PERGAMON

Neuropsychologia 41 (2003) 221–228

NEUROPSYCHOLOGIA

www.elsevier.com/locate/neuropsychologia

Capuchin cognitive ecology: cooperation based on projected returns

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Abstract

Stable cooperation requires that each party's pay-offs exceed those available through individual action. The present experimental study on brown capuchin monkeys (*Cebus apella*) investigated if decisions about cooperation are (a) guided by the amount of competition expected to follow the cooperation, and (b) made instantaneously or only after a period of familiarization. Pairs of adult monkeys were presented with a mutualistic cooperative task with variable opportunities for resource monopolization (clumped versus dispersed rewards), and partner relationships (kin versus nonkin). After pre-training, each pair of monkeys ($N = 11$) was subjected to six tests, consisting of 15 2 min trials each, with rewards available to both parties. Clumped reward distribution had an immediate negative effect on cooperation: this effect was visible right from the start, and remained visible even if clumped trials alternated with dispersed trials. The drop in cooperation was far more dramatic for nonkin than kin, which was explained by the tendency of dominant nonkin to claim more than half of the rewards under the clumped condition. The immediacy of responses suggests a decision-making process based on predicted outcome of cooperation. Decisions about cooperation thus take into account both the opportunity for and the likelihood of subsequent competition over the spoils.

Keywords: Capuchin monkeys; Cooperation; Ecology

1. Introduction

Observers of social primates often assume great social and ecological knowledge in their subjects, which knowledge permits individuals to engage in cooperative pursuits based on expected outcomes. Primates may be able, for example, to predict the amount of competition likely to follow the joint acquisition of a resource. They may seek or avoid certain partnerships for this reason. The present study is the first to use controlled methods to investigate ecological decisions about cooperation, paying attention to both the adaptiveness and speed of the decision-making process.

1.1. Evolution of cooperation

Behavior that serves the interests of others is treated as a paradox by biologists since natural selection is supposed to favor organisms that promote their own interests. Why would animals be prepared to suffer costs in order to help others, sometimes literally giving their lives so that others may live? Should not such behavior have been weeded out in the course of evolution? Ever since Kropotkin's *Mutual Aid* [30], the solution to this puzzle has been that one way in which the cost of helping may be recovered is through return-benefits. This "You scratch my back, I'll scratch yours" principle was first formalized in modern evolutionary terms by Trivers as "reciprocal altruism" [45]. Since then it has been central to the explanation of cooperation among unrelated individuals (for related individuals, see below).

Trivers' theory deals with how cooperation could have come into existence. As such, it knows no exceptions, that is, the theory applies to organisms from fish to humans. However, one should not take this to mean that mutual help in human society is basically the same as that in fish. The above framework only deals with the *ultimate* reasons for reciprocal exchange. That is, it hypothesizes why animals engage in such behavior, and what evolutionary benefits it provides. It says nothing about how cooperation is achieved, which is commonly referred to as the *proximate* explanation. Even if mutual help evolved for identical ultimate reasons in a wide range of species, it can be achieved in a great variety of proximate ways [3].

Stable cooperation among unrelated individuals requires that each party's pay-offs exceed those available though individual action. The underlying cost/benefit calculation may

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PII: S0028-3932(02)00152-5

have occurred either in the evolutionary past, in that natural selection has favored cooperative pursuits [18,23], or during an individual's lifetime based on experience. Even though the learning of cooperation benefits is implied by many observational studies of mammals and birds, a conclusive demonstration requires experimental manipulation. One would need to show that animals estimate the outcome of future interactions in light of previous ones with the same partners. These estimates may cause them to favor certain partners over others because of (a) the proven effectiveness of these partners in cooperation, and (b) return benefits derived from cooperation with them. The latter benefits may occur either right-away if the partner relinquishes or shares the pay-offs of the cooperation (tolerance), or—in case all benefits do go to the partner—after an interval. In the second case, the partner returns the received service or one of an equivalent value (reciprocation). The first case is known as *mutualistic cooperation*, the second as *reciprocal altruism*. In either case, one expects reiterated interactions to lead to the development of stable partnerships characterized by trust, predictability, tolerance, and reciprocity [45].

