

## Reciprocal Food Sharing of Gibbons<sup>1)</sup>

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The social relationships between animals of a species are often reflected in the way in which they respond to food. Filial and sexual relationships, competition, and dominance may be manifested in the character of food related activities. Indeed, sometimes the manner in which animals respond to food is used to characterize the relationship between them.

Relationships between members of animal groups often have been studied in situations where there is a limited supply of incentives. In studies of food competition among primates, it has been shown that rhesus monkeys and pairs of adult chimpanzees manifest clear dominance relationships with one animal of a pair obtaining and keeping a large proportion of the food. These dominance relationships may be modified by the female sex cycle and by food motivation of the animals (Nowlis, 1942; Maslow, 1936), nevertheless, one animal of a pair retains almost all of the food. In these species, food rarely passes from one animal to the other, although occasionally the dominant animal may take food from a subordinate. There may be a transfer of food between juvenile chimpanzees, but again it is most often the dominant animal who gets the food (Nissen and Crawford, 1936; Nowlis, 1941). Reciprocal sharing of food occurs between pairs of young chimpanzees, but it is not common.

We have recently observed reciprocal food sharing in a group of 12 gibbons kept in a laboratory.\* All of the animals, juvenile and adult, show this behavior to some degree: however, it appears to be far more prominent in juveniles.

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\* Carpenter has demonstrated this behavior in his film, *Characteristics of Gibbon Behavior*, and has described it as representing mild competition.

In adults, food either is not transferred between animals, or the transfer is ordinarily uni-directional.

A typical instance of reciprocal food sharing involves an *attempt* by one animal to take food held by another, either by grasping the food or by holding the partner's hand and taking the food. Each food sharing attempt results in either a *success*, a *failure*, or a *split*. That is, the animal making the attempt gets either all of the food, none of it, or in the case of soft foods, he may break off a piece. Many attempts may be made until some of the food is obtained, and if the attempt has been successful, the original holder may try to recover some of the food. The holder of the food usually permits the animal seeking food to get part of it without protest. However, in some circumstances he will resist by keeping the food out of his partner's reach and only rarely will threaten or fight. It should be pointed out that we have never observed one gibbon offer food to another.

This series of studies was undertaken in order to analyze variables affecting the food sharing of gibbons. The factors of motivation, availability of food, social relationships and individual differences were all related in some way to food sharing attempts and their degree of success. The interplay of these factors illustrates the multidimensional nature of food sharing in juvenile gibbons and thus has significance for understanding various aspects of gibbon behavior.

### Experiment I

The first phase of the series was devoted to determining the extent to which dominance, as measured by food retrieving, is characteristic of young gibbons and how food sharing attempts are related to this measure. In the first study, pairs of animals were observed in a situation where one piece of food was available to either of them.

Three pairs of juvenile gibbons were tested in a 92 × 36 × 25 in. outdoor cage constructed of 2 × 4 in. turkey wire over a metal pipe frame. On each of six mornings, ten trials were presented to each pair. A trial consisted of throwing a quarter of a banana onto the floor of the cage and observing the animals until the food had been consumed. The two observers sat in sight of the animals, two feet from the cage. One described the behavior of the animals, while the other kept a protocol. The behaviors noted included: the first animal to retrieve the food, food-sharing attempts by each animal, and the results of each attempt.

As may be seen in Table I, food retrieving in juvenile gibbons can scarcely be considered as a sensitive index of social dominance. No animal was the first to pick up the food on all trials, although one animal of each pair tended to get the food more often. The number of food sharing attempts varied widely between subjects, and the animal who initially had picked up the food made fewer attempts. Certain members of a pair were more successful, but success was in no way related to initial access to the food.

## Experiment II

The results of the first experiment showed that the animal who did not obtain the food initially made more food sharing attempts. In order more satisfactorily to separate dominance characteristics from attempts to obtain food from a partner, a second experiment was performed in which both animals received the food initially equally often.

