow reaching and pulling the rope, we attached a small, handheld, opaque white PVC pipe. At the right tension, pulling on the PVC pipe would reliably lift the plastic bin. The PVC pipe could contain a single blueberry inside depending on the condition presented. We used two PVC pipes of the same dimensions and appearance to avoid contamination of blueberry leftovers after the trial.

The table with wooden plank would be set up at a distance so that it could not be grabbed by subjects and the ramp was placed underneath so that blueberries would roll down and land in front of the enclosure gate. E2 would then distract the two subjects to an opposite or adjacent side of the subjects' enclosure with a handful of blueberries or cereal pieces while E1 tied the end of the purple rope with the PVC pipe onto the mesh gate of the enclosure, roughly at the experimenter height, approximately 2 meters to the right or left. The distance and location of the rope was kept constant for all trials of each pair; however, because the enclosures differed in layout, the rope would go to the most convenient side. This way, we ensured that the rope had proper tension to be pulled by gibbons and lift the plastic bin as well as be distant enough from the ramp so that a subject could not easily pull on the rope and obtain food from the ramp at the same time.

Procedure

Individual solo pre-testing of the mechanism of the apparatus was not possible because the separation of the pairs was prohibited.

Three conditions were tested: Test, Altruistic, and No Food. In the Test condition, the following procedure was performed. E1 would place five blueberries in the plastic bin on the apparatus. To gain the attention of the subjects, E1 would call the subjects names and show the food, if they were not already focused on the food/experimenter. Once both subjects had observed the five blueberries placed in the plastic bin, E1 would squeeze a single blueberry on top of the PVC pipe, so that the blueberry would be clearly visible. The rope and pipe would be set up so that the pipe was just far enough from the enclosure (at approximately 30-50 cm) in order for subjects to need to pull on the rope to obtain access to the pipe and blueberry. Consequently, pulling the rope would also lift the plastic bin and drop five blueberries down the ramp, accessible to subjects. The experimenter would also call the names of the subjects when placing

the single blueberry in the pipe. A choice was recorded when one of the subjects pulled the rope. If no subject pulled the rope within 90 seconds, the trial ended and was recorded as no pull. If an experimenter error was made, up to 3 repetitions of the trial would be completed. Environmental conditions such as rain would also end test sessions to be continued the next day.

In the Altruistic condition, there was no single blueberry placed in the PVC pipe (but still followed the same procedure of calling the subjects and mimicking putting a blueberry in the pipe). In the No Food condition, no blueberries were used in the trial. In order to control for time and actions, we used the same procedure of calling the subjects and touching both the box and the PVC pipe.

Design

The six pairs participated in 6 sessions of 15 trials each. Five trials of each condition were presented within a session in a pseudorandomized order where no condition was done more than twice in a row. In total, 540 trials were completed. There were no dropouts or removed subjects. One set of trials for one pair had to be continued on the next day due to rain. 8 trials were lost due to errors in video recording. One trial was excluded from model 3 due to a failure of the apparatus.

Coding and statistical analysis

Two cameras on tripods recorded footage concurrently. One was placed to the side of the experimenter in order to capture a wide view of the trials, specifically to show the positions of the subjects, their choices and if they obtained blueberries. The other was placed close to the ramp to accurately count the quantity of blueberries obtained by each subject. For all trials we coded the act of pulling or not pulling and the ID of the puller (actor subject) and non-puller (passive subject in those cases in which one gibbon pulled). We also coded the number of blueberries each subject ate and whether the actor subject ate the blueberry from the pipe. Next, we coded whether a passive subject was present in front of the ramp at the moment the plastic bin was lifted and at the moment the actor arrived at the release location. Additionally, we coded instances of cofeeding and displacements. Cofeeding was coded when individuals feed within a distance of 1 meter⁵⁵. Displacements occurred when an individual left her spot due to the partners arrival. Additionally, we calculated the latency from the start of the trial (last frame experimenter touches the handle) until the individual releases (opening of the plastic bin).