The same calculation does not necessarily apply to related individuals since helping kin has its own benefits, i.e. increased inclusive fitness for the helper [26]. When it comes to kin, therefore, we assume animals to weigh the costs of cooperation against two potential benefits rather than one. This biases partner choice in favor of kin as evident from, e.g. the matrilineal alliance network among female cercopithecine primates [31,32] and fraternal alliances in chimpanzees, lions, and dolphins [6,25,38]. This is not to say that cooperation among nonkin is rare or absent: it is quite common [18]. For example, high-risk, high-stake collaborations among unrelated individuals have been observed during power struggles in both captive and wild chimpanzees [8,36].

Here we follow a previous definition of cooperation as "... the voluntary acting together of two or more individuals that brings about, or could potentially bring about, an end situation that benefits one, both, or all of them in a way that could not have been brought about individually" [3]. This definition suits our focus on process rather than outcome and reflects our interest in proximate mechanisms. It is also clear that this definition is geared more towards the mutualistic end of the spectrum of cooperation than the reciprocity end. Mutualistic cooperation delivers pay-offs to all parties simultaneously, such as when several hyenas together bring down a wildebeest. Since in mutualistic cooperation parties work directly for their own share of the reward, Dugatkin speaks of "no-cost cooperation" ([18], p. 32). But even though this kind of cooperation offers more certain rewards than reciprocal altruism, in which there is a time lag between cooperative acts and return benefits, mutualism is far from risk-free, because the sharing of pay-offs among cooperation partners does not need to be equal. Mutualism, too, is contingent upon the outcome of reiterated interactions.

1.2. *Capuchin monkeys*

To date there has been far more naturalistic than experimental research on cooperation in primates. The literature offers fine-grained analyses of group hunting by wild chimpanzees [1,2], "market" effects in the choice of alliance partners by male baboons [37], and reciprocity in the spontaneous alliances of macaques and chimpanzees [11,17,43]. In contrast, even though laboratory work on primate cooperation goes back to the 1930s [7], few experimental studies have been conducted. What is especially lacking is the experimental manipulation of "economic" variables, such as the relation between effort, reward allocation, and reciprocity. Recently, this situation has changed thanks to experiments on brown or tufted capuchin monkeys (*Cebus apella*).

The *Cebus* genus is particularly suited for cooperation research. These monkeys show high levels of social tolerance around food and other attractive items, sharing them with a wide range of group members [12,22,28,29,44]. This level of tolerance is unusual in nonhuman primates [21], and its evolution may well relate to cooperative hunting in the natural habitat. Perry and Rose [39] confirmed reports in [35] and [20] that wild *Cebus capucinus* capture coati pups (*Nasua narica*) and share the meat. Since coati mothers defend their offspring, coordination among nest-raiders conceivably could increase capture success. This was also suggested for hunting by capuchins on squirrels (*Sciurus variegatoides*) [40]. Even if these situations probably do not reach the complexity of cooperative hunting in chimpanzees, a convergent, hunting-related evolution of food sharing in capuchins and chimpanzees has been proposed [40].

Despite these and other indications of cooperation among wild capuchins, however, tests of their cooperative abilities in the laboratory initially failed due to opaque cause-and-effect contingencies. These tests relied on electronic or other invisible devices, which capuchin monkeys fail to understand [3,5,47]. In contrast, a classical paradigm [7] has led to quick successes. In this paradigm two individuals need each other's help to pull food towards themselves. The set-up is entirely mechanical and intuitive: the monkeys can see how their actions cause food to move towards themselves and can feel the effect of their partner's pulling. In a series of experiments, we demonstrated close coordination among subjects [34]. For example, the success rate in the pulling task dropped dramatically if monkeys were prevented from monitoring each other's actions, thus indicating their reliance on information about the other's behavior.

Cooperation partners shared rewards through a mesh partition, doing so more often after having needed each other's assistance than in control tests in which they pulled alone [16]. The conclusion from this and other work has been that capuchins cooperate on a reciprocal basis. The observed reciprocity may result from the monkeys responding to their partner's general social attitude [14]. This mechanism, dubbed "attitudinal" reciprocity, is considered simpler than so-called "calculated" reciprocity, which relies on mental scorekeeping of given and received favors. The latter mechanism has thus far been demonstrated in chimpanzees only [3,13].