The procedure was the same as in the first study except that one animal of the pair was handed the food on the first five trials of a session, and the other animal received it on the second five trials. The order of this presentation was balanced over days, so that each animal received the food from the experimenter equally often in both ordinal positions. Three pairs of animals were used with two pairings different from before. The results of the experiment may be seen in Table 2. Each animal was considered separately so that the data in the table represent the average number of attempts made by each animal and the results of these attempts under the four conditions of the experiment. Analysis of variance indicated that regardless of which animal of the pair was considered, one who was given the food (S) made fewer attempts ( $p < .01$ ) than did his

**Table 1.** Food Sharing When There Is Free Access to Food

Pair	name	Initial holder %	Mean number of attempts	R e s u l t s		
				Per cent Success	Per cent Split	Per cent Failure
I	<i>Spade</i>	17	9.8	22	21	56
	<i>Lone</i>	83	1.6	6	25	69
II	<i>Ted</i>	58	1.2	0	8	92
	<i>Ben</i>	42	4.3	4	29	67
III	<i>Burma</i>	19	6.0	18	65	17
	<i>Becky</i>	81	2.9	3	24	72

**Table 2.** Food Sharing When Food Is Distributed Equally

Conditions	Mean attempts per condition	R e s u l t s		
		Percent Success	Percent Split	Percent Failure
S I	5.00	40	37	23
S II	3.50	33	19	48
P I	23.67	35	29	36
P II	14.50	39	34	26

partner (P). No matter which member of the pair received the food, there were more attempts ( $p < .05$ ) in the first half of the session (I) than in the second half (II). This may have reflected a reduction in food motivation over the session. There were significant differences in the number of attempts made by the different subjects ( $p < .01$ ). The patterns of successes, splits, and failures were not different in the first half of the session from the second half, nor were they affected by whether the subject making the attempt had been given the food or whether his partner had received it.

### Experiment III

The first two experiments of the series showed that attempts to obtain food from a partner were reciprocal. That is, the level of attempts was determined more by which animal had the food than by dominance relationships. The data also suggested that motivational factors may be important, and the second phase of the series therefore investigated the effect of hunger on food sharing.

All pairings of five juvenile gibbons were tested in an  $84 \times 48 \times 36$  in. outdoor cage similar in construction to that of the previous experiments. The observation procedure was the same as in those experiments except that five instead of ten trials were used in every session. The banana was thrown onto the floor to start a trial, and the time taken for the food to be consumed was noted. The trial was discontinued after 75 sec. if the food had not been eaten in that time.

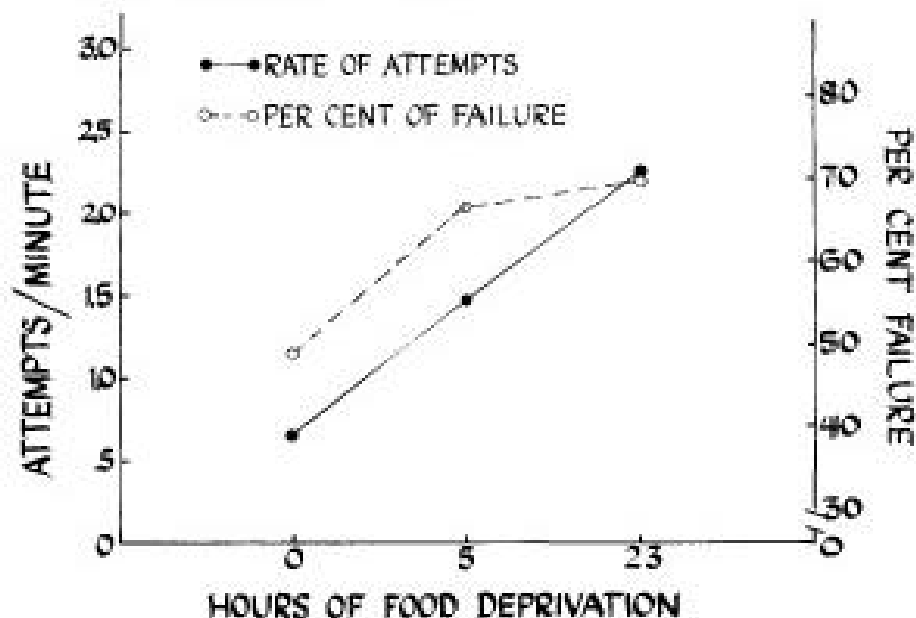
The animals of each pair were deprived of food for 0, 5 or 23 hr. prior to testing but were otherwise kept on a diet of milk and fruit. Deprivation periods were presented in a random order. The animals were separated, but in sight of each other, for one hour prior to testing. All experimental sessions were run at 3:00 p.m.