All analyses were conducted with R statistics (version 3.4.4). We used Generalized Linear Mixed Models (GLMMs) to investigate gibbons' binary choices (models 1, models 3-6). Variables were z-transformed when required. Every full model was compared to a null model excluding the test variables. When the comparison between the full and the null model was significant, we further investigated the significance of the test variables and/or their interactions. We used the "drop1" function of the *lme4* package⁵⁶ to test each variable significance including interactions between test predictors. Non-significant interactions were removed and a new reduced model was produced when necessary. A likelihood ratio test with significance set at $p < 0.05$ was used to compare models and to test the significance of the individual fixed effects. We ruled out collinearity by checking Variance Inflation Factors (VIF). All VIF values were

closer to 1 (maximum VIF value = 1.02). For every model we assessed its stability by comparing the estimates derived by a model based on all data with those obtained from models with the levels of the random effects excluded one at a time. All models were stable. We also fitted a mixed-effects Cox proportional hazards model (Model 2) to analyze gibbons' latencies to act. For this purpose, we used the "coxme" function from the *coxme* package⁵⁷. The results of Model 2 are reported as hazard ratios (HR). An HR greater than one indicates an increased likelihood of acting (e.g. releasing the rewards) and an HR smaller than 1 indicated a decreased hazard of acting. In addition, to obtain the p-values for the individual fixed effects we conducted likelihood-ratio tests.

The interobserver reliability was great based on the 19% of the data that was coded by a second rater. Cohen's Kappa values were calculated to assess the reliability of gibbons' decisions and actions. Pearson R^2 values were calculated to assess the reliability of the latencies to manipulate the handle and release the rewards and the quantity of rewards that each individual ate (participation and IDs of actor and passive partner: Cohen's Kappa = 1; latencies to manipulate the handles: Pearson R^2 = 0.99; food consumption and number of rewards obtained: Cohen's Kappa = 1, Pearson R^2 = 0.96; passive individual in front of the ramp: Cohen's Kappa = 1; passive individual in front of the ramp by the moment the subject arrived to the rewards' location: Cohen's Kappa = 0.8; occurrence of cofeeding or displacements: Cohen's Kappa = 0.76).

Declarations

Ethical Statement

The current research was purely behavioral and non-invasive. The current research has been approved by the IACUC committee of the Gibbon Conservation Center (GCC) and complied with the rules of the IACUC office at University of California, San Diego. The current research was carried out in compliance with the ARRIVE guidelines.

Statement of informed consent

the person in Fig. 1 is the first author of the study and authorizes the consent to public the image.

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Additional information

The authors declare no competing interests.

Author contributions:

ASA and FR designed the study. ASA and RB conducted the study. ASA and FR discussed the data analysis. ASA and RB coded the data. ASA and FR analyzed the data. ASA drafted the manuscript. ASA, RB and FR edited the manuscript.

Data availability: The data is located in the dryad repository:

https://datadryad.org/stash/share/vEjtboMhIKHTShoqSF49f_Po2XGZc2avM8PsDRMoLN8.

