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Do Capuchin Monkeys Display a Sensitivity to Unequal Effort Contributions in a Snowdrift Scenario?

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An abstract of
A thesis submitted to the Faculty of the
James T. Laney School of Graduate Studies of Emory University
in partial fulfillment of the requirements for the degree
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Abstract

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The existence of altruism presents a conundrum for evolutionary theory, and assessing the existence and features of this behavior in non-human primates can potentially contribute to evolutionary explanations of human cooperative behavior. Basing our experiment on the "Snowdrift" game, we looked for whether individual capuchin monkeys adjust their own behavior in response to the effort levels of a partner monkey in a cooperative task. We found no evidence that the capuchins adjust their own behavior based on an assessment of a partner's contributions. Instead, the monkeys behavior was consistent with individual learning that is based on the food rewards received for behavior within each session.

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Introduction

Background

Problem of Altruism

The evolutionary stability of altruism presents a great challenge to evolutionary biology (Hamilton 1964; Maynard-Smith & Szathmary 1995; Frank 1998). Altruism is costly to the acting individual but beneficial to its recipient. Therefore, by the principles of both natural selection and 'rational' self-maximizing behavior, altruism should not occur, or exploitation of altruistic (cooperative) individuals should predominate. Yet, cooperative behavior is found throughout the history of life, from the evolution of chromosomes out of discrete DNA molecules (Maynard Smith & Szathmary 1995) and the sharing of sucrose products in yeast (Greig & Travisano 2004), to its critical role in the formation and maintenance of human and non-human animal societies (Maynard Smith & Szathmary 1995; Crespi & Choe 1997; Dugatkin 1997).

Hamilton's theory of kin selection provides a partial solution to this conundrum: when cooperative acts occur between relatives, the inclusive fitness of the actor is increased because the actor's genome is partially shared with the recipient (Hamilton 1964). However, quite a few species display cooperation between non-relatives (Fehr & Fischbacher 2003). Robert Trivers (1971) proposed the idea of reciprocal altruism, whereby the cost of helping is offset by the likelihood of the benefit being returned at some point in the future. Therefore, stable cooperation could theoretically occur in any individuals interacting repeatedly, related or not, because the payoffs for cooperating individuals over time can exceed those of individual action. Both of these theories provide *ultimate* level explanations. That is, they explain why organisms might cooperate and how it is evolutionarily beneficial to do so. Neither theory, however, explains how cooperation might be accomplished and what animals need to know or learn to be successful at it - the *proximate* level of explanation. The ultimate reasons for cooperation could, theoretically, be the same across all species, but the way it is accomplished probably is not.

Behavioral Economics

Over the past decade, a number of controlled experiments have found that chimpanzees (Melis *et al.* 2006a; Melis *et al.* 2006b) and capuchin monkeys (de Waal & Berger 2000; de Waal & Davis 2002; Mendres & de Waal 2000; Brosnan *et al.* 2006) engage in cooperative behavior, at least with related individuals. During this same period, other studies have begun to investigate different "economic" variables as potentially underlying the cooperation found in these primates, such as reward distribution, reciprocity and effort recognition (de Waal 2006). These studies have found that capuchin monkeys respond negatively to unequal reward distributions and reciprocate when a partner shares food or assists in a task. The role of effort recognition in capuchins is less clear, but a few recent studies have made promising headway towards an answer. A study by van Wolkenten et al. (2007) showed that capuchins are at least sensitive to their *own* effort within a token exchange paradigm, while a study by Romero et al. (in prep), which utilized principles of 'game theory,' suggests that capuchin monkeys are also sensitive to the efforts of others in a cooperative task. Most recently, Takimoto *et al.* (poster) found that capuchins change their food container choices depending upon others' effort in a joint labor task.

Capuchin Monkeys

Capuchins, from the genus *Cebus*, show levels of social tolerance that are unusually high for non-human primates, sharing food and other desired objects (de Waal & Davis, 2003). The evolution of this tolerance is thought to relate to their cooperative hunting in the wild (Rose 1997). Consequently, they are an excellent fit for cooperation research.

Game Theory

Game theory, introduced by John von Neumann and Oskar Morgenstern in 1944, provides a mathematical framework for studying the costs and benefits involved in strategic interactions between 'players', as in the case of cooperation. Maynard-Smith and Price (1973) integrated concepts of game theory and evolutionary biology by treating species and genes as players in the strategic interactions described by game theory. This allowed for an economic analysis of interactions both in terms of payoffs and in terms of biological fitness. Axelrod and Hamilton (1981) then embedded the concept of reciprocal altruism within game theory, and the creation of new mathematical models of the evolution of cooperation followed (Nowak & Sigmund 2004; Doebeli & Hauert 2005).

Most game-theoretic models used to study cooperation have been based on the classical prisoners' dilemma (PD) game. In this game, players can cooperate (C) or defect (D), and the payoffs can occur as illustrated below, where b and c represent the benefits and costs, respectively, of choices:

Prisoner's Dil.	C	D
Payoff to C	$b - c$	$-c$
Payoff to D	b	0

Figure 1

To be considered a prisoners' dilemma, the payoffs must be T>R>P>S. In other words, the temptation (T) to defect against a cooperating partner must carry a greater payoff than that of cooperating for mutual reward (R), and the net gain of mutual defection (P, for punishment) must be greater than that of being suckered (S) into unilateral cooperation.