1.3. The present study

Group hunting is characterized by a phase of coordination followed by a phase in which the parties collect around the captured prey. The latter phase decides who gets what for their efforts. In our current experiment, we mimicked this situation by allowing individuals to move around freely during the pulling task instead of being confined to separate areas, as done previously. This way, cooperation partners could compete over the acquired resource. We further manipulated (a) opportunities for competition by presenting the resource in clumped versus dispersed distribution, and (b) the tendency for competition by comparing related and unrelated pairs.

Numerous primate studies indicate greater tolerance and more co-feeding among kin than nonkin [9,10,21,41,48]. In previous studies on our capuchins, we had been unable to compare kin and nonkin pairs since our colony did not yet include kinship relationships among adults. At present, however, daughters of females in the colony have grown up so that five adult kin pairs are available for testing.

The objective of our study was two-fold. First, to analyze decision-making regarding cooperation. Are decisions in accordance with models which predict that food distribution affects the intensity of competition and the "steepness" of the social hierarchy [46]? Is cooperation favored if hard-to-obtain foods are sharable? These questions can be addressed by manipulating the potential for competition after cooperation, which we accomplished by having monkeys face a cooperation task with variable partners and variable food distributions. As such, the project looks at the ecological conditions favoring cooperation.

Second, in investigating how cooperative tendency varied with the potential for competition we were interested in the speed of the decision-making process. Do monkeys need to learn incrementally which specific conditions are favorable for cooperation or do they make instantaneous adaptive decisions? In the first case, the pros and cons of each specific condition need to be learned through direct experience, hence behavior will gradually change in response to any new condition. In the second case, there is a fast adjustment to new conditions since decisions are based on the generalization of existing social knowledge.

Both questions—the first regarding the role of food distribution and competition, the second regarding the speed of adjustment—are relevant to models of the evolution of cooperation. Imagine a genetic variant that cooperates readily with any member of its group to obtain resources, yet is a slow learner. The variant would have enormous trouble distinguishing profitable from unprofitable partnerships: it would need to go through many reiterated interactions before it understands which partners and situations provide optimal pay-offs. Each time a new situation arises, it would need to go through this learning process. Unless the cooperative tendencies of this individual selectively favor kin, they would impose serious costs. On the other hand, a highly discriminating individual, who quickly generalizes knowledge across a variety of conditions, would avoid wasting time and effort on partners or situations unlikely to yield benefits. This individual would take full advantage of its cooperative tendencies. The speed and nature of the decision-making process are highly relevant, therefore, to the question of how cooperation may have evolved.

2. Methods

2.1. Subjects and housing

Subjects were adult *Cebus apella* from two different social groups housed in a shared facility at the Yerkes Regional Primate Research Center, since 1991. When testing began, one group included two adult males, five adult females, one subadult, and six juveniles. The second group included two adult males, five adult females, two subadults, and seven juveniles. The monkeys were housed in indoor–outdoor pens, with one group having 25 m^2 total surface and the other 31 m^2. Outdoor sections were separated from indoor sections by a wall, but two small doorways allowed the monkeys to move between indoor and outdoor. Each indoor section was further subdivided into two sections by a chain-link fence, with two small (monkey-size) doorways and one door accessible to people. The two social groups were visually separated by an opaque screen, which did allow auditory contact. The floors in each indoor pen were covered with wood chips. Monkey chow and water were available ad libitum and trays of fruit, vegetables, bread and protein juice were given to both groups in the late afternoon. No food deprivation occurred prior to testing, which every day was completed before the afternoon meal.

We only used same-sex pairs in the cooperation tests, and always paired monkeys from the same social group, drawing from both groups. All subjects used were fully adult (i.e. over 5 years of age). Our criterion for inclusion (see below) resulted in 1 male–male and 10 female–female pairs in the study. Of the female pairs, half were related, in all five cases a mother and adult daughter.

2.2. Training

Of the 13 adults in the study, 6 had previous experience with the pulling apparatus described below. Yet, of the 11 pairs in the study, only 3 had ever been used as pulling pair before. In previous studies, they had been placed in a small test chamber, each partner confined to a position right behind one of the pull bars [16,34]. In the present study, on the other hand, the two monkeys were free to move around in a much larger cage, hence the need for them to learn to approach the tray when the cups were baited and select positions at different bars before pulling together. None of the pairs had been in this particular situation before.