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Figures

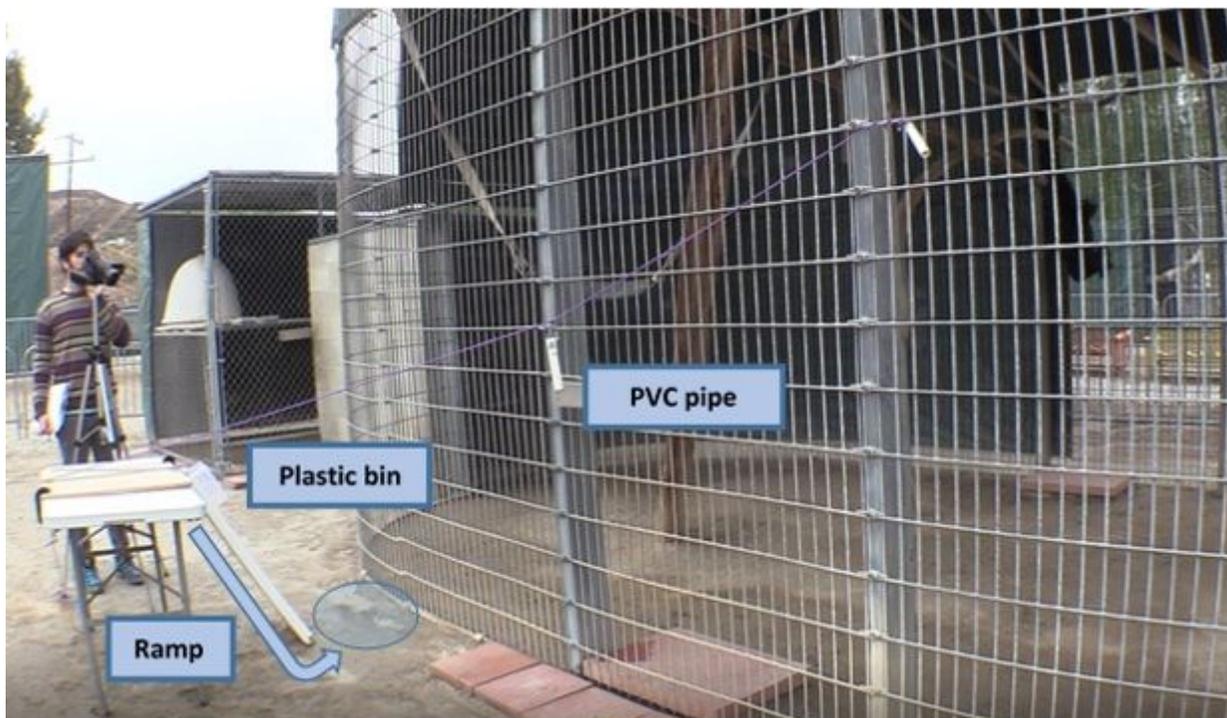


Figure 1

Proportion of released trials across conditions. The box plot represents the median and q1 and q3 quartiles. The dotted line represented the fitted values of the model.



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Proportion of released trials across conditions. The box plot represents the median and q1 and q3 quartiles. The dotted line represented the fitted values of the model.