The problem of cooperation in the prisoners' dilemma is therefore described by evolutionary game theory as follows: because defecting while a partner cooperates guarantees greater fitness than mutual cooperation, and because cooperating when a partner defects is more costly than mutual defection, the strategy of defecting 'strictly dominates' the strategy of cooperating. That is, regardless of what one's partner does, the best strategy is always to defect in a one-shot interaction, making defection the only evolutionary stable state. As mentioned, however, repeated, or 'iterated' interactions between players creates the opportunity for reciprocity, and mathematical models have shown that this opportunity can lead to the evolution of stable cooperation from a population initially containing several different strategies (Nowak and Sigmund 1992, 1993). In these models, two strategies were most successful in maximizing benefits for individual players, and both involved cooperation.

One strategy, known as *tit-for-tat,* involves cooperating in an initial interaction, then punishing previous defection and rewarding cooperation in subsequent interactions. That is, a player defects if their partner defected in the most recent interaction between the two, and cooperates if their partner cooperated. The second strategy involves repeating a strategy that worked in a previous interaction and changing any strategy that didn't, and is therefore referred to as *win-stay, lose-shift*, or *Pavlov strategy*. Both strategies create a situation in which the probability of an individual's cooperation on a current trial (t) can be predicted by what a partner did on a previous trial (t-1).

Empirical work has found that human players apply both the TFT and Pavlovian strategies successfully in the IPD (Wedekind & Milinski 1996). Although several animal studies purport to be using an IPD framework (Gardner et al. 1984; Lombardo 1985; Milinski 1987; Dugatkin 1988), empirical work with primates is lacking, largely because of the difficulty in translating the PD/IPD scenario to use with primates. Further, even the existing animal studies have been criticized on the grounds that the experiments do not actually conform to the Prisoner's Dilemma (Clements & Stephens 1995).

The Prisoner's Dilemma paradigm has been more generally criticized as being conceptually appealing but generally lacking applicability to nature (Kun et al. 2006), and indeed, has failed to produce any convincing support of its validity in non-human studies (Clements & Stephens 1995).

Snowdrift Game

Different social dilemmas predict different cooperation strategies. The iterated snowdrift game (ISD), also know as the Hawk-Dove game, predicts higher rates of cooperation among non-relatives than the widely used iterated prisoner's dilemma (IPD) (Sugden R. 1986). In the snowdrift scenario, two strangers are stranded in their vehicles by a snowdrift. They can choose to work together in clearing the snow with shovels, or one can remain in their car and allow the other to do all of the work. Of course, if both strangers take this gamble and defect, then both remain stranded. Thus, the snowdrift game features immediate direct benefits for cooperative acts and shared costs of cooperation (payoff matrix shown below), whereas the IPD features neither of these.

Figure 2

Snowdrift	C	D
Payoff to C	$b - c/2$	$b-c$
Payoff to D	b	0

For these reasons, snowdrift leads to an evolutionary stable state of cooperation in mathematical models and is thus thought to represent many systems in which cooperation may have evolved (Doebeli & Hauert, 2005; Kummerli et al, 2007). For example, during cooperative hunting, some animals may invest heavily in the hunt, while other animals invest little to nothing but share in the catch. In other words, it is possible for animals to cooperate in the hunt or exploit others, but if no one hunts, no rewards are shared, consistent with the SD payoff matrix (Doebeli & Hauert, 2005). Because the snowdrift dilemma encourages cooperation and is based on the resources expended by organisms in order to achieve payoffs, it is a promising model for studying the role effort plays in cooperation of social species. Further, it is easier to implement into an experimental setup for non-human primates than other dilemmas, such as the iterated prisoner's dilemma.

The limited data generated by studies of humans support the model. These studies have shown that: 1) ISD does in fact lead to higher rates of cooperation than other games, namely the IPD; 2) as in the IPD, *tit-for-tat* and *Pavlov* strategies are most successful, and 3) unlike in the IPD, males and females show no difference in their rates of cooperation (Simpson 2003; Kummerli et al. 2007).

The Prisoner's Dilemma has served as a catalyst of biological theorizing for nearly three decades now. Despite this, there is no empirical evidence to support the model in non-human animals. Because the PD has failed to produce more than conceptual appeal, notable opposition to the paradigm has arisen (Noë 1990; Clements & Stephens 1995). The snowdrift paradigm represents an alternative paradigm for testing cooperation in animals, and is as theoretically appealing as the Prisoner's Dilemma. Until the aforementioned Romero study (in prep), no animal studies had been conducted using the snowdrift paradigm.

Aims and Rationale

This study aimed to replicate the basic finding of the Romero study that capuchins exposed to a snowdrift dilemma via a bar-pull paradigm show cooperation patterns that indicate sensitivity to the effort contributions of partners. This study further aimed to investigate the effect on this sensitivity of social relationship and subject sex, and the use of primary versus secondary reinforcers.

Social Relationship

The nature of the social relationship between partners was included as an independent variable because it is thought that in socially tolerant and cooperative species, close relationships are more oriented towards communality, whereas distant relationships are governed by contingency rules, such as equity (Walster et al. 1978; Clark & Grote 2003; Brosnan & de Waal 2003) and reciprocity (Trivers 1985; Roberts & Sherratt 1998; Brosnan & de Waal 2002). Both genetic relatedness and the strength of the social relationship have been found in studies of non-human primates to decrease sensitivity to reward inequity (Brosnan et al., 2005; Brosnan et al., 2006) and loosen the contingency of reciprocity (de Waal, 1997; Brown & Brown 2006).

It was therefore predicted that capuchins' sensitivity to a partner's effort in the snowdrift paradigm would decrease with social closeness. Three levels of social relationship were used to create testing pairs: 1) kin, ingroup members (excluding kin that are not socially close), and 2) ingroup, non-kin members and 3) outgroup members. Data from regular 'global' observations in the lab, which provide time-sampled information about affiliative relationships between monkeys, will be used to create these matches.