Training turned out to be extremely easy, with all pairs scoring at least one success on the task within the very first three trials. This particular task apparently comes natural to capuchin monkeys, as noted before [34]. After running two standard tests (see below) on 14 pairs of adults, we dropped three pairs with a success rate under 50%. The remaining 11 pairs went on to the study.

2.3. Testing procedure

Before testing, two individuals were separated from their group using a trained capture procedure: subjects entered a transport box and were kept apart until the rest of the group had been moved to the outdoor section of their housing area. We then placed both subjects in the front section of their group's indoor housing, which was 213 cm high for both groups with a surface area of 270 cm × 360 cm for one group, and 270 cm × 290 cm for the other group. The test apparatus consisted of a counter-weighted tray that hooked up to the outside mesh of this indoor cage (Fig. 1; [34] provides a different depiction). Two metal pull bars were attached to the tray and protruded approximately 10 cm through the mesh into the cage. The bars were 75 cm apart. The tray, which supported six small transparent food cups, was in full view of the monkeys.

After testing, pairs were returned to their group. To avoid undue stress, we did not separate dependent young from mothers when mothers were being tested. No individual was tested more than once per day. Each videotaped test consisted of 15 2-min trials at the beginning of which two small apple slices were placed in two of the transparent cups on the tray making for four slices in total. The two baited cups were placed symmetrically on both sides of the tray, creating three distinct reward distributions illustrated in Fig. 1: C, clumped (both cups together in the middle); S, standard (cups lined up with pull bars); and D, dispersed (cups at the extremes of the 150 cm long tray). We ran six tests per pair of monkeys, all on different days. The testing order was the same for each pair. Table 1 shows the testing order. Test 5 was a rotating test with regularly alternating trials of types S, D, and C, such that, e.g. C-trials were number 3, 6, 9, 12, and 15.

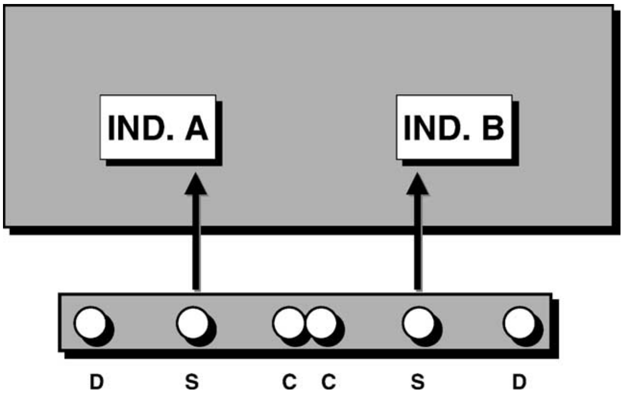


Fig. 1. Adult monkeys A and B were separated from their group in a large indoor mesh cage. Outside the cage was placed a tray on a track. The monkeys had bars to pull the tray towards themselves, but could accomplish this only by working together. At the beginning of each trial, two small apple slices were placed in two of the transparent bowls on the tray: in both S bowls for standard, in both D bowls for dispersed, and in both C bowls for clumped reward distribution.

Table 1
Each pair of subjects was subjected to six separate test sessions, each test consisting of 15 trials

Test number	Test type	Trials
1	Standard (S)	15 trials, all standard
2	Standard (S)	15 trials, all standard
3	Clumped (C)	15 trials, all clumped
4	Dispersed (D)	15 trials, all dispersed
5	Rotating	5 groups of 3 trials of each type (S, D, C)
6	Standard (S)	15 trials, all standard

For each pair, tests were conducted in the below order, never more than one test per day. Standard tests 1, 2 and 6 were combined in the analysis since no differences between them were found.

If the monkeys pulled hard enough, the tray would lock into position, permitting them to empty the cups without holding on to the pull bars. Individual strength was periodically tested to determine the maximum weight each individual could pull by placing them alone in the test chamber and letting them perform one or two pulls for high reward to see the maximum weight they could pull. During pair tests, the tray was counter-weighted such that the strength of both was necessary. Following a successful pull and food collection, the tray was released back into distant position by remote and remained in place until the next food drop.