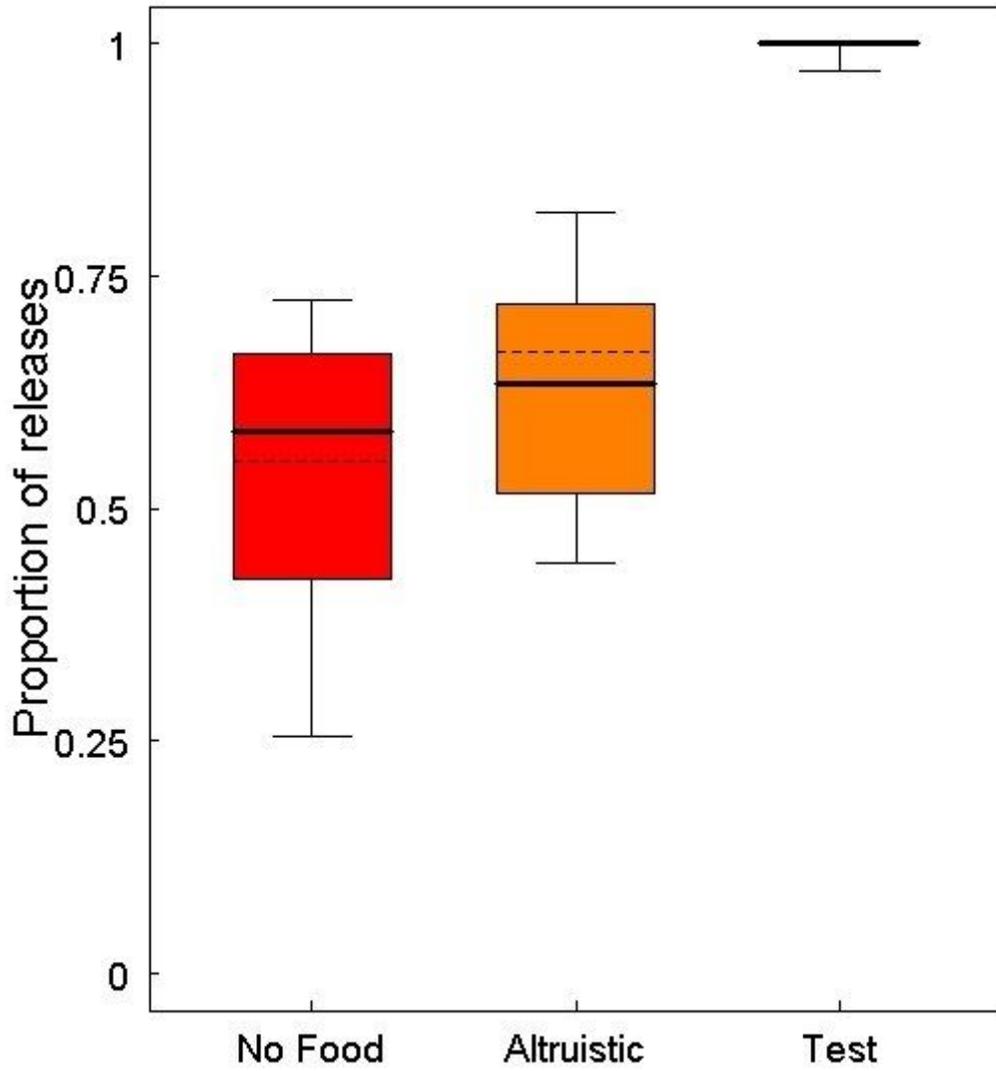


Figure 2

Proportion of food obtained per individual (out of the 5 released rewards) in relation to the percentage of Altruistic (left) and Test trials (right) in which they participate. Each color represents one dyad. Squares represent females and dots represent males.