Primary vs. Secondary Reinforcer

Type of reinforcer was included as an independent variable for comparison of performance using direct versus indirect rewards. Most –but not all- of human-based literature uses secondary reinforcers or other indirect reinforcers (e.g., money, extra credit points) as payoff in social dilemma scenarios, whereas the majority of non-human animal studies examining similar social scenarios (including the previous study by Romero, in prep) use direct food reward. Money is in many ways equal to primary reinforcers in its effects on human behavior (Delgado *et al.,* 2004), and therefore its use in a human study is just as 'immediate' as food rewards in an animal study. On the other hand, a study of chimpanzees suggests that the incentive salience of food rewards creates different task performance than when abstract symbols are used (Boysen & Berntson 1995). Therefore, a direct comparison of performance using primary vs. secondary reinforcers was still of interest in this study, and had the potential to aid comparison with some human-subjects studies.

This study used cucumber slices as a direct food reward consistent with Romero et al. (in prep). Additionally, small, identical marbles were used as a secondary reinforcer in other sessions (further description in methods).

The effect of reinforcer type is difficult to predict. On the one hand, the presence of food might be such a motivating stimulus that the sensitivity to others' efforts are diminished, resulting in higher rates of cooperation. On the other hand, precisely *because* food is highly prized, monkeys may become more sensitive to effort in its presence, and therefore show greater cooperation when a secondary reinforcer is used. Therefore, this variable is an exploratory one and no directional prediction is made.

Sex

Male and female *Cebus apella* (and humans, among other primates) have faced different adaptive pressures in the history of their evolution, and as a result, female-female relationships are normally closer and more stable than either male-male or male-female relationships (Fragaszy et al. 2004, pp. 212-214). The difference between male-male and female-female relationships seems to be diminished in captivity though, with male-male relationships becoming more like the tolerant female relationships.

Still, the difference in nature of these relationships would predict higher rates of cooperation in females. However, female brown capuchins are more reciprocal (i.e., show more of a contingency between giving and receiving) in grooming and sharing food than males (de Waal 1997; di Bitetti & Janson 2001), suggesting that females might be more sensitive to an economic variable like effort. Therefore, the prediction of this study is that females will show a greater sensitivity to effort.

Methods

Subjects

Subjects were 12 (8 female, 4 male) adult and sub-adult brown capuchin monkeys (*Cebus apella*) housed in two separate social groups at the Yerkes Regional Primate Research Center.

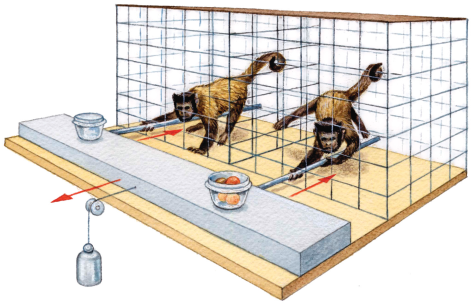
The monkeys were housed in indoor-outdoor pens, and the two groups' pens are separated by an opaque screen which allows for auditory contact, but not visual. Monkey chow and water are available *ad libitum* in addition to afternoon feedings of bread, fruits, vegetables and a protein solution.

Testing Chamber

During testing, participating individuals were isolated from other group members by entering a test chamber. The testing chamber measures 144 x 60 x 60 cm. Paired individuals (pairings described later) were separated by a transparent, plexiglas divider in the center of the testing chamber.

Bar-pull Apparatus

The bar-pull apparatus employed in this study is similar to that used by Crawford (1937) for use with chimpanzees and has been used extensively in this laboratory to study cooperation in capuchin monkeys (de Waal & Berger, 2000; de Waal & Davis, 2002; Mendres & de Waal, 2000; Brosnan et al. 2006). The bar-pull has a tray and holes for two bar-handles that can be used by the monkeys to pull the tray within reach. Rewards can be placed into transparent cups on the tray, directly above each bar. The tray can be counterweighted so that pulling the bar to retrieve rewards requires effort. The apparatus locks into place after every 1.5 inches that the tray is pulled forward, so that the tray cannot slide backwards. The tray also locks completely into place after the tray it is pulled all the way in, preventing backward and forward motion. After each trial, the tray is released back into original position.



Maximum Pulling Weights and Habituation

Prior to testing, individuals were habituated to the bar pull apparatus and maximum pulling weights determined. Maximum pulling weights were established as follows: once individuals demonstrated that they could successfully complete the bar pull task to retrieve a cucumber reward (the food reward to be used in testing), the amount of resistance applied to the bar pull was increased incrementally until monkeys cannot, or will not complete a successful pull. Before being included in tests, individuals must also demonstrate that they can successfully complete the bar-pull task in the 'marble' condition described below.

Rewards

Cucumbers were used as the food reward in all trials, consistent with the previous snowdrift study by Romero (in prep). For 'marble' sessions, two small, identical marbles were used.

Testing

Sessions

The pairing conditions described below created a total of 8 sessions for each individual. Each session consists of 35 trials. Only same-sex pairs were used, and no individual was ever tested in more than one session on a given day.

Independent Variables

Social Relationship (Independent Variable 1)

Each individual was exposed to 4 pairing conditions: 1) pulling with a kin member, 2) pulling with a non-kin member, and 3) pulling with an outgroup member, and 4) baseline 'solo' pulling. All pairs were same-sex and matched as closely as possible on maximum pulling weight. During solo sessions, both bars and food containers were present consistent with paired sessions, but only one reward was presented. The bar-pull was weighted with 80% of an individual's maximum pulling weight during solo sessions, and 80% of the stronger member's maximum weight during paired sessions.