2.4. Data collection, analysis, and predictions

Data were coded from videotapes, which included a time statement. Our main measures were success rate (i.e. trials in which the subjects pulled in the tray to the point that food collection took place) and food allocation (i.e. number of apple slices appropriated by each subject out of the four slices available per trial). The only behavioral measure open to judgment was bar pulling (both successful and unsuccessful) by either or both individuals on an all-occurrence basis over the entire 2-min period of each trial. In order for an action to be classified as a pull, it required exertion of force on the bar *toward* the subject, i.e. mere bar touches or pushing of the bar did not count as pulls. Interobserver agreement on this item was 92.4% with a Kappa coefficient of 0.675 [34]. All analyses respected individual variation, considering the behavior of individual subjects under various conditions. Statistical comparisons were within-subject or pair.

Competition was expected most under the clumped condition (C). The critical comparison condition for C was not the standard (S) but the dispersed condition (D), because in both the C and D conditions the baited cups were well to the side of the pulling individuals, outside arm's reach, thus requiring them to lock the tray into place before releasing the pull bar and collecting the rewards. Standard trials seemed easier given that the monkeys could pull and reach into the cup at the same time, hence had no need to pull hard enough to lock the tray into place. Given these two aspects—the potential for competition and the cup locations—the predicted order of difficulty of the task, from least to most difficult, was from standard, then dispersed, to clumped.

3. Results

Videotaped tests were first analyzed on percent success defined as the proportion of trials in which a completed pull occurred, i.e. in which the tray was pulled close enough to permit at least one subject to obtain at least one of the four apple slices. Remember that without substantial tray movement rewards would remain out of reach. Since tests of the S-type (tests 1, 2, and 6) showed no significant differences, a single S-score combined the results from all three *S*-tests.

A first ANOVA on success under the three conditions (S, D, and *C*-tests), found significantly different outcomes: $F_{2,20} = 16.2$, $P < 0.001$ (Fig. 1). As expected, the monkeys performed best on *S*-tests, but remember that the most critical comparison concerned the C and D conditions (Section 2). Therefore, from here on statistical tests will focus on this two-way comparison.

The next question was if the effects of food distribution were gradual or immediate. First, the drop from D to C conditions proved demonstrable in the very first five trials of both test types (paired $t = 1.90$, $P = 0.043$, one-tailed). Fig. 2 shows pooled results for all 11 pairs combined in each of 15 consecutive trials per test. It shows a gradual drop in performance over the duration of all three test conditions (Spearman correlation with trial number, $N = 15$, for *S*-test, $\rho = -0.54$, $P < 0.05$; *D*-test, $\rho = -0.93$, $P < 0.01$; *C*-test, $\rho = -0.86$, $P < 0.01$). Performance in corresponding trials was the lowest under the C condition, an effect that was visible in the very first trial and maintained throughout the test.

Second, the rotating test (test 5), in which C-trials were interspersed with the other two types of trials, showed essentially the same results as tests of a single condition, with lower success in C than D trials (paired $t = 1.94$, $P = 0.041$, one-tailed). Thus, the negative impact of clumping on cooperative performance was instantaneous and undisturbed by alternation with other conditions.

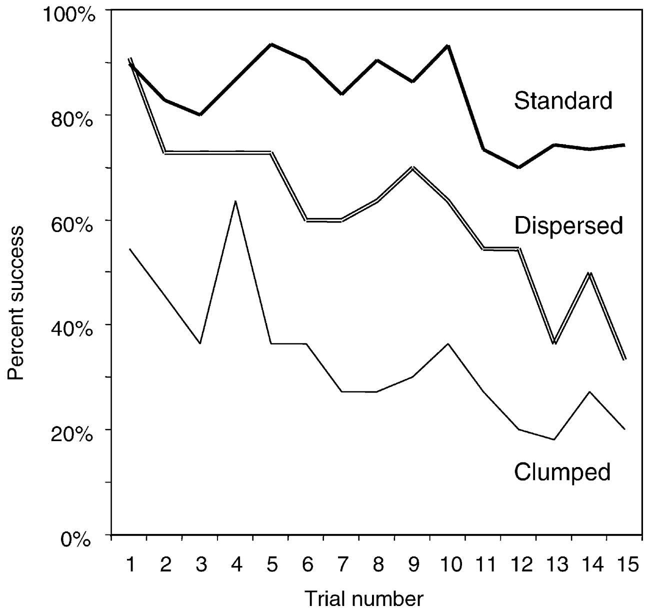


Fig. 2. Percentage of trials with successful cooperation for 15 consecutive trials per test condition. Since the data on all 11 pairs are pooled for each trial number, this graph shows no error data.