The basic procedure for analyzing the results was to regard the data for the different pairings as replications of the experiment for any individual. Thus, since an animal was paired once with each of four other animals, the experiment was considered replicated four times for each S. This was done to control for the effects of individual pairings. The basic datum analyzed was the sum over the five trials of a session.

Analyses of four measures were carried out: time for consumption of foods, number of food sharing attempts, rate of attempts (attempts/time), and food sharing failures per attempt.

Mean time scores summed over five trials shows that the speed of food consumption was directly related to deprivation ( $p < .001$ ), and that the rate of attempts was higher when the animals were deprived ( $p < .01$ ). The degree to which the animals were successful in attempts to get food from their partner is reflected in the failure scores. The proportion of failures was higher in the

**Fig. 1.** The relationship of food sharing attempts and failures to food deprivation when both animals are equally hungry.



deprivation conditions ( $p < .05$ ). In general it appears that the five hours of food deprivation had nearly the same effect as did 23 hr.

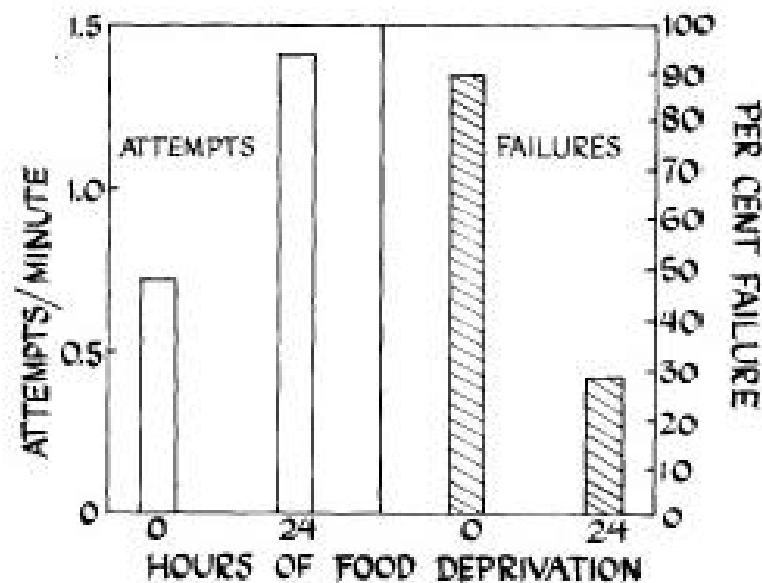
#### Experiment IV

In this experiment, members of a pair were differentially satiated to determine whether food sharing patterns between members of a pair could be reversed by changing the deprivation state of the individuals.

Three pairs of juvenile gibbons were tested in the same situation as the first experiment. The animals were 0 or 23 hr. food deprived with the same procedure as in the previous experiment except that one animal of a pair was hungry and the other satiated. Which animal was deprived was alternated over the four days of the experiment so that each animal served in each deprivation condition twice. There were eight trials on each day and banana was given to each S on alternate trials.

The experiment therefore was a  $2 \times 2$  design in which a subject or his partner received food when S was hungry or satiated. The results were analyzed in a similar manner to Experiment II. Each S was considered separately with respect to rate of attempts and per cent failure under the four experimental conditions.

**Fig. 2.** Food sharing attempts and failures when the subject under consideration and his partner are at different hunger levels.



The results presented in Figure 2 are consistent with Experiment II in showing that an animal had a higher rate of attempts when his partner (P) received food than when it was given to him ( $p < .05$ ). When his partner received food the animal who was hungry attempted to get food at a greater rate than when he was satiated, but this effect was not statistically significant.