Primary vs. Secondary Reinforcer (Independent Variable 2)

For each pairing condition, 2 sessions were conducted- one in which members of a pair pulled for a cucumber slice on each trial (primary reinforcer), and a second in which monkeys pulled when cued by the presence of small marbles (secondary reinforcer). During cucumber sessions, a small wedge of cucumber was placed into the transparent cup directly above each bar, so that a successful pull resulted in monkeys being able to directly retrieve the reward from their respective cups. For marble trials, one marble was placed into each of the transparent containers directly above each bar (i.e., one marble for each monkey), but the containers were closed and did not allow for the monkeys to retrieve the marble. Instead, the completion of each successful pull of a marble was coincided by the presentation of a cucumber slice by the experimenter to both monkeys, so that the marble served as a secondary reinforcer. That is, the sight of the marbles served as a cue to pull, and pulling was rewarded with cucumber wedges the same as those in cucumber trials. Cucumber slices are not visible to the monkeys before completion of a pull and no exchange of the marble occurs.

Thus, each monkey participated in the following conditions as a within-subjects design:

Figure 3

Cucumber	**Marble**
Solo	Solo
In-group kin	In-group kin
In-group non-kin	In-group non-kin
Out-group	Out-group

Individuals proceeded through each of the pairings and each reward condition in a randomized order. The side of the testing chamber that an individual pulled from was counterbalanced across pairings (e.g., on left for solo cucumber, on right for solo marble).

Measures

Trials

To initiate each trial, rewards (cucumber or marble) were held above the bar-pull apparatus for approximately 3 seconds, after which the rewards were placed in the transparent containers described above. Once the rewards had been made available, monkeys had 15 seconds to complete a ‘successful’ pull and an additional 30 seconds to consume their cucumber reward.

Dependent Variables

Pulling

A successful pull was defined as any instance in which an individual pulled a reward within its own reaching distance. This definition excludes partial pulls in which a pull is initiated but not carried out to the extent that a reward is brought within reaching distance. If pulling doesn’t occur within 15 seconds, the rewards were removed and the trial counted as a ‘no pull.’

During each session, the number of trials in which successful pulls were completed by individual or cooperative effort were recorded, as well as trials in which no successful pulling occured.

Cooperation

Pilot data show that cooperative pulling can occur in a synchronous or an asynchronous manner, such that an individual approaches the bar but waits for cooperation, or initiates a pull alone while a partner completes the pull. Because of this, immediate pulling versus waiting for a partner was recorded, as were instances in which one individual initiated a pull while the other completed it. To do this, four levels each of non-cooperative and cooperative pulling outcomes were defined. ‘Approach’ of the bar in these definitions refers to a monkey contacting the bar with at least one hand, but not applying any or enough force to advance the bar.

For non-cooperative pulling:

Immediate pull: a successful pull is initiated by only one individual within 2 seconds of approaching the bar.

Waiting before pulling: a monkey approaches the bar and holds this position for at least 2 full seconds before a pull is completed, without partner's cooperation.

Give-up: an individual approaches the bar, remains in this position for at least 2 seconds, but then 'gives up' and leaves the bar, not successfully completing a pull.

Aborted pull: a monkey initiates a pull (i.e., makes any forward progress on a pull) at any point during a trial, but neither the initiating individual, nor the partner, successfully complete the pull. That is, a monkey only partially completes a pull.

For cooperative pulling:

Immediate pull: a successful pull is initiated by at least one of the individuals within 2 seconds of approaching the bar, and completed by both individuals.

Waiting before cooperative pulls: a cooperative pull is initiated after one or both of the individuals waited at least 2 seconds after approaching the bar.

Immediate half and half: one monkey initiates a pull within 2 seconds of approaching the bar, only to release contact from the bar. The other monkey then completes the pull.

Waiting half and half: one monkey waits at the bar as defined above, then initiates a pull, only to release contact from the bar. The other monkey then completes the pull.

Control for pretended or apparent cooperation

In order to verify that both monkeys were pulling, and that one individual wasn't simply holding the bar but not actually putting forth effort- a force sensor was placed between each bar and the bar-pull tray (this is the point where force is applied in pulling). The sensors themselves added no resistance but produced a measure of each individual's force contribution. While the precise force applied by each monkey is not of interest, the ability to detect when a monkey is contributing negligible or no effort is crucial. Therefore, the force sensors were calibrated so that if either bar was pulled at approximately 30% of the total effort needed to retrieve rewards, a corresponding LED for that bar would illuminate. This provided a binary score for pulling versus pretended or apparent pulling.

Free Trials

To ensure that any 'non-pulling' wasn't due to a loss of interest in the reward, at the end of each session an additional 5 'free' trials were conducted in which the bar-pull tray was locked into place adjacent to the testing chamber and monkeys could reach rewards without having to pull.

Trials that were deemed invalid due to environmental distractions, etc. were also recorded.

Thus, the dependent measures for this study were coded as shown below:

Figure 4

Ai	Individual A pulls alone within 2 sec
A2	A waits ≥ 2 sec, then pulls alone
Bi	Individual B pulls alone within 2 sec
B2	B waits ≥ 2 sec, then pulls alone
AG2	A gives up after waiting ≥ 2 sec
BG2	B gives up after waiting ≥ 2 sec
Aa	Individual A aborts a pull
Ba	Individual B aborts a pull
Ci	Cooperative pull initiated within 2 sec
CA2	Cooperative pull after A waited ≥ 2 sec

CB2	Cooperative pull after B waited ≥ 2 sec
IHHA	A initiates in ≤ 2 sec, B completes pull
IHHB	B initiates in ≤ 2 sec, A completes pull
WHHA	A initiates after ≥ 2 sec, B completes pull
WHHB	B initiates after ≥ 2 sec, A completes pull
Z	No pull
X	Invalid
	Note: Individual 'A' is always used to indicate the individual on the left side of the testing chamber, while 'B' is for the individual on the right.