When data were split according to whether a pair consisted of either a mother and daughter or two unrelated adults, we found kinship to matter in a manner consistent with the pay-off calculation hypothesis. Controlling all of the above variables, our main statistical comparison of the clumped versus dispersed condition was a repeated-measures within-subjects ANOVA with two factors (condition: C or D; trial block: first, second, or third five-trial block) with social relationship (kin or nonkin) as a between-subjects factor. The outcome was a significant effect of condition ($F_{1,9} = 9.71$, $P = 0.012$), trial block ($F_{1,9} = 13.38$, $P = 0.005$), and social relationship ($F_{1,9} = 13.2$, $P = 0.005$) as well as the interaction between all three factors ($F_{1,9} = 7.11$, $P = 0.026$). Cooperative success dropped under the clumped condition, especially in nonkin pairs: kin succeeded 5.1 times more often than nonkin under this condition (Fig. 3).

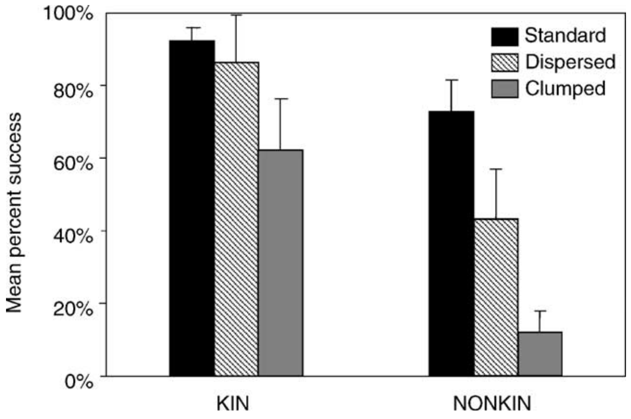


Fig. 3. Percentage of trials with successful cooperation under each of three conditions (standard, dispersed, and clumped) divided for related and unrelated pairs. The graph provides mean success (+S.E.M.) per pair: $N = 5$ for kin and $N = 6$ for nonkin.

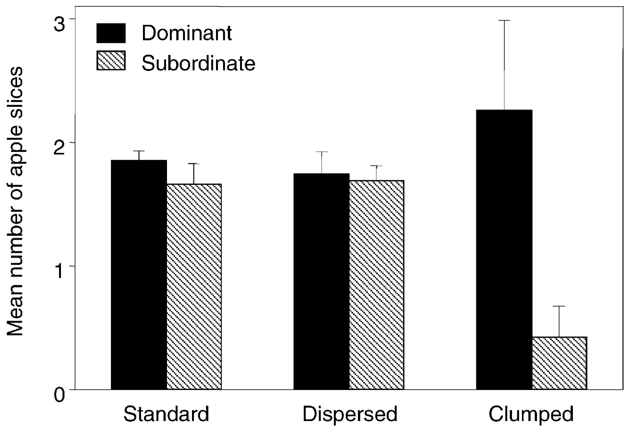


Fig. 4. Mean + S.E.M. number of apple slices (out of a total of four provided) obtained per trial by dominant vs. subordinate cooperation partners under three conditions (standard, dispersed, and clumped). This graph concerns unrelated pairs only.

Comparing rewards collected by the subordinate and dominant partner in *C*-tests, kin failed to show a dominance bias ($t = 0.03$, d.f. $= 4$, NS), whereas nonkin did show such a bias ($t = 2.67$, d.f. $= 3$, $P = 0.038$). The division of apple pieces in clumped tests was approximately equal in related pairs (i.e. a mean of 49.4% of pieces for the subordinate), yet biased in unrelated pairs (i.e. a mean of 20.8% for the subordinate). This bias existed in clumped tests only (Fig. 4).