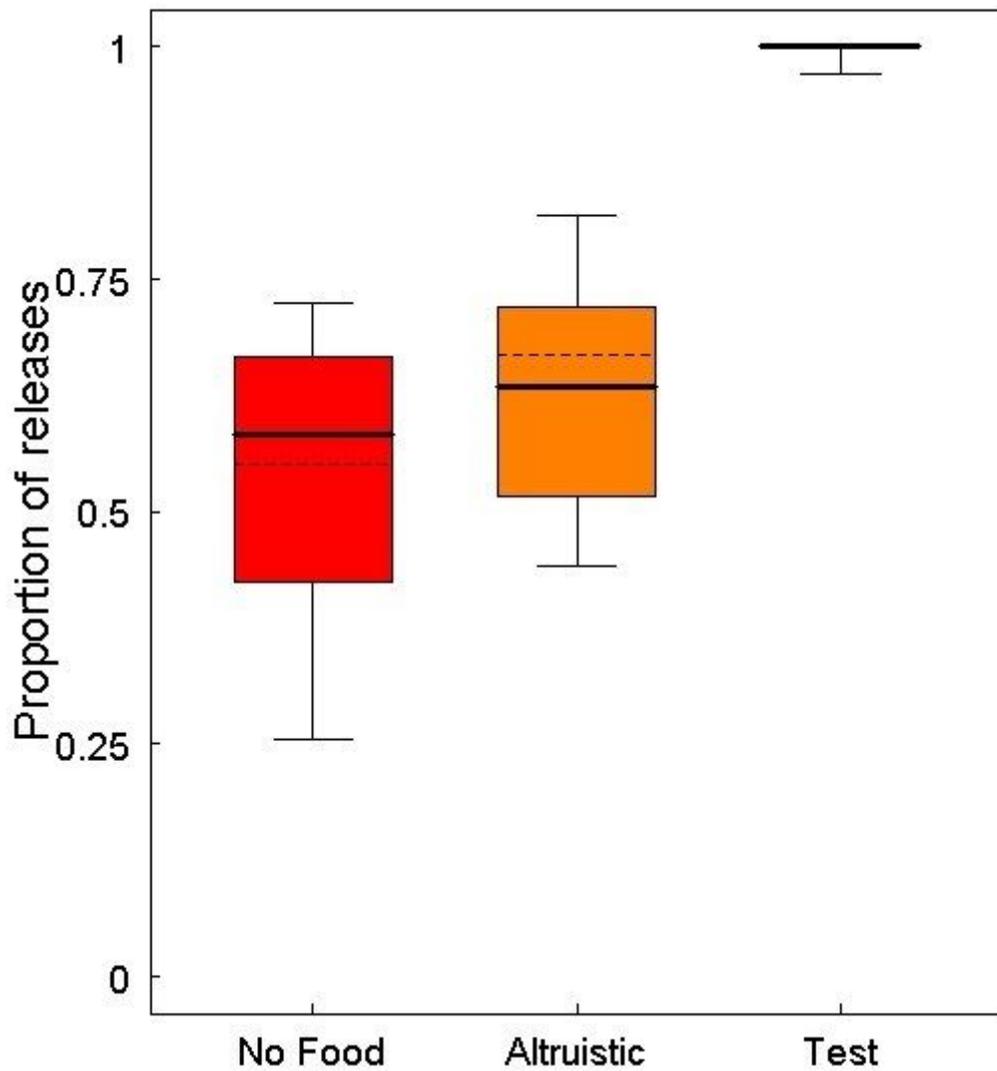


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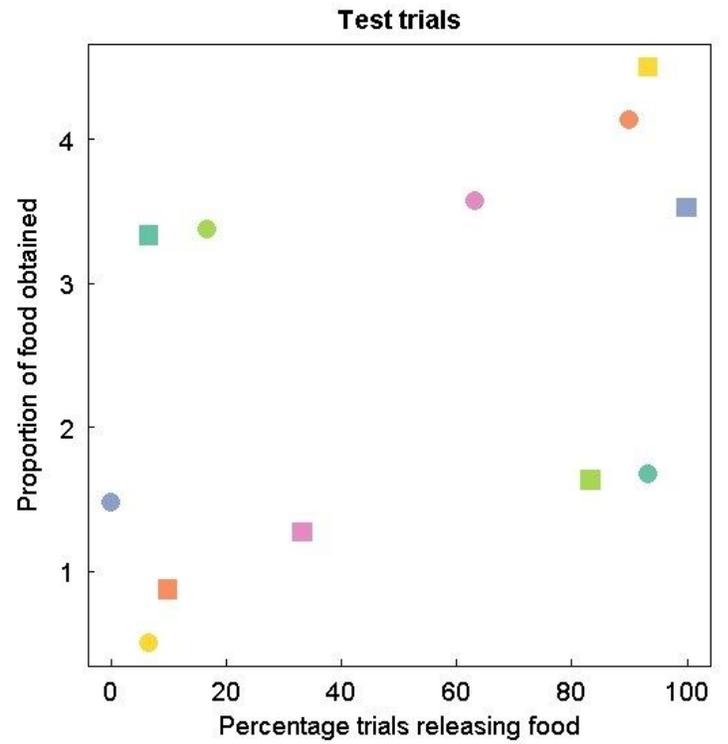
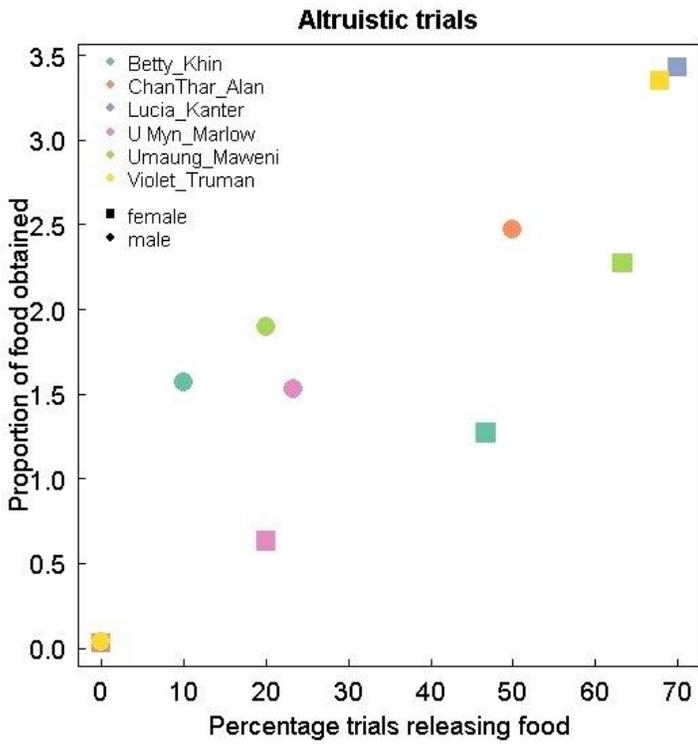