For additional analyses, coding of 'fake-pulling' versus blatant non-pulling was done as follows:

A	A pulls independently
B	B pulls independently
C	A and B pull cooperatively
Z	No pull
Afb	A mimics pull by grasping the bar and remaining fully oriented to pull, but does not trigger force sensor.
Bfb	A mimics pull by grasping the bar and remaining fully oriented to pull, but does not trigger force sensor.

Figure 5

Data Collection

All tests were recorded on digital video, and measurement of dependent variables made from the video.

Analyses

Data analyses followed several steps:

1) To test for a bias toward pulling more or less when testing on one side of the testing chamber versus the other, a t-test was performed for each monkey comparing their

total pulling behavior on the left side of the chamber to their pulling behavior on the right side of the chamber.

Mixed Factorial ANOVA were used to examine the effect of subject sex, reinforcer type and social pairing type on both cooperation and overall pulling rates.

2) To test whether the monkeys' behavior seemed to be independent of what their partner did, a chi square test of independence was used to compare the observed behavior of monkeys to what would be expected by chance if the monkeys were acting independently of one another. If we refer to the two monkeys in a pair as monkey A and monkey B, then the following relationships would be expected if monkeys are acting independently of their partner's behavior:

Equation 1) $P(C|A) = (P(A|A) + P(C|A))* (P(B|A) + P(C|A))$

&

Equation 2) $P(Z|A) = (1-(P(A|A) + P(C|A))) * (1-(P(B|A) + P(C|A)))$

In both equations: A = solo pull by monkey A, B = solo pull by monkey B, C = a cooperative trial and Z = a trial in which neither monkey pulls. Therefore, $P(C|A)$ denotes the proportion of trials where a solo pull by monkey A was followed by a trial in which both monkeys pulled (C). Likewise, $P(A|A)$ is the proportion of times that monkey A pulls alone following a trial in which A had pulled alone. $P(B|A)$ is the proportion that monkey B pulls following a trial in which monkey A pulled alone and so on.

In short, Equation 1 calculates the expected proportion of trials where cooperation would occur by chance if both monkeys were behaving independently of one another (i.e., the chance that their 'solo' pulls would overlap, resulting in cooperation). Equation 2 calculates the expected proportion of trials where non-pulling would overlap by chance (i.e., trials where neither monkey pulls). Again, a chi square test will be used to compare these expected values to actual values derived from the data.

3) To further discriminate the potential role of individual learning in the monkeys performance (i.e., how independent one monkey's behavior is from its partner), equation 3 was used:

Equation 3) $B1/B2 = b(r1/r2)^a$

This is a recent extension of a thoroughly studied and empirically validated equation introduced by R.J. Herrnstein in 1961 (McDowell, *submitted*). The equation attempts to identify all potential behaviors and reinforcements in a given scenario, and in so doing, identifies patterns in data that aren't accounted for by simple reinforcement. *B1, B2, B3*, etc represent the behavioral outcomes exhibited in an experiment. In this experiment, only two basics outcomes were measured, pulling or not pulling, and they are represented by *B1* and *B2*, respectively. The terms *r1* and *r2* represent the reward outcomes for *B1* and *B2*, respectively. In this experiment, pulling (*B1*) *always* resulted in a food reward, so the value of *r1* was defined as 1. If a monkey did not pull (*B2*), then whether or not they received a food reward was determined by their partner- if their partner pulled, then a non-pulling monkey received a reward. Therefore, the value of *r2* for any given session was determined by the ratio of a partner's pulling to non-pulling.

The exponent, *a*, in this equation reflects how strongly the ratio of reward (*r1, r2*) controls the ratio of times spent engaging in the two behaviors (*B1, B2*). This is important because even in situations where a behavior always results in reward (e.g., *B1-r1* of this experiment), animals do not exhibit this behavior one hundred percent of the time, even in experimental scenarios. This value has been shown to be fixed at approximately 0.8 in vertebrate species (Wearden & Burgess, 1982), and so a value of 0.8 was used in these calculations.

The factor, *b*, is called the bias parameter, and as used here it shows any biases in pulling that aren't explained by the behavior-reward relationships explained above.

These bias terms were calculated for a) each complete session, b) the first 17 trials of each session and c) the final 18 trials of each session.

To assess any potential differences in behavior between the first and last half of sessions, the first 17 and last 18 trials were compared using a dependent samples t-test.

The calculated bias parameters of entire sessions (all 35 trials) were then subjected to a 2x3 Factorial ANOVA with social group (Ingroup kin, Ingroup nonkin and Outgroup) and reinforcer type (Cuc versus Marble) as factors.

Finally, bias terms were compared to zero in T-tests. This is important because a bias term of zero suggests that all behavior has been accounted for by the behavior-reward relationships defined in equation 3.

4) To determine any potential contingencies in the monkeys' behavior, each session was analyzed in a trial-by-trial fashion. That is, could one monkey's behavior in a session be predicted by what the other monkey did during that session. To do this, the proportion of each behavioral outcome (pull or not pull) at trial *t* given *x* on trial *t-1* was calculated. In the example below, the data are from a session in which a monkey named Bailey was paired with another female, Bias. Following trials in which both monkeys pulled, Bias pulled roughly 92% of the time. Following trials in which Bailey pulled alone, Bailey pulled again roughly 81% of the time, and so on.