Finally, we investigated the rate with which parties pulled on the bars. This was done to test the expectation that the drop in success under the clumped condition was due to the subordinate, i.e. the individual who stood most to lose. Fig. 5a and b illustrates that number of pulls per trial deviated most from the standard rate for subordinate nonkin under the C condition. Only under this condition did nonkin subordinates pull significantly less frequently than their dominant partners ($t = 2.05$, d.f. $= 5$, $P = 0.048$, one-tailed). Related pairs showed a nonsignificant trend in the opposite direction under all conditions, i.e. more pulling by the subordinate than the dominant.

4. Discussion

This study demonstrates that capuchin monkeys in an experimental task decide to cooperate based on their chances at obtaining rewards. At the start of testing, the monkeys were familiar with the test apparatus and their partners, but not with two out of three conditions presented. Differential cooperative tendencies under varying food distributions were visible in tests in which all trials were of the same condition as well as in tests in which different conditions alternated.

As expected, the monkeys cooperated best under the standard condition. This condition different from the other two in that each subject could directly reach into their cup from the pulling position. Since there was no need to pull hard enough to lock the tray into position, this condition required less effort than the other two. It is for this reason that the most critical comparison concerns the other two conditions in which the rewarded cups were equally displaced from the pull bar, meaning that the monkeys needed to first lock the tray into place before collecting any rewards (once released by the monkeys, the tray would otherwise be pulled back immediately by the counterweight). Since the monkeys were trained on the standard condition and since standard tests were part of the testing schedule, results from these tests are presented for completeness sake. Our main analysis, however, focused on clumped versus dispersed food distributions.

The analysis showed that under all conditions success decreased over the course of the 15 trials per test, probably due to dropping food motivation. Success rate was the lowest under the clumped condition, particularly if the partners were

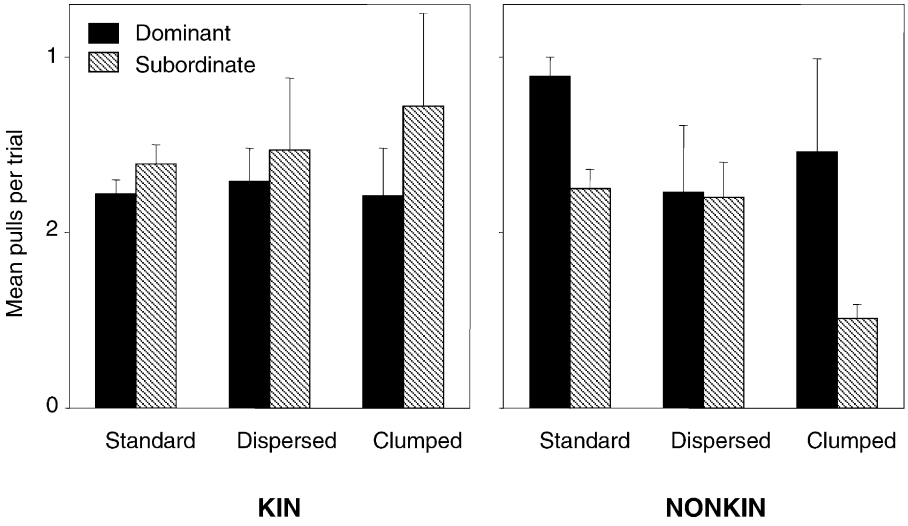
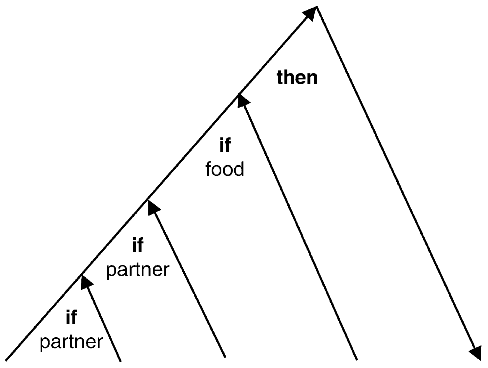


Fig. 5. Mean + S.E.M. number of pulls and pulling attempts per trial made by dominant vs. subordinate partners under three conditions (standard, dispersed, and clumped). On the left side for related, on the right side for unrelated pairs.