Figure 3

Details of the study setting. The arrow and the circle represent the movement of the food rewards rolling down and the area where the rewards land.

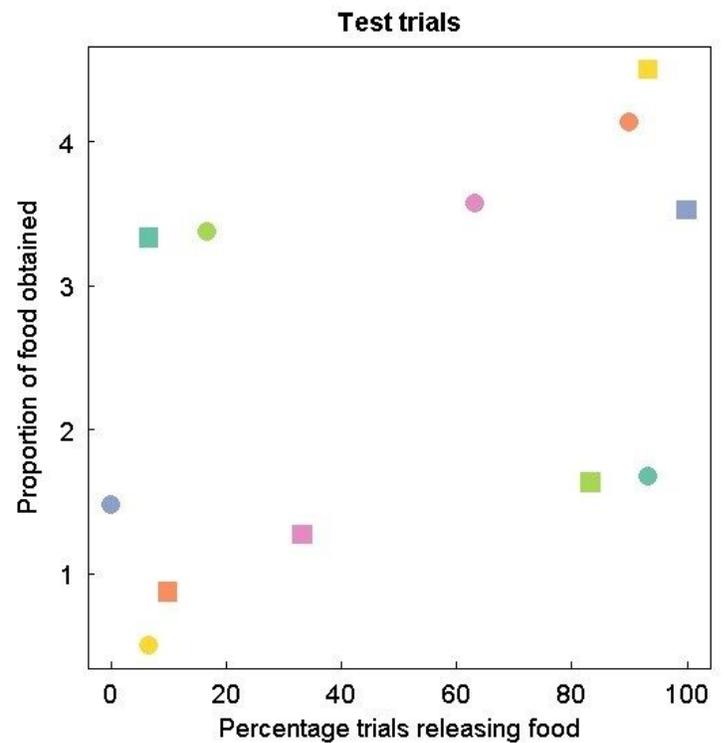
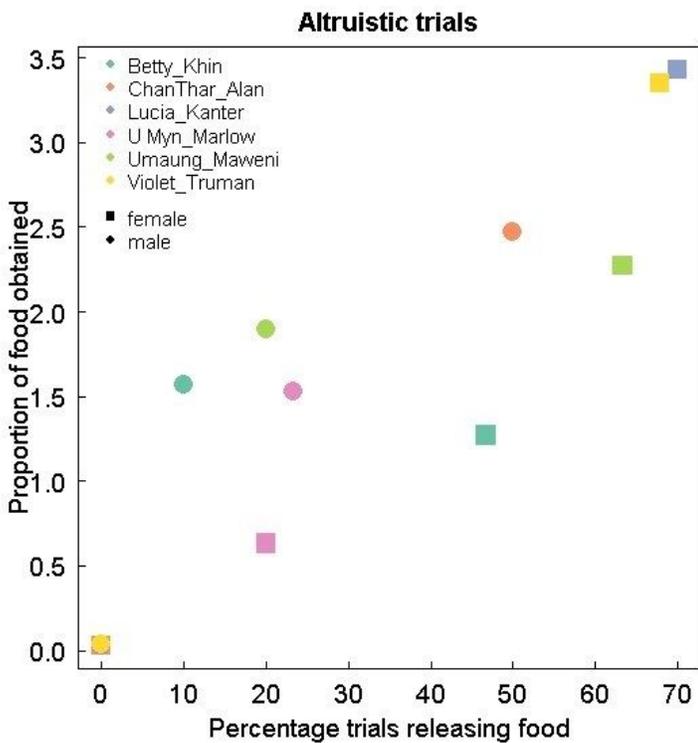


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