Bailey's Behavior t-1	Trial t Bailey Pulls	Trial t Bailey Does Not Pull	Prop. Of Pulls
Both Monkeys Pulled	12	1	0.923076923
Only Bailey Pulled	13	3	0.8125
Only Bias Pulled	4	1	0.8
Neither Pulled	1	0	1

Differences in these proportions were then calculated as follows: for each session, a monkey's proportion of pulling following a solo pull was subtracted from a monkey's proportion of pulling following both monkeys pulled. In the example above, this would be 0.9230 – 0.8125 = .1106, showing that Bailey was more likely to pull after a cooperative trial than one in which she pulled alone. This was repeated for the proportions of pulling following a partner's solo pull and neither monkey pulling (e.g., 0.8 – 1 = -0.2). This creates a value (referred to from here as 'difference values') showing whether a monkey was more likely to pull following cooperation or solo pulling and whether he or she was more likely to pull following a partner's solo pulling or a trial where neither monkey pulled.

This allows for the detection of several types of contingencies in behavior. Any monkey who showed a trend toward not pulling in response to a partner who never pulled might be showing an awareness of, and reaction to their partner's effort. Further, if a monkey consistently follows cooperative trials by not pulling, then the monkey might be exploiting her partner. Similarly, a monkey who rarely pulls following a partner's solo pull might be characterized as free loading, and finally, any monkey interested in food rewards should show at least some pulling behavior following trials where neither monkey pulled. In the example above, Bailey's behavior can be said to display a type of contingency, in that she is more likely to pull following a cooperative trial than a trial in which she pulled alone.

The method of analysis outlined here in step 4 allows for each individual session to be assessed for a pattern of contingent behavior (such as the Bailey example above), but also allows for larger-scale analyses. It is important to note, however, that when visualizing the data at the level of a single session, virtually all sessions appear to have *some* type of contingency. This is because a monkey would have to pull an equal proportion of the time following all four possible outcomes. Therefore, the data were analyzed as described in the following two paragraphs- on an overall level and on the level of individual monkeys, across sessions.

The difference values, as well as the absolute values of the difference values, were pooled by social pairing and reinforcer type and compared to zero (which represents non-contingent behavior) in one-sample t-tests. Testing the absolute values of the differences allows for the detection of *any* overall pattern of contingency in the data, while the non-absolute values tell the *direction* of a contingency (toward pulling or non-pulling).

Finally, the difference values of each individual monkey across sessions (i.e., 6 values per monkey) were compared to zero (again, a value of zero represents no contingency) using t-tests. This was to assess whether any individual monkey, regardless of overall patterns in the data, displayed a consistent pattern of contingent behavior throughout testing.

5) The same difference values calculated in step 5 were subjected to a 2x3 Factorial ANOVA (again, reinforcer x social pairing) to assess any differences in contingent behavior based on the experiment's independent variables.

6) Finally, the difference values of each monkey across sessions (i.e., 6 values per individual) were subjected to a Pearson's correlational test to determine if monkeys behavior in any one of the session types correlated with their behavior in any of the other session types. For example, did monkeys behavior in ingroup, kin, cucumber sessions

correlate with that of outgroup, marble? This analysis was aimed at determining if the monkeys acted in a consistent way across sessions, or if behavior varied more from one condition to the next.

7) The force sensors installed on the barpull apparatus allow for a distinction to be made between real and apparent or 'pretended' pulling (for definitions see page 16). Further, they allow for a distinction between apparent pulling and obvious cases of non-pulling. To assess whether monkeys responded differently to partners who might appear to be pulling, but aren't (apparent pulling) than partners who were obvious in non-pulling, a comparison was made between the rate of pulling by partners when each of these behaviors occurred using a t-test.

Differences in behavior when a partner fake pulled versus blatantly non-pulled were subjected to a 2x3 Factorial ANOVA (again, reinforcer x social pairing) to assess any differences in response to this behavior based on the experiment's independent variables.

Results

General descriptive statistics of the data showed that the total amount of pulling per session occurred as follows:

Table 1

Social Pairing	**Mean number of pulls per session**	**Standard Deviation**
Solo Sessions	26.13	8.30
Ingroup kin Pairs	19.25	8.55
Ingroup non-kin pairs	19.32	11.31
Outgroup pairs	17.38	9.65

This shows how many times the monkeys successfully pulled in the tray per session as a function of social conditions, collapsing across reinforcer type.

The total amount of cooperative trials per session are shown in table 2:

Table 2

Social Pairing	**Mean number of cooperative pulls per session**	**Standard Deviation**
Solo Sessions	0.00	0.00
Ingroup kin Pairs	6.88	2.24
Ingroup non-kin pairs	7.00	4.85
Outgroup pairs	5.5	5.17

This shows how many times monkeys cooperated per session as a function of social conditions, collapsed across reinforcer type.

The overall percentage of trials that each behavioral outcome occurred was as follows:

Table 3

Only one monkey pulled	69% (33% monkey A and 36% monkey B)
Both monkeys pulled (cooperative)	18%
Neither monkey pulled	13%

These percentages include all partnered sessions' data combined.

Results from the steps of analysis outlined above (see Methods section) are as follows:

1) T-tests revealed no bias toward pulling more or less on one side of the testing chamber versus the other for any monkey.