The outcome of the food sharing attempts reflected deprivation level of the two animals. When the animal under consideration was hungry and his partner satiated there was a significant reduction in failures over the case when the partner was hungry and the subject satiated ( $p < .05$ ). This contrasts with the previous experiment in which failure was an increasing function of deprivation when both animals were deprived. As in Experiment II, whether the food was given to the subject or to his partner did not significantly affect the outcome of the attempt.

#### Experiment V

At feeding time we have observed that even when a large quantity of free food was available some of the gibbons would still indulge in reciprocal food sharing. One hypothesis for dealing with this phenomenon concerns the proximity of food as a primary stimulus for the securing and eating of the food. Thus, an animal without food, who is in proximity to a cagemate with food might be more likely to try to secure food held by the cagemate than to secure

free food located further away. Since the gibbon tends to travel, rest and eat at high locations we hypothesized that free food available at high locations along the sides of the living cage would decrease the frequency of food sharing attempts from that which occurs when free food is available on the floor of the cage.

The Ss were four gibbons (*H. lar.*). The animals were housed and tested together in a 148 × 24 × 90 in. outdoor cage which contained two platforms at either end, about 5 ft. from the cage floor, a swing, and plywood panels along the sides.

Food was located in the cage according to each of the test conditions. Under the High condition, the food was placed by means of wood screws onto the sides of the plywood panels approximately 5 to 6 ft. from the cage floor. Under the Low condition, food was scattered along the floor of the cage.

The animals were 22 hr. food-deprived upon entering the test situation. The amount of food (apples, oranges, cooked sweet potato and bananas) was held constant under both conditions. Approximately 90 pieces of food (divided into quarters) were used at each test session. Test sessions lasted 25 minutes and food sharing attempts, results of each attempt and vertical location of animals (i.e., whether an animal was above or below the middle of the cage) were recorded during one minute intervals. Each test condition was replicated three times in an alternate sequence on separate days.

**Table 3.** Food Sharing Attempts and Results as a Function of Food Location

	Number of Attempts		P	% Failure	
	High	Low		High	Low
<i>Burma</i>	9	67	<.01	22.2	26.9
<i>Becky</i>	12	72	<.01	41.7	55.6
<i>Britt</i>	3	14	<.05	66.7	28.6
<i>Kerry</i>	—	3	=.25	—	00.0

The main results of this experiment are presented in Table 3. The table shows the number of attempts to secure food from another animal and the results of such attempts for each animal as a function of the location of the food. The four animals responded in the predicted fashion, three of them significantly. That is, attempts were more numerous when food was scattered on the floor of the cage than when food was high. The proportion of failures to obtain food was not affected by the experimental conditions.

The record of vertical location of the animals showed that high locations were preferred and that in all but one instance, food sharing took place above the middle of the cage.

## Experiment VI

The results of the previous study show that proximity of food can be important in determining the level of food sharing behavior. Other observations have indicated that as more preferred foods are consumed, food sharing attempts gradually increase. The next study investigated the effects of food availability on the progress of food sharing over time. It was predicted that if only one piece of food was available, attempts initially would be maximal and would decrease as the food was consumed. If three pieces of food were available, each animal would initially eat one of the three and sharing would be low. However, in this condition, as food became scarce, attempts would increase and then decrease once more when the food became depleted.

All pairings of six juvenile gibbons were tested in a  $92 \times 48 \times 25$  in. outdoor cage similar to those of the previous experiments. Each pair was deprived of food and caged together for 23 hr. prior to testing. The pairs were tested under each of two conditions in a given test session. Under one condition a single piece of cooked sweet potato (3 in. cubed) was placed on the floor of the test cage, and under the other condition, three pieces were similarly placed. The sequence of conditions was counter balanced and the experiment replicated twice for each pair. The number of attempts and successes were recorded during