Ready for trial	Dominant	Kin	Clumped	Cooperate
	Dominant	Nonkin	Clumped	Don't cooperate
	Dominant	Nonkin	Dispersed	Cooperate
	Subordinate	....	....	Cooperate

Fig. 6. If-then decision tree for the conditions presented in this experiment in which the partner decides to cooperate, or not, based on its dominance rank vis-à-vis the partner, the tolerance to be expected in relation to food (kin vs. nonkin), and the ease with which food can be monopolized (dispersed vs. clumped). Below the tree are presented four out of the eight possible decision paths, all of which lead to cooperation except if the partner is an unrelated dominant and food is clumped.

unrelated. All of these effects (food distribution, trial number, and kinship) were found to be significant. This means that the monkeys based decisions about cooperation on anticipated pay-offs, taking into account both the possibility and likelihood of competition with their partner. In tolerant relationships, as found among kin, monopolization opportunities were largely ignored, but not in the more competitive relationships among nonkin.

Further support for this interpretation came from data on reward allocation and pulling rates. These data showed that food allocation was imbalanced under the clumped condition but only for unrelated pairs. This was caused by the ability and tendency of unrelated dominants to claim the majority of apple slices. The observed pulling rates confirm that it was the subordinate which lost interest in the task under the clumped condition with unrelated partners. In related pairs, in contrast, subordinates (i.e. daughters) pulled slightly more than their partners (i.e. mothers) under all conditions.

Decisions to cooperate seemed to follow the hierarchical decision tree proposed for symbol- and tool-use in chimpanzees [33], and adapted for social problem solving [15]. Accordingly, decision-making follows an if-then syntax according to which several conditions need to be met before a behavior will be shown. Thus, if the partner is kin it does not matter if the food is clumped or dispersed: cooperativeness is high in both partners. If the partner is unrelated and dominant, however, food monopolizability becomes an issue, and cooperative tendency dwindles. Fig. 6 illustrates some of the options under the if-then decision tree tested in the present series of experiments.

It is correct to speak of "decision-making" since we found absolutely no evidence that preference for one condition over another required direct experience with the presented test conditions. The distinction between food distributions was visible from the very first trial onwards. Even more convincingly, the monkeys singled out the clumped trials for less cooperation in tests in which these trials alternated with other conditions. Thus, rewarded trials did not throw them off decisions about trials representing a more challenging condition. As argued in the Introduction, speed of decision-making is a critical aspect of adaptive cooperative behavior.

The decisions observed were probably based on a lifetime of exposure to dominant versus subordinate partners, and kin versus nonkin, under competitive food conditions. The monkeys thus showed an ability to flexibly generalize previous knowledge to the novel conditions of our experiment. Likely, the same ability to reach quick decisions about profitable cooperation underlies the capuchin's natural interactions around food sources that are more easily acquired by several individuals than by one, as in the group hunting documented in the field (see Section 1).

It is particularly important to stress the generalizability of knowledge and the complexity of the variables that enter into social decision-making given that social considerations are almost entirely absent from traditional learning research. For example, there is no mention of cooperation or almost any other socio-emotional skills (e.g. conflict resolution, alliance formation, empathy) in a recent 700-page book on human and animal cognition [42]. Many biologists, in contrast, believe that the social milieu has provided the main impetus for the evolution of intelligence in the large-brained order of primates [19,27]. Thus, "planning" and "foresight" are terms used in relation to chimpanzee power struggles [8], and social intelligence is accorded special status [4,24]. The assumption that primates are born politicians, extraordinarily sensitive to the reactive social field within which they operate, is supported by the present study.

Acknowledgements

Research was supported by a grant from the National Science Foundation (IBN-0077706) to the first author, and a grant from the National Institutes of Health (RR-00165) to the Yerkes Regional Primate Research Center. We are grateful to Marietta Dindo, Cara Dzubow, Laura Mullen, and Hiral Patel for assistance with the experiments, and to three anonymous referees and Ralph Adolphs for helpful comments on the manuscript. We also thank Richard Wagner for construction of the apparatus, and the animal care and veterinary staff at the Yerkes Primate Center. The Center is fully accredited by the American Association for Accreditation of Laboratory Animal Care.

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