A 2x2x4 Mixed Factorial ANOVA with sex as a between subjects factor and within-subjects factors Reinforcer Type (Cucumber vs Marble) and Social Pairing (Ingroup Kin, Ingroup non-kin and Outgroup) was used to compare the mean number of pulls per session found. No significant main effects or interactions were found.

A 2x2x3 Mixed Factorial ANOVA with sex as a between subjects factor and within-subjects factors Reinforcer Type (Cucumber vs Marble) and Social Pairing (Ingroup Kin, Ingroup non-kin and Outgroup) was used to compare the mean number of cooperative trials per session. No main effects or interactions were found.

2) The expected values produced by equations 1 and 2 (see: methods) as well as the actual observed values from the data are shown below:

Table 4

A Pulled in Preceding Trial	**Expected**	**Observed**
Cooperation	0.21	0.13
Neither pulls	0.17	0.10
B Pulled in Preceding Trial		
Cooperation	0.22	0.16
Neither pulls	0.15	0.09
C Occurred in Preceding Trial		
Cooperation	0.45	0.38
Neither pulls	0.11	0.04
Z Occurred in Preceding Trial		
Cooperation	0.11	0.10
Neither pulls	0.46	0.44

In the leftmost column, the 4 possible outcomes of a given trial (n) are shown in bold. Beneath each emboldened outcome are the outcomes of interest for a subsequent trial (n+1).The 'expected' column shows the proportion of each outcome expected by chance. The 'observed' column shows the actual occurrence of each outcome.

A chi-square test of independence found no significant difference between the observed and expected values for either cooperation or mutual non-pulling.

3) The bias terms computed using equation 3 are shown below:

Table 5

BIAS TERMS	ALL TRIALS	LAST 18	FIRST 17
All DATA	-0.080	-0.218	0.058
INGRP KIN	-0.044	-0.306	0.216
INGP NONKIN	-0.052	-0.137	0.031
OUTGRP	-0.142	-0.257	-0.027

A positive value here represents a tendency toward pulling that isn't explained in terms of behavior-reward relationships, while a negative value shows a tendency toward non-pulling. A value of zero, if it existed, would represent behavior that is perfectly accounted for by the behavior-reward relationships defined in the above equation.

A dependent, paired sample t-test found no significant difference between the bias terms of the last 18 trials of sessions compared to the first 17 trials.

Because no difference was found between the first 17 and last 18 trials, the bias terms from complete session data (i.e., all 35 trials per session) were used in a 2x3 Factorial ANOVA. No main effects of social group (Ingroup kin, Ingroup nonkin and Outgroup) or of reinforcer type (Cuc versus Marble), nor any interaction effects, were found.

Two-sample unequal variance T-tests showed no significant difference between bias terms and zero. T-tests also revealed no difference amongst any of the bias terms.

4) No contingencies in the monkeys' behavior were found at either the group level or at the individual level.

One-sample t-tests with the overall data found that the absolute values of the differences (see Methods) did not differ significantly from zero in any case. One-sample t-tests (overall data) of the non-absolute values of the differences also, accordingly, did not differ significantly from zero.

T-tests further revealed that no individual monkey displayed any consistent contingency in behavior across sessions. In fact, only five out of the 52 sessions in this experiment showed a pattern that would suggest that cooperation occurred in a contingent manner. In other words, there were only five sessions in which cooperative trials were more likely to be followed by another cooperative trial than by one of the monkeys pulling alone. The most frequent pattern of behavior was instead that monkeys were most likely to pull the bar following a trial in which they pulled alone.

5) The same difference values exposed to a 2x3 Factorial ANOVA (reinforcer x social pairing) yielded no significant main effects or interactions.

6) Pearson's correlational tests found no significant correlation of the behavior in any session type with one another.

7) A paired-samples t-test showed that overall, monkeys pulled significantly more when a partner was obvious in non-pulling than when a partner seemed to pull, but did not actually pull (apparent pulling) (t(28)= -4.433, p<.0001).

The 2x3 ANOVA found no significant main effect of social pairing or reinforcer type.

Discussion

The hypotheses of this study were that 1) capuchin monkeys would show a sensitivity to effort by adjusting their own behavior based upon the effort level of a partner in a cooperative task, 2) this sensitivity would be weakest in related pairs and strongest in unfamiliar pairs (social pairing), 3) this sensitivity would be modulated (direction not predicted) by subject sex, and 4) this sensitivity would be modulated (direction not predicted) by reinforcer type (direct versus indirect).

Hypothesis 1

The data provide no support for the hypothesis that capuchins show sensitivity to partner effort by adjusting their own behavior in the snowdrift task.

Step two of the data analyses found that the capuchins' rates of behavior in partnered sessions did not differ statistically from chance. That is, the level of cooperation and mutual non-pulling did not differ from what would be expected if two partners completed a session totally unaware of one another; their pulling behavior would be expected to overlap by chance a certain number of times, creating 'cooperative' trials and their non-pulling behavior would be expected to overlap a certain number of times, creating mutual non-pulling trials.

Further, step three of the analyses found that the monkeys' behavior was consistent with a model of individual learning based on rewards. If the snowdrift game is conceptualized as a Pavlovian task in which, from an individual monkey's perspective, pulling a bar always results in a reward, and not pulling a bar intermittently results in a reward, then one can attempt to account for a monkey's behavior based on these behavior-reward relationships. The equation in step three of analyses is designed for just this, and includes a factor, b, that represents the amount of each behavior in each session *not* accounted for by the behavior-reward relationships in the model. Therefore, a bias term (b) of zero means the data have been accounted for by behavior-reward relationships. Since the bias terms in these data were found to not differ statistically from zero, then the monkeys' behavior can be said to be consistent with the model, which is one of individual learning within sessions.