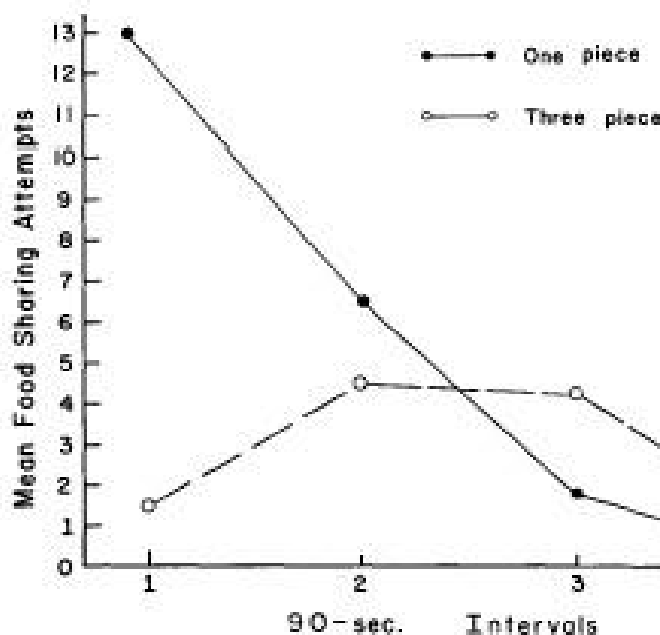


Fig. 3. Food sharing attempts under two conditions of food availability.



successive 15-sec. intervals on time-ruled paper. The test was terminated when food was no longer available.

The single piece of food was naturally consumed in a shorter period of time ( $\bar{X}=120$  sec.) than were the three pieces ( $\bar{X}=225$  sec.). As predicted, food sharing attempts (for each S summed over pairings) manifested different functions over time (see Fig. 3), with the single piece showing a regular decrement over time and the three-piece condition increasing and then decreasing.

Analysis of variance of the number of attempts over 90-sec. intervals showed the Food Conditions  $\times$  Intervals interaction to be significant ( $F=13.24$ ;  $df=3/15$ ). This interaction derived from the fact that the Intervals effect was significant for the condition in which there was one piece of food ( $F=14.96$ ;  $df=3/15$ ), but not when three pieces were presented ( $F=1.22$ ;  $df=3/15$ ). A significant difference between conditions during the first interval ( $t=5.72$ ;  $df=5$ ) was no longer in evidence during the next three time intervals.

### DISCUSSION

The significance of food sharing in juvenile gibbons lies partly in its reciprocal character. The fact that one gibbon of a pair often takes food from another and then, in turn, may relinquish the food reflects the fact that unidirectional dominance is not well developed in these animals. Since adult gibbons do not share food as readily as do juveniles, this may be partly a function of maturation and may indicate that status relationships among immature animals are less differentiated than relationships among adults.

This is not to say that young animals respond in the same way to one another. In our experiments, the gibbons behaved differently depending upon the S with which they were paired, both in the degree to which they made attempts and the number of successes they made. However, this did not ordinarily reflect different amount of unidirectional tendencies as much as it did pair differences in the degree to which food was transferred. That is, in some pairs food transfer occurred, and the transfer was reciprocal, while in others, the animals simply kept away from one another.

In addition to maturational, social, and individual factors, motivation level and availability and proximity of food determine the level of food sharing. A high level of attempts is expected when an animal is hungry and food is available but scarce or difficult to get to. The greatest number of successes results when the partner is satiated. These motivational and ecological factors show that food sharing must be considered within the context of the normal feeding behavior of gibbons. Carpenter in his field study (Carpenter, 1940) has reported an instance in which an infant took food from its mother. It may be that food sharing attempts are an infantile method of obtaining food in young gibbons who do not yet have the motor facility required for a successful active, arboreal existence.

Two of our animals showed a relatively high level of food sharing apparently associated with a fear of going to the floor to retrieve food. They would wait until a partner had gotten some food and traveled to a high level in the cage and then they would obtain their ration from the partner. This, of course, is not in the classical dominance pattern. Rather, it appears to be an adaptation for obtaining food by a hungry young animal who is not yet completely independent.

### SUMMARY

Young gibbons freely take food from one another. This pattern contrasts with food sharing activities in adults and in other primate species in which the dominant member of a pair retains most of the available food. Six studies were reported which showed that the number of attempts to obtain food and the degree of success of these attempts is conditioned by individual differences, hunger and proximity and availability of food. It was concluded that food sharing represents an important dimension in social relationships of young gibbons and that it serves as a behavioral mechanism by which gibbons who have difficulty in obtaining food in their predominantly arboreal environment can survive.

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