Just to help further explain this model, imagine that overall, the monkeys had a largely negative bias term (b), which was found to differ statistically from zero. This would mean that the monkeys displayed more non-pulling than could be explained by the model. This would not answer *why* they displayed more non-pulling, but one could, for example, hypothesize that the monkeys might be 'freeloading' on partners when the opportunity presents itself, which would be revealed in the contingency analyses of step 4.

Even in the absence of large-scale, mean differences in behavior, it seemed possible that patterns of contingency between partners pulling could exist in the data. In other words, perhaps by looking at the data from each session in a trial-by-trial manner, evidence of monkeys adjusting their behavior based on their partner's behavior could be found.

Step four of analyses found no such contingency, however. There was no suggestion in the data that monkeys were more likely to pull the bar following a cooperative trial (trial in which both monkeys pulled), nor were they more likely to not pull the bar following a trial in which neither monkey pulled. Instead, individual monkeys were most likely to pull the bar if they had pulled alone on the previous trial. This was true at an overall level of the data, as well as for individual monkeys.

The analyses of step four suggest that most monkeys pull only when they must, i.e., when a partner is not pulling, while other monkeys just always pull at relatively high rates. For a monkey to only pull when they must does not require a recognition of a partner's effort, per se, because monkeys need only make the connection that they aren't receiving food for non-pulling. These analyses therefore add to step two and three in suggesting that, in this particular task, the monkeys' behavior is best explained by individual learning.

Hypotheses 2, 3 and 4

Hypotheses two, three and four predicted that social pairing, subject sex and reinforcer type, respectively, would all affect the monkeys behavior in the snowdrift paradigm. The data did not support any of these hypotheses.

Step one of analyses found no effect of social pairing, subject sex or reinforcer type on total pulls per session, although a main effect of social pairing was very nearly significant ($p = .07$).

There was a main effect of social pairing on the total amount of cooperative trials per session. This however, should be expected given that solo sessions were included as a level of social pairing, and monkeys *cannot* cooperate during solo sessions. Pairwise comparisons verified that, in fact, solo sessions differed from all other levels of social pairing in level of cooperation, but no other levels differed from one another. Therefore, this main effect can be attributed to the solo condition.

Social pairing, subject sex and reinforcer type were also found to have no effect (nor interaction effects) on the bias terms calculated in step three, nor the difference values calculated in step five of analyses. Together, these steps suggest no effect of any of these independent variables on the monkeys behavior in this study.

Step six of analyses was aimed at determining if the monkeys acted in a consistent way across sessions, or if behavior varied more from condition-to-condition. The results did not show any correlations. This result resonates with the model used in step three of analyses in that monkeys behavior seems to be dependent on what rewards they get for their behaviors, and therefore can vary greatly from session-to-session independent of type of partner or reinforcer used.

Apparent or pretend versus obvious non-pulling

The exploratory analysis of apparent or 'pretend' pulling allowed by the force sensors found that monkeys pull significantly more when a partner is conspicuous in non-pulling (e.g., in the corner of the test chamber instead of near the pulling bar) than when a partner fake pulls. This is in line with other findings. If monkeys are paired with a partner who isn't even approaching the bar, then the monkey's only way of retrieving food rewards is to pull alone. In other words, if a monkey finds that they must pull to get any food, they will. This is consistent with the findings of step four of analyses.

Summary and Conclusions

No hypotheses of this study were confirmed by the data. It should be pointed out, however, that steps one and six of analyses included tests that nearly reached significance. This might suggest that greater statistical power would have found some positive results.

It should also be pointed out that some of these negative results represent very interesting findings. The fact that reinforcer type made no difference in any measure of behavior is particularly interesting. By definition, primary and secondary reinforcers should affect behavior differently, though there was no evidence of that here. This raises several possibilities, but perhaps most likely are that a) the monkeys in the capuchin lab are so accustomed to interacting with secondary reinforcers via experiments that they have taken on characteristics comparable to that of primary reinforcers (similar to money in humans), or b) this experiment simply was not sensitive enough to detect any differences that might be caused by the use of different types of reinforcers.

That social pairing had no affect on behavior is extremely surprising. Regardless of whether monkeys pay attention to one another's effort or not, it is surprising that their behavior in the task was not statistically different when an unfamiliar monkey was present. Again, however, a main effect of social pairing on total pulling per session did border on significance, so perhaps greater statistical power would lead to a positive finding here.

The fact that subject sex made no difference in any measure of behavior is interesting, although might be most easily attributed to the low number of males available for this study.

Overall, it seems that if capuchins are sensitive to the effort levels of others, this experiment was not sensitive enough to detect it. Instead, the monkeys behavior was consistent with individual learning that is based on the food rewards received for behavior within each session. Most simply, if individual monkeys had to pull to get food, they would; if they did not have to pull to get food, then they wouldn't.

There is another possible approach to analyzing snowdrift data, however. Instead of looking only for evidence of cooperative behavior in the ISD, one can look for evidence of any sort of 'coordination.' Coordinated events include not only instances in which two actors work together, but also the instances in which neither actor works (mutual defection). If two actors differ significantly from chance in their level of coordination, it could show a trend of either cooperation *or* of negative response towards non-cooperation (mutual non-cooperation). Although it is unclear whether this type of analysis is appropriate for these data, it is a potential avenue for analyses of future experiments.

Currently, a follow-up study is underway which uses an experimental manipulation of clumped versus dispersed rewards. The hope is that, in contrast to this study, which relied on statistical mining of the data, the experimental manipulation will lead to an obvious response to effort inequity.

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